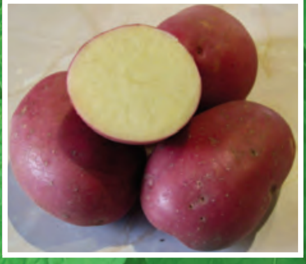
Growing the Potato Crop

John J. Burke



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Preface

Worldwide, the potato is the third most important food crop, after rice and wheat, in terms of human consumption. As a foodstuff, potato has widespread acceptance across cultures and social classes. More than a billion people worldwide eat potato, and global total crop production exceeds 300 million metric tons. A growing world population heightens the threat of increase in hunger rate and the associated search for food security. This is best illustrated by the case of China, which is now the world's largest consumer of potatoes. Furthermore they expect that potatoes will provide 50% of the increased food production needed to meet demand during the next 20 years.

In many countries, with growing populations, the area available for expanding potato production is constrained. Increases in crop yield will therefore have to come from improvement in productivity. While impact evaluation studies show the potentially high returns on investments in research on potato technologies, worldwide there is relative underinvestment in roots and tuber research. Such research requires significant capital investment. A less expensive approach to improving productivity among potato farmers in Sub-Saharan Africa is to invest in up-skilling the potato farmers.

A first step towards this objective is to up-skill the Extension Workers and Potato Crop Specialists, who advise the farmers; that is the primary objective underlying the publication of this book. The author is aware that already many excellent textbooks exist, dealing with specialised potato topics. This publication should be regarded as a training manual and is intended purely for educational purposes. It aims to provide practical guidelines to improve crop productivity, combined with an elucidation of the scientific principles underpinning those guidelines. Extension Workers, Potato Crop Specialists and Undergraduate Students are the target readership.

The focus of the book is improving potato productivity in sub Saharan Africa. Hence the emphasis for example on the use of appropriate technology, such as farmer constructed diffused light stores to facilitate seed tuber sprouting. Due to the scarcity of land, farmers in this region are often forced to abandon traditional crop rotation practices and plant successive potato crops. The dangers associated with such practices are highlighted. Intercropping is an established practice in traditional agriculture. The value of this practice in potato production is discussed. Currently most potatoes grown in this region are consumed fresh. As living standards and disposable incomes increase, the switch to consuming processed product will occur, mimicking consumption trends in the rest of the world. Crop quality will then assume a greater significance than that required to satisfy the fresh market. Factors, which influence tuber quality, such as crop nutrition, irrigation, crop maturity and tuber storage are addressed. The book is not intended as a literature review and furthermore, to streamline reading by a non-scientific audience, citations are not included. This deficit can be overcome however, by typing a phrase or sentence into an Internet search engine and the reader will be directed to the source

The author wishes to thank the potato experts who generously publish state-of-the-art information on the Internet, dealing with diverse aspects of the potato crop. This resource has been utilised extensively while compiling the book. A sincere thanks to copyright holders who gave permission for the use of their photographs and diagrams. A special word of thanks to site owners, who grant unrestricted use of content for educational purposes.

While the information contained in this publication has been formulated in good faith, the contents do not take into account all the factors, which need to be considered, before putting that information into practice. Accordingly, no person should rely on anything contained herein as a substitute for specific professional advice.

Foreword – John O'Shea

Five generations of my family have grown potatoes on the banks of the river Suir in the South East of Ireland. A passion for producing and delivering top quality potatoes to our customers, drives everything we do, from our determination to farm sustainably and in harmony with nature, to our commitment to innovation and continuous improvement. From an early age I was acutely aware of the importance of best practice in Potato agronomy, over the years we have worked with many consultant agronomists who have kept us up to date with the latest developments in Potato research and production.

From my first trip with Vita to Ethiopia in 2012, I recognised two areas that needed to be addressed if the productivity of potato production in Ethiopia was to improve.

Firstly the Vita agronomists on the ground are key to the success of the project and it is very important that they have the communication and technical skills necessary to enable them to transfer their knowledge to the farmers. The ongoing education and training of both the Agronomists and subsequently the farmers will ensure that the productivity of potato production and the quality of finished product improves.

The second area that needs to improve is the quality of seed potatoes. Increases in productivity can only be achieved if farmers have access to clean seed.

To address these issues, we invited John Burke to join our team. John spent his career working with Teagasc, the national body providing integrated research, advisory and training services to agriculture and the food industry in Ireland. Since joining Vita as a Volunteer Agronomist he has focused attention on the production of clean seed, free from virus and bacterial wilt.

This book addresses the broad span of topics associated with potato growing in sub Saharan Africa. It will provide front line staff with a manual that can be distilled and translated into local languages to provide farmers with a scientific basis to guide their decision-making.

The book is our gift to the potato farmers of sub-Saharan Africa.

John O'Shea and Family,
O'Shea Farms,
Piltown,
Co. Kilkenny,
Ireland.

Foreword, John Weakliam, C.E.O., Vita

The potato farmers of Ethopia battle with seemingly insurmountable odds to produce food for the family table and sell some to earn a little cash. Their insurmountable odds include old and diseased seed tubers, lack of fertilisers and fungicides, tiny land holdings, far away and unfriendly markets, the list is endless. Despite all that, the farmers persevere with great resilience because potato has no peer in busting hunger and breaking poverty. In Ireland, we know that diseased potato caused famine and we also know that healthy potato makes for a wealthy farmer as well as a great meal. Potato farmers know all this too. They know that if you overcome the odds, you can have bigger yields, more food and more money than wheat, barley or any other crop.

Vita started work in partnership with the Ministry of Agriculture with potato farmers in Ethopia in 2012. We learned that know-how was the key to changing lives and that Ireland had the very best of know-how. We started working with the Irish State Agriculture Agency, Teagasc and through Teagasc we met John Burke. John spent his working career engaged in research in crop agronomy. He has dedicated the past four years of his life to sharing a lifetime of experience with farmers in Ethopia.

In a spirit of true partnership and shared learning, potato experts in Africa and Ireland have been able to identify the key obstacles in the potato value chain which have stymied the potato reaching its full potential as a hunger-busting crop. Bacterial wilt, or brown rot as it is called in Ireland, is one such obstacle and another related obstacle is virus prevalence in seed tubers. There are many more critical risks to potato production and this book identifies almost all of those.

This book combines farmer-friendly language with scientific rigour and will more than earn its keep not only in Ethopia but through the Irish Potato Coalition network, across seven countries of Eastern and Southern Africa. The Irish Potato Coalition was established to promote best practice in potato production. The efforts of National Ministries and partners, Vita, Teagasc, CIP and other Coalition partners are being directed to support as many of the four million potato farmers as possible to achieve best practice, improved productivity and more sustainable livelihoods. In this regard, this book will be a key guide to best practice.

A generous financial grant from a Vita donor has defrayed the cost of publishing this book. It is intended that the book will be distributed for free and no financial reward from the publication will accrue to Vita or the author.

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Section 1

The Potato

Introduction

The potato (*Solanum tuberosum*) is fundamentally important as a staple food of humanity. Potatoes are grown and eaten in more countries than any other crop; they are grown in all the continents except Antarctica. In the global economy they are the fourth most important crop in total production and the fourth largest contributor to human caloric consumption, after the three cereals, rice, wheat and maize. As a food crop, the potato is the third most important in the world after rice and wheat in terms of human consumption. More than a billion people, in over 100 countries worldwide, eat potato and global total crop production exceeds 380 million metric tons. Potato is considered the highest yielding crop per hectare of arable land and it will grow in agro-ecologies where other crops will fail. Should growth of the world population continue at the current pace, then within two decades, global demand for food is projected to increase by 50 per cent, demand for water by 35-60 per cent, and demand for energy by 45 per cent. The high yielding potato crop will play a significant role in meeting this increased demand for food.

The crop has a high consumer acceptability by all socio-economic classes. Demand for potatoes is expected to rise with the expected rise in the standard of living in developing countries. Growing the potato provides humanity with an efficient tool to capture and store some of the limitless energy of the sun, which the potato utilises to efficiently convert carbon dioxide, water and nutrients to edible dry matter.

While consumption of fresh potatoes is declining in the western world in favour of processed product, fresh potato consumption is increasing in developing countries. The increasing popularity of the potato in these countries is due to the high nutritional value of the tubers, combined with the ease of its cultivation by vegetative propagation. Potato provides a balanced source of starch, vitamins and minerals to many communities. The potato is rich in the nutrients that humans need. A plentiful supply has often staved off hunger and in some cases facilitated enormous increase in populations. On the other hand potato scarcity, due to destruction of the crop by a pathogen, such as for example in Ireland in the 1840's or Germany in 1917, has resulted in famine and death from starvation.

Origin and history of the potato

Botanists and historians have extensively researched the origin and history of the potato and even today there is still widespread disagreement regarding the precise details. The center of origin of the potato crop is the western coast of South America. The genus Solanum comprises about 1,500-2,000 species (Fig. 1a). There are more than 4,000 varieties of native potatoes, mostly found in the Andes. They come in many sizes, shapes, skin colours and flesh colours (Fig. 1b).

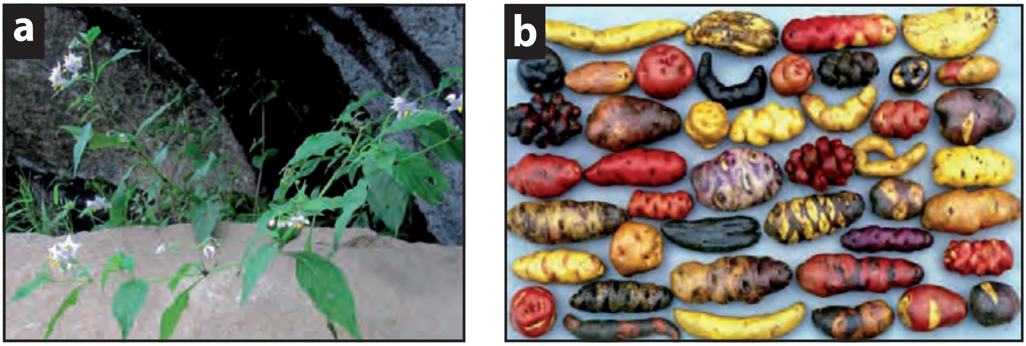

Figure 1.
A wild Solanum plant growing in a rock crevice at the Incan ruins at Machu Picchu, Peru, (a). Selection of native Peruvian potato varieties (b). (Photos (a) Author . (b) © CIP. With permission)

Many member of the *Solanaceae* family are too bitter to eat, their important biodiversity includes natural resistances to pests, diseases, and climatic conditions. It is not known for how long humans, as hunter-gatherers, collected and consumed wild potatoes. There is evidence that that humans first started to cultivate potatoes in the Andes, on the borders of lake Titicaca. Material collected from archeological sites and subjected to radio carbon dating, suggests that domestication of the potato began about 8,000 years ago. Thereafter by breeding and selection, yield improved and the area over which the crop was planted ranged from the hot dry semi desert of the Peruvian coast, to an altitude of 4,500 m above sea level in the Andes Mountains and extended southwards to an area we know today as southern Chile. A major attribute of the potato is adaptability, which allows it to prosper in a wide range of diverse environments. The potatoes we consume today are descendants of the first domesticated potatoes grown for human use (Fig. 2).

At high altitude in the Andes another property of the potato was exploited. Tubers comprise some 20% dry matter and 80% water so they freeze readily at low temperatures. Farmers spread the tubers on the ground and next morning they crush the frozen tubers by walking on them. High daytime temperatures evaporate some of the moisture. The freeze/thaw cycle is repeated three times and produces a flour-like material known as chuño, similar to that produced today by modern freeze-drying. This can be stored for years then prepared for consumption by adding water to rehydrate the powdered product.

Extending the crop growth range to southern Chile was fortuitous, since at its' center of origin in the southern tropics, around the border between modern day Peru and Chile, the potato produced tubers under short day conditions. But when people moved further south and when the potato was grown under the long days prevailing at these low latitudes, tuber formation was delayed. Further crossing and selection produced types that formed tubers early after planting and provided high yields during the short summer season at the low latitudes.

Figure 2.
A market stall in Ollantaytambo, Peru.
At least sixteen different potato varieties are offered for sale (Photo © Author).

Subsequently when the tubers were transported to Europe some lines were pre adapted for growing under similar day lengths, at corresponding latitudes in the northern hemisphere. Ever since humans first began to grow potatoes, we have been picking the 'best' potato plants (with the biggest or tastiest potatoes, for example) to grow for our use. Just by doing this we began to change potato plants to suit our needs. Just as we do today, in current breeding programmes, our ancestors bred potatoes for improved yield, quality, texture, and resistance to disease.

If there is controversy about the origin of the potato crop, there is even further disagreement about its transportation to North America and Europe. The credit for transporting is assigned both to returning Spanish conquistadors, who invaded South America in the 1500's and also to subsequent English explorers. The potato was introduced to Ireland sometime before 1600 and it flourished in the Irish climate and soil. The ease of growing, harvesting, and preparing potatoes also contributed to their rapid success. By 1650, potatoes had become widely grown in Ireland. During the 1700's the potato became established as a food crop in mainland Europe, driven mostly by food scarcity caused by wars and by the demand for food to supply an increasing population. Expansion in planting during the 19th century meant that it was credited as being the staple food crop that fed the expanding urban population, which fueled the Industrial Revolution.

Following its introduction to Europe, the potato was subjected in each country to breeding and selection to provide high yields under diverse local environmental conditions and to satisfy flavour and quality requirements of local consumers.

The potato was similarly brought to other countries around the world such as India, Japan and China in the late 1600's. While there is some evidence of it being brought to Africa at this time also, it was really in the 19th century that the potato was brought there by missionaries and explorers

Major roles of the potato crop

At least six major roles can be assigned to the potato tuber:

- As a hunger-relieving crop
- As food, either fresh, processed or as animal food
- As a propagule, from which to produce the next crop
- As a feed stock in industry for starch and alcohol
- As an item of commerce
- As a resource of biodiversity

The potato as a hunger-relieving crop

A disturbing aspect of our world today is the unevenness of food distribution. The world has the capacity to produce enough food for every person on the planet, yet millions go hungry every day and solving world hunger remains a complex issue. Notwithstanding the huge increase in global food production over the past 50 years, many individuals and communities – mainly in rural areas – do not have physical or financial access to food year round. In some countries there is such excess levels of food that between 10 and 30 percent of it is wasted. Yet in other countries, a short distance away, people suffer from malnutrition and hunger. People are malnourished if their diet does not provide adequate calories, protein and micronutrients for growth and maintenance, or if they are unable to fully utilize the food they eat due to illness (under-nutrition). The causes of hunger are many and complex, but having access to a locally grown high yielding, nutritious crop can alleviate the worst effects. The potato meets these requirements. It is ideally suited to places where land is limited and labour is abundant, conditions that characterize much of the developing world.

Potato can be described as a "fast food" i.e. it grows rapidly and can produce a usable yield in as little as 75 growing days, with a full yield in 100 to 120 days. They are fast to cook, requiring a simple cooking pot and a fire. They are produced locally and not subject to the dramatic price fluctuations of internationally traded food, such as cereal grains.

The potato as food

Potato is one of the most important crops in the world today. Potato produces more protein and calories per unit area per unit time and per unit of water than any other major food plant. One hectare of potato can yield two to four times the food quantity of grain crops. Potatoes are up to seven times more efficient in using water than cereals. It has been estimated that it takes 1000 to 2000 litres of water to produce 1 kg of wheat and 10,000 to 13,000 to produce 1 kg of beef, whereas potato can produce between 4 and 7kg per 1000 litres of water. Another important aspect of potato, the ratio of edible to non-edible components (harvest index HI) is much greater than in wheat, rice and maize. The potato produces more nutritious food more quickly, on less land, and in harsher climates than any other major crop - up to 85 percent of the plant is edible human food, compared to around 50% in cereals.

Potato is a versatile, carbohydrate-rich food, highly popular worldwide and prepared and served in a variety of ways, making them a good source of energy. Freshly harvested, it contains about 80 percent water and 20 percent dry matter. About 60 to 80 percent of the dry matter is starch. In addition, the potato is low in fat. They are a valuable source of at least 12 essential vitamins also minerals and some micronutrients. They are very rich in vitamin C - a single medium-sized potato contains about half the recommended daily intake - and contain a fifth of the recommended daily value of potassium.

On a dry weight basis, the protein content of potato is similar to that of cereals. Potato has the highest protein content (around 2.1 percent on a fresh weight basis) in the family of root and tuber crops, and furthermore, the protein is of a fairly high quality, with an amino-acid pattern that is well matched to human requirements. Because of the well-balanced amino acid composition, potato proteins have a high biological value, higher than offered by any other vegetable protein and close to whey and egg protein.

Potatoes have generally been regarded as one of the least allergenic foods at our disposal. Potatoes contain a wide variety of chemical compounds such as proteins, glycoproteins and alkaloids. Some of the allergens in potatoes are sensitive to heat, so if potatoes are cooked, they no longer have the potential to cause a reaction.

Historically, most potatoes were consumed fresh, i.e. simply boiled. In recent decades however, processed potatoes — crisps, French fries and hash browns, for example — have grown more popular worldwide as the technology to freeze the vegetables has improved. For example, in several European countries some 50% of the crop is consumed after processing. In the U.S., processed potatoes comprised 64% of total potato use during the 2000s, compared to 35% in the 1960s. The FAO estimates that processed food now accounts for 80 per cent of all global food and beverage sales. This change in consumption patterns reflects growing urban populations, changes in traditional male-female roles within the family, more female participation in the workforce, higher levels of disposable income, diversification of diets and lifestyles that leave less time for preparing the fresh product.

With an emphasis on crop production for processing, there is constant demand for improvements in tuber quality. The concept of quality embraces biological traits (e.g. proteins, carbohydrates, and minerals); sensorial traits (e.g. flavour, texture); and industrial traits (e.g. tuber shape, cold sweetening, starch quality). Since most quality traits are genetically controlled, breeding programmes can successfully meet the requirements of a changing and demanding world. Besides being important in human diet, potatoes are also used as animal feed. This trend will expand in developing countries as incomes improve and consumers switch from vegetable to animal based protein, such as meat and dairy products. Cattle can be fed up to 20 kg of raw potatoes a day, while pigs fatten quickly on a daily diet of 6 kg of boiled potatoes. Chopped up and added to silage, the tubers cook in the heat of fermentation.

The potato as a propagule – the seed potatoe

Potatoes are mainly propagated by vegetative methods (cloning). Vegetative reproduction ensures a uniform crop, contrary to what would happen with sexual propagation. The progeny tubers are genetically identical to the mother tuber. Since potato is a vegetatively propagated crop, planting material is subject to degeneration over time, caused by the build-up of virus diseases and other degenerating factors that are transferred from one generation to the next. The use of planting material of low quality leads to reduction in crop yields and quality and causes yield reductions on over 5 million hectares of potato in the developing world. The degeneration of seed potatoes takes place when farmers either sow their own seeds, retained from the previous harvest, rely on informal production or purchase "seed" potatoes from traders in their local market.

Seed borne fungal or bacterial diseases act as a serious limiting factor to potato production worldwide. Fortunately many of these pathogens produce visible symptoms and therefore the infected tubers can be eliminated prior to planting. Virus diseases represent another extremely important pathogens of potato. This is due to their potential for transmission in a symptomless form, from generation to generation, in seed tubers, which causes degeneration of the planting material. While virus diseases are seldom lethal to the plant, they lead to reductions of plant vigor, quality and yields. Reported effects of virus infections on yields are generally highly variable, but can reach up to 90%.

Low seed potato quality is a major constraint of potato production in developing countries. Two factors can be at play here – the inability of the seed supply system to provide adequate quantities of clean seed or the inability of poor farmers to purchase the expensive certified seed. Recognising the problems associated with clean seed supply, CIP (International Potato Center) had pioneered the development of the three-generation (3G) seed multiplication strategy as an approach that helps to substantially improve the quality of the seed. The concept underlying the 3G strategy is to reduce the number of multiplications between *in vitro* plantlets to making seed available to farmers, to prevent contamination with diseases and viruses transmitted by vectors. However, it requires availability of a certain infrastructure such as laboratory and greenhouses for mass production of plantlets *in vitro* and of mini tubers. Then it needs skilled personnel to complete the field multiplication steps.

No single technological fix will resolve the potato seed problem; it will have to be accompanied by a broad, systemic approach aimed at the general improvement of the entire seed system in a particular region. Good quality seed is essential to high yields and is usually the most costly input to potato cultivation, accounting for 30-50 percent of production costs. In many developing countries the scarcity and greater expense of such high quality seed tubers at planting time may force potato farmers to plant inferior seed, or to depend on expensive, imported seed, which may or may not arrive in time for the optimum planting dates. The improvement of seed quality will contribute significantly to enhancing farmer efficiency and competitiveness.

The potato as a feedstock for starch and alcohol

Potato starch is a very refined starch, containing minimal protein or fat. It is a fine, tasteless powder with excellent "mouth-feel". The starch is therefore used to provide viscosity or act as a 'binder' in sauces and soups. It provides higher viscosity than wheat and maize starches, and delivers a tastier product. Potato starch tolerates higher temperatures than maize starch. It is used as a binding agent in cake mixes, dough, biscuits, and ice cream. Potato starch is now often valued for its indirect uses, such as in animal feed and biofuel.

In Eastern Europe and Scandinavia, crushed potatoes are heated to convert their starch to fermentable sugars that are used in the distillation of alcoholic beverages, such as vodka and akvavit.

Potato peel and other "zero value" wastes from potato processing are rich in starch that can be liquefied and fermented to produce fuel-grade ethanol. A study in Canada's potato-growing province of New Brunswick estimated that 44,000 tons of processing waste could produce 4-5 million liters of ethanol.

Potato starch is widely used by the pharmaceutical, textile, wood, and paper industries as an adhesive, binder, texture agent, and filler, and by oil drilling firms to wash boreholes. Potato starch is a 100% biodegradable substitute for polystyrene and other plastics and used, for example, in disposable plates, dishes, and knives.

Potato flour is made from whole potatoes (most of the time even the peel is included). The potatoes can be raw or cooked. Either way they are first dried then ground into flour. The result is a heavy, cream-colored flour with a distinct potato flavor.

The potato as an item of commerce

The growth in population and increasing urbanization and specialization led to the need to produce larger quantities of food and then transporting it over longer distances. Unlike wheat, rice and maize, which are internationally traded commodities the potato crop is largely consumed locally. This helped to protect the potato from the food price hikes in 2007-08 caused mainly by the diversion of grain from food to ethanol production. Potatoes are exported mainly as fresh, seed or as frozen product. The market for frozen product is the most globalized one, with the highest market integration and highest price transmission. The USA exported 3 million tonne in 2014, while the European Union exported 1.1 million tonne to Saudi Arabia. In many African countries the import of frozen French fries is prompted by the requirements of the lucrative tourist and hotel trade. Potatoes however, are commonly regarded as a bulky, perishable commodity with high transport costs and limited export potential, confined mostly to cross-border transactions.

These constraints have not hampered the international potato trade, which has doubled in volume and risen almost fourfold in value since the mid-1980s. This growth is due to unprecedented international demand for processed products, particularly frozen French fries and dehydrated potato products. To date, developing countries have not been beneficiaries of this trade expansion. As a group, they have emerged as leading net importers of the commodity.

International trade in potatoes and potato products still remains thin, relative to production, as only 7% of output is traded. That value however, is higher than for rice, where only 5% of output is traded. High transport costs, including the cost of refrigeration, are major obstacles to a wider international market place for potato. Despite these constraints, world potato trade was worth at least US$12.2 billion in 2015. In countries that lack a properly functioning potato seed certification scheme, importing certified seed potatoes might appear to be the answer. But importing seed potatoes is different to importing cereal seed. Seed potatoes are highly perishable and will deteriorate in days if not stored under proper conditions, e.g. refrigerated container. When seed tubers are shipped across international borders the costs usually double due to transport costs, tariffs and compliance with phytosanitary requirements.

While potatoes may not rate highly in international trade, they are very valuable as a source of family income when sold by the farmer in the local market or to mobile potato traders. This type of local marketing is fraught with controversy and discussion abounds regarding the ethics. When farmers, organize in marketing co-operatives, they can resolve many of the problems associated with local seed trading and as there is strength in numbers, it would prevent the trader from taking unfair advantage.

The potato as a reservoir of biodiversity

When humans first started the domestication process over 8,000 years ago, the biodiversity (variation of life forms within ecosystems) of plants and animals at large was changed, and huge amounts of the original biodiversity were lost. Humans rely on biodiversity; at least 40 per cent of the world's economy and 80 per cent of the needs of the poor are derived from biological resources. For potatoes, the richer the diversity, the greater the opportunity for the emergence of traits which can permit the crop adapt to new challenges and changing conditions.

In the year 1800, the world population first reached I billion. The population doubled between 1950 and today. Furthermore the UN forecasts a population of 9.2 billion for the year 2050. The demands on natural resources and biodiversity are growing even faster, because the global economy has quintupled in the last 50 years. As the amount of land available for agricultural use continues to decrease worldwide, more pressure on the soil resource base and the environment is to be expected.

Biodiversity is nature's bulwark against unfavourable change. Genetic diversity ensures that crops have within their genetic makeup the capacity to adapt to changing environments; a natural weapon offering them the flexibility to deal with unforeseen events such as climate change, and giving them greater chances to resist pests and diseases.

The history of the potato provides a grim warning of the need to maintain genetic diversity in our staple food crops. In the 19th century, Ireland was heavily reliant on only a few varieties of potato, and unfortunately those contained little resistance to the devastating fungal disease known as late blight. When late blight destroyed the 1845-1847 potato crops, widespread famine followed.

The potato has a richer genetic diversity than any other cultivated plant. In the center of origin in South America, potato genetic resources include wild relatives, native cultivar groups, local farmer-developed varieties ("landraces"), and hybrids of cultivated and wild plants. The biological traits inherited over aeons are carried as genetic code within the DNA of the potato genes and these traits will ensure the crops' survival. In both potato and sweet potato it is easy to see genetic diversity in the fantastic variety of tuber shapes (Fig. 1), flower, skin, flesh colours, and tastes that they show. But while these are the visible traits, it is the invisible traits, which exist at the molecular level, like resistance to disease and drought that provide a valuable genetic repository that can be mined by breeders and farmers.

Wild potatoes display a wide variation in appearance and taste. They occur in a variety of shapes and colours. Due to the presence of poisonous alkaloids, the tubers of some species taste extremely bitter. This bitter taste is induced by the presence of the glycoalkaloids - α-solanine and α-chaconine. The evolutionary role of glycoalkaloids is both that of feeding deterrent to discourage predators including animals and insects and to protect against adverse effects on hosts from fungi, bacteria, viruses, and insects.

There is an ever present demand from today's potato-based agricultural systems for new potato varieties to combat pests and diseases, increase yields, and sustain production on marginal lands. The chances of success are enhanced if breeders have access to the entire potato gene pool. The prerequisite of the ancient agriculturalists was to identify useful or edible species. A selection process to identify the more productive cultivars followed. Today farmers, amateur and professional breeders maintain that quest for more productive cultivars.

The selection process, in the quest for new cultivars, necessarily results in a reduction and simplification of the immense biological diversity of nature, at both the species and genetic level. Natural biodiversity is the "mine" from which this resource base is derived. If we allow it to be destroyed, we destroy our own safety net. The traditional potato varieties may not provide the highest yields but they are highly prized for their unique flavour and cooking qualities. They are a genetic resource and will repay any effort to protect and preserve them. It is important to support farmers to maintain this potato diversity. The diversity of wild potato plants is a valuable resource for modern potato breeders, who may be able to breed useful traits found in wild potato species, such as the ability to resist disease, into the potato plants we grow as crops.

Constraints on potato production

In countries, where agricultural productivity is low, population growth rates are high and the ability to import food are severely constrained, one of the most important objectives is to accelerate agricultural growth. Improving potato productivity would help address the issues of food supply and food security.

There are biotic and abiotic constraints to crop production. Many constraints derive from the biological characteristics of the potato itself. These include the low multiplication rates of seed tubers, and the technical difficulties and costs associated with maintaining seed quality through successive multiplications. Maintaining seed quality is an ongoing problem due to the potato's susceptibility to soil and seed-borne insect pests and diseases. Seed tubers are also bulky: two to three tonnes of seed per hectare are typically required. Stringent phytosanitary restrictions limit the movement of potato germplasm, seed tubers and fresh ware potatoes.

Potatoes have high fertilizer requirements but low utilization efficiency – nitrate is readily lost from the root zone. A long-term approach may be to reduce this loss by developing potato cultivars which utilise N more efficiently. Post-harvest, fresh potato tubers deteriorate quickly in tropical and subtropical environments, especially in the lowlands. Today the global food system is subjected to increasing pressures from two directions. The world population is growing and patterns of food consumption are changing due to globalization, rising income levels and urbanization. These factors contribute to the demand for animal derived protein products and particularly processed food. The demand for biofuels is also impacting on the supply of land available for food production

To help offset these additional demands, there is no longer a vast pool of available under utilised fertile land. Increasingly there are moves to bring marginal land into production. Meanwhile, topsoil degradation and erosion are reducing the available agricultural land pool.

Crop productivity must increase to meet the food requirements of the world's growing population. Achieving this objective will put considerable pressure on global water resources. While globally there should be sufficient water for future agricultural requirements, in many regions surface and ground water is becoming less available due to urban and industrial water use rising. The combination of low water supply and high human demand may lead to regional shortages of water for future food production.

This is happening against a background of climate change, where rising temperatures, changing patterns of precipitation and more extreme weather events are likely to negatively affect the conditions for agricultural production in many regions of the world. There is potential for improvement however, since in both dry-land and irrigated agriculture only about one-third of the available water (as rainfall, surface, or groundwater) is used to grow useful plants.

Another constraint to potato production is the risk from pests and pathogens. Since the 1940's there has been a non-ending stream of new pesticides designed to control fungi, weeds and insect pests. Because of overuse and misuse, many of these products are now redundant due to the development of resistance. In recent years the cost of bringing a new agrochemical to the market has soared owing to rigorous testing protocols and the requirement to meet ever more stringent regulations with regard to the effects on target and non-target organisms; so consequently the production cycle for new compounds has slowed dramatically. We must therefore use the available compounds with care and discretion, so as to prolong their useful life.

An abiotic constraint to potato production relates to the soil. The top 30cm of soil has nourished the farmer's ancestors since they settled there. It is truly their most valuable asset – even priceless - and if it is protected from erosion, degradation and contamination by persistent pathogens it will continue to provide sustainable yields of potatoes and nourish the generations yet unborn.

Tillage, monoculture, pesticide use, erosion and soil contamination or pollution, generally have negative effects on most soil organisms, reducing the soil's capacity to maintain its function. This has numerous facets including decreased soil organic matter content, loss of soil structure, loss of soil through wind and water erosion. On the other hand, the application of organic wastes, moderate use of mineral fertilisers, crop rotations, irrigation in dry and drainage in wet areas generally have positive impacts on soil organism densities, diversity and activity. These latter practices will support sustainable potato production without the need for excessive amounts of expensive external inputs.

Summary

Why Plant Potatoes?

- The potato is an easy crop to grow and the generous yield will provide ample compensation for the effort expended.
- Let's say you have 1ha of farm land. If you grew potatoes, you could meet the energy needs of 22 people. If you used this land to produce beef or eggs, you could meet the energy needs of 1 person.
- Potatoes produce more energy per day on a given area of land than any other crop. Compare to a grain crop, for example. Only 33% of a grain plant is edible, versus 75% of a tuber plant.
- Potatoes take 2-3 months to mature and can be stored for long periods of time. They are an efficient means of converting solar energy, land, water, and labor into nutrition.

Speaking of water…

- It takes 25 litres of water to produce one potato.
- It takes 40 litres to produce one slice of bread.
- It takes 40 litres to produce one glass of milk.
- It takes 70 litres to produce one apple.
- It takes 135 litres to produce one egg.
- It takes 2400 litres to produce one hamburger.

Sources accessed in the preparation of this section.

Lutaladio, NeBambi. Ortiz, Oscar. Haverkort, Anton. Caldiz, Daniel, (2009). Sustainable potato production – Guidelines for developing countries. Publ . FAO 91 pp.

Gastelo, Manuel; Kleinwechter, Ulrich and Bonierbale, Merideth, (2014). Global Potato Research for a Changing World. Pub. International Potato Center (CIP) 54pp.

F.A.O AGP - Agriculture and soil biodiversity

F.A.O (2008). International Year of the Potato.

Section 2

Botany of the potato plant

Introduction

The potato can be defined as having an annual cycle and a perennial cycle. In the annual phase, food synthesised in the leaves passes to the ends of the stolons, which swell and form the tubers we call potatoes. Since the potato tuber is a stem, it has leaf scars and lateral buds; these constitute the familiar 'eyes'. Each one of these can produce a new shoot in the following year (the perennial phase), using the food stored in the tuber. The old tubers shrivel and rot away at the end of the season

Potato - Scientific classification

Plant classification is the placing of known plants into groups or categories then grouping successive categories into a hierarchy. The act of classification can be defined as 'the grouping of individuals so that all the individuals in one group have certain features or properties in common'

According to the rules of taxonomy potatoes are classified as:

Order:	Solanales
Family:	Solanaceae
Genus:	Solanum
Species:	Solanum tuberosum

Cultivar is the lowest rank. A cultivar is a cultivated variety, a particular plant that has arisen either naturally or through deliberate hybridisation, and can be reproduced (vegetatively or by seed) to produce more of the same plant. A cultivar is also defined as plant or grouping of plants selected for desirable characteristics that can be maintained by propagation.

There are more than 4,000 varieties of native potatoes, mostly found in the Andes (Fig. 1). There is at least a further 1000 cultivars either in cultivation or in collections around the world.

Potato cultivars are roughly classified into four types based on their purpose: table use, food processing, starch production, and other purposes, including colorful potatoes. Consumption of table use potatoes continues to gradually decrease in many countries. In contrast, consumption of potatoes for food processing such as potato chips, French fries, frozen croquettes, and packed salads, has greatly increased since 1970. This is driven by increase in urbanization and the growth of the socio-economic group defined as "middle-class".

Figure 1.
A selection of potato cultivars. (Photo © CIP. With permission)

Potato ploidy level

Ploidy is a measure of the number of sets of chromosomes in the nucleus of a cell. In common with many other important crops, potato is a polyploid. Just as in hybrids, polyploids have been observed to be more vigorous than their diploid parents. This may include bigger leaves as well as an increase in height. The polyploids can also be more disease and pest resistant.

The effect of polyploidy on crop production has yet to be determined, but its prevalence in a broad range of crop species suggests certain advantages. Polyploidy is an important mechanism in plant speciation that has been associated with geographical and environmental range expansions. Polyploidy in potato results from genome doublings (autopolyploidy) rather than genome combinations (allopolyploidy).

The cultivated potato belongs to a species, *Solanum tuberosum*. Domestic potato cultivars are highly heterozygous autotetraploids. Potatoes may be classified into different ploidy levels, based on a haploid number of 12, ranging from diploid (2n=24) to hexaploid (6n=72), and including triploids, tetraploids, and pentaploids. The cultivated potato is a highly heterozygous tetraploid (4n=48); many wild species are diploid but may range up to hexaploid. The tetraploid cultivated potatoes are not diploidised, so that there are four interchangeable genes at each locus.

Botanical description

The potato plant is an herbaceous perennial (a plant whose growth dies down annually but whose roots or other underground parts survive) in that it lacks a woody stem and

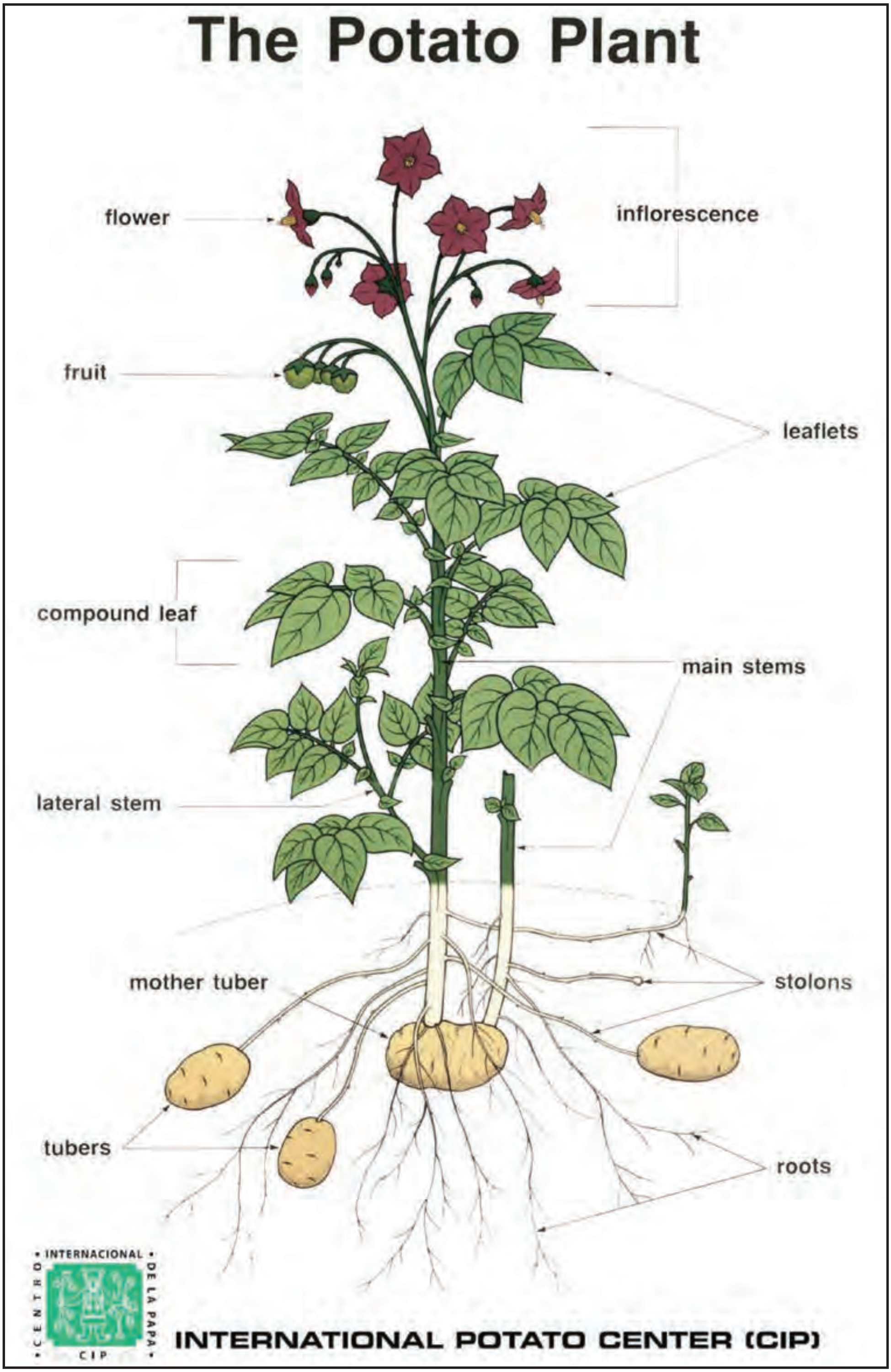

Figure 2.
The potato plant (Image © CIP. With permission)

lives more than two years. Under normal cultivation it is grown as an annual, with the above ground stem dying back at the end of the growing season. The tubers provide the perennial dimension – but this only happens when plants are not harvested at the appropriate time and allowed to regrow as "volunteer potatoes".

The above ground portion – the stem, and the collection of stems – the canopy, is the most recognizable characteristic. Two types of stem are recorded: determinate and indeterminate. The stems on determinate cultivars will typically grow to between 75 and 95 cm. tall. Indeterminate stems can attain heights of 2.0 meters depending on the number of successive axillary stem orders formed (They are called "axillary" because they form in the angle between the leaf and the stem: this is the leaf "axil."). These values however are not absolute as they can be modified by factors such as physiological age, soil nutrient status and soil moisture status (excess moisture – water logging - restricted growth or moisture scarcity and again restricted stem growth). Growth habit may range from fully erect, through rosette to completely prostrate.

The below ground portion – the tuber. The potato tuber is an enlarged portion of an underground stem, in which case these underground stems are termed stolons. The stolon can often grow through the side of the ridge and emerge above ground. Stolons emerging from the soil in this manner will go on to form a stem and leaves. The term stolon is commonly used in the potato literature for both rhizomes and stolons.

Although potato tubers grow underground, they are not roots. Growing underground does not make a plant part a root, and, similarly, growing above ground does not make a particular plant part a shoot. As discussed above roots and shoots are defined by where they form during the development, of the plant embryo. Plants usually produce shoots that grow aboveground, where their leaves are exposed to the sunlight that is needed for photosynthesis, and roots grow below ground, where they take up water and extract nutrients from the soil. Some plants, like potatoes, are specialized to produce shoots below ground (as well as above ground).

The Potato Stem

The stem is generally considered to be the central structure of the potato plant. The stem is a collection of integrated tissues arranged as nodes and internodes. Nodes are locations where leaves attach to stems, and internodes are the parts of stems between nodes. The stem supports leaves and turgor pressure in stems provides a hydrostatic skeleton that supports young plants. Leaves are also supported by a stem's internal structure of collenchyma and sclerenchyma. It supports the flowers and has nodes from which new shoots and sometimes new roots can arise, is usually found above-ground, but stems can be modified and found below-ground as well. Stems of potato plants are green and photosynthetic, however photosynthesis in stems is not significant compared to leaves.

Potato plants grown from true seed have one main stem; but when propagated from 'seed' tubers the potato normally produces a number of stems and these are categorised either as main stems (Fig. 2) or secondary/lateral stems. Main stems originate from the tuber eye and because the eye may contain several buds, more than one stem may emerge.

Stem colour is generally green or mottled green (Fig 2 a); occasionally it may be red-brown, or purple (Fig. 2 b). Main stems show partial apical dominance. Stems are round to angular, usually triangular, in cross section. Wings or ribs are often formed at the angle margins. These wings can be straight, undulate or dentate (Fig. 2 c). Stems range from nearly hairless to densely hairy. Stems may be solid or partly hollow due to the disintegration of the pith cells.

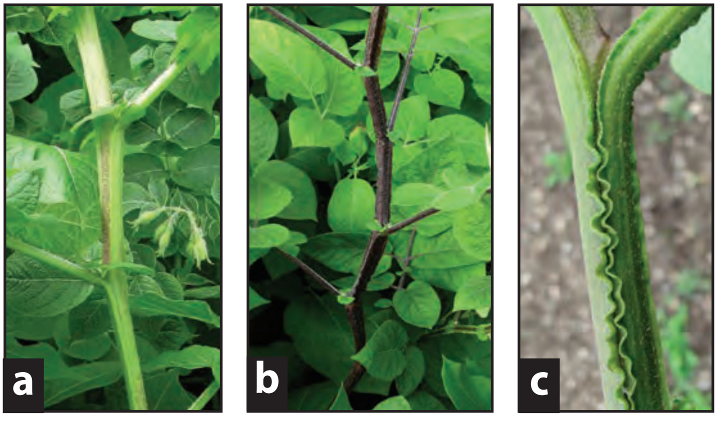

Figure 2.
Stem type and colour (a & b). Dentate wings (c). (Photos © Author)

The potato main stem plays a major role in determining tuber yield. This is achieved through interstem competition, whereby stems compete for water, nutrients and light. The intensity of competition controls the number of tubers formed per stem and then goes on to influence the size distribution of the tuber crop. The main stems terminate in an inflorescence. With determinate cultivars, no further growth takes place. With indeterminate cultivars, a bud in the axil of the leaf subtending the inflorescence may elongate to produce a secondary stem, which forms leaves and again terminates in an inflorescence. This is sometimes known as a 1st order apical branch. After this branch terminates in an inflorescence, a 2nd order branch may develop and the process continues until the onset of canopy senescence. The number of levels or orders produced per stem depends on factors such as cultivar, physiological age of seed and environmental conditions. Indeterminate cultivars require a long growing season to ensure that their potential yield is attained.

Main stem branches

Axillary buds are young dormant branches. These buds have different development potentials. They are called “axillary” when they form in the angle between the leaf and the stem; this is the leaf “axil.” When an axillary bud elongates, it forms a branch. Branches tend to replicate the basic structure of the shoot system, in being composed of stem and leaf components.

Axillary buds forming in the axils of leaves just above the soil level of the main stem may begin to elongate until it forms a branch. These lateral stems are branches of main stems.

Main stem branches can also arise from nodes below soil level. These branches can go on to form roots, produce stolons and form tubers (Fig. 2). They behave independently of the main stem.

Leaves

Leaves are the most active and conspicuous organs of the potato plant. Their most important function is absorbing sunlight for use in photosynthesis. When all or most leaves are arranged at or near the base of short stems and are near the soil surface, the plant has a rosette or semi-rosette habit.

The potato leaf is pinnate; that means that leaflets are attached along a common axis; there is a terminal leaflet and therefore an odd number of leaflets (Figs. 3a and 3b). Three to four pairs of leaflets are generally present. The leaflets are borne on petiolules; they are ovate (i.e. they have a tapering point). Secondary leaflets (Fig. 3b) fill the spaces between the primary leaflets and serve to increase the amount of light intercepted.

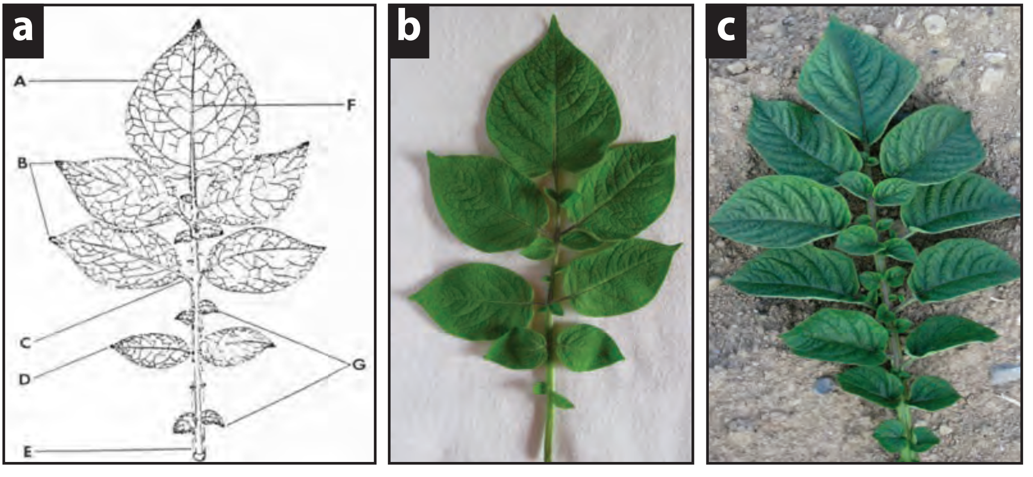

Figure 3.
Diagrammatic illustration of a potato leaf:
A Terminal leaflet. B Primary leaflets. C Petiolules. D Secondary leaflets. E Petiole.
F Midrib. G Tertiary leaflets (a); Primary, Secondary and Tertiary leaflets (b & c).
(Photos b & c © Author)

Roots

Potato plants may develop from true seed or from seed tubers. Plants grown from seed form a slender taproot with lateral branches. Under conventional agriculture, potato plants grown from tubers form adventitious roots at the base of each sprout and, later, above the nodes of the underground part of each stem. Occasionally, roots may also grow on stolons. In comparison with other crops, the potato root system is poor. Therefore, good soil condition is necessary for potato growing. The type of root system varies from light and superficial to fibrous and deep.

Potatoes produce more roots in the upper soil layers than many agricultural crops (Fig 4a). In early growth, roots are almost entirely confined to the top 20cm. of surface soil. After extending horizontally to a distance of 30 to 60cm. or more, the roots turn more or less abruptly downward and penetrate the 60 to 90cm. zone of soil. Branching is very profuse throughout the root extent, and at maturity, laterals occur to the root tips. Usually the branches are relatively short but so numerous and well rebranched that despite the poorly developed root system, the absorbing system is very efficient.

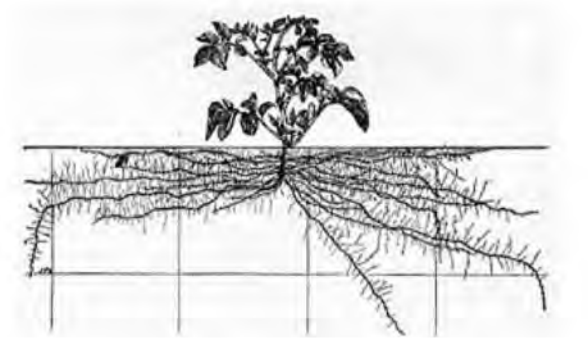

Figure 4a.
Development of a potato root system at 56 days old (Source, Weaver 1926)

Figure 4b.
Illustration, showing white fleshy stolons with tubers attached and brown-coloured fibrous roots. (Photo © Author)

Stolons

The stolon is an underground modification of the stem. The formation of stolons normally begins at the lower nodes on the stem and progresses acropetally. Stolons (technically rhizomes) have elongated internodes and have leaf scales located alternately on their surface, in the same manner as the aboveground stems. Buds developing at the base of the stem produce shoots, which grow horizontally at first (they are diageotropic stems) and then down into the ground. In conditions that are noninductive for tuberisation, e.g. long day, the stolons often grow upward and emerge out of the soil to form a new shoot. However, In tuber-inducing conditions, e.g. short-day, the stolons grow under-ground until the tip of the stolon swells to form the tuber. In potato, stolon swelling is confined to the tip. Under repeated cycles of stress imposition, stress relief, a phenomenon called 'chain tubers' occurs. This gives the impression of multiple swelling events (Fig. 5d B).

Although they resemble roots superficially (Fig. 4b), they can be distinguishable from roots by the presence of the following features; presence of nodes and internode; presence of scale leaves, buds and adventitious roots at the nodes; an internal structure resembles that of aerial stem and not of root.

Tubers

Many adaptations for asexual propagation involve underground plant parts. In some cases the structures are true roots, but most are modified underground stems. The common potato isn't a root, but is a tuber. A tuber is the botanical name for the swollen end of a fleshy underground stem (a stolon), which arises from a below-ground axil at the base of the stem.

Tubers are enlarged structures of the potato plant; used as storage organs for nutrients; used for the plant's perennation (survival through the winter or dry months); used to provide energy and nutrients for regrowth during the next growing season, used as a means of asexual reproduction and used for consumption.

The underground stems (stolons) grow horizontally outwards in the soil and are modified to store starch for subsequent growth (or for consumption). The tuber can be defined as a stem because it has many nodes called eyes, with spaces between eyes known as internodes. The potato is an example of a shoot that has become specialized for storage. Each tuber is irregular in shape due to the deposition of food materials (starch). The importance of tubers is reflected in the fact that some 75 to 85% of the dry matter produced by the plant accumulates in the tuber.

Tubers are covered by a corky skin, with a number of small depressions. These depressions, which comprise a C-shaped leaf scar with a subtending axillary bud, are called eyes (Fig. 5a). Eyes of potatoes are really axillary buds, which contain several small buds at each site. These buds can expand to form shoots and roots that grow on to make whole plants. As with stems of other kinds of plants, we can look along the length of the potato tuber to find its nodes and internodes. They are arranged in a downward spiral pattern from the terminal end to the point of attachment of the stolon. The small, scale-like leaves have usually worn away before the potato is harvested; however, we can readily find the so-called "eyes" that are the nodes of the potato stem; each eye represents a node. A big scar at one end of a potato marks its attachment to the stolon. This is often referred to as the "heel end" of the tuber while the terminal end, with its apical bud, is referred to as the "rose end" (Figs. 5b and 5c)

Figure 5.
A tuber eye with its C-shaped leaf scar and axillary bud (a); Stolon attachment heel end (b); rose end (c). (Photos © Author)

While normally tubers form at the tips of stolons, occasionally tubers form along the stolon itself, resembling beads on a string, (these are referred to as "chain tubers")(Fig 5d). This phenomenon is observed when growth is interrupted by early drought followed by growth resumption after irrigation or rainfall. Under experimental conditions, repeated cycles of high nitrogen/nitrogen withdrawal can also result in the formation of "chain tubers," demonstrating that nitrogen levels play an important role in the control of tuber formation.

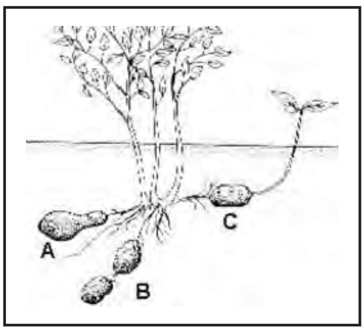

Figure 5d.
Various scenarios, resulting in the formation of chain tubers. (Image courtesy aardappelpagina)

Tubers can actually form on other parts of the plant above ground, normally from axillary nodes on the stem. These aerial tubers are usually formed only on injured or diseased plants, where translocation of assimilates below ground has been prevented, or in plants grown in very strong inducing conditions.

Potatoes can be grown by cutting a single potato into fragments that each contains an eye. When planted, the axillary bud of each potato piece will begin to grow outward from the eye to form an entirely new plant that will have an above-ground shoot with stems and leaves and below-ground roots. That new plant will also have the ability to form underground new potatoes.

The potato tuber for consumption

Potato tubers come in a variety of shapes, which can be round, oblong, flattened, or elongated. Skin and flesh colors: range from purple, pink, gold and yellow, but most common are red and white skins; white and cream coloured flesh.

Quality is one of the most important aspects related to potato tubers. Quality parameters vary according to market specification and to utilization requirement. Two major categories exist. The first category groups "external quality", aspects comprising skin colour, tuber size and shape, eye depth. These traits are deemed very important for fresh consumption where the consumer "shops with their eyes" and furthermore, external traits are most likely to influence consumer's choice. The second category comprises "internal quality" aspects including nutritional properties, culinary value, after-cooking properties or processing quality. Internal quality is given by traits such as dry matter content, flavour, sugar and protein content, starch quality, type and amount of glycoalkaloids. Potato varieties have a range of subtle flavors.

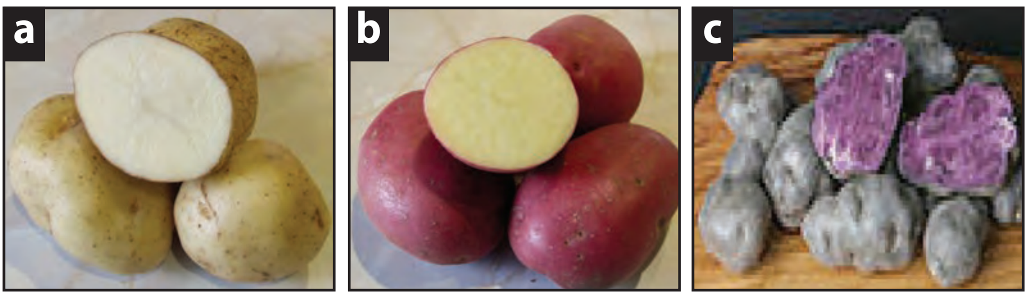

Figure 6.
Examples of tubers having white skin, white flesh (a), red skin, yellow flesh (b) and 'black' skin, purple flesh (c) (Photos (a&b) © Author, (c) Courtesy Wikipedia)

Growing potatoes from true seed

True Potato Seed (TPS) is the actual botanical seed produced by the potato plant. Found in tiny seed balls resembling tomatoes, TPS is occasionally formed after the potato has finished flowering (Figure 7b). Potato crops are normally planted using the potato 'seed' tuber, but planting from TPS has several advantages.

The peculiarities of potato genetics cause plants grown from TPS to be markedly different from the parent plants and from each other. This diversity helps ward off incidences of plant disease while offering growers an opportunity to develop their own varieties. Plants grown from true seed exhibit great variation; selecting material from within this variation is the basis of potato breeding.

TPS can be collected and saved. TPS can be stored in a cool, dry place for about eight months before planting them indoors into trays and transplanted out to the field.

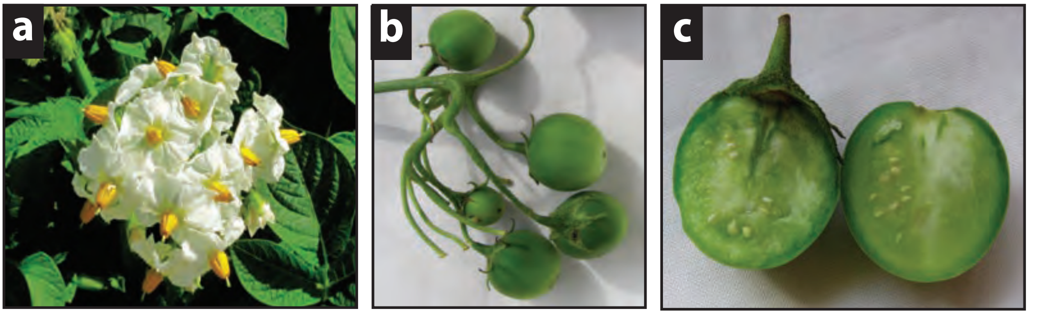

Figure 7.
Potato flower (a) and potato fruit (berry) (b), berry showing true potato seed (c). (Photos © Author).
(**Note**: *Potato berries, which resemble tomatoes, contain toxic compounds known as glycoalkaloids, of which the most prevalent are solanine and chaconine. They must never be consumed, especially by children.*).

The potato flower

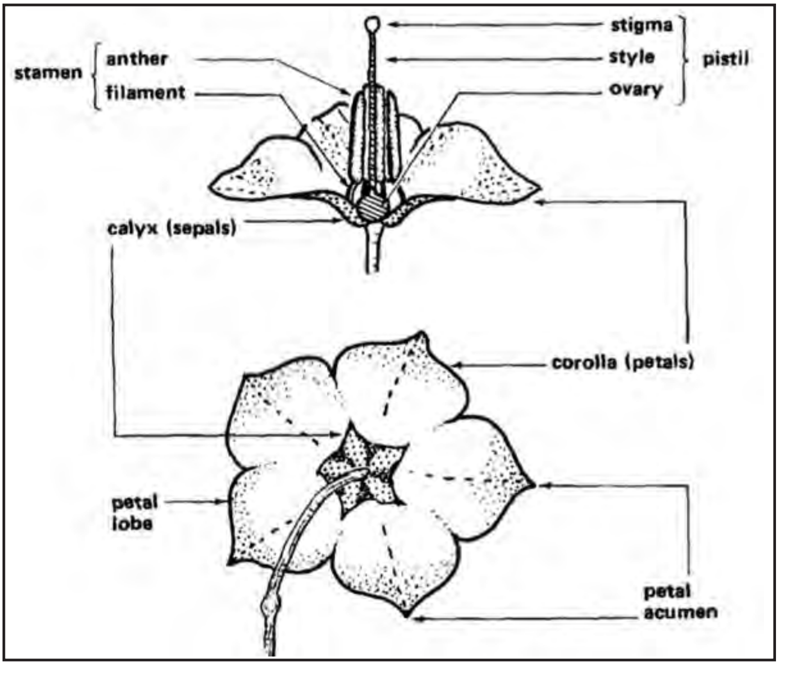

Figure 7d.
Diagrammatic representation of a potato flower (Image © CIP. With permission)

Breeding a new potato cultivar

The objective of all potato breeding programmes is to develop potato cultivars that are genetically superior to the existing cultivars and that satisfy or exceed the standard cultivar for yield and grade in the fresh and processing markets. To achieve these objectives, parental lines with desired traits are crossed and progenies are evaluated.

The potato plant contains a wealth of genetic resources. While containing only 12 chromosomes, cultivated varieties have four copies, for a total of 48 chromosomes. When the potato plant reproduces, usually though self-pollination, the chromosomes (along with the genes they carry) are reshuffled, distributing themselves randomly to the seeds. Each seed will develop into a plant with unique characteristics. Each of these plants will produce tubers that are widely different from tubers on neighbouring plants, they will range in tuber shape, they will vary in skin and flesh colour while others will demonstrate excellent disease resistance. Some will be worth growing out for generations, while others will grow poorly and have to be discarded.

The modern, tetraploid cultivated potato has four sets of chromosomes and this means that the cultivated potato cannot easily be crossed with many wild potatoes, which are mostly diploids. Therefore the majority of breeding with potatoes involves crosses between tetraploid genotypes followed by recurrent selection based on phenotype. Parents are selected to be diverse in order to minimize homozygosity and inbreeding depression, and test crosses may be performed in order to determine which parent combinations are desirable. Although molecular markers are increasingly used, selection is typically applied at the phenotypic level. Due to the heterozygosity and tetraploidy of *S. tuberosum*, traits are expected to segregate in the F1 generation, and large populations are typically generated, on the order of tens of thousands. From the F1 generation, tubers will be removed and planted, representing the first clonal generation. The clones will then be put through a series of field trials in an increasingly diverse range of environments over a number of years, and selection will be applied to reduce the number of clonal lines until only one or at most, a few remain.

Breeding methodology

Potato breeding is now largely carried out by research institutes or professional breeding organisations, with considerable investment in infrastructure, where the crossing is carried out in a controlled environment (Fig 8). But it can be done on a small scale, even by amateur breeders and with a lot of luck! they could develop a successful new variety.

Potatoes produce flowers that can be either self-pollinated, or cross-pollinated, to produce fruits, containing true seed. Potato flowers being bisexual facilitate self-pollination. They posses all four essential parts of a flower; calyx, corolla, male elements and female elements (Figs. 7d and 9).

Figure 8.
Glasshouse with parent plants being prepared for crossing. (Photo © Author)

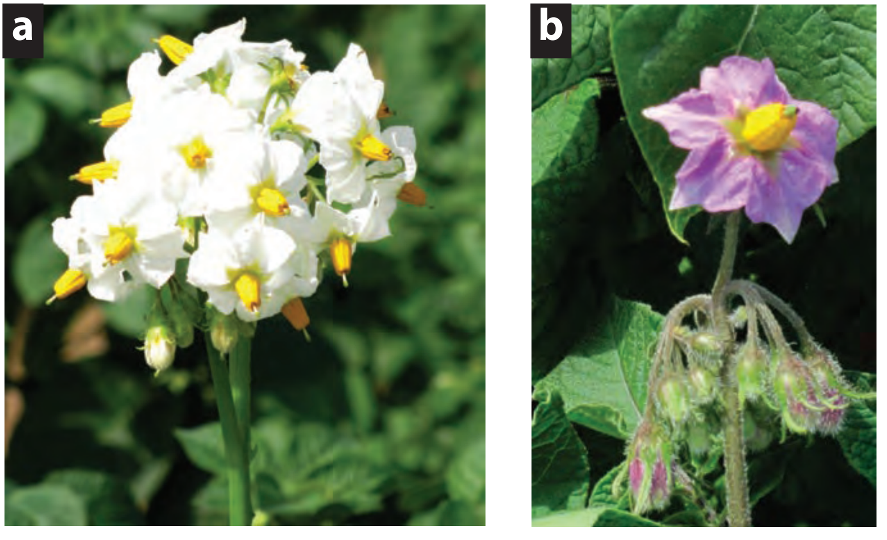

Figure 9.
Potato flowers, showing white and purple petals, yellow anthers, with stigma and style protruding. (Photos © Author)

The first step in a breeding schedule is to select potato varieties or genotypes with complementary traits for use as parents. Next decide which will be used as the female parent. The flowers should still be closed, (Fig. 10a) with the petals fully formed but adhering to each other. The petals are gently pulled apart and the anthers exposed. Unless the breeder is certain that the plant is self-sterile, the anthers are removed

(Fig10b). This step is referred to as emasculation and is done the day before the flower opens. Otherwise, when the anthers mature, a small aperture appears at the tip and this allows pollen to emerge and deposit on the stigma, allowing the plant to self-pollinate.

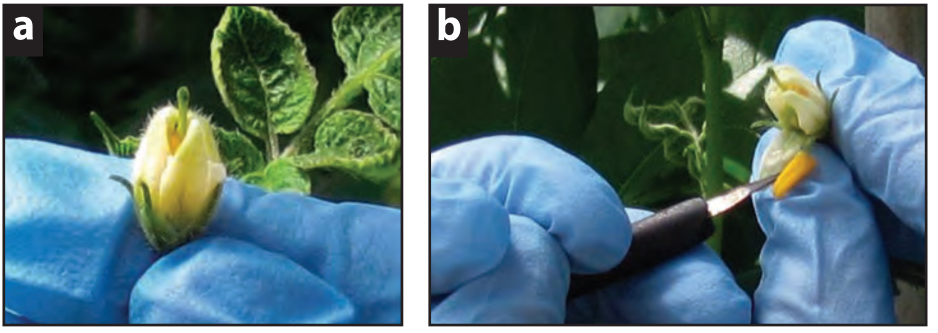

Figure 10.
Flower with petals still closed (a). Emasculating the flower (b). (Photos © Author)

The flower, with the stigma, style and ovary exposed, is now ready to receive the pollen (Fig. 11). A small label, containing data on the parents in the cross, is attached by string to the flower

Figure 11.
The flower on the female parent ready for pollination. (Photo © Author)

A male parent is selected for the cross. The five anthers are arranged tightly around the pistil of the flower, or they may be loosely arranged. The pollen is stored in the anthers and when it is 'ripe' it assumes a dust-like quality. It is removed by splitting open the anther. A pen nib or blunt scalpel can be used (Fig. 12). Excess pollen can be collected, dried and stored in small glass vials for future use. Make sure that the pollen is not sterile.

Figure 12.
Collecting pollen from an anther using a pen nib. (Photo © Author)

A small amount of pollen is collected on the pen nib and applied to the flower stigma (Fig. 13a). Up to 200 such parental crosses are completed each year in a typical breeding programme. After pollination, a label is attached, carrying details of the parents used (Fig. 13b).

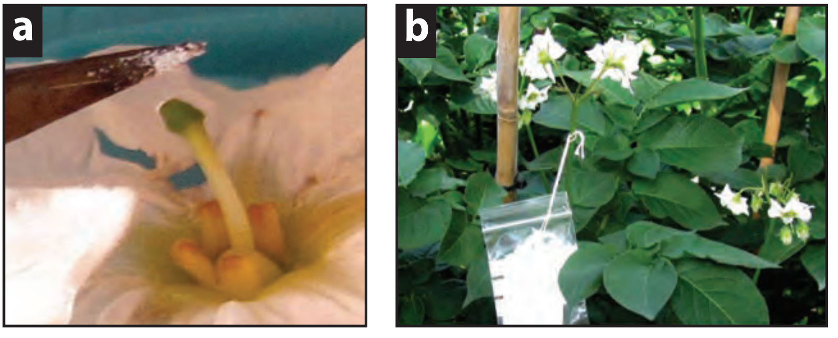

Figure 13.
Pollinating the potato flower (Photos © Author)

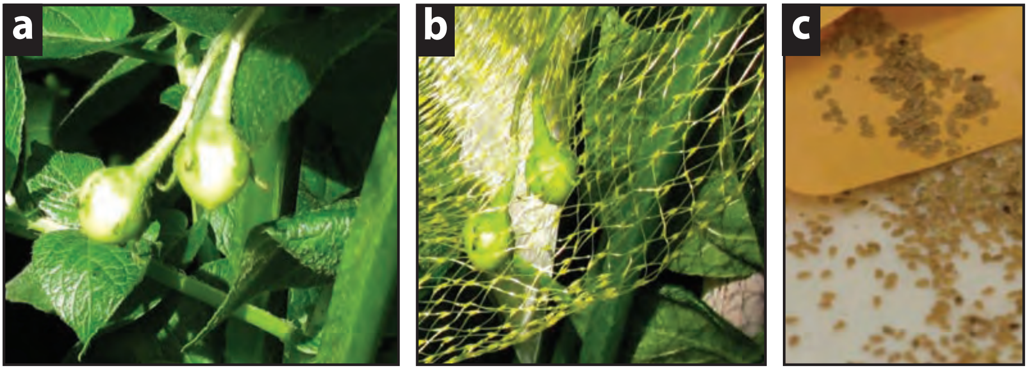

Figure 14.
Berries containing true potato seed (a). Secured in a net for protection (b).
True potato seed extracted, dried and prepared for storage (c). (Photos © Author)

If pollination is successful a berry (or fruit) is formed (Fig. 14a). This will contain up to 200 true potato seed. Each seed is a sibling of every other seed in the berry, but genetically different from all the other seeds. When the berries are ripe they are collected from the stems and stored until the seed is extracted. This is accomplished by cutting the berry open and placing it in water for about three days. As the mixture ferments, the seed separates from the flesh and can be collected, dried and stored (Fig. 14b).

The seed is sown in trays (Fig. 15 a&b) and crossses wil vary in the amount of seedlings that emerge. Trays will typically contain about 300 seedlings.

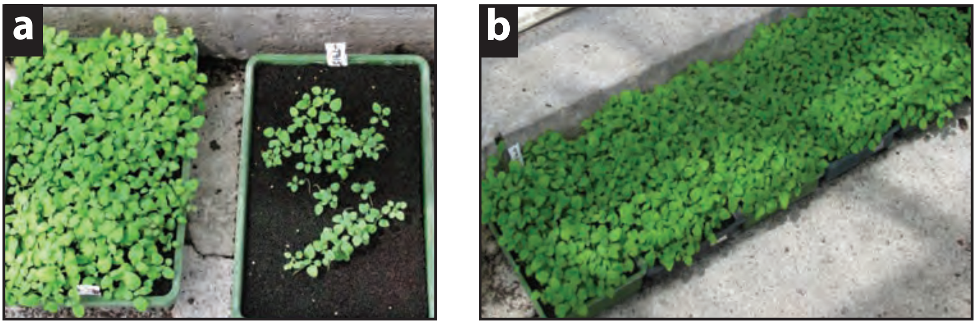

Figure 15.
Variation in the levels of germination and emergence of true potato seed (a) and trays containing seedlings with high levels of emergence (b). (Photos ©Author)

After emergence the seedlings are transplanted to pots and grown on to produce small tubers (Fig. 16). Each seed therefore can be the basis of a potential new variety. In the first year the seedling is planted and its progeny (4-6 tubers) is evaluated visually; then either selected for progression or discarded. Typically, from about 100,000 seedlings planted, only some 3000 will be retained after the initial selection and advanced for further evaluation.

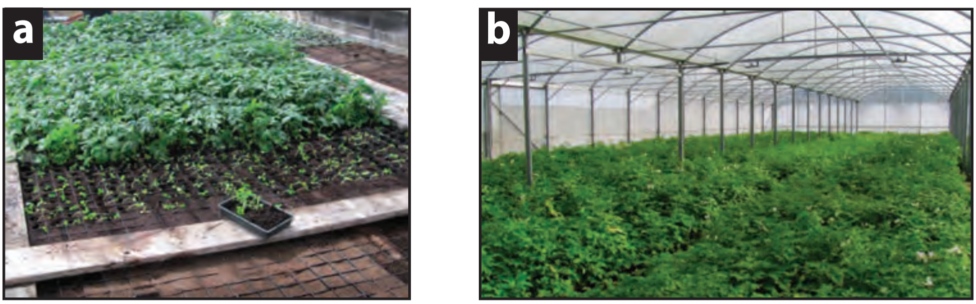

Figure 16.
Planting potato seedlings grown from true seed (a)
The seedling crop at maturity (b) (Photos © Author).

Selected tubers from the pot grown plants are multiplied vegetatively, ensuring that there is no further segregation and therefore the selection is relatively easy. Over several more seasons this number of seedlings will be constantly evaluated using increasingly rigorous selection criteria and unsuitable clones discarded..

Initially selection is for basic agronomic and commercial traits such as foliage, length of stolons, tuber shape, number, size and distribution, skin colour and flesh colour. The selection percentage is decided by the breeder – too severe and there is a risk of discarding a potentially useful cultivar; too vague and unsuitable clones are carried for longer than necessary – wasting resources. At later selection stages further traits such as foliage maturity, disease resistance, yield, specific gravity, cooking quality and fry colour are assessed

Breeding a new potato cultivar is not a quick route to success. From the first year when the crosses are made, to the release of a successful new cultivar, it is expected that 12 to 15 years will elapse. From the initial 100,000 seedlings planted in pots, finding one new commercially acceptable variety is considered a success

Typical flow chart for the development of a new cultivar is presented in Tables 1 and 2.

Table 1.
A typical potato breeding and selection scheme,
showing the progressive reduction in seedling numbers

Year	Task
1	Select parents and crossing – 100,000 true potato seed
2	Raise seedlings in nursery – 90,000 seedlings
3	Single plants in the field – 75,000 plants
4	5 Tuber lots – 2,500 seedlings
5	20 Tuber lots – 300 seedlings
6	40 Tuber lots – 35 seedlings
7-12	National List Trials – Approx. 35 seedlings – 1 New Variety

Table 2.
Details of activities at advanced selection stages

Year	Task
5	Replicated 20 tuber lots; initial screening for insect resistance.
6	Replicated 40 tuber lots; screening for insect resistance and quality characteristics
7	Replicated yield trials; Continuing assessment of quality characteristics
8	Pre National List trials at a range of locations to assess reaction to various agroecologies
9	National List trials
10	National List trials
11	Granting of Plant Breeders Rights for New National Variety
12	Seed Multiplication of the New Variety under the Seed Certification Schem

Summary

The cultivated potato belongs to a species, *Solanum tuberosum* and is a highly heterozygous tetraploid (4n=48);

Potato cultivars are roughly classified into four types based on their purpose: table use, food processing, starch production, and other purposes.

The stem is the potato's most recognizable characteristic. Two types of stem are recorded: determinate and indeterminate.

The potato tuber is an enlarged portion of an underground stem; it provides food reserves and meristematic potential.

True Potato Seed (TPS) is the actual botanical seed produced by the potato plant.

The majority of breeding with potatoes involves crosses between tetraploid genotypes followed by recurrent selection based on phenotype.

Sources accessed in the preparation of this section.

Canadian Food Inspection Agency, (2015). The Biology of Solanum tuberosum (L.) (Potatoes)

Huaman, Zosimo,. (1986). Systematic botany and morphology of the potato plant CIP., Lima, Peru. 22 pp.

Struik, P. C. (2007). Above-ground and below-ground plant development. Pages 219-236 ***in*** D. Vreugdenhil, J. Bradshaw, C. Gebhardt, F. Govers, D. K. L. Mackerron, M. A. Taylor, H. A. Ross, eds. Potato biology and biotechnology: Advances and perspectives. Elsevier Science B.V., Amsterdam.

Weaver, J. E. (1926). Root development of field crops. Publ. McGraw Hill Book Company N.Y.

Section 3.

Tuber Dormancy

Introduction

Potato tubers are swollen underground stems, formed by swelling at the tip of underground stolons in a series of processes consisting of: the cessation of growth at the apex, swelling of the stolon and enlargement of the tuber by cell division and cell expansion. As the tuber elongates, a growing number of lateral bud meristems (termed eyes) are formed in a spiral arrangement on its surface. When tubers attain their final sizes, they assume a deep (internal) dormancy, which is caused by a hormone–mediated signal.

In a potato tuber, dormancy is defined as the physiological state in which autonomous sprout growth will not occur within two weeks, even when the tuber is stored in conditions favourable for sprout growth. This onset of dormancy is associated with the cessation of meristematic activity at the stolon tip during tuber initiation. Tuber dormancy deepens further following the death/destruction of the canopy.

The basis of dormancy

Dormancy is a hormone induced physiological state. Dormancy gradually develops in potato tubers from the moment cell division in the stolon tip ceases and the tuber starts to expand. During dormancy, biochemical reactions and physiological processes continue to occur within the tuber, but they do not manifest as morphological changes.

There are two possible definitions of potato dormancy; total dormancy which covers the period from tuber initiation to the end of dormancy or post harvest dormancy. This latter description covers the period after harvest and following wound healing when the tuber enters a biochemically 'quiet' phase.

Plant dormancy is classified into three categories: endodormancy, paradormancy and ecodormancy. In potato tubers the dormancy is defined as "endodormancy" and is due to the interaction of the endogenous hormones abscisic acid (ABA) and ethylene that mediate suppression of meristem growth. ABA is considered as a positive regulator of dormancy induction and most likely also maintenance.

Dormancy and sprouting are controlled by the interactions of major plant growth regulators, predominantly the ratio of gibberellin (GA) and abscisic acid. ABA has been suggested as important to maintain dormancy, whereas the role of GA has been clearly determined in dormancy breakdown. Abscisic acid is synthesized in the haulm during the field growth stage and is transported, via the stolon, to the tuber.

Unlike cereal seeds, potato tubers remain hydrated throughout their life, but dormancy ensures that metabolic activity continues at a very slow pace. The development of dormancy is a gradual process and in some respects it parallels tuber initiation. To permit tuber initiation to commence, the apical meristem of the stolon must become dormant – otherwise stolon extension growth will continue. With this cessation of cell division in the stolon tip, longitudinal cell division in the subtending nodes commences. This characterizes tuber initiation and is accompanied by buds in the eyes becoming successively dormant until finally the apical bud becomes dormant. The role of the tuber in vegetative propagation of the crop is defined by the reactivation of these dormant meristems

The role of tuber dormancy

After maturation, dormancy serves to protect tubers as organs of vegetative reproduction under conditions unfavorable for growth. During this dormancy period, tubers are highly resistant to pathogen attacks. This preserves the reserves of starch and protein required to support future sprout growth. Dormancy is thought to be an adaptation to enable the tuber to survive periods unfavourable for growth. In colder climates, it prevents sprouting when tubers would be exposed to extreme temperatures. These low temperatures would kill the sprouts if they were present. Potato sprouts are extremely frost sensitive

Dormancy and tuber metabolic activity

Metabolic depression is generally associated with dormant tissue and this extends also to potato tubers. Tubers are living organisms and as such, they respire. Respiration is a process that consumes glucose to maintain cell functioning, and generates carbon dioxide, water and heat. In some respects it can be considered the reverse of photosynthesis. The less the potato tubers respire, the less they will shrink in storage, and the less likely they are to break dormancy and sprout prematurely.

The rate of respiration could almost completely be explained by the factors: storage temperature, degree of sprouting, storage duration, and the interactions between these factors. Tuber respiration (a gross indicator of metabolic activity) is high, following harvest. This increase is essential to provide the energy required for callous formation and wound healing. When these processes are completed and the tubers are in store, the respiration rate declines and remains low throughout dormancy. Another rise in metabolic activity is observed coinciding with dormancy break. This is represented by a decline in macromolecules and an increase in their monomeric constituents, illustrated by an alteration in the starch/sugar ratio.

Genetic control of tuber dormancy

Cultivated potato varieties demonstrate a wide range of values for the length of the dormant period. Cultivars emerging from modern breeding programmes generally have short dormancy duration, whereas long tuber dormancy is generally found in wild potato populations. Because dormancy duration is not related to a cultivar's earliness of maturity, it is possible to breed late maturing varieties, which display relatively short dormancy and early varieties which display relatively long dormancy.

Bud break

The dormancy observed in postharvest potato tubers is defined as endodormancy and results in the suppression of meristem growth. Dormancy is characterized by the absence of visible bud growth. Dormant eyes will not sprout even if the tubers are stored under conditions, which are conducive to sprouting. The only portions of a tuber that can grow are the tiny clusters of cells in depressions on the tuber surface known as eyes. Dormancy is considered to have terminated when 80% of the tubers have produced sprouts approximately 2mm long.

Figure 1.
Bud break on a seed tuber. (Photo © Author)

Prior to the appearance of visible bud growth, hormonal activity commences in the tuber. This triggers the onset of enzyme activity and the degradation of starch to sucrose. The availability of sucrose is one prerequisite for bud break. In the absence of sucrose, no bud break occurs. Storage proteins are broken down to polypeptides and amino acids. After dormancy, the tuber bud 'awakens', sprouts start to grow intensively (Fig. 1), ultimately with the formation of roots at their bases. Tuber sprouting is usually initiated from its apical bud, located opposite the basal tuber-stolon connection site

Dormancy duration

The length of the dormancy period is under environmental, physiological and hormonal control. The dormancy period depends on the genetic background and is affected by preharvest and postharvest conditions. The duration of the endodormancy period is primarily dependent on the genotype, but other factors, such as growth conditions of the crop and storage conditions after tuber harvest, are also important.

Tubers from a fully mature crop have longest dormancy. Tubers from a crop affected by heat or water stress or infected with disease have shorter dormancy.

Each variety and field has its own period of natural dormancy and when that period expires the eyes begin to sprout. Wounding the seed tuber – in practical terms by cutting the seed – reduces the period of dormancy and induces sprouting.

Dormancy duration is also affected by tuber size, with small tubers (minitubers) having dormancy duration approximately 140 days. By contrast, dormancy for 100g seed tubers approaches 90 days.

The effect of temperature on dormancy duration

Tubers stored at warm temperature will sprout weeks before those stored in the cold, producing a single bud. Over the range of 3^0C to 25^0C the length of tuber dormancy is inversely proportional to storage temperature. The effect of temperature on dormancy break is not absolute, since for any given temperature the duration varies for different cultivars. When dormancy is released, sprouting of the apical bud may be inhibited by cold temperature (enforced dormancy).

The effect of desprouting

In some potato cultivars, the development of the apical sprout inhibits the development of secondary sprouts. When the seed tubers are required as planting material for another crop of seed tubers, desprouting – or removal of the dominant sprout, will permit dormancy break at secondary eyes. The seed tuber will now produce multiple sprouts.

If a crop is destined for processing, large tubers are required, then single sprouts are useful. Seed growers, by contrast, require a high population of tubers in the 35-55mm size grade. The most effective way to produce a crop with this size distribution is to plant seed tubers, which already have formed multiple sprouts. The increased number of sprouts per seed tuber will likely produce a plant with multiple stems. The resulting interstem competition for light, water and nutrients will restrict tuber size development and result in an increased population of tubers of the required size grade. If this practice is to be successful, the desprouting should be carried out immediately after the apical sprout has formed. Delaying desprouting wastes seed tuber reserves, which have been invested in sprouts which are now discarded.

Breaking dormancy

When only one crop per year is grown, dormancy duration is rarely significant. In regions where more than one crop is produced, long dormancy is a severe disadvantage as it delays the target planting date for the subsequent crop. During dormancy, potato tubers cannot be induced to sprout without some form of stress or exogenous hormone treatment. Seed tubers, where dormancy is interrupted chemically, often produce a single apical sprout. This sprout gives rise to a single stem, which will then produce a few large tubers. These seed tubers can be considered as physiologically young and would be expected to provide a high yield if a long growing season could be availed of.

Tubers have been subjected to a range of stresses to promote dormancy break:

Gibberellic acid

Gibberellic acid (GA_3) promotes the growth and elongation of cells. Freshly harvested tubers are cleaned and dipped in a 5-10ppm solution of 10 to 20 minutes. Treatment with GA_3 tends to promote the emergence of a single apical sprout. If a multi-sprout seed is required (to produce a crop of seed size tubers) the apical sprout can be rubbed off and subtending eyes will sprout.

The effectiveness of GA_3 in breaking dormancy was enhanced when a trace element mixture was combined.

Thiourea

Thiourea is an organosulphur compound. It has a molecular structure similar to urea, except a sulphur atom replaces the oxygen atom. Seed tubers can be soaked in a 1% aqueous solution for one hour. Entry to the tuber is gained through cuts and bruises sustained during harvesting. If wounds have healed then a couple of cuts should be made to the heel end of the tuber.

Ethanol

Ethanol or ethyl alcohol or 'drinking alcohol' is the principle type of alcohol found in alcoholic beverages. When mini tubes were treated in a solution of 0.5% ethanol plus 1% sucrose, they broke dormancy at 3 to 5 days after treatment.

Temperature treatments

When potatoes are held in store, fluctuating storage temperatures shorten dormancy more than constantly high temperatures. Dormancy break is promoted by keeping tubers in the dark at 18 to 25^0C until sprouting occurs. This treatment works well for early maturing cultivars.

A variation on the raised temperature treatment just described is to provide a cold shock by holding the tubers at 4^0C for 2 weeks and the storing them at 18-25^0C until sprouts develop. In the absence of controlled environment stores, this treatment is not very practical.

Summary

When tubers attain their final sizes and no further assimilates arrive from the shoot, they assume a deep dormancy; during this phase, sprouting will not occur even if the tubers are held under optimal conditions.

Dormancy is controlled by the interactions of major plant growth regulators, predominantly the ratio of gibberellin (GA) and abscisic acid (ABA).

Dormancy serves to protect tubers as organs under conditions unfavorable for growth. During this period, tubers are highly resistant to pathogen attacks.

Prior to the appearance of visible bud growth, hormonal activity commences in the tuber. This triggers the onset of enzyme activity and the degradation of starch to sucrose.

Tubers stored at warm temperature will sprout weeks before those stored in the cold, producing a single bud.

Fluctuating temperatures in the store shorten dormancy, compared with a constant temperature.

Sources accessed in the preparation of this section.

Fernie, A. R., Willmitzer, L. (2001). Molecular and Biochemical Triggers of Potato Tuber Development. *Plant Physiol.* **127**: 1459-1465.

Hartmann, A., Senning, M,. Hedden, P., Sonnewald, U., and Sonnewald, S. (2011). Reactivation of Meristem Activity and Sprout Growth in Potato Tubers Require Both Cytokinin and Gibberellin. *Plant Physiol.* **155**: 776–796.

Muthoni, J., Kabira, J., Shimelis, H. and Melis, R. (2014). Regulation of potato tuber dormancy: A review. *Aust. J. Crop Sci.* **8**: 754-759

Struik, P.C, Wiersema, S.G. (1999). Seed potato technology. Wageningen University Press. The Netherlands.

Van Ittersum, M.K., Scholte, K. (1992). Relation between growth conditions and dormancy of seed potatoes. 2. Effects of temperature. *Pot Res.* **35**: 365 - 375.

Section 4

Sprout Growth

Introduction

Potato tubers serve as organs for vegetative propagation by providing a source of substrate and energy to produce the next generation. The potato seed tuber carries the genetic potential to deliver both high yield and desirable qualities. These characteristics and qualities are passed on unchanged and undiluted thorough successive generations. It also contains water and the metabolites including carbohydrate reserves required to sustain sprout elongation during emergence, before the new leaves can support growth. The shoot meristems, which form in the eyes of seed tubers, are referred to as sprouts (or shoots). The development of sprouts is the first sign that dormancy had ended and the first stage of vegetative growth of the potato plant. This is an advantage conferred on potato, in that growth can commence before the 'seed' is planted in the ground; but is not possible in other crops.

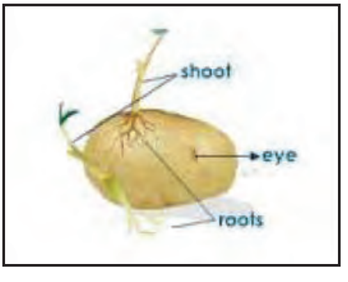

Figure 1.
Diagrammatic representation of the seed tuber and its developmental components.
(Image © tutorvista.com. With permission)

Sprouts possess multiple nodes and have meristematic tissue and leaf primordia present both at each node and at the top, or distal end of the sprout. Sprouting is a hormone mediated process. There is some evidence that the hormone indole acetic acid (IAA), an auxin, plays a crucial role in sprouting. IAA is known to promote apical dominance and through this mechanism, it suppresses the sprouting of lateral buds. At the earliest visible stage only small white buds are present, but as growth progresses, sprout branching occurs when apical dominance is overcome, this may happen following damage to the apex.

Potatoes are one of the few vegetable crops that are grown from a vegetative propagule, the seed tuber, as opposed to a true seed, such as for example barley or maize. Whereas barley and maize seeds are dried before storage, 'seed' potato is stored fully hydrated. It is important therefore that the seed tubers be stored carefully under cool conditions with diffused daylight, to prevent excessive sprout growth and the associated depletion of starch reserves

Seed tuber size

The effect of seed size on tuber size distribution and total tuber yield has been investigated extensively. When seed tubers are planted whole, they are usually graded by size. Two sizes are common 35-45 mm and 45-55 mm. As a general principle, seed tubers less than 35 mmm produce one or very few mainstems, leading to the development of a few large tubers. Furthermore, if the newly emerged shoot, arising from a small tuber, is damaged by frost, there may not be sufficient reserves to produce the additional growth to replace the damaged tissue.

Excessively large seed tubers can produce too many stems per hill, increasing tuber set and reducing tuber size, as well as increasing the cost of seed. A solution for large tubers is to cut them. An experienced person should only attempt this task, as several criteria must be applied to ensure success. The large tuber must be cut to ensure at least one eye per seed piece. Seed piece for optimal productivity should range 43 to 85 g. Cutting knives should be sterilised regularly to avoid spreading infection. Wound healing prior to planting should reduce the risk of seed piece decay before emergence.

Number of sprouts per seed tuber

After a dormancy period of typically 12 to 16 weeks, dormancy is broken and the apical bud sprouts. With the onset of sprouting, the tuber turns into a source organ supporting growth of the developing sprout. This is accompanied by structural and metabolic changes. Endogenous plant hormones play a critical role in the regulation of dormancy duration and bud break.

The first bud to produce a sprout is generally the apical bud (Fig. 2a). This is the bud located at the opposite end of the tuber to the stolon attachment point. During the early stages of sprouting this apical sprout exerts dominance over the lateral buds. Tubers planted at this stage of sprouting may have only a single stem or at most a very few stems. Farmers growing crops for ware want few mainstems as this condition results in fewer and larger tubers

As storage is extended this dominance of the apical sprout is weakened and sprouts emerge from the lateral eyes. There is a tendency for tubers with multiple sprouts to produce multiple stems. Farmers, growing crops for seed, aim to produce multiple stems per seed tuber (Fig. 2b), as this increases the number of daughter tubers, which develop.


Figure 2.
Seed tuber with single sprout (a); multisprout (b) (Photos © Author)

Sprout length

The objective is to produce short thick sprouts with a green colour. Short sprouts are associated with thickening at the basal end and therefore are not easily 'rubbed off'. These sprouts have shortened internodes, well developed leaves and they have a characteristic green colour due to the presence of functioning chlorophyll. The ideal sprout length should not exceed 12mm. Sprouts of this dimension can resist breakage during transport and planting (Fig. 3). When sprouts emerge above the soil following planting, they are normally referred to as 'stems' or 'shoots'.


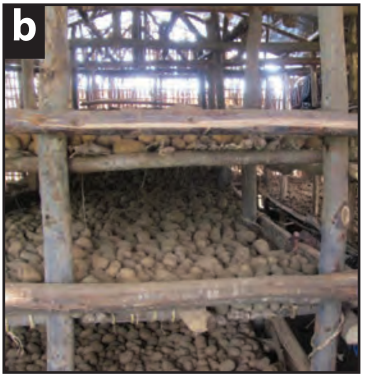

Figure 3.
The ideal type of sprout, short, green and resistant to rubbing off (a); the ideal storage conditions to produce short green sprouts. (Photos © Author)

When potato sprouts grow in darkness, they are white, etiolated and spindly due to lack of light (Fig. 4). Growing long sprouts depletes the starch reserves in the tuber and when these tubers are planted subsequently, there may be insufficient starch reserves remaining in the seed tuber to support the elongation of the sprouts until they emerge above the soil. Long sprouts are readily broken off during handling or planting (Fig. 4). Producing new sprouts to replace them will further deplete the starch reserves in the seed tuber.

Figure 4.
Long sprouts, which are readily broken off during handling and planting.
(Photo © Author)

Physiological age

At any one time the seed tuber has two ages; its chronological age and its physiological age. Chronological age is the tuber age, measured from either tuber initiation or harvest, without reference to environmental conditions. Chronological age is more accurate when calculated from tuber initiation as this relates to a fixed point in tuber development. Measuring chronological age from harvest date is of course much easier but less informative, as harvest date bears little relation to tuber development. Different seed crops with the same harvest date can have different physiological ages, with some seed sprouting and the other remaining dormant. This is due to variation in the environmental experiences of the different crops.

Physiological age is defined as the physiological condition of a seed tuber at any time; it is the internal age of the seed resulting from biochemical changes taking place within the tuber throughout its development. Physiological age can also be defined as the state of the seed tuber, which influences its production capacity. In practical terms it describes the readiness of the seed tuber to grow and growing in this instance means sprout formation, which implies that the physiological age of the seed will have an impact on how the new crop grows. Physiological age depends on both the chronological age and environmental conditions. The onset of dormancy in the apical zone at the tip of the stolon undergoing transition to tuber formation is sometimes recorded as the starting point for accumulation of physiological age. Physiological age is affected by two factors, which influence internal biochemistry:

- Genetic predisposition and
- Environmental stress during field growth.

Genetic predisposition is defined by the cultivar. Environmental stresses in the field are primarily moisture, temperature, nutrients, pest injury, and mechanical damage.

In storage, stresses are temperature, moisture, aeration, bruising, and disease. During post-harvest storage, potato seed tubers undergo considerable changes in their physiological state. These influence their sprouting capacity, which consequently influences the yield of the crop. The storage temperature regime experienced by the seed tubers, post dormancy break and prior to planting. is a significant determinant of physiological age.

Potato variety also affects physiological age. Some varieties have a long dormancy period and will have physiologically younger tubers than varieties that break dormancy early in storage and commence sprout growth. When sprout growth in three cultivars (early maturing, medium and late maturing) was compared, the sprouts were longer in the early, than in the medium, than in the late maturing type.

Physiological age has important practical implication for potato growers. In regions where it is possible to plant two crops per year, growers need cultivars, which are ready to sprout soon after the first crop is harvested. It is very risky to plant dormant seed since they may not sprout and then the tubers are wasted. But even when small sprouts have formed prior to planting the seed is still 'young' and normally only a single or at best a very few shoots establish.

At the other extreme, in regions where the climate is only suitable to permit one crop per year, then the seed must be stored for up to 7 months. Unless the grower has access to controlled temperature storage the seed tubers will break dormancy and produce excessive sprout growth prior to planting. Again this has significant practical implications for the grower as such seed will produce a restricted canopy and a reduced yield.

Several economic and agronomic reasons can be advanced to support the use of physiologically aged seed. There is often a significant price premium paid for the first crops of potato brought to market. The price premium will nearly always compensate for the yield reduction resulting form early harvest. Planting physiologically aged seed will significantly reduce the yield penalty associated with early harvest.

Where a short growing season in expected due to the early onset of drought or of defoliating diseases such as *Phytophthora infestans*, physiologically ageing the seed will also produce a commercially acceptable tuber yield, despite an abbreviated growing season.

Measuring physiological age

It is widely recognised that planting seed tubers of differing physiological ages will produce widely different results – expressed as variation in tuber yield and tuber size distribution. Due to the effect of physiological age on crop growth and development, the topic has been researched extensively for more than 50 years.

Currently there are two concepts to express physiological ageing. One method assumes that physiological age is the accumulation of age from the date of tuber formation until that seed tuber is planted. There is no difficulty defining the factors that influence physiological age, but how to measure the impact of environmental and storage factors? A physiological age index has been developed which factors in both chronological and physiological age. It "utilises the haulm killing date of the seed crop and the end of the incubation period of the seed tubers, measured under standardized conditions" (Caldiz et al. 2001).

Another method assumes the clock of physiological ageing commences with the break of dormancy and accumulates with sprout growth. Sprout growth is largely temperature dependent and ceases when tubers are stored at 4^{0}C. A practical approach to measuring accumulation of physiological age is to note the date of dormancy break (sprouts 1-3mm) then commence logging the accumulation of day-degrees greater than 4^{0}C. An accumulated value of 200 day degrees >4^{0}C will provide seed tubers which are capable of early emergence and establishment, then a high yield at early harvest. For maximum yield at late harvest, physiologically young seed should be planted.

Table 1
Characteristics of young versus physiologically old seed

Young Seed	Old Seed
Slow emergence	Rapid emergence
Fewer stems per hill	More stems per hill
Longer tuberisation period	Uniform tuber set
Low tuber set	Higher tuber set
Long tuber bulking period	Shorter tuber bulking period
Larger tubers at harvest	Smaller tubers at harvest
More foliar growth	Less foliar growth

Sprout growth rate

Sprout growth is a heterotropic process, relying on the remobilization of assimilates stored in the seed tuber. Since the energy required to power sprout growth is derived from respiration, it would be expected that soil temperature would exert a significant influence. Below 2^{0}C no growth takes place and the sprout will not emerge. The planting depth of the seed tuber will also influence the time from planting to emergence and seed tubers with longer sprouts at planting would be expected to emerge sooner. Sprout growth rates of between 0.5 mm and 2.0 mm per day degree have been recorded and a typical value might be accepted as 1.0 mm dd^{-1} above a base temperature of 2^{0}C.

Sprout disorders

Little potato disorder

At very high levels of physiological age, a disorder known as "little potato" formation is observed. Small tubers are formed on stolons emerging from the seed tuber before the sprouts emerge above ground. This disorder is also observed when 'warm' seed is planted into cold soil that has not warmed sufficiently before planting.

Coiled sprout

The most common characteristic is bending (coiling) thickening and swelling of sprout internodes, coupled with non emergence from the soil. This is most commonly observed when seed with high levels of physiological age (long sprouts) are planted in cold soil. Deep planting also enhances the development.

Figure 5.
Some examples of sprout disorder. (Photo © CIP, with permission)

Figure 6.
Daughter tubers formed directly on sprouts
(Photo © Author)

	**Dormant**	● Potatoes do not sprout at all ● Dormancy period varies depending on cultivar ● Chemical and non chemical means of breaking dormancy
	**Young**	● Young seed is characterised by apical dominance ● Minimal sprouts ● Sprouts come of apical end of tuber ● Fewer stems per tuber ● Fewer tubers but large in size
	**Middle aged**	● Multiple sprouts ● Loss of apical dominance ● Multiple stems (eg 3-6) per plant ● High number of tubers per plant, but reduced size. ● Middle aged seed that has been de-sprouted should be considered old seed
	**Old**	● Excessive branching of sprouts ● Sprouts weak and do not produce vigorous plant ● proliferation stems that lack vigour to bulk tubers
	**Little tuber disorder**	● Small tubers form on the sprouts giving rise to little tuber disorder ● This seed age should not be used.

Figure 7.
Diagrammatic representation of various sprouting stages (Photos © Author)

Summary

Ideally, prior to planting, potato seed tubers should be firm and still holding the shape they had at harvest time.

Shriveling of the skin, the appearance of wrinkles and the development of a soft spongy feel accompany excessive sprout growth.

Physiologically young seed produces vigorous stems, whereas seed tubers with excessive physiological age produce stems with reduced vigour.

Sources accessed in the preparation of this section.

Caldiz, D. O., Fernandez, L. V. and Struik, P. C. (2001). Physiological age index: a new, simple and reliable index to assess the physiological age of seed potato tubers, based on haulm killing date and length of the incubation period. Field Crops Res. **69**: 69-79.

Caldiz, D. O. (2010). Physiological Age Research during the Second Half of the Twentieth Century. *Potato Research* **52**: 295-304

Daniels-Lake, B.J. and Prange, R.K. (2007). The Canon of Potato Science: 41. Sprouting. *Potato Research*, **50**:379.

Reust, W., (1986). EAPR Working Group – Physiological age of the potato. Potato Research, **29**: 268-272

Section 5.

Soil Preparation and Seed Potato Planting

Introduction

Planting the potato crop presents the farmer with a range of choices: where to plant the crop, how to prepare the seed bed, what variety of potato to plant, what distance between seed tubers, what distance between rows, also what fertiliser to apply. A high yield of tubers is achieved when all the foregoing issues are addressed correctly.

Where to plant the crop

Growers with small landholdings may not have much choice in deciding where to plant. Nonetheless some rules apply. Planting potatoes in the same area of ground during successive seasons will encourage the buildup of pathogens and pests, which attack the crop. It is essential therefore to consider crop rotation – or in other words, how long has it been since the last potato crop planted in this area of the farm and what other crops have been planted since. Repeatedly planting potatoes exposes the site to the risk of infection with bacterial wilt. Volunteer potatoes carry over the disease during the break crops and the infection spreads. Crop rotation and its' role in containing the spread of bacterial wilt will be considered in **Section 18**.

Soil type is a further consideration when deciding where to plant the crop. While again it is recognised that a farmer may have limited choice, it is fortunate that potatoes will grow well on a range of different soil types. The ideal field in which to plant a potato crop, will have a deep, well-drained and friable soil.

In addition to tolerating a wide range of soil types, potatoes can tolerate a range of soil pH values. Unlike other vegetables, potatoes can produce high yields when grown in soils with pH 4.8-5.5. An advantage of growing at such low values is that common scab is unlikely to cause a problem at pH values below 5.4.

However, despite their tolerance of low pH values, the highest yields are obtained at values of 6.0 – 6.5.

What variety to plant

The major choice is between deciding to plant home saved seed of local varieties or to plant clean seed from one of the new improved varieties. Planting new improved varieties, using the modern agronomy and applying granular fertiliser can provide yield increases of at least 3-fold compared with planting local varieties using traditional procedure.

Note: *Purchasing seed tubers from an unknown source, exposes the farmer to significant risk. Seed tubers may show no visible symptoms and yet they may carry virus or even worse, bacterial wilt. A concerted effort is required to educate farmers regarding the risk from purchasing and planting seed from an unknown source. Cheap seed, that contaminates your field, is not a bargain!*

Preparing the seed bed

For a good seedbed, the ratio of air, soil and water must be optimal. A biochemical process known as respiration supplies the energy required for the sprout to extend and push up through the soil then finally emerge overground. Through respiration, starch in the seed tuber is converted to sugar. Oxygen is necessary to facilitate the breakdown of this storage starch and convert it to the sugar required to support sprout growth and extension.

When potatoes are planted in fields where the soil is prone to compaction, tillage operations should not be conducted when the soil is wet. Compacted soil contains less oxygen and restricts the movement of water down to the root zone. Growers should exercise caution with soil compaction - the seed bed must be sufficiently firm that the rootlets come immediately in contact with the soil particles, yet the soil structure must be open enough that the roots can readily penetrate.

Potatoes grown from seed tubers initially form adventitious roots at the base of each sprout. At later growth stages, roots grow from above the stem nodes that are covered with soil. Potatoes are a shallow rooted crop with a poor capacity to explore a large volume of soil. The vast majority of the roots will be found in the zone 0-0.6 m deep. Because of this they require a well-tilled seedbed since both roots and tubers are sensitive to soil compaction.

Soil moisture has a marked influence on seed tuber emergence. If the soil is too dry following planting, emergence is delayed and the number of mainstems is reduced. Conversely, seed potatoes will not grow well if planted into wet soil. The oxygen required for tuber respiration and associated sprout growth will be excluded and this will impact negatively on plant emergence. Growers should try to ensure that the soil is loose and well draining but capable of retaining moisture.

The soil should be free from clods with a finely crumbled lose layer that can retain moisture but not restrict air supply. Time spent preparing the seed bed is time well spent. The success of the crop is highly influenced by the ease with which the roots can explore the soil volume and the capacity of the soil volume to retain moisture and nutrients.

Planting the crop

Select disease free seed

Inspect seed for disease symptoms prior to planting – ***a diseased seed tuber cannot produce a healthy plant!*** and in addition – planting diseased tubers will introduce pathogens or add to those already present in the soil.

Some disease symptoms can be treated, but if others are present, then the seed lot should be rejected.

If more than 20 small or 10 large Rhizoctonia sclerotia are visible on one side of the seed tuber, consider using a different seed source. Seed with less than 20 small or 10 large sclerotia should be treated before use. Treating the seed tubers with a mixture of the fungicides flutolanil and mancozeb has been shown to provided effective treatment for Rhizoctonia

Seed lots with less than one half of one percent (0.005) of tubers with Fusarium dry rot symptoms can be used if the diseased tubers are removed and seed treatments are used on the remainder of the lot. Again treating the seed tubers with a mixture of the fungicides flutolanil and mancozeb has been shown to provided effective treatment for Fusarium and reduced both the number of decaying seed tubers and the level of sprout rot

Tubers with five percent or more of the surface affected with silver scurf should not be used for seed. Silver scurf is caused by the fungus *Helminthosporium solani*. No seed treatment has been shown to be highly effective in controlling the pathogen that causes this disease.

Seed lots with more than one percent of the tubers showing blackleg symptoms or soft-rot symptoms caused by *Pectobacterium carotovorum* (Formerly known as *Erwinia carotovorum*) should not be used. Seed tubers generally acquire blackleg infection via the stolon. The symptoms will be therefore likely be first observed at the heel end and are normally easy to detect. Another possible entry route for the pathogen into progeny tubers is via the soil. After the blackleg disease has induced decay to the belowground stem and seed tuber, the infectious bacterium spreads from infected tissue into soil water and is subsequently distributed throughout the root zone, thus bringing it into contact with the progeny tubers. Bacterial cells enter lenticels of the progeny tubers and either become inactive, or if conditions are favorable, immediately initiate decay.

The presence of pinkeye, early blight or late blight lesions on the tubers could provide a source of inoculum for new crop infections. This seed should not be used. Know the source and history of a seed lot and try to avoid those that have had heavy infection with Verticillium spp.

A bacterium-like organism *Streptomyces scabies* that overwinters in fallen leaves and in the soil causes potato scab. It infects tubers when it enters through pores (lenticels) in stems, through wounds and directly through the skin of young tubers. The organism can survive indefinitely in slightly alkaline soil but is relatively scarce in highly acid soils. It is transmitted to plants by infected seed tubers, wind and water. The organism is also spread in fresh manure, since it can survive passage through the digestive tract of animals

Seed-borne scab can contaminate a field without a history of scab infection, so therefore seed tubers displaying scab infection should be used only in fields with a history of scab. Seed with scab should be treated to control this disease. High levels of scab on the seed warrant rejection of the seed lot. Adjusting pH of the fields greatly aids in the control of scab. Keeping soil moist during tuber initiation and during early tuber development may have a dramatic effect on common scab infection. Maintain proper soil moisture during the logarithmic phase of tuber growth. Avoid overwatering.

The “five percent rule” is a useful aid to guide the selection of seed lots. A seed lot with five percent or more total defects is too high to use. Seed cost is a large outlay in potato growing. Each grower should strive to use the highest quality seed obtainable.

Effect of varying the row width

The general range is 60 to 90 cm. When drills are formed manually and infinite choice of row widths is available. Greater constraints are experienced when using machinery to prepare ridges. Under conditions of late planting, with consequent restricted growing period and the likelihood that canopy development will be limited and not be sustained, a row width close to 60cm might be selected. Also for seed crops, where the objective is to produce a large number of moderately sized tubers, a row width of 60 cm is desirable. By contrast, where a long growing season is expected, water and adequate fertiliser are available and ware sized tubers are desirable, then consider a row width of 75 to 80 cm. This will permit maximum light interception by the canopy without the risk of mutual shading by leaves growing in close proximity to each other

Figure 1.

Demonstrating the effect of varying in row seed tuber spacing (Photo © Author, Diagram © Aardappelpagina, With permission).

Effect of varying the in-row spacing

The primary factors controlling seed piece spacing are consumer demand, market need (seed or ware crop) and the associated economic return. The cost of seed tubers represent some 50% of the cost of establishing a potato crop so careful consideration should be given to optomising seed piece spacing. The principles underlying the effect of varying in-row spacing are best illustrated in a practical training session (Fig. 1)

As with row width, a wide range of values is possible but in general, distances of 18 to 25 cm are typical. Cultivar characteristics such as tuber number per plant, average tuber size and days to maturity need to be considered before deciding on in-row spacing's. Cultivars with high tuber set need wide spacing to produce ware size tubers, while cultivars with low tuber set, need close spacing to avoid producing extra large tubers. Excessively large tubers may develop defects such as hollow heart, knobs and growth cracks

The main stems is widely considered the unit of potato crop production. When growers seek to maximise tuber yield in a specific fraction they will attempt to achieve this objective by manipulating the stem population.

Close seed spacing, with it's related high stem density per unit area, induces mutual shading of leaves and limits the photosynthetic capacity to provide assimilates to bulk each tuber. Wider than optimal spacing results in a delay in attaining full ground cover and failure to capture all of the available photosynthetically active radiation; consequently, reducing carbohydrate supply to the tubers. The choice of seed piece spacing gives the grower the opportunity to manipulate tuber size towards the most desirable fraction for the intended market

A range of options for optimum interplant spacing to maximise yield in seed and ware fractions is presented in Table1.

Table 1. Inter-row and intra-row spacing for seed pieces depending on the intended purpose of the crop.

Crop Purpose	Seed Size	Within Row Spacing	Between Row Spacing
Seed Crop	45-55 mm	10-20 cm	65-75 cm
	35-45 mm	10-20 cm	60 cm
Ware Crop	35-55 mm	30-40 cm	75 cm

For table potatoes, the density is 40 000 plants/HA or 15-20 stems per m^2.

For a crop intended for seed production, the density may be as high as 60,000 plants/HA or 30 stems per m^2.

Effect of seed size

Seed tuber size is one of the most recognizable attributes of seed quality, with large seed having the highest rates of survival, growth and establishment. The importance of this factor has long been recognised by growers so consequently, the topic has been researched extensively. An example of one such study compared the performance of 20 g seed tubers with that of seed tubers weighing 100g. The performance of the small seed demonstrated lower yield per stem and lower leaf weight per stem compared with the larger tubers. Seed tubers heavier than 100 g produced more sprouts with longer length and produced a higher ground cover and yield compared to small potato seed tubers.

Seed size not only has an effect on stem number, but also on the early development of the crop through possessing a larger number of eyes and greater reserves of water, carbohydrate and mineral nutrients. These attributes will produce and sustain an increased number of main stems.

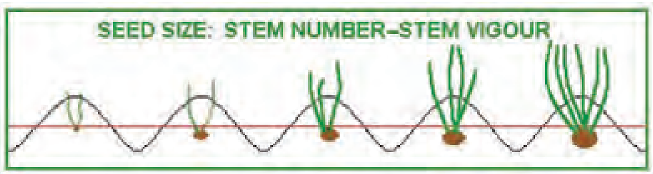

Figure 2.

Graphical illustration of the effect of planting seed tubers of increasing size.
(Diagram © Aardappelpagina, With permission)

Variation in seed tuber size can result in significant variation in tuber yield. There is a complicated relationship between seed tuber size and seed tuber weight; furthermore, it can vary between cultivars due to variation in tuber shape, and can vary between years and even between batches grown at different locations in the same year. An example in illustrated in Fig. 3 – where a 40mm tuber can vary between 38 and 56 g.

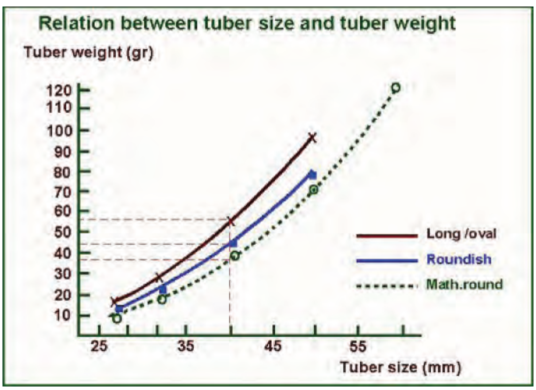

Figure 3

Graphical representation of the relation between seed tuber size and weight.
(Diagram © Aardappelpagina, With permission).

Regulations governing the size of seed tubers vary depending on the country of origin or based on import requirement. Tubers ranging 35 to 55 mm are widely accepted as providing satisfactory results when planted under normal conditions.

Beware of planting 'small seed' (<35mm); should the sprouts suffer damage from a late frost episode, the reserves in the small seed tuber may not be sufficient to support the regrowth and there will be blank spaces.

Effect of stem density on yield and tuber size

Mainstem density significantly influences the crop yield and tuber size distribution. Main stems act as independent entities and increasingly, the main stem is regarded as the unit of plant density. The number of stems per m^2 is a more accurate statistic to express crop density than number of plants per hectare.

Total yield increases until a density of approximately 15-20 stems per m^2 is reached. With a further increase of stem density the yield remains more or less similar, but the average tuber size decreases (relatively more small tubers (Fig. 4). Unfortunately it is notoriously difficult to predict main stem emergence by referring to any of the seed matrices, size, number of eyes, physiological age etc.

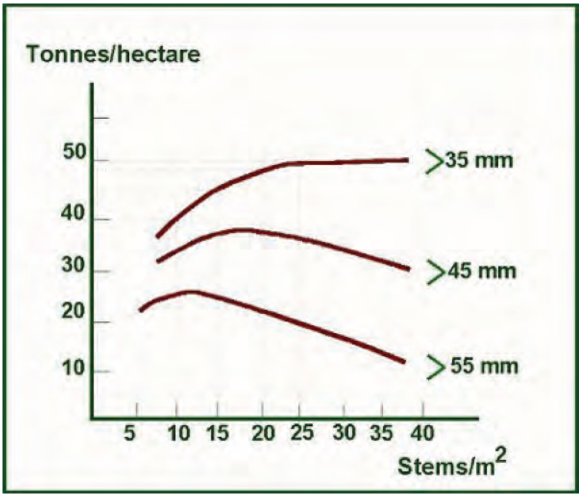

Figure 4.
Graph relating stem density, yield and tuber size. (Diagram © Aardappelpagina, With permission).

Planting depth

The seed should be covered with a layer of soil of sufficient depth to prevent the ridge from drying out too soon. Moisture stress after planting will delay emergence. Cooler temperatures, resulting from the deep cover, promote stolon growth and tuber formation. Consider a planting depth of 20 cm. from the seed piece to the top of the ridge.

When selecting a planting depth, a second consideration is to ensure that the stolons will not grow to the edge of the ridge and expose the ends of the tubers to the light. Greened tubers cannot be used for human consumption. Again, aim for a width of 25 cm at the top of the finished ridge.

When drill formation and ridge building is carried out by hand, the grower can select the optimum planting depth. During subsequent tilling and hilling operations, more soil can be heaped onto the ridge until the desired depth is attained. A wide hill is preferable to a high hill and this point should be considered when selecting an inter row spacing. A wide high hill also protects the root system from moisture and temperature stress during the tuber bulking phase. In addition, a wide hill affords protection to the potato roots during interrow cultivation to remove weeds and during 'hilling up'.

If heavy rains are expected the top of the ridge should tend towards a sharp point. By contrast, if low rains are expected a flatter top should be formed, since this will permit capture of the available moisture and direct it downwards towards the plant roots.

Summary

A successful crop can be grown by selecting, the correct planting date, planting the seed tubers at the optimum density (dictated by the target market) and at an even and correct depth.

Effort expended to source and select clean seed tubers will be rewarded.

Remember the Golden Rule:

- Plant clean seed
- In clean soil
- Harvest a clean crop.

Sources accessed in the preparation of this section.

Güllüoglu, Leyla. and Arioglu, Halis, (2009). Effects of seed size and in-row spacing on growth and yield of early potato in a Mediterranean-type environment in Turkey. African J. Agric. Res. **4:** 535-541.

Otroshy, M. and Struik, P.C. (2008). Effects of Size of Normal Seed Tubers and Growth Regulator Application on Dormancy, Sprout Behaviour, Growth Vigour and Quality of Normal Seed Tubers of Different Potato Cultivars. *Research Journal of Seed Science*, **1**: 41-50.

Wright D.N., Bishop J.C., Harvey O.A., Baghott K.G., Voss R.E. & Timm H. (1977). Potato preplant tillage practices. Leaflet 2682, University of California.

Section 6.

Crop Nutrition

Introduction

After emergence, the potato plant sustains growth by utilising assimilates produced in the shoot and by the uptake of water and nutrients by the roots. All the essential nutrients must be supplied at optimal rates to produce vigorous plants, necessary to support maximum tuber growth. Nutrient deficiencies limit canopy growth and shorten canopy duration, resulting in reduced carbohydrate production and tuber growth rates. Excessive fertilizer applications can modify the partitioning of assimilates and cause nutrient imbalances that delay or slow tuber growth rates. Either deficit or excess fertilizer situations can reduce tuber-bulking rates.

Central to the understanding of potato crop nutrition is the knowledge of how soils hold nutrients and how the plants use them. A fertile soil combines a mixture of a variety of minerals, many different types of organic matter in different stages of decay, and a large population of living microorganisms. The complex make-up of the soil permits it to hold a large quantity of water, which it provides to plants.

In addition to water, the soil supplies the plants with the thirteen mineral nutrients required for normal growth and development. These nutrients (in the ionic forms taken up by the root) are nitrogen, phosphorus, potassium, sulfur, calcium, magnesium, iron, manganese, boron, chlorine, zinc, copper, and molybdenum.

These mineral nutrients exist in two forms, both as constituents of the soil particles and as dissolved ions in the soil water. Root uptake systems facilitate taking these nutrient ions and water from the soil and moving them into the root tissues.

Soil pH

Soil pH or soil reaction is a measure of the acidity or alkalinity in soils. pH values normally range from -1 to 14, with 7 being neutral. A pH below 7 is acidic and above 7 is alkaline. Soil pH is sensitive to changes in soil management processes resulting from human activity. Soils become acidic in reaction with increasing number of years in cultivation. Acidic conditions are also induced:

(1) When heavy rainfall leaches away the basic ions calcium, magnesium, potassium and sodium.
(2) When carbon dioxide, formed in the soil, from the breakdown of organic matter and root respiration, dissolves in soil water to form a weak organic acid.
(3) When urea and DAP are oxidised, strong inorganic acids such as nitric acid is formed.

Soil pH is a commonly measured soil property. It is considered a most useful and informative soil parameter because of its relationship to many aspects of soil fertility and plant growth.

Soil pH controls many chemical processes that take place in the root zone and it specifically affects plant nutrient availability by controlling the chemical forms of the nutrient. The optimum pH range for most plants is between 5.5 and 7.0, however many plants' such as potato can thrive at pH values outside this range.

Soil pH influences potato plant growth through influencing the solubility and availability of nutrients. Fourteen of the seventeen essential plant nutrients are obtained from the soil. But before a nutrient can become available to plants, it must first be dissolved in the soil solution.

A pH range of approximately 6 to 7 promotes the ready availability of most plant nutrients (Fig. 1). At high pH values (6-7), the availability and uptake of certain elements such as Ca and Mg increase. By contrast, low soil pH values can bring elements such as aluminium to toxic levels of solubility.

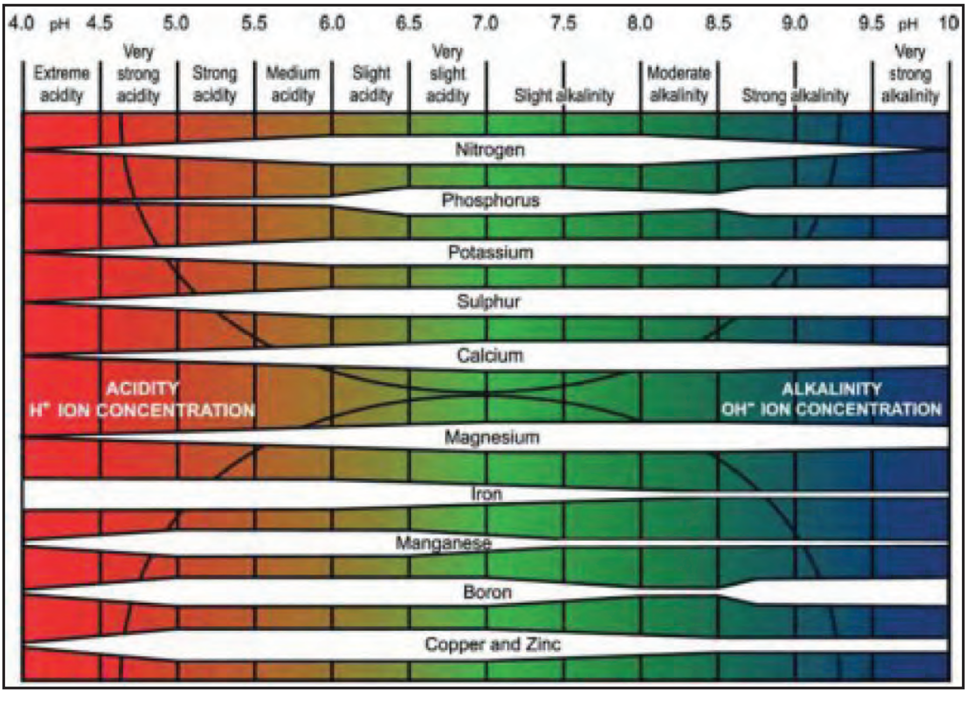

Figure 1.
Influence of soil pH on nutrient availability. (Ref. Truog 1946).

Plants take up nutrients as ions, that is, within charged atoms or molecules. Ions can also affect important soil factors like pH, nutrient availability, water retention, and ultimately plant growth. Positively charged ions are called cations and negatively charged ions are called anions. Cation Exchange Capacity (CEC) is the measurement of a soil's ability to bind positively charged ions (cations), which include many important nutrients. Again in the simplest terms, cations are key in the chemical bonding process that allows certain types of soils to retain vital nutrients. Thus the higher the CEC, the higher the soil fertility.

The availability of most macronutrients (nitrogen, phosphorus, potassium, sulfur, calcium, and magnesium) decreases as soil acidity increases (Fig. 1). Therefore, application of lime to moderately acid soils tends to increase the availability of these nutrients. On the other hand, the availability of most micronutrients is decreased as soil pH increases. Under these conditions, nutrient deficiencies may occur in response to excessive lime application.

Negative effects of soil acidity on plant growth are generally not only caused by a single factor, but several that affect normal plant development. The main factors that typically affect plant growth in acidic soils includes toxicity of hydrogen ion (H^+), aluminum, and manganese as well as deficiency of essential nutrients such as phosphorus, magnesium, and micronutrients. Despite crop tolerance to moderate acid conditions, nutrient use efficiency can be affected by soil pH. Soil acidification is a progressive problem in all cultivated soils, which leads to loss of organic matter, soil compaction, release of metals to toxic concentrations and excessive clay weathering. Soil acidity affects root development, leading to reduced nutrient and water uptake.

Aluminium toxicity is a widespread problem in acid soils. Aluminium is present in all soils, but dissolved Al_3^+ is toxic to plants; Al_3^+ is most soluble at low pH. Above pH 5.2 little Al is in soluble form in most soils. Aluminium is not a plant nutrient, and as such, is not actively taken up by the plants, but enters plant roots passively through osmosis. Aluminium inhibits root growth; lateral roots and root tips become thickened and roots lack fine branching; root tips may turn brown. In the root, Al has been shown to interfere with many physiological processes including the uptake and transport of calcium and other essential nutrients, cell division, cell wall formation, and enzyme activity.

The contribution of urea and soluble phosphate fertilisers such as DAP to soil acidification is not being addressed in potato growing regions in Sub-Saharan Africa. Potato growers rely on urea and DAP for soil nutrition. It is widely recognised that both those products contribute to soil acidity. For every kilogramme of urea and DAP fertiliser added to the soil 6.6 kg and 7.9 kg respectively of calcium carbonate is required to neutralize the acidity.

Adding lime to the soil not only increases soil pH but also replaces hydrogen ions, thereby eliminating most major problems associated with acid soils. It also contributes two nutrients, calcium and magnesium to the soil. Furthermore, lime increases the availability of added phosphorus and increases the availability of nitrogen by hastening the breakdown of organic matter. Liming materials leave no objectionable residues in the soil.

A number of factors affect the amount of lime required to ameliorate soil acidity; among them, existing soil pH, soil structure and the amount of organic matter. In addition, various crops have varying requirements for soil pH and consequently the amount of lime required

Soil organic matter

Soil organic matter (SOM) is a dynamic and large reservoir of carbon, which is subject to change due to changes in management practices and crop rotation sequences. It constitutes one of the most complex components of agricultural soils. Organic matter plays a vital role in regulating the flow and supply of plant nutrients and water flow, also determining physical attributes of soils.

SOM is a soil component consisting of plant and animal residues at various stages of decomposition, cells and tissues of soil organisms, and substances synthesized by soil organisms. SOM increases soil fertility by acting as a reserve of plant nutrients, especially nitrogen, phosphorus, and sulfur, along with micronutrients, which are then slowly released upon SOM mineralization. As such, there is a significant correlation between SOM content and soil fertility. Organic matter retains plant nutrients and prevents them leaching to deeper soil layers. Microorganisms decompose organic matter, which contributes to mineralization and immobilization of N, P and S. Thus, they contribute to the gradual and continuous liberation of plant nutrients. Soil organisms retain available nutrients that are not taken up by the plants. In soils depleted of organic matter, these nutrients would be lost from the system through leaching and runoff.

The bacterial activity that releases nitrogen from organic matter and certain fertilisers is particularly affected by soil pH; bacteria operate best in the pH range of 5.5 to 7.0. Acidic conditions are particularly detrimental to soil bacterial activity.

Soil organic matter affects both the chemical and physical properties of the soil and also its overall health. The properties influenced by organic matter include: soil structure; moisture holding capacity; diversity and activity of soil organisms. Increasing the topsoil organic matter by 1% will increase the capacity of each hectare to hold an additional 100,000 liters of water.

Soil testing

Prior to planting a potato crop, it is advisable to have the soil tested to determine the pH value and the level of macronutrients. Conventional practice in Sub-Saharan Africa is to apply urea and DAP at standard rates, irrespective of crop history or soil type. It is to be hoped that soil testing will become widely available and that the practice of standard application will soon be at an end.

Crop Nutrition

Potato plants require three factors for growth: light, water and nutrients. The nutrients can be supplied from either chemical or biological sources. Farm-yard manure being an example of a biological source. But before it becomes available for plant growth, the FYM must be broken down to its chemical constituents. These chemical elements, when dissolved in water, become constituents of the soil solution. Plant roots absorb elements from this medium. Because potatoes have a poorly developing root system, it is obligatory that all the essential nutrients be supplied at the right rate, the right time, and in the right location to ensure the crop delivers its yield potential.

The total collection of nutrients required by potatoes can be subdivided into three categories, based on demand. The highest requirement is for the macronutrients, nitrogen, phosphorus and potassium. Potatoes have a lower demand for a group of nutrients referred to as secondary nutrients, sulfur, magnesium and calcium. In trace amounts potatoes require the micronutrients, iron, manganese, zinc, boron, copper, chlorine and molybdenum. The macronutrients, N, P and K are rarely present at sufficiently high levels in the soil to provide an economic yield and therefore must be supplemented by the farmer. The secondary nutrients and micronutrients are generally present in the soil at adequate levels to sustain crop growth, except as described earlier, when they are unavailable due to inappropriate soil pH values. In such cases, it would be cheaper to adjust the soil pH, than to apply the micronutrient as a supplement. Finally the essential elements C, H and O are available from the air as carbon dioxide or from the soil as water.

Macronutrients

Nitrogen nutrition

Agricultural crops have a considerable dependence on inorganic nitrogen and 85–90 million metric tonnes of nitrogenous fertilizers are added to the soil worldwide annually. Due to the cost associated with manufacture, nitrogen is one of the most expensive nutrients to supply and commercial fertilizers represent a major cost in potato crop production.

Nitrogen is a key element in potato growing and required by the plant's roots and shoot throughout the growing season. Nitrogen gas makes up 80% of the earth's atmosphere, but this gaseous nitrogen is unavailable for plant growth. Bacteria play an essential role in making atmospheric N available for plant growth.

Some of the nitrogen required to produce a crop of potatoes will be available from soil resources (Fig. 2) but this will normally need to be supplemented by additional supplies. Nitrogen is an essential component of proteins, nucleic acids and enzymes. Along with magnesium, it is a major constituent of chlorophyll, the green coloured compound that traps sunlight and utilises the solar energy to manufacture the products required for growth and development. Pale green new leaves, yellowing of older leaves, slow growth and stunted growth, are likely symptoms of nitrogen deficiency.

Protein synthesis describes the production of proteins required for plant growth. Potato plants have a high requirement for nitrogen to produce the amount of protein required by the leaves, roots and tubers.

Nitrogen fertiliser exists in many chemical and physical forms. Potato plant roots can take up several chemical forms of nitrogen. The most common are ammonium (NH_4^+), nitrate (NO_3^-) and urea ($(NH_2)2CO$). Natural processes in the soil can convert one

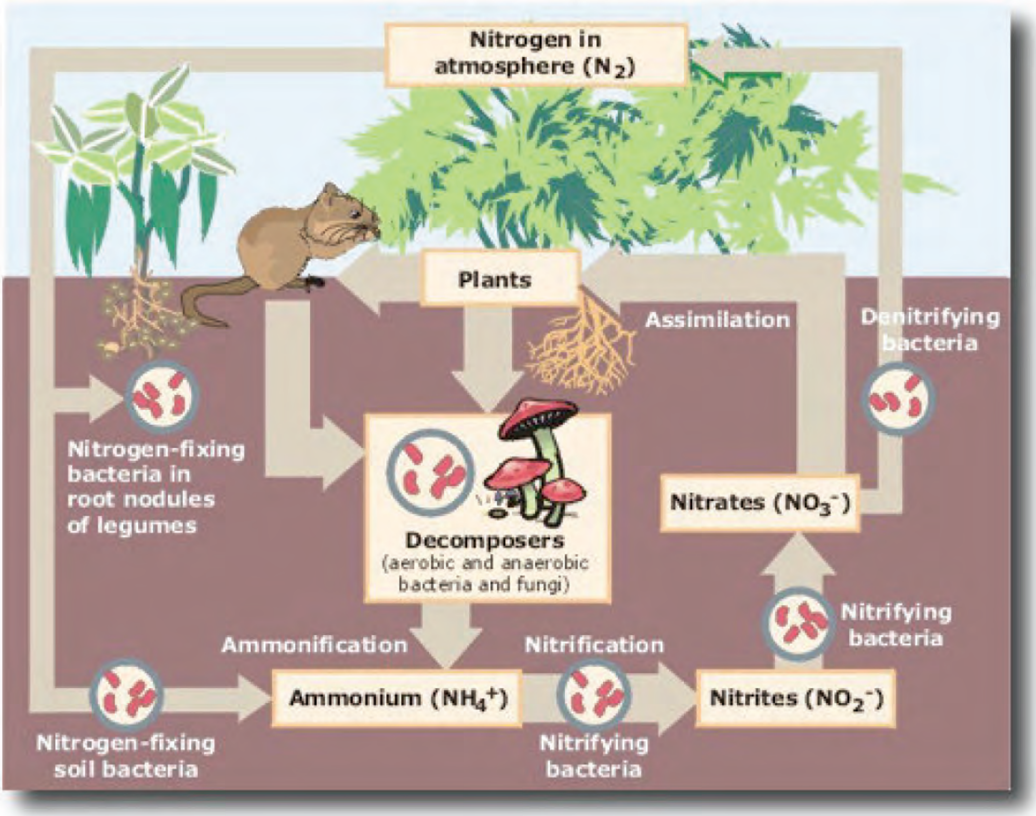

Figure 2.

Nitrogen cycling pathways through the soil, plant and bacteria (Ref. Wikipedia)

form to another. The nitrogen in urea is completely water-soluble. Upon application, urea nitrogen changes rapidly to NH_4-N. Urea nitrogen therefore is readily available to plants on application to the soil.

Urea is the most widely used dry nitrogen fertilizer in the world. After application to soils, urea is converted into ammonia, which can be held in the soil or converted into nitrate. Ammonia volatilization following fertilization with urea can be substantial, and if urea is applied to the surface of the land, without immediate incorporation into the soil, considerable loss of nitrogen can occur.

Hydrolysis of urea by urease produces ammonium carbonate. With surface-applied urea, alkalinity of pH 9 or higher can develop under the urea granule or pellet, and ammonia will volatilize into the air. Volatilization occurs on bare ground, on debris, or on plant leaves. Urea is readily soluble in water, and rainfall or irrigation after its application will move it into the soil and lessens volatilization losses. Use of urease inhibitors has been suggested to lessen the volatilization losses of ammonia from surface-applied urea. Manufactured urea is identical to urea in animal urine

Currently there is considerable interest in the efficient use of N in agriculture. This arises not only because the different forms and pathways by which N can be lost from soil can have adverse environmental impact, but also because losses of such an expensive input are a direct cost to growers. There is much evidence to show that N is used more efficiently on soils with more organic matter, and presumably a better structure, so that roots explore the soil more effectively to locate the nutrients. In a study, to compare the yield response of potatoes to increasing levels of N, the response to N was always larger on soils with more soil organic matter (SOM) irrespective of the amount of N applied, and the recovery of the applied N was greater where the yields were larger.

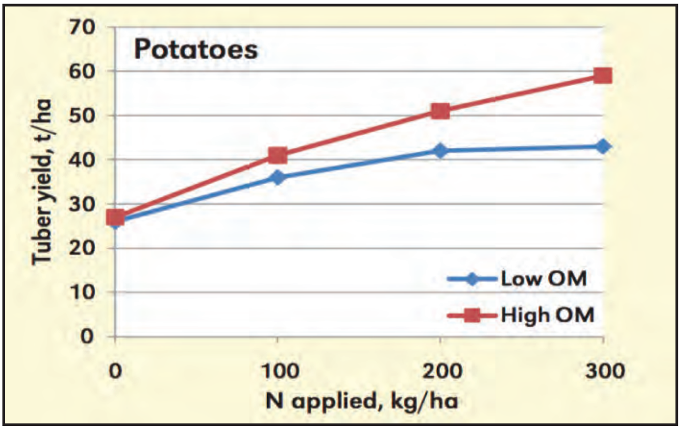

Figure 3.
Potato yield response to applied N when planted in soil with two levels of SOM, 1.3 and 3.4%, respectively. (Ref. Johnson, 2009)

Unless it is possible to add large amounts of organic materials, it is not easy to increase SOM in many arable-cropping systems. However, every attempt should be made to conserve and increase SOM wherever possible because it improves soil structure and thus the ability of plant roots to explore the soil and find the nutrients required to optimize growth and yield. This is especially so in relation to the acquisition of N and P and thus their efficient use in agriculture

Crops vary in their demand for nitrogen. Potatoes, because they need to produce a large canopy in a very short time, have a high requirement for nitrogen (Fig. 3). Furthermore, this canopy must be sustained over the growing season, while it traps solar energy and produces sugars and other products required for growth. Potatoes need to take up nutrients, including nitrogen, throughout all of their field growth phase.

While adequate supplies of nitrogen can produce a high yield of tubers through sustaining a vigorous canopy (Fig.4), excessive applications can delay the onset of tuberisation and reduce yield, in situations where the growing season is restricted due to shortage of water or infection with late blight. This reduction in yield is caused by excessive partitioning of assimilates to the shoot, at the expense of the tubers.

Figure 4.
A vigorous potato canopy. (Photo © Author)

Phosphorus nutrition

Phosphorus is the second most important macronutrient next to nitrogen in limiting crop growth. Phosphorus is involved in an array of process in plants such as in photosynthesis, respiration, in energy generation, in nucleic acid biosynthesis and as an integral component of several plant structures such as phospholipids.

Crop yield is limited by phosphorus in about 40% of the world's arable land. Total phosphorus is about 0.1 percent by weight of the soil, but only one percent of that is available. Of the part available, more than half comes from the mineralisation of organic matter. Plant dry weight may contain up to 0.5% phosphorus. Phosphorus is a limiting nutrient in several Sub-Saharan soils. Many studies indicate that total-P and available-P are low and P-sorption capacity is relatively high. The low availability of P in the soil is reflected in the low content of active P forms.

Roots absorb P ions from the soil solution. Plants can only absorb phosphorus from the solution phase but not directly from the solid phase. Solid forms must be converted to liquid and then chemically converted to the mono- or diprotonated phosphate (HPO_4^{2-} and $H_2PO_4^-$) before the phosphorus is available to the plant. The ability of the plant to absorb P will depend on the concentration of P ions in the soil solution at the root surface and the area of absorbing surface in contact with the solution. The P availability to plants may be limited by its low abundance in the soil, but also, and very commonly, by its adsorption onto various soil minerals.

In acidic soils, phosphorus may be adsorbed by iron or aluminium oxides, and various clay minerals. Many of the most fertile and productive soils in tropical zones are derived from volcanic material containing allophane minerals, which have a large phosphorus fixing capacity. Phosphorus deficiency is often the major limitation to crop growth on these soils, particularly where previous cropping has caused a depletion of soil organic matter and increased acidification. Phosphorus deficiency is also common on highly weathered tropical soils and siliceous sands; in fact, few soils are naturally well endowed with this nutrient.

Phosphorus can be present in soils in two forms, inorganic and organic. In most agricultural soils, 30-60% of the P is present in inorganic forms, although this fraction can vary from 5-95%. Phosphorus availability is controlled by solubilisation and precipitation of phosphate in inorganic forms and through the mineralisation and immobilisation of the organic fraction.

Inorganic forms of soil phosphorus consist of apatite (the original source of all phosphorus), complexes of iron and aluminum phosphates, and phosphorus absorbed onto clay particles. The primary inorganic form of P is found in crystalline Al and Fe compounds in acid soils and associated with Ca compounds in alkaline, calcareous soils. These are the most stable forms (least soluble) of P. Chemical weathering releases the plant-available monohydrogen phosphate (HPO_4^{2-}), and dihydrogen phosphate ($H_2PO_4^-$). These anions can interconvert readily, and the predominant species at any given time is determined by the pH of the soil solution. This chemical weathering reaction is slow, so very little plant available P is derived from inorganic sources in the soil.

The solubility of these phosphorus compounds as well as organic phosphorus is extremely low, and only very small amounts of soil phosphorus are in solution at any one time. Organic phosphorus is found in plant residues, manures and microbial tissues. As with organically bound N, organically bound P is not available to plants and organisms because it cannot be absorbed into root cells without first being released from the organic molecule through mineralization. Decomposition of OM provides much of the P required by plants, with the remainder being provided by applied fertilisers. Three general types of compounds make up the bulk of the organic phosphorus in plants, namely: phytin, phospholipids, and nucleic acids. Organic P forms include both relatively labile pools such as phospholipids and nucleic acids but also more resistant pools such as humic acids.

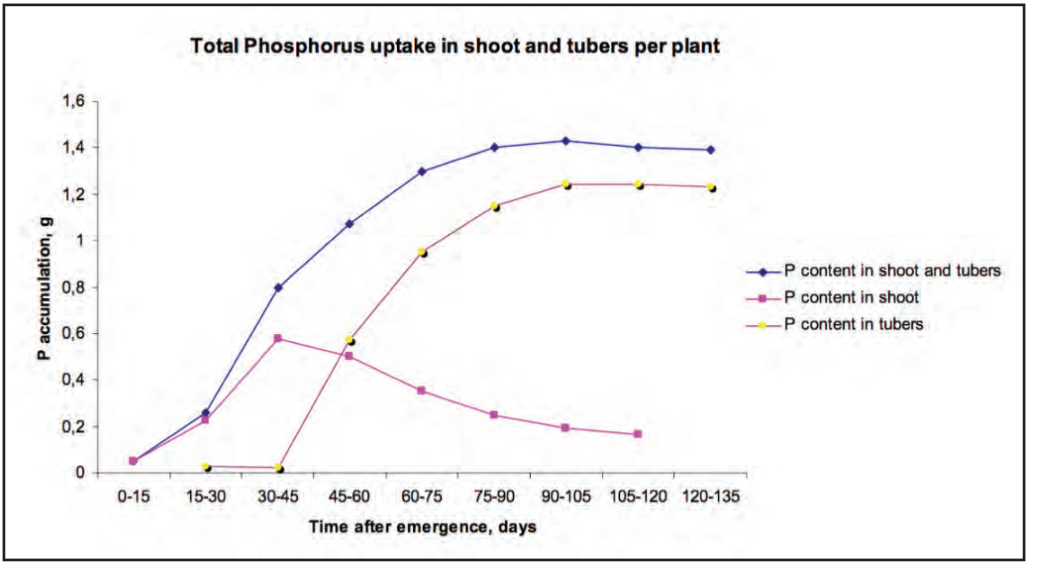

Figure 5.
Phosphorus uptake in shoot, tubers and shoot + tubers per plant over time.
(Ref Kolbe and Stephan-Beckmann, 1997).

Despite its importance in plant growth and metabolism, phosphorus is the least accessible macronutrient and hence the most frequently deficient nutrient in most agricultural soils because of its low availability and its poor recovery from the applied fertilizers. The low availability of phosphorus is due to the fact that it readily forms insoluble complexes with cations such as aluminum and iron under acidic soil condition; whereas the poor P fertilizer recovery is due to the fact that the P applied in the form of fertilizers is mainly adsorbed by the soil.

Phosphorus is never readily soluble in the soil but is most available in soil with a pH range centered around 6.5. Extremely acid and strongly acid soils (pH 4.0-5.0) can have high concentrations of soluble aluminum, iron and manganese, which may be toxic to the growth of some plants. Plants absorb most of their phosphorus from the soil solution as orthophosphate ($H_2PO_4^-$), regardless of the original source of phosphorus. Typical daily uptake of P per potato plant is shown in Figure 5. The most widely applied form of P in Sub-Saharan African potato growing is di-ammonium phosphate. DAP application significantly lowers soil pH, exchangeable Ca and Ca saturation and increases soluble Al and exchange acidity

Phosphate deficiencies in potato

Potato has been described as the crop species with the greatest susceptibility to P deficiency. Root size, shoot size (leaf size and stem growth) as well as tuber yield and quality (set, number, size, specific gravity, starch synthesis and maturity) all have been shown to be impacted by P deficiency. To ensure an optimum yield, potatoes require adequate phosphorus from the earliest stages of growth.

Phosphorus plays a role in photosynthesis, respiration, energy storage and transfer, cell division, cell enlargement and several other processes in plants, since it is a part of the structure of DNA, RNA, ATP and phospholipids in membranes. Most metabolic processes including cell division, cell expansion, respiration and photosynthesis are reduced by phosphorus deficiency.

It is more difficult to diagnose phosphorus deficiency than a deficiency of nitrogen or potassium. Often the only symptom of phosphorus deficiency is a general stunting of the plant during early growth. Some crops, tend to show an abnormal discoloration when phosphorus is deficient. The plants are usually dark bluish-green in color with leaves and stem becoming purplish. The upper side of the leaves will therefore acquire a darker green color. The lower side of the leaf and the stem often turns purple, The purplish color is due to accumulation of sugars that favors the synthesis of anthocyanin (a purplish-colored pigment), which occurs in the leaves of the plant although it is more common to observe yield loss without these symptoms. Chlorophyll and chloroplast formation is less affected than cell and leaf expansion,

Large differences between symptoms among potato cultivars occur, and some will show purple color even though they are not deficient. In other cases, tuber yield is reduced due to P deficiency, even though no visual symptoms are apparent. Deficiency symptoms in potatoes can be observed as stunted plants with shortened internodes and poor root systems which can be seen right from the early stages of growth. Under low P conditions, a greater proportion of total carbon production is used in root respiration than at adequate P levels. Therefore, overall haulm growth is retarded by P deficiency, while root growth is less severely affected, resulting in an increased shoot/root ratio, although, tuber set is negatively affected by P deficiency.

When potatoes were grown on P deficient soils there was a positive relationship between P fertiliser application rates and both stem height and leaf area index. Studies showed that the fertiliser application increased yield due to increased radiation interception rather than to increased conversion efficiency. This is also in line with further research, which suggested that the mechanism by which P fertilizer may increase yields is through increased ground cover and radiation absorption.

When soil phosphorus is limiting, older leaves curl upwards and may develop necrotic spots on the margins. The tubers may have rust-brown colored blotches and plants are shorter with thinner stems. One possible result of lack of phosphorus in the soil is that leaf stomata fail to open normally and this can result in plant temperature rising by 10% higher than normal.

While potatoes are very responsive to applications of fresh soil phosphate, the economic optimum rate is often very difficult to define. Rates will depend on soil type and soil test results. In the absence of soil testing facilities, growers are forced to rely on standard applications, without reference to soil P status.

Potassium nutrition

Potassium, along with nitrogen and phosphorus, is an essential plant macronutrient that is taken up by crops from soils in relatively large amounts (Figures 6 and 8). Although potassium is not a constituent of any plant structures or compounds, it plays a part in many important regulatory roles in the plant. Potassium is especially important in its interaction with nitrogen throughout the growth cycle as it helps to improve nitrogen uptake from the soil and the subsequent conversion of this nitrogen in the plant to amino acids and ultimately protein. Potassium plays a critical role in enzyme activation, water use, photosynthesis, transport of sugars, protein synthesis, and starch synthesis in plants. Adequate potassium in the field results in higher crop yields and higher nitrogen-use efficiency. Crops respond to additional potassium levels when nitrogen is sufficient, and greater yield response to nitrogen occurs when potassium is sufficient

Fertiliser materials containing potassium include such as muriate of potash (KCl), sulfate of potash (K_2SO_4), double sulfate of potash and magnesium (K_2SO_4 $2MgSO_4$), and nitrate of potash (KNO_3).

Plants differ in their ability to take up K depending on several factors. The factors that affect availability of K in the soil and resulting plant uptake are soil factors, plant factors, and fertilizer type and management practices. The chief soil factor is the soil itself and especially the clay content. The cation exchange capacity (CEC) of the soil reflects the soil's ability to hold K and other cations and store them in the soil for crop uptake. Clay minerals and soil organic matter are the soil constituents that contribute to CEC. In general, the higher the CEC of the soil, the greater the storage capacity and supplying power for K.

The major plant factor influencing K uptake is the crop, since crops differ in their ability to take up K from a given soil. This is associated with the type of root system and surface area of the roots. Grasses, for example, have a much greater capacity to take up K than potatoes. Grasses having many more fibrous, branching roots, increasing the K absorbing surface.

Potatoes take up more potash than many other arable crops. In the six weeks after plant emergence, the crop will take in at least two thirds of the total K uptake. During peak vegetative growth, potatoes may require 10 kg K_2O/ha per day from the soil. Maincrop potatoes contain the maximum quantity of potash about 80 days after emergence and this may be more than 500 kg K_2O/ha for high yielding crops (Fig. 6). As the tops die back and the plant matures, some potash is returned to the soil. By harvest more than 75% of the maximum K uptake is found in the tubers, which typically contain around 5.8 kg K_2O per tonne of tubers

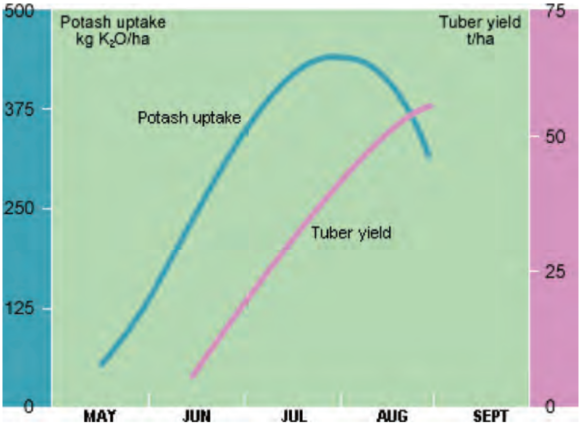

Figure 6.

Patterns of potassium uptake during the linear phase of tuber bulking for a crop growing in the temperate zone. (Diagram. © PDA, UK. With permission.)

K efficiency describes the capacity of a genotype to grow and yield well in soils low in available K. All the major economically important plants have displayed genotypic differences in efficiency of K uptake and utilization. The biochemical basis of K-efficiency is complex, comprising a mixture of uptake and utilization efficiency mechanisms. An example of K efficiency is illustrated for improved K uptake where a cultivar may have a larger surface area of contact between roots and soil and increased uptake at the root–soil. An example of increased utilization efficiency is where cultivars display better translocation of K into different organs, greater capacity to maintain cytosolic K^+ concentration within optimal ranges and increased capacity to substitute Na^+ for K^+. It was shown that a more K-efficient potato cultivar could take up more K per plant due to its higher K influx and this higher influx resulted because of its capacity to use higher non-exchangable soil K. Regression analysis indicated that the capacity to use non-exchangable K is the main factor controlling the K efficiency of different potato cultivars; followed by root length to dry matter accumulation ratio and K influx.

The potassium in the soil may be found in reserves or pools. The pools for K are described as: soil solution (K very available), exchangeable (K less available), non-exchangeable (K hardly available) and fixed (K rarely available). The dissolved K ions in soil solution are readily taken up by crop roots and generally comprise between 2 to 5 mg/l in normal agricultural soils. The next most "available" fraction in the soil is "exchangeable" potassium. These represent the two accessible fractions upon which we can rely on for growing our crops.

Potassium has two major roles in the plant. First, it is involved in the activation of enzymes that are fundamental to metabolic processes, especially the production of proteins and sugars. This metabolic function requires only small amounts of K. Second, K plays a biophysical role, by maintaining the water content and thus the turgor of cells. The osmotic function of K^+ can be partially substituted for by Na^+. Turgid cells are essential for leaf vigor so that photosynthesis proceeds efficiently. Carbon dioxide enters the leaves through the stomata. This function is regulated by the guard cells. Potassium regulates expansion and contraction of the guard cells and therefore controls entry of carbon dioxide into the leaf. Low levels of potassium can result in inefficient stomatal activity, reducing the level of photosynthesis.

The relationship between the water, nitrate and potassium content of the cell, controls the movement of both through the plant, as well as the transport of sugars produced by photosynthesis to roots and storage organs like tubers. Potassium improves the ability of plants to resist diseases, insect attacks, cold and drought stresses and other adverse conditions. It promotes the development of a vigorous root system and increases the efficiency of the uptake and use of N and other nutrients. It is vitally important that a lack of potash does not diminish the crop's ability to respond to nitrogen. It is also important that there is enough potash available to satisfy the peak uptake by the crop. This is often very high, even if only temporarily, and occurs at flowering. Potassium increases both the yield and quality of agricultural produce. Much larger quantities of K are needed for this physiological function than for its biochemical role in plants.

As the potato crop is harvested and the tubers removed from the field, so potash is taken away in that crop material. This must be replaced otherwise future crops will be grown in soil with a reduced potash level, and lower yields will then occur.

Plants also have a naturally occurring defence mechanism when infected by a pathogen. The infection triggers an increased production of certain chemicals that form part of the plant's defence mechanism. Potassium plays an important role for both the production and the transport of these compounds to the site of infection. When a shortage of K exists, the amount of natural antifungal compounds is reduced, so once the fungus has penetrated the cells, the plant's susceptibility to disease is increased.

Potash deficiency in potato

Potassium deficient potato plants grow slowly and have poorly developed root systems. Potassium is highly mobile in plants and is readily translocated from older tissue at the base to the upper newer leaves. In K deficient plants, the initial symptoms normally appear on the older leaves displaying as yellowing of the leaf margins. The upper leaves of K deficient potato plants are smaller, crinkled and darker green than normal with small necrotic patches. Middle to lower leaves show marginal scorch and yellowing. Early indicator: dark green crinkled leaves, though varieties differ in normal leaf color and texture. If potassium deficiency is severe, there will be bronzing on the leaves (Fig. 7), A shortage of potassium leads to greater drought susceptibility, a reduction in photosynthesis and restricted movement of water nutrients and sugars around the plant. Insufficient K promotes lower tuber dry matter through reduced photosynthesis, and a consequent reduction in starch production. Tuber quality is also affected where potassium deficiency causes the accumulation of reducing sugars, which provide undesirable, dark colored chips. A further consequence of K deficiency is internal blackening of potato tubers resulting from excess of tyrosine. Two further markers of tuber quality, bruising and hollow heart can be reduced by K application. Potassium fertilization improves the quality of potatoes for processing.

Figure 7.
Typical symptoms of potassium deficiency in potato leaves – crinkling and bronzing. (Photo © PDA, with permission)

Potassium plays a vital role in maintaining the turgidity (rigidity) of plant cells. Because of its importance in turgor maintenance, potassium is essential to obtain maximum leaf extension and stem elongation in potato haulm. This helps to achieve rapid ground cover so maximising interception of sunlight and thus the rate of growth in the critical early periods of the growing season, which is of particular importance for short season crops such as potatoes. In severe cases, of K deficiency haulm growth is so retarded that the leaf canopy may not meet between the rows, with consequent reduction in radiation interception. Another symptom of K deficiency is uneven growth throughout the field, with serious consequences for tuber yield and quality.
There can actually be a significant loss of yield and a reduction in tuber quality without any visible symptoms of K deficiency in the leaves. By the time symptoms are visible, is likely that potential yield loss will already have occurred and furthermore, it is not likely that this can be dissipated by top dressing with K.

Increasing the application of potassium has been shown to increase tuber yield. This is achieved by increasing average tuber size and weight. The source of fertiliser can be important. Use of sulphate of potash instead of muriate of potash may be beneficial where larger numbers of small-medium size tubers are required such as for seed. The benefit will be more pronounced under dry or stressed growing conditions.

Tuber dry matter and specific gravity were more affected with sulfate of potash than muriate of potash. The quality parameters like dry matter, specific gravity, starch contents, vitamin C, chip color and taste are improved with K application.

In general, an inverse relationship is found between available soil K and the severity of disease. It is a common practice to add K fertilizers to reduce certain diseases. With potatoes, K fertilization has been found to decrease the incidence of several diseases, such as late blight, dry rot, powdery scab and early blight.

Secondary Nutrients
(Ca, Mg, S)

Note: *The phrase 'secondary element' refers to the quantity but not the importance of the element required to sustain plant growth. A deficiency in a secondary nutrient is just as detrimental as a deficiency in nitrogen, phosphorus or potassium.*

Calcium

Calcium should be considered a most important nutrient, and more than simply just an ameliorant to adjust the pH scale. It plays a major role in the physiology of the plant, strengthening its physical structure, increasing nutrient uptake and protecting from disease. Calcium is involved in both the structure and function of all plant cell walls and membranes. An additional role for calcium is in cell signaling by acting as secondary messenger and maintaining the integrity of plasma membrane. It plays a regulatory role in maintaining the cation anion balance. In its role as a secondary messenger, calcium induces the opening of K channels in leaves, especially guard cells.

The primary roles of calcium:

- As a soil amendment, calcium helps to maintain chemical balance in the soil, reduces soil salinity, improves water penetration and promotes good crumb structure.
- Promotes cell division and elongation
- Facilitates nitrate uptake and metabolism
- Calcium plays a critical metabolic role in enzyme activity and carbohydrate removal.
- Calcium neutralizes cell acids.

Calcium is an essential nutrient for plant growth. It performs critical functions in the soil surrounding the roots and also within the plant. Calcium has an important influence on soil properties, especially as it prevents dispersion of clay and maintains a friable crumb structure in soil. It is not considered as a leachable element. Many soils are high in calcium, but often it is present in insoluble forms such as calcium carbonate and therefore not readily available for root uptake. Plants growing in these soils can show calcium deficiency symptoms.

All soils contain Ca (and Mg) in the form of cations (positively charged ions, Ca^{++} and Mg^{++}) that attach to the soil clay and organic matter. These cation minerals interact with negatively-charged particles of clay and humus and in this way they are held in the soil. The plant takes up calcium and magnesium in the form of cations. The soil parent material determines the relative proportion of these elements, as well as the total amount present in the soil.

High levels of other cations such as magnesium, ammonium, iron, aluminum and especially potassium, will reduce the calcium uptake in some crops. A common misconception is that if the pH is high, adequate calcium is present. This is not always true.

In potatoes, inadequate supplies of calcium cause growth abnormalities like internal brown spot and hollow heart. These responses are worsened in acidic soils. Tuber Ca concentration may be increased through fertilization and Ca application can increase tuber Ca concentration and reduce the occurrence of internal brown spot. Up to 40% of tuber Ca may be absorbed directly from the soil solution through the tuber periderm.

Adequate calcium nutrition can also improve potato skin finish, while reducing problems with blackspot and bruising. Abundant tissue calcium also increases the tubers' resistance to attack by soft rot bacteria during storage and may improve the performance of seed potatoes.

In plants, calcium is regarded as a non-mobile element i.e it is not mobile in the phloem transport system. Thus, if the plant becomes depleted in calcium, it cannot remobilize it from older tissues, in a manner comparable with nitrogen. It is an important constituent of cell walls and can only be supplied in the xylem sap. Should transpiration be reduced for any reason, the calcium supply to growing tissues will rapidly become inadequate. Water movement governs calcium movement within the plant - tissues that use the most water due to evapo-transpiration accumulate the most calcium. Therefore it might be expected that leaves and stems of potato contain about five times as much calcium as the tubers This is explained by the fact that the leaves and stems lose far more water than the tubers, because the tubers are constantly surrounded by moist soil.

While the nutrient is involved in photosynthesis and plant structure, other functions attributed to calcium are: the neutralization of organic acids; inhibition of some potassium-activated ions; and a role in nitrogen absorption. A notable feature of calcium-deficient plants is a defective root system. Calcium deficiency causes stunting of root systems. Roots are usually affected before above ground parts. The concentration of calcium in lower in roots than in leaves.

With rapid plant growth, the structural integrity of stems that bear flowers is strongly coupled to calcium availability. Calcium is a critical part of the cell wall that produces strong structural rigidity by forming cross-links within the pectin polysaccharide matrix. Depleted calcium in plants leads to a deterioration in cell membrane, loss of cell compounds and eventually death of cell and plant tissue. Calcium additionally plays a role in cell structure, in regulating cell and plant functions as a secondary messenger and in various plant functions from nutrient uptake, changes in cell status (of the plant) in reacting to the environmental and disease stresses. Heat stress in particular tends to elongate stem length while reducing leaf size in many crops. Calcium helps overcoming heat stress effects by improved stomatal function and other cell processes. Calcium's role in the development of heat shock proteins that help plants tolerate stress to prolonged heat is also significant.

Calcium is often referred to as the plant's 'first line of defense'. Some organisms infect plants by penetrating cell tissue using enzymes known as pectinase. These enzymes dissolve pectins. A higher calcium content in plants, with higher concentration of pectins holding cells together will give plants a greater ability to withstand these enzymes. Virulent stains of fungal pathogens produce oxalic acid. Pectinases and oxalic acid are involved in pathogenesis. Calcium is sequestered from the leaf to form calcium oxalate. In such cases, the increase in calcium levels in leaf tissue or calcium in foliar applications will decrease the pathogen's ability to invade the leaf. Fungal pathogenic infection is also reduced with increased calcium uptake by plants.

Calcium too, plays a major role in the quality of many crops. Increasing tuber calcium content promotes longer storage life and resists a range of physiological break down.

Symptoms of calcium deficiency:

- Necrosis at the tips and margins of young leaves,
- Deformation of affected leaves,
- Highly branched, short, brown root systems,
- Severe, stunted growth, and
- General chlorosis.

It must be remembered that these problems are caused by an inadequate supply of calcium to the affected tissues. These deficiencies can occur even when the soil appears to have an adequate presence of calcium.

Ca^{2+} is not usually limiting under field conditions, however there are several defects that can be associated with low levels of this ion, including poor root development, leaf necrosis and curling. Symptoms of calcium deficiency are not as well defined as those for magnesium. In most situations, tubers are small and deformed while the foliage appears normal. Inadequate supplies of calcium cause tuber growth abnormalities like internal brown spot and hollow heart.

High tuber calcium has been associated with improved storage ability. Even though there is only slender evidence that Ca fertilizer treatment will alter yields, they may affect tuber size distribution.

Magnesium

Magnesium is best known for its central role in photosynthesis, where it is present as the central atom of each chlorophyll molecule. It is also involved in various key steps of sugar production as well as the transport of sugars in the form of sucrose from the leaves to the tubers. The plant uses these sugars for energy and also for structure. When Mg is deficient, the movement of carbohydrates from the leaves to other parts of the plant is slowed. This results in reduced growth of other plant organs like roots and the reproductive parts that are harvested. Magnesium is also involved in protein production where it serves as a 'building block' of ribosomes, the organelles that synthesize proteins in cells. In potatoes, magnesium uptake mirrors that of phosphorus (Fig. 8).

Magnesium has unique roles in plant physiology. As a carrier, it is also concerned in numerous enzyme reactions as an effective activator, in which it is closely associated with energy-supplying phosphorus compounds. Magnesium also helps to activate specific enzyme systems. Enzymes are complex substances that build, modify, or break down compounds as part of a plant's normal metabolism. Magnesium acts as a cofactor in all phophhorylation processes. Phosphorylation is a fundamental process of energy transfer and occurs in photosynthesis, glycolysis, tricarboxylic acid cycle and respiration.

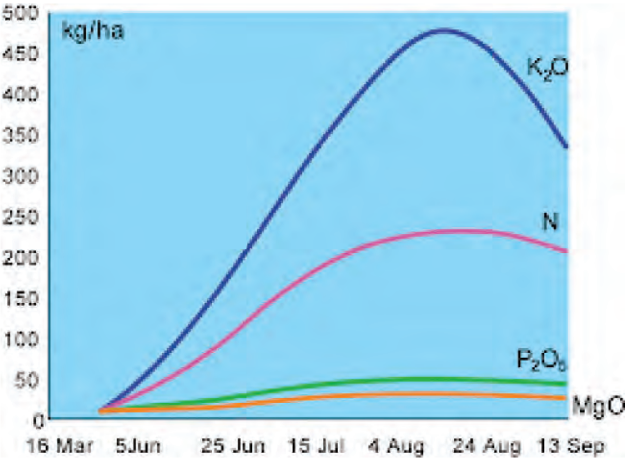

Figure 8.

Nutrient uptake of a 55t/ha crop of potatoes (**Note:** *These details refer to a crop grown in a temperate zone in the Northern hemisphere*). (Diagram © PDA UK.)

Consequently, magnesium is very mobile in plants, and, like potassium, when deficient, is translocated from older to younger tissues, so that signs of deficiency appear first on the oldest leaves and then spread progressively to younger and younger tissues. That means that Mg deficiency symptoms appear first near the base of the plant and are characterized by interveinal chlorosis and sometimes by the accumulation of reddish pigments (anthocyanins) at the leaf margins. Magnesium increases NPK uptake and thereby increases yield and promotes uptake and translocation of phosphorus.

Magnesium is abundant in the earth's crust. It is found in a wide variety of minerals.

Rocks that are dominantly basaltic are magnesium rich. Besides the divalent Mg^{+2} ions occurring in the soil solution, magnesium is either adsorbed to cation exchangers such as organic matter or clay particles in the exchangeable fraction or it is bound inside the crystals of soil silicates. Only the first two fractions are available to plants.

Magnesium becomes available for plant use as these minerals weather or break down. The magnesium can be categorised as:

- That contained in parent rock material, largely insoluble and largely unavailable to plants.
- That held loosely in the soil (exchangeable magnesium is present in the soil as the positively charged cation (Mg^{+2}) and as such capable of being held in the soil by the negative charges present on the clay-humus complex).
- That which is present in the soil solution for immediate plant uptake.

These pools are similar to the soil sinks for potassium, although there are some important differences. Unlike potassium, magnesium does not move between non-exchangeable sources into the exchangeable pool easily and this process is chiefly driven by pH (the more acid the conditions, the faster the mobilisation).

Magnesium is held on the surface of clay and organic matter particles. Although this exchangeable form of Mg is available to plants, this nutrient will not readily leach from soils.

The electrical charge on magnesium is also weaker and is therefore more easily lost to lower soil zones than potash, particularly on sandy or acid soils. Mg deficiency is usually only been observed on very acid soils. These soils usually have a sandy loam, loamy sand or sand texture. Plants are deficient in Mg when grown in soils having low pH, sandy in nature and highly leached soil with low Cation Exchange Capacity. A Mg deficiency is not likely to occur until the soil pH drops below 5.5.

In potatoes, the loss of the green color begins on the tips of the lower leaves when there is a mild Mg deficiency. When the deficiency is more serious, the yellowing progresses between the veins toward the center of the leaf. In the advanced stages of Mg deficiency, leaf areas between the veins show small brown dead spots.

Note: *Diseases, herbicide damage (**Section 7**), and environmental factors also cause leaves to die prematurely. So, care should be taken in identifying a Mg deficiency. If in doubt, use plant analysis to be sure*.

The concentrations of calcium and magnesium in potato tuber pith and cortex were analysed. The cortex as defined here refers to the tissue exterior to the vascular ring. Whereas the cortex of the tuber was found to contain about half of the weight but only contained 60 to 80% of the tuber calcium. Magnesium was distributed evenly throughout the tuber on a tissue weight basis

Sulphur

Sulphur is classified as a secondary element, along with Mg and Ca, but it is sometimes called "the 4th major nutrient". Some crops can take up as much S as P. Sulphur is one of the key secondary elements essential for optimal plant growth. It is taken up from the soil solution by the plant in the sulphate form (SO_4^{2-}).

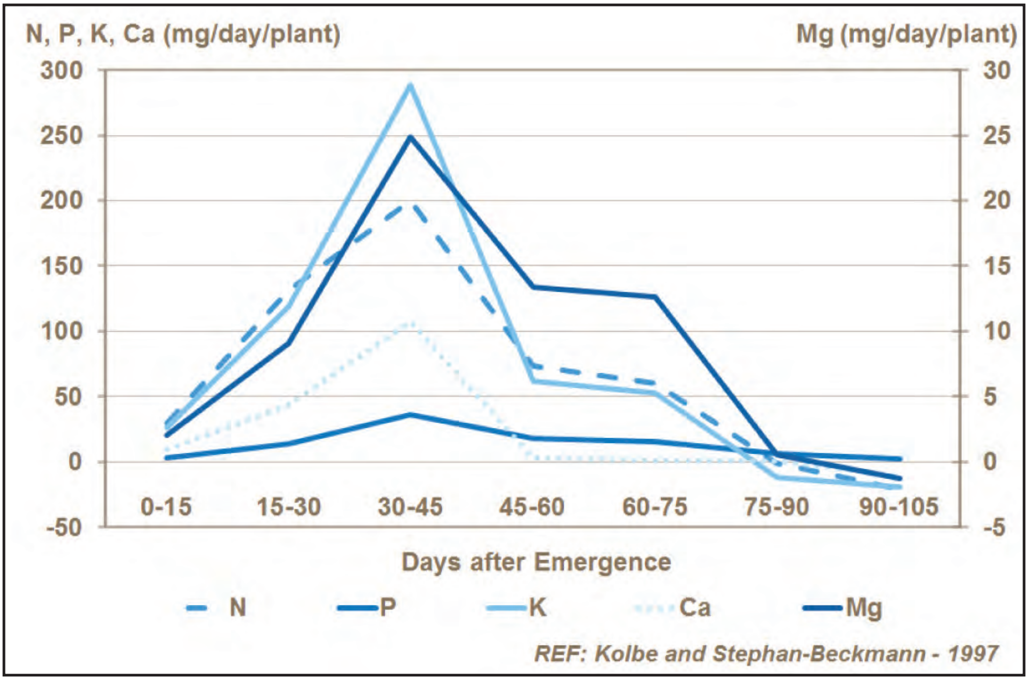

Figure 9.

Daily rate of nutrient uptake for five major nutrients by the potato plant

Sulphur is present in various forms in the environment. Up to 95% of the total sulphur in the soil is associated with organic matter. Other sources of sulphur in soils are animal manure and irrigation water. In the soil, sulphur is present as organic sulphur compounds, sulphides (S-), elemental sulphur (S0), and sulphate (SO_4^{2-}). Plants cannot absorb organic or elemental sulphur. For plants to utilise sulphur from the soil it must be in the sulphate form. Therefore organic sulphur and elemental sulphur must be converted to the sulphate form in the soil.

In the plant, sulphur is a component of methionine, cysteine and cystine, three of the 21 amino acids, which are the essential building blocks of proteins. The sulphur containing amino acids are essential in human nutrition. They cannot be synthesized in the human body. It is their content in the tuber that makes the potato so valuable in human nutrition. Sulfur supply to the growing plant has been recognized as a major factor influencing protein quality. In potatoes, the biological value of proteins was reduced from 94 to 55 by sulfur deficiency at high N supply. (*Biological value is a measure of the proportion of absorbed protein from a food, which becomes incorporated into the proteins of the human body. It captures how readily the digested protein can be used in protein synthesis in humans.*)

Sulphur is also a component of key enzymes and vitamins in the plant and is necessary for the formation of chlorophyll even though it is not one of the constituents.

Sulphur is essential for many growth functions in plants including nitrogen metabolism, enzyme activity and protein synthesis. It improves the use efficiency of nitrogen and phosphorus. Generally, sulphur-deficient plants have short and/or spindly stems. Sulfur deficiencies in potatoes appear similar to nitrogen deficiencies. All leaves are pale yellow and are smaller in size than normal. The youngest leaves are a brighter yellow. This should not be confused with iron deficiency, which looks similar but the veins stay green. Since sulphur is only moderately mobile within the plant, the deficiency is manifested as yellowing of the young (top) leaves. With nitrogen deficiency, yellowing affects the older, lower leaves first. Generally, plants require about a tenth as much sulphur (S) as nitrogen (N), but sulphur deficiencies restrict plant growth as surely and severely as nitrogen deficiencies

Factors contributing to increased incidence of sulphur deficiency include less sulphur being added to the soil due to the increasing proportions of high-analysis, sulphur-free fertilizers, such as urea and diammonium phosphate (DAP).

Sulfur is usually low in sandy soils. Except in extremely deficient soils, potatoes do not usually respond to sulfur applications. If soil test sulfur is less than 7 parts per million and/or tissue sulfur is less than 0.18 percent, then 20 kg sulfur/Ha (use a sulfate source) should be banded at planting.

Sulphur is lost to the soil when potatoes are harvested and removed. Typically 1tonne of potato tubers will remove 4.5 kg of S

Micronutrients

(Fe, Mn, Zn, Bo, Cu, Mo, Cl)

To ensure an optimum tuber yield, it is essential to achieve an appropriate balance between macronutrients and micronutrients.

Iron

Iron is abundant in the soil in many rocks and minerals. Plant roots absorb Fe from the soil solution most readily as (ferrous) Fe^{2+} but in some cases also as (ferric) Fe^{3+} ions. The solubility of Fe oxide minerals in soil is very low, so when $F3^{+}$ ions predominate the plant roots reduce the Fe^{3+} ions to Fe^{2+} ions before they move into the root across selective membranes. This process involves the root excreting a variety of organic compounds and acids into the soil.

Iron deficiency (resulting in chlorosis) is most likely to occur on highly calcareous soils (pH higher than 7.8). Symptoms of iron deficiency first appear in the youngest leaves. The interveinal areas are chlorotic but the veins remain green. In cases of severe deficiency, the entire leaf is chlorotic. Iron is necessary for the formation of chlorophyll. It is not very mobile within plants so plants invest iron in the growth of new leaves, therefore iron chlorosis shows first and more severely on the newer growth at branch tips.

Be careful with making a diagnosis of iron deficiency since zinc and manganese deficiencies also result in similar leaf symptoms. However iron chlorosis appears first on the younger or terminal leaves and under severe conditions, it may progress into older and lower leaves. By comparison, zinc and manganese deficiencies typically appear first on older leaves

Manganese

Manganese deficiency. Night frosts can cause similar symptoms. Exercise caution with diagnosis, as Magnesium deficiency is similar but here yellowing usually starts on older leaves. Manganese deficiency is normally limited to high pH soils, where manganese in the soil is unavailable for the plants. Manganese deficiency occurs on medium to low pH soils, if the soil preparation has created a loose soil with high oxygen content.

Deficiency symptoms include intercostal yellowing on entire leaflets usually starting on younger leaves. Necrosis at leaf edge may be due to severe deficiency but it occurs usually in spots along the line of the veins.

Most likely to occur on organic soils, Sandy soils, High pH, Cold wet periods.

It's role in plant growth, to boost bulking. Increases the yield of tubers. Improves disease resistance. Improves skin finish. Increases tuber dry matter content. Increases starch levels.

Zinc

Zinc deficiency in potato results in stunted growth and small leaves. Furthermore it causes younger leaves show interveinal chlorosis and necrosis, which occurs in irregular patches. Whitish spots develop within the brown necrotic tissue. Symptoms may also start on older leaves.

Deficiency is likely to occur in organic soils, high pH soils, soils rich in phosphorus or soils receiving high phosphorus application. Cold wet conditions exacerbate symptoms.

Zn is important for healthy green foliage also improved tuber yield and quality.

Boron

Boron deficiency can be confused with Ca deficiency, which also affects the growing points and leads to their 'dying off.' Ca deficiency also causes leaf necrosis, which is seen at the edge of the leaf and not between the veins as with boron deficiency. Potato has a relatively low requirement hence deficiency symptoms occurs mainly on soils with poor boron content (weathered sandy soils) or soils with a high fixing capacity (recently limed, peat soils, pH > 7)

The primary role of boron is in the cell walls, where it provides cross links between polysaccharides to give structure to cell walls. Boron also plays roles in formation of sugar complexes for translocation within plants, and in the formation of proteins.

Boron deficiency induces thickening of the young leaves also crinkled and bordered by light brown tissue, which extends to the intercostal areas. The growing points and the shoot tips die off. In severe cases, the leaf margins are cupped upward.

Deficiency symptoms are induced by sandy soils, alkaline soils, soils low in organic matter, high levels of nitrogen, high levels of calcium, cold wet weather, periods of drought.

Boron is important for improved crop development and improved tuber quality. It reduces incidence of internal Rust Spot and incidence of internal browning.

Copper

Copper is important for healthy green foliage and improved yield. Copper plays roles in photosynthesis and respiration, including the final transfer of electrons to oxygen. Copper helps form lignin in cell walls, which provide support to hold plants upright. Copper deficiency causes permanent wilting of potato plants. Particularly young leaves roll inwards, they develop a dark green colour and plants become stunted. Leaf tips and margins may die off without preceding chlorosis. Normally potatoes are not sensitive to copper deficiency. Symptoms are seldom visible in the field. Deficiency symptoms are made worse by organic soils, chalky soils, sandy soils, reclaimed heathland and high nitrogen applications.

Molybdenum

Deficiency symptom description – a general yellowing of older leaves, while young leaves become uniformly yellow-green. Crop deficiencies of molybdenum are rare. Within the plant, Mo is primarily used in the production of enzymes that regulate various plant functions. The most well known of these Mo-containing enzymes regulate nitrogen nutrition – the critical reaction involving the conversion of nitrate into proteins (nitrate reductase).

Young plants can show deficiency symptoms if seed potatoes were grown on soils with low Mo content. Yellowing of leaf blades is similar to nitrogen or sulfur deficiency. The symptoms are made worse by acid soil, low pH and low levels of soil organic matter.

In plant metabolism Mo is important for nitrogen metabolism, pigment and chlorophyll synthesis and is beneficial for growth and yield.

Chlorine

Chlorine is an essential micronutrient, which is taken up by potatoes in significant quantities. In soils and plants, it exists as chloride. In plant nutrition, chlorine is applied as the chloride salt of calcium, magnesium, potassium and sodium. In soil, chlorine is readily soluble where it occurs in aqueous solution as the chloride anion (Cl^-) and in this form plants can readily take it up, through an active uptake process. Existing as an anion (i.e. carrying a negative charge) it does not adsorb to soil particles and moves readily with the water in the soil. Chloride ions are taken up by the root and move in the xylem to the shoot. Only small portions return to the roots via the phloem.

In plant growth and development chloride participates in several physiological processes. Its' functions include osmotic and stomatal regulation, evolution of oxygen in photosynthesis, and disease resistance and tolerance. An effective exchange of gases between the plant and the surrounding air is critical for photosynthesis. Chloride plays an essential role in stomatal regulation where the plant's stomata, open and close to allow gas exchange and minimise water loss. The opening and closure of stomata is mediated by fluxes of the potassium ions (as K^+) and accompanying chloride anions (as Cl-).

Studies with isolated chloroplasts have indicated that Cl^- is an essential cofactor for photosynthesis, where it is required for the photochemical reactions necessary for splitting water (known as the Hill reaction) and oxygen evolution, in photosystem II.

The potato crop is considered highly responsive to chlorine. In the potato, chlorine concentration is highest in the leaves, followed by the stem and lowest in the tubers. Potatoes for fresh consumption and seed potatoes are considered partly chloride tolerant whereas potatoes for processing are considered chloride sensitive, therefore choose sulphate of potash and avoid application of KCl. Rainfall deposits atmospheric chloride in significant amounts in coastal regions, but this source decreases with increasing progression inland. Where muriate of potash fertiliser is not regularly applied, chloride deficiencies can occur.

Summary

- All the essential nutrients must be supplied at optimal rates to produce vigorous plants, necessary to support maximum tuber growth.
- Nutrient deficiencies limit canopy growth and shorten canopy duration, resulting in reduced carbohydrate production and tuber growth rates.
- Nitrogen is a key element in potato growing and required by the plant's roots and shoot throughout the growing season.
- Phosphorus is involved in an array of process in plants such as in photosynthesis, respiration, in energy generation, in nucleic acid biosynthesis and as an integral component of several plant structures such as phospholipids.
- Potassium is especially important in its interaction with nitrogen throughout the growth cycle as it helps to improve nitrogen uptake from the soil and the subsequent conversion of this nitrogen in the plant to amino acids and ultimately protein.
- The phrase 'secondary element' refers to the quantity but not the importance of the element required to sustain plant growth. A deficiency in a secondary nutrient is just as detrimental as a deficiency in nitrogen, phosphorus or potassium.
- To ensure an optimum tuber yield, it is essential to achieve an appropriate balance between macronutrients and micronutrients.

References

Kolbe H., Stepha-Beckmann, S. 1997. Development, growth and chemical composition of the potato crop (Solanum tuberosum L.). I. leaf and stem. Pot. Res. 40:111- 129.

Kolbe H., Stephan-Beckmann S. 1997, Development, growth and chemical composition of the potato crop. II. Tuber and whole plant. Potato Res., **40**, 135-153.

Truog, E. (1946). Soil reaction influence on availability of plant nutrients. Soil Sci. Soc.of Am. Proc. **11**, 305-308.

Nitrogen cycle. (2016). Wikipedia, The Free Encyclopedia. https://simple.wikipedia.org/w/index.php?title=Nitrogen_cycle&oldid=5421713

Sources accessed in the preparation of this section.

International Plant Nutrition Institute (IPNI). https://www.ipni.net/publication

Johnston, A.E., Poulton, P.R. and Coleman. K. (2009). Soil organic matter: its importance in sustainable agriculture and carbon dioxide fluxes. *Advances in Agronomy* **101:**1-57.

Potash Development Association (UK). Leaflet No. 15. Potash for potatoes. http://www.pda.org.uk

Waterer, D., 2005. Calcium nutrition of potatoes, problem and potential soultions. Manitoba Agri., pp: 1-3

Section 7.

Early Development – Planting to Emergence and Weed Control.

Introduction

The period from planting to emergence normally extends from 14 to 28 days. Several factors determine the number of days after planting (DAP) to emergence. This interval between planting and emergence is the most vulnerable stage of the potato crop. The period is deemed to have ended when the sprouts emerge above the soil surface. Optimum sprout development is highly influenced by the quality of the seed, its physiological age, sprouting stage, as well as by the proper soil conditions, especially temperature and moisture at planting time. The effects of seed quality, physiological age and sprouting stage have already been discussed

Factors affecting the number of days from planting to emergence

Seed tuber size

Sprout growth rate is influenced by the seed tuber size. The seed tuber provides reserves of food and water to sustain sprout growth until it emerges from the soil and until the new expanded leaves commence photosynthesis. The seed tuber size therefore constrains the reserves of food and water available to maintain sprout growth. Sprouts growing from a large seed tuber have more ready access to a larger pool of assimilates than sprouts growing on a small seed tuber. Sprouts on large seed tubers demonstrate higher relative growth rate compared with sprouts on small seed during both the pre emergence and post emergence phases. Sprouts from large seed tubers emerged significantly earlier than sprouts from small tubers. At planting time, the sprouts on large seed tubers were slightly longer and thicker, which resulted in earlier germination and crop establishment. This ensured that plants established faster since the shoots were not yet photosynthesizing but were relying solely on the remobilisation of metabolites from the mother tubers.

When a small seed tuber has a number of sprouts, the competition for access to limited reserves impairs the sprout growth rate. It is proposed that this competition is not for local metabolites but for growth factors distributed throughout the tuber since it has been shown to be independent of the distance between the competing sprouts. A further advantage of planting large seed is observed where in the event of damage to the newly emerged shoots by frost or hail, a large seed tuber will possess sufficient reserves to allow rapid regrowth.

Sprout length

The ideal sprout length at planting is 8 to 12mm. Longer sprouts risk being rubbed off during handling, especially if sprouts are formed in darkness or under low light levels. When potato seed tubers are sprouted in a diffused light source (DLS), considerable thickening will have occurred at the base by the time the sprout attains a length of 12mm. This thickening serves to provide increased stability and resist rubbing off. Also on a 12mm sprout, the root primordia will have expanded and in addition, lateral stems will have begun to expand (Fig. 1). These structures developing on the sprout provide additional stability during handling and planting and reduce the risk of removal.

Figure 1.

A seed tuber with sprouts at the ideal stage of development. (Photo © Author)

Because the sprouts have already commenced growth, the number of days after planting to emergence will be reduced. Rapid establishment is crucial when the field growth phase may be cut short by adverse environmental conditions or an onset of defoliating pathogens like late blight.

Planting depth

Conventional sized seed tubers (35-55mm) can be planted 15 to 20cm deep. Tubers in this size grade provided they have not accumulated high levels of physiological age, will have sufficient reserves of water and metabolites to sustain sprout growth until they emerge above the soil surface and assume independent growth.

Note: *When seed tubers are scarce the small seed tubers (<35mm) from clean, healthy stock will also establish plants. However, the initial planting depth should be shallow, to compensate for their limited reserves of water and nutrients. The planting depth can be brought to the desired value subsequently by "earthing-up" during successive cultivations*

Soil tilth and texture

Potato sprouts display negative geotropism, they grow upward towards the surface. Growth progress will be restricted by adverse soil conditions. Potatoes thrive best when planted in soil with an open texture, well aerated and having high levels of organic matter. Potato sprouts display heterotrophic growth, relying on the mother tuber for energy supply and as a source for water and remobilized structural components. These steps are powered by respiration, and are limited when there is a constraint on ready access to oxygen from the soil. Heavily compacted or water logged soil leads to the development of anaerobic conditions which will retard sprout emergence.

Large clods, resulting from failure to produce a fine seedbed, will delay emergence, as the sprout must circumvent the obstacle. Potatoes are renowned for their poor rooting capacity. A fine tilth will facilitate root outgrowth and ensure that root hairs have the opportunity to explore soil pores and absorb water and nutrients.

Soil temperature

Post planting soil temperature moderates sprout growth. Research evidence shows optimum growth rate occurring at soil temperature of 20^0C. Sprout growth rate has been researched extensively. There is a consensus that a typical growth rate is 1mm per ^{0}Cday (degree day) above a base temperature of 2^0C.

While sprout elongation rate is optimised at 20^0C, soil temperatures above 25^0C retard or even inhibit emergence, reduce plant establishment and the number of main stems per plant. Soil temperature values in this range are likely to be encountered in the sub-tropics.

Do not plant seed tubers in soil where the temperature has been less than 7^0C for 3 consecutive days before planting. Planting seed tubers, with advanced physiological age, in soil at low temperature can result in the physiological disorders "coiled sprout" or "little potato disorder" discussed earlier.

Soil moisture

The moisture required to facilitate sprout emergence is normally supplied from the seed tuber. Very small seed tubers (or minitubers) may lack adequate carbohydrate and water reserves. For this reason they should be planted at a shallow depth to facilitate rapid emergence, then additional soil earthed-up during subsequent tilling. But again exercise caution – this area at the top of the ridge is prone to drying under high temperature.

Irrigation (particularly furrow irrigation) should not normally be considered due to the possibility of water logging and the consequent reduction of oxygen in the rooting zone, with the attendant risk of seed tuber decay. Soil moisture content, 70%

to 80% of field capacity is adequate at this growth stage. If the soil were irrigated to a higher water content and heavy rain fell, flooding could result with disastrous consequences for the emerging crop.

Weed Control in Potato

Introduction

A 'weed' is often defined as a plant growing in the wrong place. But then if this definition is applied rigidly, a wheat plant is regarded as a weed if it is growing in a potato crop! A more common sense definition is a plant, which has no commercial or nutritional value and is growing in competition with an agricultural crop.

Worldwide, weeds are the most costly category of agricultural pests and cause more yield loss of agricultural crops and add more to farmers' production costs than insect pests, crop pathogens, root-feeding nematodes, or warm-blooded grazing pests.

Weeds are highly competitive and successful plants. They exhibit rapid seedling growth and an ability to reproduce when young, especially when they experience stress. Weeds mature quickly compared to most crop species, and many species thrive under a broad range of conditions. They can tolerate a wide range of adverse environmental conditions, such as drought stress and soil compaction. Weeds can scavenge and compete for resources, and they respond rapidly to favorable growing conditions and produce vast quantities of seeds.

Four broad factors govern the success of weeds in their competition with the crop:

- Weed density,
- The time of emergence,
- The size of the weed relative to the height of the potato canopy at any stage and,
- Existence of allelopathy, the ability of a weed species to secrete inhibitory substances into the soil surrounding the roots.

Weeds in potato crops

Potatoes are normally planted in the most fertile field on the farm. They receive additional fertiliser and water when it is available. It is not surprising therefore that the conditions which favour potato growth also favour the growth of weeds.

As with all crops, potatoes need to be protected from weeds, diseases and pests. Weeds compete with potatoes for light, nutrients and water and if not controlled will reduce

- Crop growth rate,
- Radiation use efficiency (RUE),
- Leaf area index and leaf area duration,
- Disturb tuber size distribution,
- Delay harvesting,
- Reduce yield and,
- Reduce quality, by lowering specific gravity.

Weeds can have a detrimental impact on tuber yield when compared to potatoes grown in weed-free conditions; the size of the reduction is a function of the density and competitive ability of the weed population. The reduction occurs because weeds use resources that would otherwise be available to the crop. Apart from these direct effects on growth and yield, weeds affect the crop indirectly by harbouring insects and diseases that attack potatoes. Weed management in potato production is one of the main cost and time consuming practices.

Many agronomic and environmental factors will influence the magnitude of yield loss. Two major loss inducing factors are the weed density, and time of emergence relative to the crop.

A grower can minimize the competitive effects of weeds on their potato crop if they can implement practices that:

- Reduce the density of weeds or,
- Adjust inter row and interplant spacing or,
- Improve uptake of resources by the crop or,
- Establish an early season size advantage of the crop over the weeds or,
- Employ the most effective timing of weed control,

All these strategies could reduce crop production costs and increase potato yield.

Weed impact on canopy development and tuber yield in potatoes

As discussed above, weeds cause reduction in growth and yield loss by several means and unless they are removed, they will outcompete the potato crop for water nutrients and light. Removing weeds by manual methods is slow and laborious. But the penalty for not controlling the weeds is severe. A study on the effect of weed competition on total potato yield ranged from yield of 22 t ha^{-1} in weed-free plots to 3 t ha^{-1} with no weed control; a yield loss of 86%. Weedy conditions also resulted in a greater number of small tubers and fewer of the desirable large grade tubers compared to weed-free conditions. Competition with weeds has been shown to impact tuber size distribution by reducing both the average tuber size and the number of tubers. In addition to negatively impacting the physiological formation of yield during the season, weeds present at harvest can be detrimental to yield. This is achieved by increasing mechanical damage to the tubers and by slowing the harvesting operation and leaving un-dug tubers in the ground, which reduces harvesting efficiency.

We need to know therefore the critical period of weed competition. In other words if potatoes and weeds are growing together, at what stage in the crop growth cycle does it experience the greatest competition and the greatest resultant yield reduction? This raises the questions–

- What is the effect of extending the period of competition, or,
- What is the effect of extending the duration of the weed free period?

How do we determine if weeds will reduce potato yield?

It is a truism that weed competition will reduce yield since the weeds compete for the same nutrients and in the same quantity that the crop is competing for, and then in addition, they are also competing for water and sunlight.

The most important decision a grower has to make regarding weeds in a potato crop revolve around timing – how long to wait before removing the weeds and how long to sustain the weed control activity without suffering a yield penalty.

To assist decision-making, three measures are employed.

“Maximum weed-infested period” (MWIP)

Weeds being discussed here are those that emerge with the crop. Then the question arises - how long after crop planting can weeds be allowed to grow before they must be removed – i.e. before they begin to compete with the crop and cause a yield loss.

Assuming that the potatoes are planted into a clean seedbed, the potatoes and germinating weeds commence their growth at the same time. Weeds that germinate with the crop usually do not affect the crop’s growth until two or three weeks after emergence – when they first become large enough to begin competing for moisture and nutrients. This initial period, during which weed can grow without reducing the crop’s yield potential, is defined as the ‘maximum weed-infested period’. The farmer needs to cultivate or otherwise control weeds before the end of this period, since if the initial flush of weeds is removed by cultivation before the end of this period, subsequent crop production will not be affected. However, failure to successfully control weeds at this stage can have a major impact on yield (Fig. 2).

“Minimum weed-free period” (MWFP)

The weeds being discussed here are the weeds that emerge later that the crop. The question then arises - how long must the crop be kept clean and free from weeds after emergence and before later-emerging weeds can be allowed to remain, without causing crop loss.

Weeds that emerge with or shortly after the crop have the greatest potential for causing economic damage if allowed to grow unchecked. Later emerging weeds have less effect, and those that emerge after a certain point in time no longer affect yield. This point is the ‘minimum weed-free period’. In a potato crop, which has the vigour to enable the canopy to provide 100% ground cover, late emerging, low growing weed species will not provide aggressive competition.

Then by combining the result of the two previous values we arrive at:

“Critical period of weed competition”

This period is defined as the time interval between two separately determined components MWIP and MWFP The “critical period” of weed interference refers to the minimum amount of time during which it is essential that the crop must be kept free of weeds in order to prevent yield loss. It represents the time interval falling between the two separate components discussed above:

(a) The minimum length of time after seeding that a crop must be kept weed-free so that later-emerging weeds do not reduce yields, and

(b) The maximum length of time that weeds which emerge with the crop can remain before they become large enough to compete for growth resources.

The critical period of weed competition has been used to determine the period when control operations should be carried out to minimize yield losses for many crops

The interval from the end of the maximum weed-infested period until the end of the minimum weed free period defines the critical period for weed control for an individual crop. Since the crop can be adversely affected either by early-emerging weeds allowed to persist into this period, or by weeds emerging during this period and allowed to grow, the weed control strategy should focus on keeping the crop clean through this time.

Then the next question arises – what level of weed control is acceptable during this period? Crops can tolerate different levels of competition even during the minimum weed-free period. Slow-growing, weed-sensitive vegetables like, direct-sown onion or carrot can suffer if weeds are allowed to reach the two-leaf stage before cultivation

In vigorous crops like beans, maize, or potatoes, one early cultivation and a second pass to remove later-emerging weeds at the two-leaf stage or even a little larger, may be sufficient.

In a young, newly emerged crop, those weeds emerging closest to crop plants compete most severely. Therefore, cultivation must effectively remove within-row weeds, as well as weeds between rows. Timing is critical for manual or mechanical within-row weeding, which works effectively when the weeds are small and the crop is sufficiently large that it can withstand the effects of cultivation.

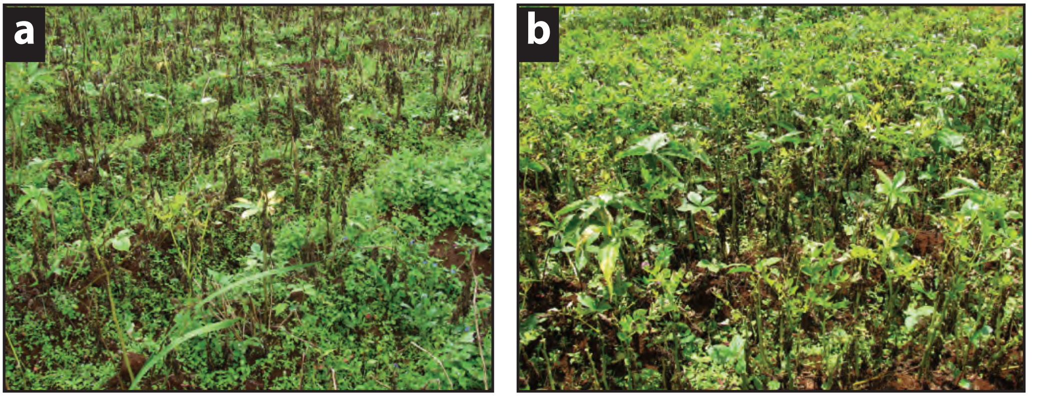

Figure 2.
Weeds emerging and growing with the canopy provide severe competition (a). Weeds emerging towards or after canopy senescence will have no effect on tuber yield (b). (Photos © Author)

The timing of weed removal after determining the critical weed control period is an important component of weed management. Critical periods of weed-crop competition for potatoes have been determined in a few environments, and only for some weed species. However, due to the diversity of climatic conditions, weed species and management techniques, these studies are site specific and cannot be extrapolated to other environments, especially tropical African countries.

Factors affecting the weed flora

Wet season and dry season response. It might be expected that soil moisture availability would influence the composition of the weed flora, promoting or retarding individual species depending on their requirement for soil moisture. A study investigating this response found that critical periods for weed control, with a 95% weed-free total yield, were estimated from 26 to 66 and from 20 to 61 days after emergence for the rainy and dry seasons, respectively. This period coincides with the period of rapid canopy growth, tuber initiation and rapid tuber bulking. Weed competition before or after these critical periods had negligible effects on crop yield.

The number of weeds per unit area and the weed species (tall or rosette type) is an obvious determinant of weed induced yield reduction. A weed density of 5.3 plants per meter of row reduced potato yield by 20 to 45% depending on the species present.

Effect of weed type

Weed flora will vary widely depending on a multitude of factors, location, altitude, soil type, moisture availability, cropping history etc. etc. It is not useful therefore to mention individual weed species here, but discuss the general concept.

Weeds can be classified as annual – growing each season from a seed; or perennial – where an underground structure such as a rhizome or storage organ allows it to perrenate. Then annual or perennial weeds can further be divided as broad leaved and graminaceous. Annual broad-leaved weeds emerge fast, become established earlier and offer more vigorous competition than annual grass weeds. They even outcompete perennial weeds at the early stage of crop growth. Growth of low growing broad leaved and grass weeds will often be suppressed when the potato canopy achieves total ground cover. These weeds get another chance to resume and prosper when the canopy begins so senesce.

Weeds (0.6 to 1.0 m) with an erect growth habit, either grass type or broad leaved, reduced yield by up to 45% and this was achieved by a decrease in tuber bulking. When the infestation was by tall (1.5 m) broad-leaved weeds, yield was reduced by impaired tuber set and tuber bulking

Methods promoting weed competition and suppression

Growers should plan a weed control program that integrates mechanical, and cultural methods to fit their weed species and production practices.

Mechanical cultivation is effective way to manage weeds early in the season, a time when weed presence is most detrimental to potato growth and yield. Weeds that emerge earlier than potatoes have been shown to be the most competitive with the crop. It is observed that the canopy of the potato crop would continue to shade out weeds emerging after initial cultivation. This timeline may vary by cultivar because of variable canopy structures. In addition, if the canopy is under stress from low soil fertility or moisture deficit, it will not be capable of competing so vigorously with the weeds. The capacity of the potato crop to provide shade competition to weeds will be significantly affected by the choice of inter-row and inter-plant spacing discussed in **Section 5.**

The choice of potato cultivars that can suppress or tolerate weed competition could be a component of an integrated weed management system to reduce reliance on herbicides. The competitive ability of 10 potato cultivars was examined. Weed competition treatments included: (1) weedy throughout the season, (2) weed-free (by hand weeding) from emergence to 4 weeks after emergence, and (3) weed-free (by hand weeding) for the entire season. Potato cultivars did not differ in ability to reduce weed biomass. Potato tuber yield was strongly related to early-season time of potato emergence and canopy closure, as well as weed competition treatments.

Although the ability to suppress weeds was similar among cultivars, differences in yield among cultivars grown in the presence of weeds suggest differential tolerances of weed competition.

Another management practice for weed control is the use of cover crops. The impact of rapeseed (*Brassica napus*), as the crop preceding potatoes, on the presence of weeds has been investigated. Rapeseed contains a compound called glucosinolate that has been found to have negative effects on weed seed germination. In a two–year study comparing rapeseed and Sudan grass covers, rapeseed produced more biomass and had a greater reduction in midseason and final weed density in the following potato crop than Sudan grass. Potatoes following rapeseed yielded higher than comparative plots following Sudan grass due to fewer weeds, while either cover did not affect the specific gravity of tubers.

A cultural method that may have an impact on weed control is row spacing. Row spacing exerts an effect through bringing forward the date of canopy closure and depriving the weeds in the bottom story of light; narrow rows could be expected to close before wider row spacing. A related factor is within-row seed piece spacing. When spacing's of 15, 25 and 35cm were investigated a small numerical decrease in weed biomass was recorded with decreasing within-row spacing, likely because of more rapid stem elongation and a greater impact on canopy closure.

Growers that have access to compost may use it to improve soil health and increase tuber yields, but compost may also increase weed competition by increasing early-season water availability and weed growth. The negative effect of additional weed competition will be overcome by enhancement of tuber yield due to the additional potassium provided by the compost

Do weeds have any useful roles?

We are conditioned to see weeds as a totally negative entity and something that must be removed as quickly as possible. However let us ask – have weeds any useful role in agriculture? Under controlled circumstances, a number of beneficial weeds can make a positive contribution.

Weeds play a crucial role in mechanically anchoring the topsoil and preventing 'blow away' by wind and erosion by water. Weeds have the capacity to germinate rapidly and colonise bare ground. They take up nutrients like residual nitrogen left after the previous crop is harvested. These nutrients might otherwise be lost thorough leaching to lower soil layers. Before planting the next crop, the weeds can be cut and dug into the soil. This procedure can contribute from 5 to 15 tonne of green manure per hectare.

Some weeds produce vigorous taproots. These can penetrate from 1 to 5m deep in the soil. They can break thorough the compaction layer, which is created by successive tillage operations and they can also seek out nutrients that have been sequestered to lower layers. These nutrients will now be returned to the above ground parts, which can be grazed or cut down and converted to mulch.

It is not difficult to imagine other useful roles for weeds, such as providing pollen and nectar for bees and perhaps even for human consumption.

Finally they must be removed before the next crop is planted and that will provide employment opportunity and paid work for farmers who require off-farm employment to supplement their income.

Weed control methods

Weeds in potato crops are controlled by two main methods, mechanical and chemical.

Mechanical weed control.

Mechanical weed removal generally involves hoeing or tilling the furrow between the drills with tilling implement fitted with tines. Traction is provided by machine or by animals. While this will effectively remove weeds from the area between the drills, the weeds between the plants will be undisturbed and these must be removed by hand hoeing.

Successful weed removal can be achieved by matching the cultivation implement to the weed stage. It is useful also to alter the cultural practices so as to best deal with different weed life cycles.

Figure 3.

A potato crop showing near perfect weed control (Photo © Author)

It is recognised that potatoes are shallow rooting and therefore extreme care must be taken to avoid damage to roots, feeding near the surface, by deep hand hoeing.

Notwithstanding the expenditure of time and labour to remove weeds and maintain a potato crop free from weeds, an excellent result can be achieved using manual operations (Fig. 3).

Note: *Use approval certification and product availability of herbicides are unique to individual countries. The data contained in the following sections is for information only and does not constitute promotion or endorsement. No advice on scheduling or application of herbicides will be provided here*

Chemical weed control

Weed control in potatoes can be effectively achieved by using herbicides. At present there is a wide range of herbicides available for weed control in potatoes. Herbicide selection will be dictated by three guidelines:

- The spectrum of weeds present or anticipated in the crop,
- The potato variety and
- Crop growth stage, and emergence.

Potatoes produced in temperate zones are normally grown in high-input systems. With access to a range of herbicides, it is not difficult to achieve a high degree of weed control, even 100% weed free. However two constraints persist: one is the requirement for adequate supplies of moisture to allow the soil-applied herbicides become washed down in contact with the germinating seed, the second constraint is, the presence of resistant weeds.

Herbicide performance depends upon weather, irrigation, soil properties, proper selection for weed species requiring control, and accurate herbicide application and timing. It is essential that prior to applying herbicide to a crop the first step must be to read the herbicide label and other information concerning the proper application and timing of each herbicide. Exceeding the recommended application rate or applying the herbicide at the incorrect growth stage, can have disastrous consequences, resulting in yield reduction or even crop loss

Contact Herbicides

These include compounds with the trade names "Basta", "Retro", and "Spotlight", which are used to kill early emerging weed seedlings. They are applied after the seedling weeds have emerged but prior to the emergence of the potato shoots. These herbicides have no residual effect, and are often applied in combination with a residual herbicide to give season long control.

Table 1. Contact herbicides for use in potato crops

Trade Name*	Chemical Name/ Active Ingredient**	Mode of Action
Basta	Phosphinic acid; Glufosinate-ammonium	Inhibitor of glutamine synthetase
Retro	Diquat; Bipyridylium	Inhibition of NADP+ reduction
Spotlight	Triazolinone; Carfentrazone-ethyl	protoporphyrinogen oxidase

* Trade names are the property of agrochemical companies and may vary in different countries and markets. **Chemical names are unchanging.

Pre Emerge Herbicides

These are generally soil acting and require rainfall soon after application to provide the best effect. "Linuron", "Sencorex" and "Defy" are typical examples of these groups. They persist in the soil for 6-8 weeks after application, and create a chemical barrier to any subsequent weed growth. Any form of soil disturbance after application will break this barrier and allow weeds to germinate.

Note: *Be sure to read the product label very carefully, as the rate of herbicide application will vary, depending on soil type. Always check varietal restrictions when using metribuzin (Sencorex), some potato varieties are extremely sensitive.*

Table 2. Residual herbicides for use in potato

Trade Name*	Chemical Name/ Active Ingredient**	Mode of Action
Linuron	Phenylurea; 3-(3,4-dichlorophenyl) -1-methoxy-1-methylurea	Inhibits photosynthetic electron transport (PS II)
Sencorex	Metribuzin; Aminotriazinone	Inhibits photosynthesis by disrupting photosystem II.
Defy	Prosulfocarb; S-Benzyl dipropylthiocarbamate;	Inhibitor of lipid synthesis - not ACCase inhibition

Herbicides are defined by their mode of action. The term 'mode of action' refers to the biochemical changes occurring in the plant between absorption and plant death. The mode of action of the herbicide will determine how and when the herbicide is applied. A herbicide will only be effective if:

- There is adequate contact with the plant, if,
- It can be absorbed into the plant and avoid deactivation, if,
- It is translocated within the plant to the site of action and if,
- Toxic levels accumulate at the site of action.

The mode of action of the Phenylurea and triazinone herbicides classifies them as photosynthesis inhibitors. Photosynthesis inhibitors result in the production of free radicals, which disrupt cell membranes. Because these compounds move upwardly in the plant's xylem, symptoms appear in the leaves. These compounds do not prevent emergence but become effective when the weed seedlings emerge, are exposed to sunlight, form leaves and begin photosynthesis.

Note *Some potato cultivars are sensitive to these compounds, so caution is advised!*

Initial symptoms are a yellowing (chlorosis) of leaf margins and tips especially of older potato leaves (Fig 4). Yellowing first occurs between the veins and moves inward to the mid-vein. As injury progresses, leaves turn brown (necrotic) and die. Younger leaves are more affected as they enlarge. Plant death is not common but loss of yield and quality is.

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Figure 4.
Potato haulm, displaying symptoms of photosynthesis inhibition induced by herbicides from the metribuzin/linuron group. (Photo © Author)

Cool weather following the application of these compounds creates conditions that favor the enhancement of herbicide injury in crops. Cool weather slows the metabolism of herbicides in the crop, which allows the herbicides to block pathways and induce injury not normally observed in potatoes. Coupled with the inherent sensitivity of some varieties, severe injury can occur. Herbicide injury symptoms can resemble nutrient deficiency symptoms (Fig. 4), but the two should not be confused. Symptoms can be very visible on the lower, early emerging leaves, but absent on new upper leaves (Fig. 4)

Potato growing and weed reduction

Cereals are sown by broadcasting the seed and covering it, or sown in narrow rows, using a seeding machine. Whichever method is used, it is not possible to effectively remove weeds, allowing perennial weeds to spread and annual weed to grow, set seed and shed the seed, before cereal crops ripen. By contrast potatoes are planted in rows so this affords the opportunity to remove weeds before they can set seed. This reduces the weed seed load in the soil and means that fewer weeds will emerge in the subsequent crop. The potato can only poorly compete with perennial grasses that propagate from stolons; these grasses can become established and spread rapidly through the potato crop. For this reason the potato is often referred to as a 'cleaning crop'. Mechanical or hand removal of weeds prevents seed set, thereby reducing the weed load in the soil and consequently the number of weed germinating in the subsequent crop.

Summary

- The period from planting to emergence normally extends from 14 to 28 days.
- Several factors, which can be modified by the grower, such as seed storage, handling during seed assembly, site tilling, planting and post planting cultivations can modify the period between planting and emergence.
- Weeds emerging before the potato plants can become a serious competitive threat.
- Weeds can have a detrimental impact on tuber yield when compared to potatoes grown in weed-free conditions.
- Manually removing weeds is labour intensive. Judicious choice of herbicide, then applying it at the correct rate and time, can reduce the amount of energy expended in controlling weeds.

Sources accessed in the preparation of this section.

Dittmar, P.J., Byrd, S. Zotarelli, L., Rowland, D. and Boyd, N.S. (2015). Weed management in potato. Univ. Florida, IFAS Extension. http://edis.ifas.ufl.edu

Masarirambi, M.T., F.C. Mandisodza, A.B. Mashingaidze and E. Bhebhe, 2012. Influence of plant population and seed tuber size on growth and yield components of potato (Solanum tuberosum). *Int. J. Agric. Biol.,* **14**: 545–549.

Monteiro, A.I; Henriques, I.II; Moreira, I.II (2011). Critical period for weed control in potatoes in the Huambo Province (Angola). *Planta daninha.* **29**. 351-362.

University of Minnesota, Extension Service. Herbicide mode of action and injury symptoms. http://www.cof.orst.edu/cof

Wiersema, S.G., (1989). Comparative performance of three small seed tuber sizes and standard size seed tubers planted at similar stem densities. *Potato Res.,* **32**: 81-89.

Wurr, D.C.E., (1974). Some aspects of seed size and spacing on the yield and grading of two main crop potato varieties: II Bulking rate. *J. Agric. Sci* (Cambridge), 82: 47–52.

Section 8.

Crop Establishment

Introduction

This stage in the crop growth cycle is characterized by rapid shoot growth; during which the canopy may double in height every week for the first three weeks. In the early phase of crop establishment, the seed tuber continues to supply metabolites as the foliage develops and grows, while in the meantime, photosynthesis increases until eventually the leaves become the sole source of food. The supply of water and nutrients required to sustain such growth can only be met by a vigorously growing root system capable of exploring the soil volume in search of macro and micronutrients.

Root Growth

Potato plants may be raised from true seed or from tubers. Plants grown from seed produce a tap-root with lateral branches. Plants, grown from seed tubers, form adventitious roots at the base of each sprout and then later a further group of adventitious roots from above the nodes on the underground parts of the stem.

Potatoes grown from seed tubers produce a fibrous root system. These roots rarely extend much beyond 60cm long, with instances where 85% of the roots were concentrated in the upper 30 cm of the soil profile. Potatoes are therefore regarded as shallow rooted, compared to cereals for example, which can root to at least 125cm depth. As a result, potatoes are often unable to exploit nutrients and soil moisture at depth within a soil profile. Consequently, water and nutrient use efficiencies are low. A well-established root system is important for subsequent growth and can allow for quick regrowth after early season defoliation from frost, hail, or insect damage.

Factors affecting root growth

Roots grow not only from the base of the stem but also on stolons and occasionally on tubers. Root primordia are often visible on the base of sprouts as the cycle of physiological ageing progresses (Fig. 1). Root growth can be considered as the result of two developmental processes, occurring simultaneously – the number of roots is increasing and the length of each root is also increasing. Potato total root lengths of 3.4 to 7.1 km m^{-3} of soil have been recorded. Root length is enhanced by the formation of branches (Fig. 1b). Whenever the roots enter an enriched layer of soil, they branch much more freely. Potassium has a very positive effect on root branching and density.

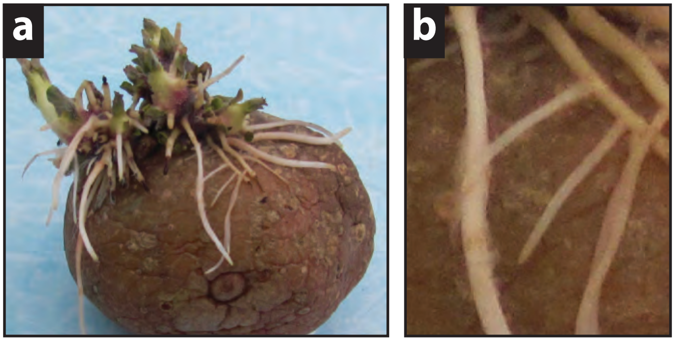

Figure 1.
Root primordia and rootlets at the base of sprouts (a).
Branch formation on roots (b). (Photos © Author)

Root growth patterns are complex. Root growth is restricted in areas where the soil is compacted but roots proliferate in areas where there is increased nutrient availability. Agricultural management practices may have a greater impact on root growth than the influence of soil temperature, mechanical resistance, macro pore continuity and available soil water, through the effects on rooting depth and root distribution with depth. Rooting depth varies with season, soil texture, and tillage, and increased rooting depth is associated with increased tillage and decreased soil moisture in surface soil layers. Therefore when considering root related growth impairments, it is often difficult to distinguish between the roles of soil mechanics and soil nutrients.

Measuring root length density can compare these variations in root growth. Root length density describes the length of roots per volume of soil. It is an important parameter in evaluating consequences of root pattern on crop water and nutrient uptake. Root length density varies with variety, stage of development, depth of the root layer, availability of soil water and nutrients, soil temperature, structure and strength. Root length density is negatively impacted by aluminum and manganese toxicity.

Potato variety and root growth
Determinancy is a measure of the crop's duration of canopy growth after it has formed the first flower. Varieties show a wide range in this character from complete indeterminancy (continues to produce leaves and flowers) to complete determinancy (canopy integrity relies on the survival of the leaves below the first flower). The determinacy of the variety will affect rooting depths. Indeterminate varieties will

have deeper roots than determinate varieties. There is some evidence also which indicates that late-maturing varieties (which are often indeterminate) root deeper than early ones.

Stage of development and potato root growth

Potatoes have a more superficial root system than many crops such as corn, wheat and most legumes. In their early growth, (when the tops are 30cm tall) roots are almost entirely confined to 20cm of surface soil (Fig. 2). After extending horizontally to a distance of 30 to 60cm or more, the roots turn more or less abruptly downward and penetrate the second and third 20cm layers of soil. Roots may also occur in the fourth 20cm layer. Branching is very profuse throughout the root extent, and at maturity, laterals occur to the root tips. Usually the branches are relatively short but so numerous and well rebranched that the absorbing system is very efficient. Both depth of penetration and lateral spread, as well as abundance and length of branches, are greatly modified by differences in the water content and fertility of the soil.

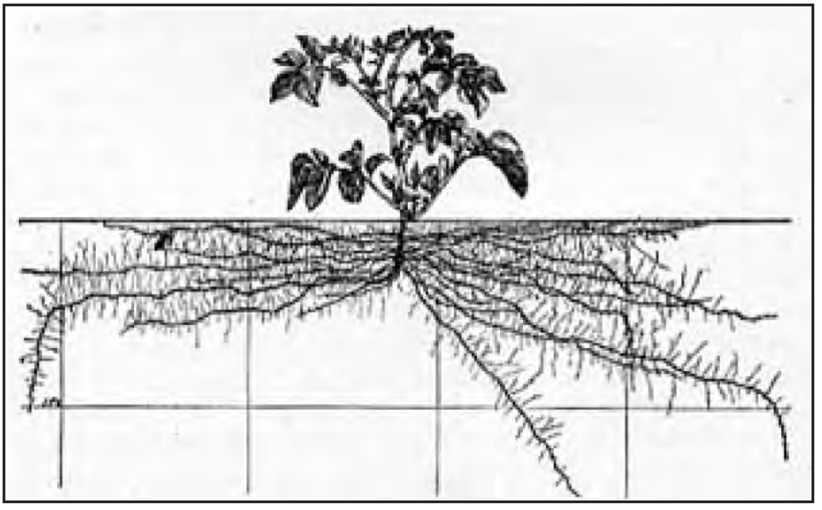

Figure 2.

Illustration of potato root proliferation. (Ref. Weaver, 1926)

When growth of the potato crop is complete the form of the root system will be almost identical with that found earlier. Practically the only difference is in its extent. Some roots will be still distinctly shallow, running their entire course in the surface 5 to 8cm of soil. The paucity of roots penetrating vertically downward beneath the plant is in striking contrast to the habit of corn and the smaller cereals. All the roots, whether shallow or deep, freely branch throughout their course, even to their tips.

Depth of the root layer

Potato roots are not distributed evenly throughout the soil layers due to the inherent nature of rooting habits and the heterogeneity of the soil profile. Surface soil layers have greater root length densities than subsurface layers, and different soil profiles have different amounts of roots. Therefore in addition to genetic influences, the soil environment and physiological condition of plants also affects root growth. Roots exploit the opportunity to take advantage of favourable features within the soil profile where physical, chemical, and biological factors encourage growth and survival.

Water availability and root growth

Root growth is promoted in moist soils and constrained in dry soil. Root growth is also constrained under water logged conditions when excessive irrigation is provided or when the soil is brought up to field capacity by irrigation and this is followed by heavy rainfall. This problem is sometimes compounded by soil compaction. Water logging results in anoxia and the accumulation of toxic substances around the roots. Prolonged wet conditions around the roots reduce plant respiration and increase root exudation to offset the adverse conditions. The root hairs (Fig. 2a) are a primary uptake site for mineral nutrients and are adversely affected by water logging.

Soil moisture deficits must also be avoided, since this has been shown to inhibit canopy and root growth and reduce tuber yield. But the potato response to drought is complex, with variation in the response between the plant parts. Moisture stress reduces total dry matter production and also reduces the proportion of dry matter partitioned into tubers, while increasing the proportion of dry matter partitioned to shoots and roots. Furthermore, drought also increased the root: shoot ratio. This indicates that root growth was maintained at the expense of shoot growth.

Nutrient availability and root growth

The root hairs are filament like projections of the epidermal (outer layer) cells. These root hairs, in conjunction with the cells of the filamentous root fibers, are responsible for the vast majority of water and nutrient uptake.

Figure 2a.
A potato root, showing root hairs.

The root and particularly the root hair (Fig. 2a) is the most important organ for the uptake of mineral nutrients. There is some evidence that when roots are growing in an environment, copiously suppliied with water and nutrients, the roots produce additional root hairs.

Plants take up nutrients from the soil using a mechanism known as cation exchange. In this process, hydrogen (H^+) ions are pumped into the soil through proton pumps located in the root hairs.

Cations attached to negatively charged soil particles are displaced by these hydrogen ions so that the cations are available for uptake by the root.

Soil Temperature and root growth

There is a consensus in the research literature that while root growth occurs when soil temperatures are between 10 to 35˚C, root growth and development is optimal at soil temperature values in the range 15 and 20˚C. Raising night temperatures over the range 0 to 20^{0}C, increases root length. Higher temperatures may inhibit root growth and activity. When potatoes are grown in the sub-tropics, soil temperatures can exceed the latter values. Root growth is often limited either by low or high temperatures. Studies investigating the effect of supraoptimal temperatures (30^{0}C) show that these high temperatures limit the allocation of assimilates to the roots. This reduces activity, such as the export of nitrate to the shoots. In potato, the root response to supraoptimal temperature is characterized by inhibition of cell division in the apical meristem and reduced geotropic response. The effect of increasing soil temperatures over the range 10 to 35^{0}C is illustrated diagrammatically below (Fig. 3)

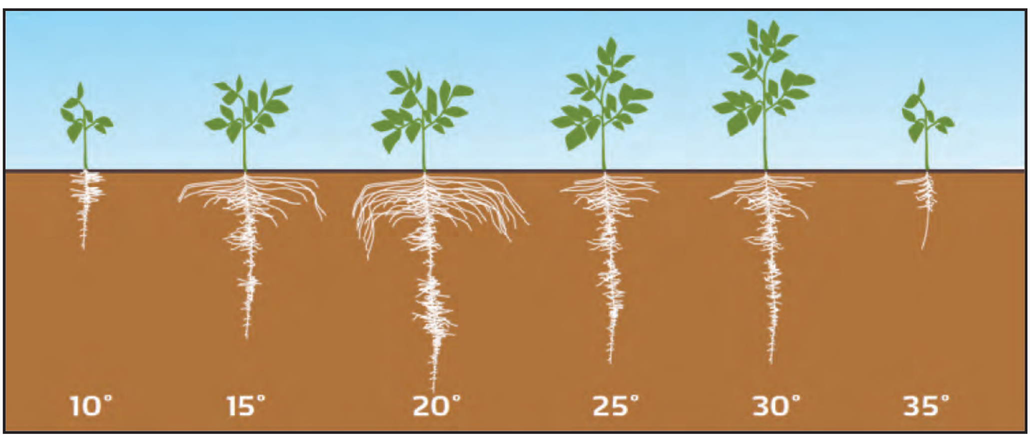

Figure 3.
Diagrammatic representation of the effect of increasing temperature on potato root growth. (Ref. Sattlemacher et.al. 1990c)

During the period, emergence to 30 days after emergence, the roots were less sensitive to temperature than top growth. But in the growth stage, 30 days after emergence to maturity. soil temperature affected root concentration in the deeper soil zone but had no effect on root distribution in a lateral direction.

Effect of soil structure and strength on root development

The physical properties of soil have significant effects on root distributions, which has been reported for many crops. Compacted soil offfers mechanical resistance and provides unfavourable conditions for root growth. This results because in addition to high resistance to penetration, the size of the pore system is reduced. There is also reduced water drainage and gas exchange, resulting in decreased O_2 transport to the root surfaces. Water logging, which induces anoxia, is a major cause of root stress in potato plants

Soil structure defines the architecture of the soil and describes the combination or arrangement of primary soil particles, sand, silt and clay into aggregates. Soil structure describes the manner in which these soil particles are aggregated. The structure affects water and air movement through soil, greatly influencing soil's ability to sustain life and perform other vital soil functions.

Soil structure exerts a major influence on plant growth. While roots grow most rapidly in soils with a good crumb structure, their capacity to take up water and nutrients may be limited by incomplete contact with the solid and liquid phases of the soil. Hard soil offers more intimate contact, but conversely the growth of the roots is so strongly inhibited that this will impair their foraging ability, resulting in the plant being deprived of water or nutrients. However, many soils, including hard soils, contain pores that offer niches to allow the roots to grow in. Soil pores exist between and within aggregates and are occupied by water and air. Macropores are large soil pores, usually between aggregates, that are generally greater than 0.08 mm in diameter. Macropores drain freely by gravity and allow easy movement of water and air. They provide habitat for soil organisms and plant roots can grow into them. These pores are prone to closure by compaction

The nature of the soil structure affects the ability of roots to grow and to supply the leaves with water and nutrients. Adverse soil structures, which restrict root growth, induces them to activate phytohormones which act as chemical messengers that alter growth patterns in the shoot. This will occur even if they are currently able to provide adequate water and nutrients.

As discussed, the soil environment has an impact on root growth, but in addition the shoot growth can also influence root growth through its ability to partition the allocation of carbon to various plant parts.

While the potato plant will grow for between 90 to 120 days and root growth is central to crop success, the roots constantly undergo change. Whereas early field growth is characterised by root expansion to meet the needs of an expanding canopy, root decay has been shown to commence 50-60 days after emergence

NUTRIENT MOVEMENT AND ROOT UPTAKE

Root uptake

Nutrient uptake systems in roots describe the mechanisms by which water and nutrients are transported to the root surface, enter the root, cross the plasma membrane and pass into the tissue that will transpot the nutrients and water to all the plant parts.

Briefly described there are a range of mechanisms by which potato roots acquire nutrients –

- The root grows out and explores the soil and it encounters the nutrient (but the roots are only in contact with 1% of the soil) or
- When nutrients, dissolved in water, move towards the roots, the process is known as mass flow. This process will move mobile nutrients such as nitrogen and sulphur. The effectiveness relies on the concentration, the higher the concentration - the more nutrient that moves in the soil solution.
- Nutrients such as phosphorus and potassium move to the root by diffusion. They are absorbed strongly by soils and are only present in small quantities in the soil solution. When the root absorbs the nutrient, the concentration in the solution close to the root declines, a gradient is created, so the nutrient diffuses from a zone of high concentration to the depleted zone. Diffusion facilitates the movement of the significant amounts of P, K and Zn to the root uptake zone

Factors in the soil either impede or facilitate nutrient movement

- *Soil structure:* soil compaction is a huge impediment to nutrient movement throughout the soil profile, where changes in density will speed up or slow down movement.
- *Nutrient concentration:* It is obvious that when nutrients are plentiful they will move more freely in the soil solution.
- *Nutrient absorption:* The soil type has a major influence on the strength of the bonds that bind the nutrients to the soil and particularly the clay particles
- *Nutrient mobility:* The major factors governing nutrient mobility in the soil are the charges on both the soil particles and on the element. Strong negative charge on soil particles with attract cations.

Table 1. Nutrient mobility in the soil

Very mobile	Nitrogen Phosphorus	Potassium Magnesium
Moderately mobile	Copper Manganese Sulphur	Iron Molybdenum Zinc
Immobile	Calcium	Boron

Uptake mechanisms of water and nutrients by roots

- The major sites of water and nutrient uptake are root hairs, along with the rest of the root surface.
- Osmosis and capillary action describe the process by which water and nutrients move into the root.
- Plant nutrients are among the particles dissolved in soil water (known as solute). The movement of soil water from areas of low solute concentration to areas of high solute concentration is known as osmosis. Osmosis defines the diffusion of soil water.
- Capillary action results from water's adhesive and cohesive forces (adhesion: defined as attraction to solid surfaces; cohesion: defined as attraction to other water molecules)
- When water moves upwards into the plant from the surrounding soil, two competing forces are active - gravity and capillary action.
- Nutrient ions move from the soil into the plant root by the processes of diffusion and cation exchange.
- Diffusion describes the movement of ions down a gradient from high to low concentration.
- The cortex cells within the root have a charged surface; these charged surfaces attract nutrient cations and an exchange process occurs. When this cation exchange reaction occurs, a hydrogen ion is released from the plant root. These H^+ ions cause an immediate decrease in the pH of the soil surrounding the plant root
- Within the plant root there are spaces between neighbouring cells; so when water and nutrients enter the root, they can move through these spaces.
- Water and nutrients enter the cortical tissue of the root by mass flow and diffusion but now the uptake and transfer of nutrients through the stele into the xylem is an active process. Having reached the xylem, the nutrients and water can be moved to the plant parts where they are required.

Three mechanisms of uptake of mineral nutrients by roots are recognised:

Simple diffusion

Describes the flux of molecules from a zone of higher to lower concentration. No transport proteins are involved, so this is a passive process with no energy input. Molecules such as O_2, CO_2 and NH_3 can move in this manner.

Facilitated diffusion

Describes the rapid movement of solutes or ions down a concentration gradient, but then the transport across the phospholipid bilayer is mediated by proteins embedded in the bilayer which can move the larger, charged, hydrophilic, and polar molecules across. The process relies on conformational change in the embedded protein. Again, this is a passive process with no energy input

– Active transport

Describes the uptake of ions or molecules by cells against a concentration gradient. A concentration gradient is created when the external concentration of ions dissolved in the soil solution is higher than the concentration inside the cell. An energy source is required to provide power for the molecular 'pumps' that move the solutes through the membrane. The requirement is to pump the solute uphill against an electrochemical gradient. There are three potential energy sources that can drive this active process: coupled carriers, ATP-driven pumps or light-driven pumps.

There is a close inerrelationship between root growth and mineral nutrient supply. There are further relationships between root parameters and genotypical differences in mineral nutrient efficiency. The size of the absorbing surface as well as the ability to explore undepleted soil layers are important factors for mineral nutrient acquisition. This ability assumes a greater significance when potato crops are grown under conditions of low fertility.

MACRO NUTRIENT UPTAKE

Nitrogen uptake

Until the potato crop emerges and the mother tuber reserves are depleted, there is no demand for soil nitrogen. However, when vegetative growth accelerates, potatoes have a high requirement for nitrogen because they must quickly establish a large canopy. Nitrogen concentration in the leaves of young potato plants was recorded at 6%. Furthermore, that canopy must be maintained throughout the tuber initiation and tuber bulking phase and this extends the requirement for nitrogen. During tuber bulking the nitrogen demand of a crop may be 2.2 to 3.0 kg/ha/day. Potato roots take up most of their nitrogen from the soil in the forms of NO_3^-, although in acid environments, ammonium (NH_4^+) is more likely to be the major source of nitrogen uptake. Urea, ammonium and nitrate are the three main sources of nitrogen, used in agriculture. Nitrogen, in the nitrate form, is the most readily available for root uptake and some of the advantages are:

- Nitrate is not volatile therefore unlike ammonium there is no need to incorporate it immediately into the soil. This makes the nitrate form suitable for top dressing,
- Nitrate is mobile in the soil – and since it is available for direct uptake by the root, it has the highest efficiency.
- Nitrate facilitates the uptake of the cations, K, Ca and Mg, while ammonium competes for the uptake with these cations, which are required to ensure high specific gravity in the tubers.
- Nitrates can be directly absorbed by the plant root and do not require any further conversion, as is the case with urea and ammonium, before plant uptake.
- Nitrate applications do not result in acidification of the soil
- The conversion of nitrates to amino acids occurs in the leaf. This reaction is fuelled by

solar energy, making it an energy-efficient process. Ammonium must be converted into organic N compounds in the roots. This reaction utilises carbohydrates, which takes from the pool of assimilates that might be directed to the tuber.

Urea is widely used in potato growing. Before it is taken up by the potato root it must be hydrolysed by the enzyme urease into ammonia and CO_2.

This breakdown begins the moment urea is applied to damp soil and happens very quickly in high pH soils. As the urea particle dissolves, the pH in the area around it is raises and there is an increase in ammonia concentration. The next process is nitrification, where ammonia is converted to nitrate, therough a series of steps, by soil dwelling autotrophic, aerobic bacteria.

The reaction rate of this nitrification step depends on having soil conditions, which favour the activity of the nitrifying bacteria. The following condition facilitate the nitrification of NH_4^+ to NO_3^- – soil temperature > 20 °C, soil pH 5,5 - 7,5 and sufficiently available soil moisture and oxygen.

But a word of caution here! In waterlogged soils, resulting from excessive application of irrigation, the oxidation of NH_4^+ is restricted due to the lack of oxygen.

Genotypical differences in the nitrate efficiency of potato plants may be due to ***uptake efficency*** (total amount of nutrient take up per unit of element available in the soil) and/or ***utilisation efficiency*** (i.e dry matter production per gram of nitrogen taken up). There is considerable differences in utilisation efficiency or differences in nitrogen acquisition by the roots. About 85% of total nitrogen uptake occurs by 45-65 days after emergence; so restricting early root growth can have serious consequences.

The amount of nitrogen that is available throughout the season strongly influences the period of maximal light interception. Higher seasonal dry matter can be achieved the longer nitrogen is maintained in the photosynthesis system

When potatoes are grown under a regime of low nitrogen availability, nitrogen acquisition is now the most important factor, so the size of the root will become critical.

Availability of N in the soil is highly dependent on N mineralization (i.e. the conversion of organic-N to nitrate-N) and N leaching processes. Haulm branching and crop productivity are affected when there are significant variations in N-mineralisation during the growing season.

Phosphorus uptake

Since phosphate is transported almost exclusively via diffusion to the root surface the size of the root system should be condisered with regard to explaining genotypic differences in crop yield under conditions of limited P-supply. Phosphate is one of the key macronutrients required for plant growth and metabolism, due to the relatively high amounts required by crops. but its availability is a limiting factor for plant development on some 40% of the worlds arable soils. Even when P levels in the soil are adequate, the mineral may not be readily available for root uptake because the preferred form for assimilation - orthophosphate (Pi), is not easily accessible to most plants and microbes, due to its adsorption to soil particles and clay minerals plus its conversion to organically bound forms.

In soils, P may exist in many different forms. In practical terms, however, P in soils can be thought of existing in 3 "pools": solution P; active P and fixed P.

The **solution P** pool is very small and will usually contain only a fraction of a kilogram of P per hectare. The solution P will usually be in the orthophosphate form, but small amounts of organic P may exist as well.

The **active P** pool is P in the solid phase, which is relatively easily released to the soil solution. As plants take up phosphate, the concentration of phosphate in solution is decreased and some phosphate from the active P pool is released. Because the solution P pool is very small, the active P pool is the main source of available P for crops.

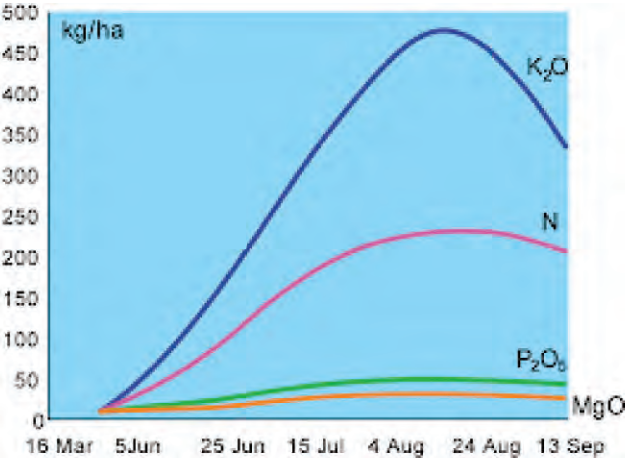

Figure 4.
Uptake patterns of the macronutrients by a potato crop yielding 55t/ha.
Note: *These details refer to a crop grown in a temperate zone in the Northern hemisphere*). (Diagram © PDA UK.)

The **fixed P** pool of phosphate will contain inorganic phosphate compounds that are very insoluble and organic compounds that are resistant to mineralization by microorganisms in the soil. Phosphate in this pool may remain in soils for years without being made available to plants

The major role of phosphorus in living entities is the transfer of energy. Adequte availability promotes early growth and hastens maturity. Since phosphate is tightly bound to inorganic or organic components of soils, root uptake is considered a metabolically active process because simple mass flow, caused by plant transpiration, can satisfy only 2 to 3% of the total phosphate demand of a crop plant. It is proposed that a proton symport mechanism drives both the uptake and internal transport processes within the plant. Such a phosphate/proton symport mechanism responsible for the energy-dependent transport of phosphate has been shown to function in potato root cells. Potato plants take up less phosphorus compared with uptake of nitrogen and potash (Fig. 4)

Potassium uptake

Successfully growing a potato crop requires large amounts of soil potassium, because this nutrient is crucial to metabolic functions such as the movement of sugars from the leaves to the tubers and the transformation of sugar into potato starch. Potato plants take up potash over the whole field growth stage, therefore a potassium deficiency will reduce the yield, size, and quality of the potato crop. This is achieved by reducing nitrogen uptake, with consequent reduction in haulm growth and light interception. A lack of adequate soil K is also associated with low specific gravity in potatoes. This response results from the reduction in the supply of sugar to the tubers especially during the critical phase of tuber bulking. In addition to the effects on yield, potassium deficiencies impair the crop's resistance to diseases and reduce its ability to tolerate stresses such as drought and frost.

The capacity of a potato genotype to grow and yield well in soils low in available K is defined as K efficiency. All major economically important plants have provided genotypes, which differ in their efficiency of K uptake and utilization. The K efficient genotypes are able to absorb higher amount of K from soil (uptake efficiency) and produce more dry matter per unit of K taken up (utilization efficiency). An example of uptake efficiency is illustrated where K-efficient genotypes of potato obtained 46% of K from the non-exchangeable pool, whereas the K-inefficient genotypes achieved only 17–25%.

A K-efficient genotype may have a larger surface area of contact between roots and soil and increased uptake at the root-soil interface. This maintains a larger diffusive gradient towards roots. However, genotypic K efficiency may not necessarily be linked to increased root growth. In contrast, a K-efficient potato genotype had half the root length of the K-inefficient cultivars, despite having similar relative shoot growth rate, but K-efficient genotypes had higher K influx than K-inefficient ones. Differential exudation of organic compounds to facilitate release of non-exchangeable K is one of the mechanisms of differential K uptake efficiency. Other mechanisms underlying K utilization efficiency are improved translocation of K into different organs and greater capacity to maintain cytosolic K^+ concentration within optimal ranges. The highest concentrations of K – over 8%, occur in the stems of potato plants during early growth.

Shoot Growth

After planting, the sprouts from the seed tuber grow toward the soil surface. Usually, more than one sprout will grow from a seed and generally more than one stem will appear from a sprout. The additional stems from a sprout are actually branches arising from nodes near the base of the mainstem. After emergence, when the stems are short and the leaves near the soil surface, the crop is often referred to as being at the rosette stage (Fig. 5).

Figure 5.
Potato shoot, early emergence phase, (Photo © Author).

This stage from emergence to canopy extension can be considered as the vegetative stage of the potato's growth cycle, when the visible portion of the plant emerges and develops. Furthermore, the plant looses reliance on the mother tuber as photosynthesis begins, providing nourishment for the growing plant

Canopy structure

The above ground portion of the potato plant is referred to as the haulm. The collective of individual plants constitute the canopy. The potato plant is a complex structure, comprising several stems, with branches, stolons, leaves, flowers, fruits and seeds.

The central element of the plant is the mainstem. The mainstems only originate directly from the seed tuber and can produce below ground branches. These branches may function as normal mainstems. The stems carry successive leaves and terminate in an inflorescence. In highly determinate cultivars, no further vegetative development occurs. In indeterminate cultivars, vegetative growth continues as a secondary stem is formed at a node subtending the primary inflorescence and terminates at a secondary inflorescence. This process may continue to tertiary level and beyond.

Canopy architecture

The mainstem is considered the unit of density in the potato crop. Potato plants grown from true seed have only a single stem but when grown from seed tubers and cut seed pieces several stems usually emerge (Fig. 6).

Factors affecting the number of mainstems emerging

Sprouts on seed tubers elongate and emerge to form mainstems. There is considerable interest in predicting the number of main stems that will emerge. The number of eyes per tuber, the number of sprouts per eye, the number of stems per sprout have been used to help predict the number of stems per plant; but with only modest success. The number of sprouts per seed tuber is influenced by the seed tuber size, physiological age, storage history, and variety.

Figure 6.
Potato plant showing six mainstems emerging from the mother tuber.
(Photo © Author).

Seed tubers, sized 1-5g might be expected to produce 2 sprouts whereas tubers 50-60g could produce 6 to 7 sprouts. It follows therefore that seed tuber size will influence the number of mainstems emerging.

Various attempts have been made to relate the number of sprouts per seed tuber at planting with the number of mainstems emerging in the field. However, not all sprouts emerge as stems and the number emerging decreases with increasing seed size. The ratio between the number present on the seed and the number emerged in the field varies with season and with year. The variation in the number of mainstems and thus the number of tubers produced per plant between seasons illustrates the importance of using the mainstem as the basic population unit. The number of stems per seed tuber influences the number of daughter tubers per unit area.

Seed tuber physiological age affects the relationship between the above ground haulm growth and the below ground growth. The physiological age of the seed tubers at planting has been shown to influence the number of mainstems emerging per tuber. When plants are grown from physiologically older tubers they tend to emerge faster, have more stems, grow smaller vines, have more tubers per plant, increase tuber-bulking rate, die earlier, and yield less. This strategy is useful when an early harvest is required to take advantage of higher crop prices in early season. Seed that is not aged excessively is preferred, particularly for high yield at late harvest. Physiological age is mainly influenced by storage temperature but the response varies between varieties.

Storage history will influence the number of main stems emerging – heat shock, cold shock, mechanical damage during handling will affect the number of sprouts, with consequent effect on the number of main stems.

Varieties vary in the number of mainstems emerging. Even when controlled for storage conditions, seed tuber size and planting methods there can be a 2-fold or even greater difference between the number of mainstems produced per tuber. This number has practical significance as the number of stems per seed tuber influences the rate of development of ground cover. Increasing the rate of development of ground cover in a restricted growing season will enhance yield formation.

Factors affecting branch formation

Mainstem branches have an crucial role in increasing canopy size. Three types of branches are recognised:

- Branches that form at nodes below-ground,
- Branches that form at nodes above-ground and
- Branches that form in the axil of the node subtending the inflorescence.

The level of determinacy will modify the orders of branches forming from the node below the inflorescence – indeterminate varieties will form several orders of branches each terminating in an inflorescence. In highly determinate varieties no axillary branches will form. An example of an axillary branch is illustrated in Fig, 7.

Figure 7.
Axillary branch formation (Photo © Author)

Branches originating below ground behave like mainstems and generally produce stolons and tubers. Branches' arising at over-ground nodes near the base of the stem form leaves and contribute assimilates to the plant and the developing tubers.

The formation of greater numbers of axillary branches at the lower plant densities, compensate for the reduction in mainstem density and intercept similar levels of photosynthetically active radiation to crops with higher planting densities.

Leaf formation

Potato leaves are arranged spirally on the stem. Leaves are compound; they consist of a midrib (rachis) and several leaflets. Each rachis may carry several pairs or leaves plus a terminal leaflet. The terminal leaflet is usually larger that the subtending leaflets. The regular arrangement of the leaf pairs may be interrupted by small secondary leaflets, interjected between the primary pairs. (Fig. 8).

Figure 8.
Leaflet arrangement on the compound potato leaf (Photo © Author).

The part of the rachis below the lowest pair of primary leaves is known as the petiole (Fig. 8).

Various factors influence the number of leaves on the mainstem. Initially the rate of formation is linear, with temperature being the major driver. Leaf/haulm growth occurs at temperatures of between 7 to 30˚C, but optimal growth is at around 20 to 25˚C. The rate is also influenced by leaf position on the stem – increasing with increasing leaf insertion number up to leaf 13 and gradually decreasing after that. Physiological ageing can markedly restrict the number of leaves per main stem and contribute to a reduction in LAI.

The number of leaves before the first inflorescence has a strong influence on the development of above-ground lateral branches. Leaf formation on lateral branches contributes significantly to canopy size. The nearer to the base of the stem that the branch emerges at, the greater the number of leaves likely to form. Basal lateral branches arising from nodes nearest the base of the mainstem can have a higher number of leaves than on the mainstem.

Canopy size

The amount of solar radiation intercepted by the potato crop is a function of the expansion and duration of the canopy. The canopy size influences the extent of photosynthesis, evaporation, transpiration and final dry matter yield. A measure of crop canopy size is required for quantification and comparison purposes. Leaf area index (LAI) is a key biophysical variable that will satisfy this role. Leaf area index is defined as area of leaf per unit of ground area. In a typical potato crop an LAI value of 3.0 corresponds to full ground cover.

Rate of attainment of ground cover is another method of comparing crop performance. Ground cover (GC) can be assessed visually by trained observers or measured using the simple grid illustrated below (Fig. 9).

Note: *The grid consists of 100 equal sections and the dimensions should be a multiple of the plant spacing. For example, when the row width is 75cm and the plants are spaced at 30cm, a frame with dimensions 75 by 90cm is appropriate. Ground cover is measured by counting the number of squares more than half-filled with green leaves.*

Figure 9.
Determining the degree of ground cover, using a grid.

Varying degrees of ground cover are illustrated in the following images

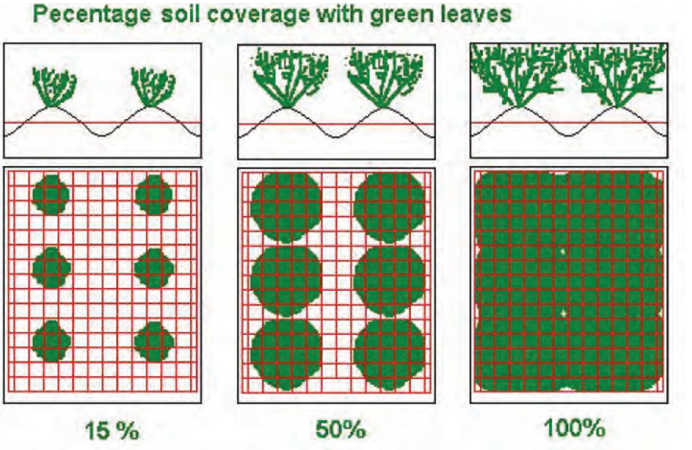

Figure 10a.
A graphical illustration of the relationship between plant height and ground cover (Diagram © Aardappelpagina.com. With permission)

Figure 10b.
Potato canopy at varying stages of ground cover. (Photos © Author)

Canopy duration
Canopy duration is the second major determinant of solar radiation interception. Factors affecting canopy duration will be explored in depth in **Section 10**.

Stolon growth
Stolons are normally formed at below ground nodes on the stems (Fig. 11). The node nearest the mother tuber is the site of formation of the first stolons. Additional stolons are then formed in acropetal succession along the stem basal nodes. The greatest number of stolons per node is generally found at the lowest node.

Figure 11.
Stolons, most with small tubers already formed (Photo © Author)

Factors affecting stolon growth

The first stolons are generally the longest and have more branches than stolons forming at nodes higher up the base of the stem, nearer to the soil surface

Stolon growth is regarded as an extension of the vegetative growth of the potato plant and therefore it could be expected that factors affecting the vegetative growth of other plant parts, might also influence stolon growth. The number of stem nodes where stolons are formed is influenced by variety and environmental conditions. Since stolons are stems, factors, which favour vigorous haulm growth, also favour stolon growth. The growth of stolons is strongly influenced by photoperiod and temperature, with the optimum temperature for stolon growth being similar to that for shoot growth.

Low levels of mineral nutrient restrict stolon initiation while increasing levels of nitrogen supply has been shown to increase the number of stolons formed. The form of nitrogen has been shown to influence stolon growth - plants supplied with NO_3-N produced more and thicker stolons than plants supplied with NH_4-N.

Other environmental factors influence stolon development. Drought enhanced stolon number but reduced the total length of stolons. Occasionally roots may grow on stolons (Fig 12). Drought also reduced the number of adventitious roots on stolons, whereas longer and more numerous stolons and stolon roots were associated with drought tolerance

Figure 12 .

Root development on a potato stolon. (Photo © Author)

Drill shape should be considered when planting different cultivars, since they produce stolons of differing lengths. A stolon not covered to an adequate depth may emerge from the side of the drill, form a vertical stem and continue normal growth.

Summary

- The crop establishment stage is characterized by rapid shoot growth; the canopy may double in height every week for the first three weeks.
- Potatoes grown from seed tubers produce a shallow root system, which has implications for nutrient uptake and water use efficiency.
- The central element of the potato plant is the mainstem. The mainstems only originate directly from the seed tuber and can produce below ground branches.
- Stolon growth is regarded as an extension of the vegetative growth of the potato plant. The growth of stolons is strongly influenced by photoperiod and temperature.

Sources accessed in the preparation of this section.

Cropwatch: Institute of Agriculture and Natural Resources. Univ. Nebraska- Lincoln. http://cropwatch.unl.edu/potato.

Epstein, E. (1966). Effect of Soil Temperature at Different Growth Stages on Growth and Development of Potato Plants 1. *Agron. J.* **58**:169-171

Passioura, J. (1991). Soil structure and plant growth. *Aust. J. Soil Sci.* **29**:

Rengel, Z and Damon, P.M. (2008). Crops and genotypes differ in efficiency of potassium uptake and use. *Physiologia Plantarum,* **133**: 624-636.

Sattelmacher, B., Klotz, F., and Marschner, H. (1990). Influence of the nitrogen level on root growth and morphology of two potato varieties differing in nitrogen acquisition. *Plant and Soil* **123**: 131-137.

Schachtman, D.P., Reid, D.P. and Ayling, S.M. (1998). Phosphorus Uptake by Plants: From Soil to Cell. *Plant Physiology* **116** : 447-453.

Smith, F.W. (2001). Sulphur and phosphorus transport systems in plants. *Plant Soil* **232**:109–118.

Wiersema, S. (1985). Physiological development of seed tubers. *Technical information Bulletin* 20. International Potato Centre Peru.

Section 9.

Tuberisation

Introduction

The major developmental event in the life cycle of the potato crop is the formation of tubers on underground stolons, either at the main stolon tip or the tip of a stolon branch.

The process of potato tuberisation represents the morphogenetic transition of an underground shoot to a tuber, which is specialised storage organ. During tuberisation, or the stolon-to-tuber transition, several changes occur in cell biological components. The changes can be classified as morphological, physiological and biochemical. They are under environmental, nutritional and endogenous regulation. Tuber formation is a complex biological process governed both by environmental factors and genes. It comprises several stages:

- Stolon formation and growth,
- Induction of tuberisation,
- Tuber initiation,
- Tuber enlargement.

The exact sequence of events leading to tuber formation is not clearly understood. Furthermore, there is an incomplete understanding of the activation of the intracellular mechanism that switches the developmental fate of stolon meristem cells, resulting in differentiation into a tuber. Tuber formation is affected by several abiotic and biotic factors, including photoperiod, temperature, levels of carbohydrates and nitrogen.

Morphological changes

Stolon formation and growth

In potato, tubers develop from underground stolons that originate from axillary buds located at basal nodes on the stem. Stolons are made up of elongated internodes and small scale-leaves. Notwithstanding that tubers are formed at the tips of the underground stolons, the stimulus that gives rise to this outcome is a consequence of processes occurring in other plant organs. The plant detects environmental cues and these combine with the phytohormone regulatory system. This triggers a sequence of processes involving biochemical and morphological changes, which culminate in the formation of tubers.

Growth regulators, including cytokinins stimulate the transition of axillary buds into stolons. These buds develop into stolons due to transverse cell divisions and cell elongation in their apical region. At the onset of tuber formation, the elongation of stolons stops.

Pre-sprouting of tubers prior to planting has been shown to increase the number of stolons formed.

Stolon branch formation
Branch formation on stolons is promoted by increasing soil temperatures. This serves to increase the number of potential tuber formation sites per main stolon and per plant. Having more than one tuber per stolon increases competition for assimilates and may significantly influence tuber number and tuber size distribution. This outcome would be particularly welcome for crops intended for seed potato production.

Induction of tuberisation
Tubers are formed on stolons. Stolons can be considered as underground branches, but when they grow through the side of the drill and become exposed to light, they will turn green, form leaves and develop as secondary branches.

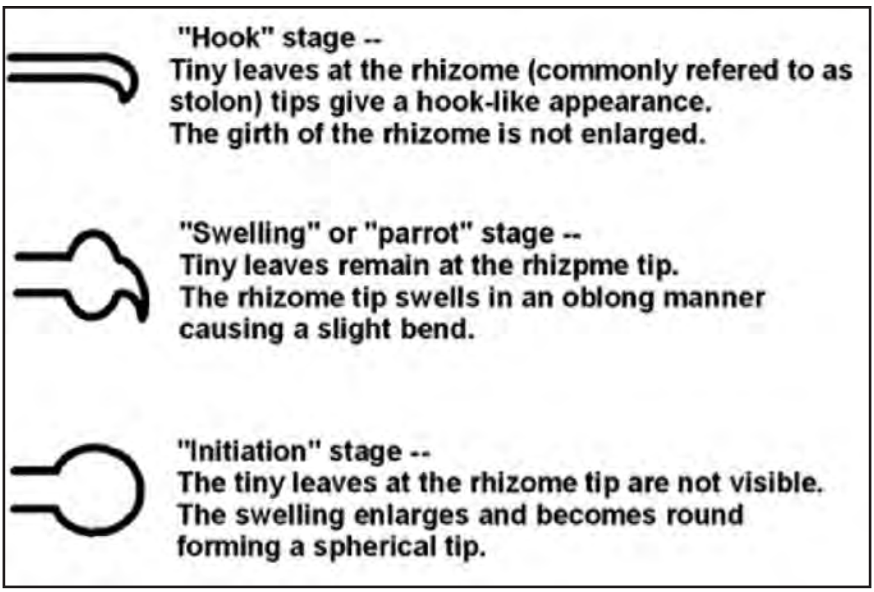

Figure 1.
Diagrammatic representation of the primary steps in tuber formation. (Ref. Pavlista, A.D (1995. With permission)

Figure 2.
Stages of tuber initiation from left – no visible swelling, sub apical swelling, "parrot stage", small tuber formed (Photo © Author)

A stolon is a diageotropic stem that is derived from lateral underground buds. These buds develop at the base of the main stem and grow horizontally underground. Usually they originate at the most basal stem nodes below the soil surface. They have elongated internodes, are usually hooked at the tip and bear small scale leaves. From 3 to 6 weeks after planting, the stolons are in the "hook" stage. This effect is produced by tiny leaves at the end of the stolon, forming a hook-like appearance (Fig. 1). After the hook stage, the stolon next goes into the "swelling" stage. This stage is characterised by an oblong swelling that forms behind the hook and accompanied by a slight "bowing" of the tip forming what resembles a "parrot" profile. Finally from the swelling stage, the stolons initiate tubers.

Tuber initiation
The start of tuberisation results in cessation of extension (or longitudinal) growth of the stolon, which is developing a tuber. The tissue that was formerly the stolon apical meristem converts into a central dormant bud, the eye. This eye, like other eyes, on the new tuber does not outgrow until the tuber attains dormancy release. When the stolon experiences conditions, which are favorable for tuber initiation, stolon elongation ceases. This is followed by enlargement of cells located in the pith and the cortex of the subapical region, i.e. the first internode of the stolon. These cells later divide longitudinally resulting in swelling of the stolon tip.

In order for tuber initiation to progress, the apical meristem must become dormant as soon as the longitudinal cell division in the stolon tip ceases. Transverse cell divisions now commence in the fourth to the eighth node. The buds in the eyes of the tuber become dormant in sequence, with the apical eye being the last one to become dormant.

The combination of these processes results in the swelling of the sub apical part of the stolon. When the swollen portion has attained a diameter of approximately 2 to 4 mm, longitudinal division stops and is replaced by randomly oriented divisions and cell enlargement. These occur primarily in the perimedullary zone and continue until the tuber reaches its final mass. Two processes are involved in tuber growth – cell division and cell enlargement. When the contribution of these processes to tuber growth was compared it was found that the rate of cell division was greater and made a greater contribution to the increase in tuber size than that contributed by cell expansion

Tuber formation commences even while stolon formation is progressing rapidly. This response suggests that the signal to cease longitudinal growth and commence radial growth is generated locally at the stolon tip.

Biochemical Changes

The role of endogenous hormones in tuber formation

All physiological processes in plants are governed and coordinated by signaling substances - phytohormones (acting in the role of chemical messengers), including auxins, gibberellins (GA), cytokinins (CK), abscisic acid (ABA), ethylene (ET), salicylic acid (SA), jasmonates (JA), brassinosteroids (BR), tuberomic acid (TA), tuberonic acid glucoside (TAG) and strigolactones. Tuber formation in potatoes is recognised as a complex process involving a number of interacting biological systems. Plant hormones have been identified as playing prominent roles in controlling different aspects of potato tuberisation. The molecular components of signal perception and transduction within the individual hormonal pathways have been elucidated using genetic and physiological studies.

Many phytohormones have been considered as candidates to influence tuber initiation. Significant effort has focused on the Gibberellic Acids (GAs) and while in excess 120 GAs have been isolated and identified in plants, only GA_1 and GA_4 are biologically active. When potatoes are exposed to short-day photoperiod and cool temperature, a transmissible biochemical signal is activated. This signal initiates the process of cell division and expansion and additionally, a change in the orientation of cell growth takes place in the sub apical region of the stolon tip. The perception of the appropriate environmental cues that instigate this change occurs in the potato leaves and the signal transduction pathway is transmitted by phytochrome and gibberellins (GA) to the subapical region of the underground stolons.

When chemicals suppressed the growth of axillary buds, or they were removed manually, tuberisation was promoted. It was concluded therefore that gibberellins were synthesised in the buds. It was further observed that high temperature stimulated the synthesis of gibberellins and export of gibberellins to the stolons, where they inhibited tuberisation.

GA is recognised as having an active role in shoot and stolon elongation. Meantime in order for a new tuber to develop changes are required in the meristem and particularly a change in direction in the plane of cell division. When there are high levels of GA at the stolon tip, this favours stolon elongation, but declining levels are required for tuber initiation. During stolon elongation endogenous GA levels are high and decrease when stolon tips commence swelling, under tuberisation inducing conditions, whereas GA levels remained high, under non-inducing conditions. The regulation of tuber formation is not achieved by gibberellins acting alone as the sole signal between the shoot and belowground parts, since stolon tips have been shown to synthesize their own gibberellins.

As stated, GA is antagonistic to tuber formation. But to facilitate the process there is up regulation of the genes involved in degrading GA during early stages of tuber development. This is followed by a rapid decrease of active GA content, that facilitate the morphological changes occurring at the stolon-tip. A gene that modifies GA concentrations has been isolated in the sub apex of the stolon at the onset of tuberisation. Modifying GA levels permits normal tuber development and growth. Tuber formation is mediated when DNA-binding proteins of potato enhance or repress the activity of specific target genes. This down regulation of GA biosynthesis genes in the stolon apex facilitates tuberisation

Because auxin is known to have an effect on many plant developmental processes, it is not surprising that it might be proposed as a candidate for involvement in tuber formation. Auxin plays a key role in developmental processes, such as lateral root initiation. The suggestion of a promoting role for auxin in tuber formation arises from the finding that auxin levels increase significantly in the stolon prior to tuberisation and then continue to remain relatively high during subsequent tuber growth.

To determine if auxin was involved in tuberisation, the auxin content of swelling stolons was quantified. Results showed that prior to tuber swelling, the auxin content in the stolon tips increased several fold. During *in vitro* tuberisation experiments there were higher levels of tuber formation from axillary buds of explants where the auxin source (stolon tip) had been excised. The response could be reversed by exogenous application of auxin. Combining the evidence from those two approaches it can be accepted that the initiation and induction of tubers in potato is a developmental process that appears to be regulated by interaction between GA and auxin (The phrase 'crosstalk' is often used in the literature to describe this response, which is a complex network of interactions and feedback circuits that determines the final outcome of the individual hormone actions.).

The regulatory role of GA in promoting stolon elongation and delaying tuber formation was outlined above. A mechanism to counteract this response is required. Abscisic acid (ABA) has demonstrated the capacity to fulfill the role of stimulating tuber formation by counteracting the effect of GA. Another factor involved in the tuberisation process is sucrose and sucrose achieves regulation of tuber formation by influencing GA levels. It is further postulated that although ABA is involved in the regulation of tuberisation, it is the balance between promoting hormones such as ABA and inhibiting hormones such as GA, which is the controlling factor.

A system for the production and directional transport of auxin in stolons has been demonstrated and it acts synergistically with a group of plant hormones, known as strigolactones. They function to control the outgrowth of axillary stolon buds, similar to the control of above-ground shoot branching. Its effectiveness was demonstrated by applying a synthetic strigolactone analogue on the basal part of the stolon, this resulted in fewer tubers.

Early research on tuberisation demonstrated that when excised stolons were supplied with a cytokinin (zeatinriboside), while growing in aseptic culture, they formed tubers. Excised stolons did not form tubers if they were grown under similar conditions, but not supplied with cytokinin. The short day exposure of stem segments, required to induce tuberisation, could be eliminated by treatment with cytokinin. Through activating cell division, cytokinins may be responsible for the creation of a strong nutrient sink, which attracts the inflow of sucrose and amino acids.

The mode of action of auxin and cytokinin are different: IAA largely increased the tuber size while kinetin application increased the number of tubers. It is proposed that this response occurs because cytokinins may have a greater impact on promoting stolon branching than on tuber induction

Jasmonic acid (JA) is a member of the jasmonate group of plant hormones. The enzymes involved in the pathway whereby it is biosynthesized from alpha-linolenic acid by the octadecanoid pathway, have been extensively characterized. The main functions of this hormone are growth related, including growth inhibition. Lipoxygenases (LOX) are nonheme iron-containing dioxygenases widely distributed in plants. LOX catalyzes the addition of molecular oxygen to polyunsaturated fatty acids that are precursors of jasmonic acid and related compounds. In plants, linolenic and linoleic acids are the most common substrates for LOX. The highest lipoxygenase activity in the potato plant was recorded in the stolons. The results indicate that lipoxygenase plays important roles in the tuberisation and tuber bulking of potatoes, possibly through the regulation of jasmonic acid biosynthesis. When JA was applied to *in vitro* explants, it enhanced tuberisation.

The following lines of evidence indicate a role for jasmonates in tuber development: many jasmonate compounds are present in potato stolons; their levels are modified as a stolon transitions into a tuber; exogenous jasmonates treatment has induced cell expansion and jasmonic acid is considered as antagonistic to GA. However, despite these responses, clear evidence is not readily available for the existence of jasmonic acid-biosynthetic enzymes in stolons or young tubers.

The technique of *in situ* hybridization showed that Lox1 class transcripts accumulated in the apical and sub apical regions of the newly formed tuber, specifically in the vascular tissue of the perimedullary region, the site of the most active cell growth during tuber enlargement. By contrast, the suppression of LOX activity correlated with a disruption of tuber formation.

The current model of tuberisation control involves complex interactions of genes, phytohormones, stimulation, inhibition and feedback loops, utilising the complex mechanism referred to earlier as 'crosstalk'. Many researchers continue to pursue the idea of a single compound controlling tuber initiation. Derivatives of JA, including a hydroxylated form known as tuberonic acid, has been nominated as the candidate to regulate tuber initiation.

Carbohydrate supply

A copious supply of carbohydrate to the stolon tip is a prerequisite for tuberisation. Carbohydrate, mainly in the form of sucrose, is produced in the leaves and transported via the phloem to the developing stolons.

An early metabolic indicator of tuber formation is an increase in the dry matter content of the stolon tip and a change in sugar metabolism. A decline in glucose and fructose contents accompanies an increase in starch content.

Starch accumulation is an important component in tuberisation and cytokinins promote the mobilisation of carbohydrates. When the activation of starch synthesizing enzymes is enhanced by cytokinins, there is an accompanying increase in starch deposition. This suggests an indirect role for cytokinins in tuber formation. Furthermore, by activating cell division, cytokinins create a strong sink for sucrose and amino acids.

This raises the question; does sucrose have a role in regulating tuberisation? Developmental studies and molecular–biological analysis present strong evidence for such a regulatory role.

When sucrose concentration in the nutrient medium of nodal cuttings was raised from 2 to 8%, stolon elongation was reduced considerably and the percentage of tuber forming stolons increased from zero to 100%. Researchers added glucose and fructose – the constituents of sucrose – to the medium but the yield was only 50% tuberisation. High levels of sucrose induced visible swelling of stolon tips. A further response of high sucrose levels was to also induce the synthesis of a specific set of proteins associated with tuber formation and involved in nitrogen storage, with patatin being the most prominent.

However the evidence for a controlling role for sucrose in tuber initiation is not so clear-cut. For sucrose to act as the major controlling factor in tuber development, it would be assumed that the stolon tips would contain high levels. This is not the case. High levels of sucrose were only recorded after visible swelling of tubers has commenced. But levels could be high in a limited number of specific cells – for example in parenchyma cells surrounding the phloem.

The interaction of sucrose with nitrogen and GA in the tuberisation step further complicates an explanation of the process. A final elucidation of the tuber formation process requires further research.

Physiological changes

Tuber enlargement

Changes in morphology and cell division occur in early phases of the stolon-tuber transition. When tubers have attained a diameter of approximately 0.8 cm, longitudinal divisions stops but randomly oriented division and cell enlargement occur in the perimedullary region and continue until tubers reached their final diameter. Tuber growth is predicated on cell division and cell expansion, but cell division plays a greater role in determining final tuber size. This phenomenon is clearly illustrated where 200-g tubers of the cultivar "Cobbler" had some 500-fold more cells than their 37-g counterparts, but only tenfold more cell volume.

Tuber initiation and enlargement are accompanied by massive changes in tuber physiology and metabolism.

Photoassimilates are generated in leaves during photosynthesis then subsequently delivered and distributed to a variety of heterotrophic tissues, which utilize the incoming carbon for growth, or store it for later use. Sucrose is the most plentiful form of transport sugar. Sucrose is first transferred to the apoplast, and then actively uploaded to the phloem followed by export from the leaf to the most demanding sink. The sucrose arriving to the developing tuber is converted to starch. When tubers are in their enlargement phase they assume the role of the largest sink of the plant and store significant amounts of carbohydrates (in the form of starch) and also significant amounts of protein. In addition, tubers lower their general metabolic activity and this facilitates their role as storage sinks.

A potato tuber is not a great source of protein since protein comprises only 2% of its fresh weight. The protein profile changes significantly during the transition from stolon to tuber. As a consequence of this change, the protein compliment is much simplified, with patatin becoming one of the most abundant. Patatin is located mainly in cell vacuoles.

In addition to changes in the protein composition, the most pronounced change observed during very early stages of tuber initiation and enlargement is the massive formation of starch, which in the mature tuber typically represents 15 to 25% of the fresh weight.

Once formed, tubers grow rapidly, reaching a maximum growth rate of up to 1.0 t/ha/day in temperate climates.

Figure 3.
Formation of tubers at nodes on the main stem (a).
Formation of tubers on sprouts (b). (Photos © Author)

Alternative forms of tuber initiation

Tubers normally form at the tips of stolons, but stolon formation is not essential for tuber formation as they can form in nodes of branches or on tuber sprouts under extreme conditions, often as a consequence of wounding or disease at the base of the stem interfering with translocation of assimilates (Fig. 3a). Tubers may also from on buds due to extreme levels of accumulation of physiological age (Fig. 3b)

Environmental Factors and Tuber Development

A long list of factors has been shown to affect tuber formation. The duration from planting to tuberisation depends on many factors, but planting date, variety, temperature, seed tuber quality, soil moisture content, nitrogen fertilisation and light have the greatest effect. Factors in the physical environment influence tuber initiation by modifying the synthesis, destruction, transport and activation of growth substances.

The effect of temperature

The majority of the currently grown commercial cultivars were developed in temperate areas and consequently they are adapted to produce their highest yields under moderate temperature regimes.

Stolon formation and extension is promoted by an increase in temperature over a wide range of temperatures. This will normally be provided by the seasonal increase in soil temperature as the growing season progresses. High air temperatures impede induction and initiation. Whereas stolon formation is not prevented by high soil temperature, elevated temperature inhibits tuber formation.

The colder the soil temperature, the more rapid the initiation of tubers and the greater the number of tubers formed. The optimum soil temperature for tuber initiation is 15 to 20˚C – especially during nighttime. Night temperatures, in particular have a strong influence on tuber initiation – high nighttime temperatures may induce high GA concentrations in the stolon tip, with consequent disruption to tuber growth. When nighttime temperatures reach 25-27˚C, there is a sharp reduction in the number and weight of developing tubers.

When grown at 15°C (below the optimum tuber initiation temperature of 20°C) tuberisation was delayed by one week. But when grown at 25°C tuberisation was delayed by three weeks. It is proposed that the slower tuberisation at 15°C probably results from slowed metabolism and growth. The delayed tuberisation at 25°C however is associated with accelerated metabolism and growth and is due to the induction of specific inhibitory effects (e.g. elevated GA) caused by the high temperature on the tuberisation process. Hence potatoes are considered a cool season crop. For success in tropical climates, cultivars must be developed that will not produce tuberisation inhibiting levels of GA, when exposed to high soil temperatures.

The response to high temperatures is not consistent; in some situations stolon development was delayed, but the final number was increased, since tuber initiation was delayed more than stolon initiation. This provided increased time and additional assimilates for extra stolon formation. There is considerable genetic variation in the ability to complete tuber formation at elevated temperatures. The response to elevated temperature varies between cultivars, with some cultivars extremely sensitive to high root and shoot temperatures, displaying a severe reduction in stolon number.

The timing of the temperature increase has significant implications for the tuberisation response. Warm temperatures during early growth, followed by cool temperatures, give better tuberisation than the reverse situation.

In addition, the high endogenous levels of JA, TA, and TAG were observed at low temperature suggesting that the increase in LOX, which is activated by low temperature, results in large amounts of endogenous JA, TA and TAG, which play a crucial role in potato tuber induction.

The effect of photoperiod.
Seasonal fluctuations in day length regulate important aspects of plant development such as the formation of tubers in potato. Day length is sensed by the leaves, which produce a mobile signal, transported either to the shoot apex or underground stems, to induce a tuberisation transition.

The potato tuber is an enlarged portion of the stolon. The transition from stolon to tuber is triggered by short days and is enhanced by exposure to short day lengths. The center of origin of the potato crop is regarded as the Andes of South America and here it evolved short-day-dependent tuber formation to provide a vegetative propagation strategy. Due to its origin close to the equator, the potato is essentially short-day dependent for tuberisation. When the crop was originally introduced to the northern latitudes it would not form tubers in the long-day conditions of spring and summer. The first task therefore for the original growers was to select lines, which formed tubers under the new long day conditions. The commercial cultivars of today are descended from those selections. However, various cultivars vary in the extent of their dependence on short day conditions to promote tuberisation. Many cultivars have no absolute requirement for short days. The currently available commercial cultivars will produce tubers under a wide range of day length conditions.

Under short-day conditions, the potato plant will have short stolons and shoots. Longer day lengths delay tuber initiation and favor the growth of the stolon and shoot. High temperatures also reduce tuber formation. Late varieties seem to be more sensitive to long day lengths or high temperature conditions.

Effect of light intensity.
Since tuber initiation is regarded as a photoperiodic response, it is likely therefore that it is also influenced by radiation intensity. Low light intensity during day light hours resulted in decreased induction to initiate tubers whether the experiments were conducted in the field or in a controlled environment.

Low irradiance, particularly when combined with high temperatures restricts tuberisation. Studies on the effect of irradiance on tuber number mainly rely on the use of artificial shading to modify irradiance. Care must be taken with the interpretation of such experiments to ensure that spectral effects are not compounding the shading response. The results of these shading experiments may be summarised as follows.

- The response to shading varied with cultivar.
- Shading delayed stolon initiation but stolon number was not affected when light levels were reduced by 50% early in the growing cycle.

- Shading prolonged the stolon elongation period and delayed tuberisation
- Finally, shading, either reduced tuber number, had no effect on final number of tubers, or increased final tuber number.

However, it is reported that shading levels, which reduced radiation by approximately 50% during the period of tuber initiation decreased tuber numbers by 20%. The shading treatment had a more pronounced effect on number of tubers growing to a size less than 50 mm compared with the number greater than 50 mm. Since the period of tuber initiation may be as short as 2 - 7 days, thus the occurrence of cloudy conditions over such a period can have a considerable impact on crop tuber numbers. Care must be taken when considering the effects of light intensity on tuber initiation so as to ensure that the effect is not confounded by unwittingly introducing variation in temperature. In a computer-based simulation of crop growth, the onset of tuber initiation was identified as the most temperature sensitive yield parameter.

While at field level, the grower cannot influence radiation, the shading experiments described above elucidate the relationship between light and tuber initiation. Further they provide a mechanism to explain seemingly anomalous responses in tuber number from similar husbandry treatments between production sites and growing seasons. As already mentioned, temperature, light intensity and nitrogen levels are all thought to exert influence through their effect on GA levels.

Effect of soil moisture

If potatoes experience a drought period during the phase between planting and stolon development this will reduce stolon numbers and then impact on tuber size distribution. Where large numbers of small tubers are required, such as in seed crops, it is essential to provide adequate moisture at stolon formation. While there is a widespread understanding that drought stress limits tuberisation, the precise molecular mechanism governing the response has not been elucidated. A possible explaination is that the drought stress response is controlled by differentially expressed genes and further that these genes achieve their effect through their involvement in phytohormone biosynthesis and also in the affiliated signal transduction pathways. Reverses in tuber growth due to interruptions in moisture supply can result in tuber malformation, growth cracks and secondary growth.

Nutritional factors

Calcium nutrition

Considerable research studies have elucidated the role of calcium in potato tuber formation. Calcium is one of the major essential nutrients and performs a central role in a number of fundamental cellular processes like cytoplasmic streaming, thigmotropism, gravitropism, cell division, cell differentiation, plant defense photomorphogenesis, and various stress responses.

While it has been shown that Ca^{2+} is required for tuberisation, supplementing the soil Ca with additional applications have also been shown to alter the tuberisation pattern. Adding Ca to the soil during tuberisation can reduce tuber number. This suggests that the tuberisation message may be modified by increased Ca levels in the soil. Since both calcium chloride and calcium nitrate additions could reduce tuber numbers, it is proposed that it is the Ca^{2+} and not the chloride (Cl^-) and nitrate (NO_3^-) anions that are inducing the response. The mechanism underlying the Ca^{2+} induced alteration of tuberisation is not known. One proposal is that a Ca/calmodulin pathway can modulate GA biosynthesis. When the soil Ca concentration is increased by adding additional forms of Ca, this may suppress the tuberisation signal by increasing the formation of GA.

Calcium in not mobile in the phloem, so this raises the question – how does the developing tuber acquire its' calcium? Some cultivars such as 'Russet Burbank' form tiny roots on the tubers and these can take up water and nutrients from the soil. Other cultivars produce roots on their stolons (**Section 8,** Fig. 12) and these can also take up soil borne nutrients, including Ca.

Nitrogen nutrition

It is a well-documented response that excess soil nitrogen delays tuber formation. This response is sometimes characterized as competition for assimilates between the production of new leaf material or the translocation of available assimilates to roots and stolons. When plants are grown under photoperiods that induce tuber initiation, a continuous N supply could offset the response and prevent tuberisation, probably through its effect on endogenous growth regulator levels. Nitrogen nutrition, photoperiod and temperature may control tuberisation by changing the ABA: GA ratio.

The mechanism, by which high or continuous N supply delays or inhibits tuber formation, is regarded as an indirect relationship. High N acts by enhancing production of the inhibiting hormone GA and depressing production the promoting hormone ABA. The resulting low ABA: GA ratio increases shoot growth and delays tuber production. This response will decrease tuber yields of early harvested potatoes but will increase LAI and yield in a season in which growth is prolonged. High levels of N supply after the start of tuber initiation again alters the ABA: GA ratio and may lead to the cessation of tuber growth and stolon formation.

The delay in tuberisation due to high N varies between cultivars. High available soil nitrogen at planting had minor effects on the time of tuber initiation for an indeterminate cultivar.

Summary

The tuberisation process:

- Involves the development and growth of the stolon
- Stolon elongation inhibition.
- Swelling of the stolon tip,
- Tuber formation is modulated by environmental and physiological factors.
- Tuberisation is reversible; the contents of the tuber may be resorbed under stress conditions before the tuber reaches a survivable size.
- The process of tuber set makes a greater contribution to final number of tubers than tuberisation.

Sources accessed in the preparation of this section.

Ewing, E.E, Struik, P.C. (1992). Tuber formation in potato: induction, initiation, and growth. *Horticultural Reviews* **14**: 89–198.

Hannapel, D.J., Chen, H., Rosin, F.M., Banerjee, A.K., Davie,P.J. (2004). Molecular controls of tuberisation. *American Journal of Potato Research.* **81**, 263-274

Krauss A, Marschner H. (1982). Influence of nitrogen nutrition, daylength, and temperature on contents of gibberellic and abscisic acid and on tuberization in potato plants. *Potato Res.*;**25**:13–21.

Menzel, C.M. (1980). Tuberization in Potato at High Temperatures: Promotion by Disbudding. *Annals of Botany*,

Pavlista, Alexander D., "EC95-1249 Potato Production Stages: Scheduling Key Practices" (1995). Historical Materials om University of Nebraska-Lincoln Extension. Paper 1584.

Pelacho, AM; Mingo-Castel, AM. (1991). Jasmonic acid induces tuberization of potato stolons cultured in vitro. *Plant Physiology,* **97**: 1253–55

Struik P.C., Vreugdenhil D., Van Eck H.J., Bachem C.W., Visser R.G.F. (1999). Physiological and genetic control of tuber formation. *Potato Res.*, **42:** 313-331.

Viola, R. (2001). Tuberization in Potato Involves a Switch from Apoplastic to Symplastic Phloem Unloading. *The Plant Cell February*, **13: 2,** 385-398.

Vreugdenhil D., Struik P.C. (1989). An integrated view of the hormonal regulation of tuber formation in potato (Solanum tuberosum L.). *Physiologia Plantarum,* **75**(4): 525-531.

Xu X, Vreugdenhil D, van Lammeren AAM. (1998). Cell division and cell enlargement during potato tuber formation. *Journal of Experimental Botany* **49**:573-582.

Section 10.

Canopy Growth and Tuber Bulking

Canopy growth

Introduction

A typical potato canopy is composed of mainstems, axillary branches and their compliment of compound leaves. The size and longevity or duration of the leaf canopy are major determinants of yield in potato crops. Critical determinants of potato canopy growth and development are appearance, expansion, and duration of individual leaves. Canopy growth and expansion can be defined in terms of extension growth of the mainstem, leaf appearance rate (LAR), leaf expansion rate (LER), basal branch and axillary branch formation. Canopy expansion and duration are affected by both environmental factors such as temperature; soil conditions such as nutrient and moisture content also agronomic factors such as stem density.

Growth of Canopy Components

Stem elongation rate, stem growth duration and final mainstem length are important characteristics of canopy growth. It may be assumed that these parameters would be influenced by growing site and by cultivar and would differ between determinate and indeterminate cultivar types. Environmental factors such as moisture stress has been shown to impact all three parameters. By reducing irrigation levels from 100% of requirement to 50%, stem elongation rate was reduced by 30%; stem growth duration was increased by 10% and final mainstem length reduced by 35%.

Maximum stem length is cultivar and site dependent, but soil nutrient availability has a greater effect than that exerted by competition for light, through altering stem density. Increasing the mainstem density enhances stem elongation rate. This can be achieved by reducing the inter plant or inter row distances.

Nitrogen partitioning during canopy expansion has been studied and the results show that a hierarchy of need within the crop dictates partitioning:

- Following tuber initiation, the tubers have priority access to available N to maintain their minimum N requirement of 0.8% by mass. Under limited N status in the soil, this allocation to the tubers, at the expense of the canopy, can induce premature senescence.
- The next priority is for structural N in the canopy – assumed to be 0.5% by mass.
- After this comes the priority for N for leaf expansion – at 2.0 g m^2.
- When excess N is available it enters a labile pool consisting of NO_3 stored in vacuoles in leaf cells – 0.4 g m^{-2}, and nitrogenous compounds stored in stems –up to 4% by mass.

Demands are filled by uptake from the soil if any N exists there and failing that, by remobilization from canopy layers at the base of the stem, to the current demander

Calculation of leaf appearance rate (LAR) is central to crop growth studies. The number of accumulated or emerged leaves on a mainstem is a defining measure of plant development and this number can be calculated by integrating LAR over time. The number of leaves is related to the timing of several developmental stages. For instance, when a certain number of leaves are emerged on the main stem, branching begins. Leaf number, also influences the leaf area that intercepts and absorbs solar radiation for canopy photosynthesis and which impacts dry matter production and crop yield. The rate of leaf appearance is generally linear during the first phase of plant growth.

A major environmental factor that drives leaf appearance in potato is temperature. Thermal time (TT), measured in units of degree-days (ºC day) expresses the time needed for the appearance of one leaf. A rate of leaf appearance has been reported at 0·53 leaves d^{-1} (one leaf per 28 °C d) and was negligibly affected by nitrogen supply. However, expressing leaf appearance in terms of TT may be subject to criticism because there are different ways to calculate TT, which can cause different results from the same data set. Furthermore, the assumption of a linear response of development to temperature is not completely realistic from a biological point of view. The rate of leaf appearance was linear over the temperature range (9–25°C) and above 25°C there was no further increase in the rate

Because leaf appearance is not related to the rate of elongation of main stems, the same number of leaves may be carried on stems, which vary considerably in height.

Leaf expansion rate is related to leaf number and nitrogen supply. Smaller leaves are found at the base of the stem; the area of individual leaves increases with leaf number until tuber initiation; reaches a maximum 12-14 and then the area declines with the higher i.e. the younger leaves. The mature leaf area was determined by the expansion rate of the leaves and that was independent of leaf number and nitrogen level.

Air temperature significantly influences potato leaf area expansion, with cooler temperatures providing the maximum individual leaf area values. There is a negative relationship between increasing temperature and growth duration, (defined as the time interval between leaf appearance and when 99% of final area was attained). Growth duration increased by about 4 days when plants were grown at a day/night temperature regime of 14/10 °C compared with growing at a day/night regime of 34/29 °C.

Differences in LAI may be due to differences in the number of leaves per plant or the size of leaves. The value is affected by seed tuber factors, such as seed tuber physiological age, photoperiod and temperature, which affect the number of leaves per main stem.

Many studies have reported a reduction in the number of leaves per main stem that emerge from seed having high levels of physiological age. The effect of photoperiod on leaf number per main stem is somewhat inconsistent, varying between experiments and cultivars. There is a general tendency to observe a greater number of leaves on stems subjected to long days compared with short days. The effect of three temperature regimes – 16, 22 and 27 ^{0}C on leaf number per mainstem on cv. 'Bintje' revealed values of 14, 20 and 32 leaves per main stem respectively.

The number of above ground stem leaves per main stems varies widely, but typically ranged from 14 to 18. Nitrogen supply did not affect the number of main stem leaves.

Basal branches contribute significantly to PAR interception and assimilate partitioning. Basal lateral branches, which are inserted in the main stems at positions near or below soil level, can produce similar or even greater numbers of leaves compared with its mainstem. Elevated growing temperatures increases the number of leaves on basal lateral branches. Basal branch formation is enhanced by physiological ageing of the seed tubers, by increasing soil nitrogen and in the presence of adequate amounts of soil moisture. Basal branch formation is impacted negatively by increasing mainstem density

Axillary branch formation is mainly associated with indeterminate cultivars and is promoted by physiological and environmental factors that promote vigorous growth. The mature area of leaves on apical lateral branches decline with increase in leaf number. Nitrogen promotes apical branching and hence the total number of leaves that appear on a plant. Nitrogen supply increases the proportion of total leaf area contributed by leaves on apical branches. The contribution by leaves on apical branches also increases with duration of growth. Leaves at an intermediate position on the stem had the greatest leaf area and the greatest leaf length. Doubling the mainstem density treatment decreased leaf area growth of potatoes when compared with single density treatment.

How Does Canopy activity affect tuber yield?

Recent developments in crop growth analysis have provided a basis whereby differences in tuber yield may be examined against a set of measurable criteria. Tuber yield is determined by:

(I) The amount of photosynthetically active radiation (PAR - light in the 400 to 700 nanometer wavelength range) intercepted by the canopy

(II) The efficiency with which this radiation is converted to dry matter and

(III) The proportion of accumulated dry matter partitioned to the canopy and the tubers.

Each of the foregoing steps can be influenced by the grower and an understanding of their contribution to tuber yield can help explain variation in yield observed between varieties, between growing seasons and between fields within a growing season.

(I) Maximising radiation interception

Radiation interception can be considered either in terms of ground cover, leaf area index (LAI) or leaf area duration (LAD). LAI describes the ratio of ground area to the area of leave's, which subtends it. The leaf area influences the fraction of light that passes through the canopy and is not intercepted. In the potato crop, peak leaf area is chiefly influenced by variety, fertiliser application and planting date. Ground cover is normally achieved at LAI 3.0, at which approximately 85% of the available radiation is intercepted. Using a grid provides a non-destructive measure of percentage ground cover (**Section 8**; Fig. 9). This value correlates well with the proportion of intercepted PAR as measured by solarimeter tubes or by destructively measuring LAI.

The grower can manipulate crop growth and development patterns to maximise PAR interception by addressing a range of strategies - and a few will be discussed here.

Factors affecting PAR interception

The obvious advantage of early planting will not be discussed further - except to caution against tilling wet soil and planting seed tubers before soil temperatures are adequate to facilitate sprout growth.

Tuber related factors

Physiologically ageing seed tubers for 200 day-degrees >4^0C has been shown to advance emergence by approximately 10 days. This is a useful strategy to combat the negative effect on tuber yield arising from a truncated growing season.

A factor which has a significant impact on PAR interception and over which the grower has complete control, is the choice of variety. Indeterminate, varieties intercepted as much as 98% of the light and maintained 95% interception for up to a month. By contrast, highly determinate cultivars often only achieve maximum interception values of 90%, and this level was maintained only for a week.

It has been demonstrated that under the short season growing conditions, cultivars, which produce canopies intermediate in size and degree of upright growth habit, appear to be most efficient in terms of maximising tuber bulking rates. Genotypes with this type of canopy structure develop rapidly and mature early, providing a high tuber yield. The ideotype of the potato cultivar which can deliver reduced leaf shading and improved leaf-angle distribution, should have leaves at the top that are more erect combined with more horizontal leaves toward the bottom of the plant. This would permit increased light penetration, and promote increased absorption of photosynthetically active radiation deep in the haulm.

Both biotic, pathogens and pests also abiotic factors nitrogen nutrition and moisture availability can result in reductions in the amount of PAR intercepted by the canopy.

Nitrogen nutrition.

Application of nitrogen has a profound influence on peak LAI and on leaf area duration and on PAR interception. Nitrogen has a direct role in the photosynthesis process since some 20 to 30% of total leaf nitrogen is utilised for the synthesis of Ribulose-1,5-bisphosphate carboxylase (RuBisCO) the most abundant protein in leaves, accounting for 50% of soluble leaf protein in potato plants

To the vexed question - how much nitrogen? - there is no single answer, as the requirements of each site must be addressed separately. However the guiding principle must be, only apply sufficient N to ensure a peak LAI which does not promote lodging – since lodging interferes with radiation interception and permits leaching which damages the environment; yet supply sufficient N to facilitate an appropriate leaf area duration throughout the growing season. Nitrogen affects dry matter production and growth by influencing the rate of leaf expansion, final leaf size and nitrogen content of leaves, but not the growth duration.

Nitrogen deficiency reduces leaf area (canopy expansion) and thus the amount of radiation intercepted. Only final leaf area and the mean expansion rate are regarded as significant functions of nitrogen availability, growth duration is not. The time to reach 95% of final size is highly variable and not related to N treatment. Leaf expansion rates, especially for higher order leaves in potato are also affected by carbon limitation.

Potato plants displaying yellow leaves is generally regarded as a symptom of lower nitrogen contents in the leaves. Low nitrogen levels may affect photosynthesis in addition to PAR interception, since there is a strong correlation between nitrogen concentration in leaves and their photosynthetic performance.

It is worth noting that increasing nitrogen application does not directly increase tuber size, but rather prolongs canopy duration and permits sustained radiation interception, which then results in increased tuber size. In order to maintain an optimum plant canopy, which will sustain tuber growth, soil nitrogen sources and split N fertilizer applications have a major role. While there is an extensive literature on the effects of nitrogen on tuber yield there is little quantitative information available on how N affects factors such as expansion, final size and duration of different organs in the potato plant.

In the research literature there are reports of contrasting responses to nitrogen application and canopy component development. It was found that leaves of field crops provided with ample N had shorter life spans than comparable ones from N-deficient crops. This may result from mutual shading of lower leaves as leaves higher up the phylum increase in size. In contrast a positive effect of high rates of N supply on the leaf longevity in the order of three weeks was observed for potato plants growing in pots. It is has been demonstrated that redistribution of N in the canopy of N-replete plants allowed the growth of lateral branches towards the end of the season, thereby maintaining photosynthetically active leaves for longer than N-deficient plants

Availability of N in the soil is boosted by N mineralization and depleted by N leaching to the lower areas in the soil profile. Nitrogen availability, haulm branching and crop productivity are considerably influenced by conditions during the growing season.

Furthermore, N uptake is influenced by plant density, which affects tuber yield quantity and quality. The latter is particularly important in relation to tuber size distribution. This strategy of close spacing/high density underpins potato seed tuber production where the emphasis is on producing a large number of small size tubers.

High N levels enhance the number of leaves on the mainstem and promote axillary branch formation. Apical branches, generally associated with indeterminate varieties, additionally contribute to PAR interception and high N also promotes these.

Moisture availability

Different levels of drought differentially affect plant canopy structure and yield. Genotypic variation is also found among genotypes in producing canopy and yield. Potato genotypes respond to moisture stress by demonstrating reduction in plant height, number of above ground shoots per plant, tuber number per plant and tuber yield. The magnitude of the reduction is a function of the different degrees of drought. Water deficit reduces yield in sensitive genotypes by reducing many yield determining parameters such as number of leaves, plant water potentials, leaf area, stem height, ground coverage, tuber growth and yield per plant. Tolerant genotypes showed comparatively less reduction in plant height, above ground shoots per plant, tuber number per plant and yield.

Drought reduces tuber yield and quality by causing stomatal closure, which limits photosynthesis, leading to reduced canopy growth. Drought affects yield, not by influencing tuberisation since similar numbers of tubers are formed; but under moisture stress conditions there is a higher degrees of tuber re-sorption. There is research evidence to show that maximum yields are obtained when soil moisture does not drop below 50% of crop available water in the soil, although it may vary 25 to 75%. These differences can be explained by climatic, plant and soil characteristics.

Biotic factors such as pathogens and pests also reduce the amount of PAR intercepted by the canopy

Pathogens

Late blight, caused by the fungus *Phytophthora infestans* causes extensive yield loss in the potato crop world wide each year. It causes this damage by invading and destroying the foliage and reducing he amount of PAR intercepted by the canopy. For any environment where potatoes are grown, there is a linear relationship between dry matter production (foliage and tubers) and the quantity of intercepted PAR. When the canopy is protected by the use of resistant cultivars, adjusting the planting date to avoid infection or by the application of fungicides, tuber yield is maintained. Cultivars that are resistant to late blight or that set tubers at low levels of intercepted radiation partly avoid the yield penalty associated with late blight infection

The fungus *Alternaria solani* causes early blight. Field experiments were conducted over two seasons to investigate the effect of early blight epidemics on

PAR interception, radiation use efficiency (RUE), and total dry matter production of potatoes. Early blight reduced PAR interception by 9% in both seasons and RUE by 17% and 28% in both seasons respectively.

Virus infection, e.g. potato virus Y, reduces canopy size and hence the amount of PAR intercepted. Diseases, which induce wilting symptoms, e.g. bacterial wilt (*Ralstonia solanacearum*), colonise the plant xylem system and prevent water uptake, thereby reducing the RUE value, or even killing the plant.

Pests

Aphids reduce the growth of the potato plant primarily by removing dry matter. This is accomplished by removing, phloem sap, which is a complex mixture of substances, including mineral ions, amino acids, organic acids and plant hormones. Since the dominant component in phloem sap is sucrose, the host's response to infestation is likely to be strongly influenced by its photosynthetic rate, and hence by PAR it receives.

(II) Conversion of radiation energy to dry matter

Photosynthesis can be described as the process of dry matter production, whereby in the presence of sunlight, water and carbon dioxide are combined to produce glucose - sucrose - starch. Radiation-use efficiency (RUE) relates biomass production to the photosynthetically active radiation (PAR) intercepted by a plant or crop. RUE is a crop-dependent coefficient widely used in the physiological interpretation of crop response to the environment and management practices.

RUE is defined as the ratio of dry matter produced per unit of radiant energy used in its production. Seasonal RUE, (g MJ^{-1}) can be expressed as the slope of the regression of aboveground biomass (g m^{-2}) obtained in successive harvests, versus cumulative intercepted PAR (MJ m^{-2}). Radiation-use efficiency is dependent on light, temperature, vapor pressure deficit and factors inherent to plant species. For example, RUE increases with increasing rate of leaf photosynthesis. Increasing soil fertility significantly increases both PAR interception and RUE. In potatoes, the amount of applied nitrogen and RUE are linked by a strong positive relationship. High nitrogen increased RUE in potatoes from 1.97 to 2.78 (g MJ^{-1}).

Similarly, a list of factors decreases RUE – including increasing leaf age, respiration and the higher energy costs associated with the biosynthesis of some plant constituents. RUE has been shown to decrease slightly during high temperatures, probably as a result of partial stomatal closure and a reduction in photosynthesis in response to high vapor pressure deficits. Also, an increase in temperature may result in a greater increase in maintenance respiration than in leaf photosynthesis. RUE also depends on the crop development phase, and the degree of infestation of plants with disease.

Differences in RUE have been proposed to explain yield differences between potato cultivars, which had similar spatial and temporal patterns of canopy development. It has also been proposed that since RUE is a critical determinant of yield differences between potato cultivars, it could be included as a as breeding criteria in the search for higher tuber yields As with radiation interception above, several factors influence the efficiency of conversion of PAR to dry matter.

Growth is never limited by carbon dioxide concentrations in the atmosphere surrounding the leaves but rather by the inability of the plant to absorb it due to stomatal closure. Ensuring an adequate supply of water will permit the efficient conversion of radiant energy to dry matter. Drought has been shown to affect radiation use efficiency, harvest index, and tuber dry matter content.

Yellow leaves generally have lower nitrogen contents, which may affect photosynthesis and hence the RUE since it has been demonstrated that there was a strong positive linear relationship between RUE and applied nitrogen. The relationship between N fertilisation and RUE is not absolute, as one study has shown no effect of N deficiency in potato on RUE.

Reported values of RUE for potato crops differ greatly among locations. In a study in Hawaii, dry matter production increased as the elevation increased from 91 to 1097 m.a.s.l., because of increases in RUE values. The researchers related the increase in RUE values to the decreased temperature at high elevations, not withstanding that light intensity was similar at both locations.

Fungicides protect the canopy from attack by late blight and reduce the yield penalty associated with infection. This response is achieved by maximising the radiation reception receipts not by increasing the radiation use efficiency.

Competition from weeds has been shown to influence potato RUE. Radiation use efficiency reduced with a decrease in duration of the weed free period and increased with increasing duration of the weed interference period.

(III) Proportion of assimilated dry matter partitioned to tubers - Tuber Bulking

Introduction

The major events of tuber bulking in potato have been defined as: cell division and expansion, together with the associated starch and protein accumulation.

Tuber bulking rate is represented as the slope of the linear curve described by the increase in tuber weight with time, while tuber bulking duration is represented by the time period between tuber initiation and senescence of foliage. The yield in the potato crop is determined by the rate and duration of tuber bulking. When senescence eliminates the active leaf area, tuber bulking ceases a short time later. Though both the rate and duration of tuber bulking are important in explaining yield differences between cultivars, tuber bulking duration is of greater importance since it seems that it is the major determinant of final yield.

It is expected that an early maturing variety will have a yield advantage over a late maturing variety if both are harvested at the linear stage of tuber bulking. However if the harvest is delayed, the opposite response may be observed – the early maturing variety, because of its early senescence, has a lower tuber yield than the later maturing variety, due to the extended growth period of the latter.

Tuber bulking is the outworking of two basic processes, tuber initiation and tuber growth. Tuber bulking duration is influenced by factors such as geographic location, environmental influences, and cultivars. This is the critical growth period for both tuber yield and quality. When there are no constraints on growing conditions, tuber growth rates remain relatively constant during this period, which is often referred to as the linear phase of tuber growth.

During this stage the tubers are the major beneficiaries of photo assimilate- they assume the role of sink – where sucrose transported from the leaves is converted to starch and stored. Tuber yield and quality depends on success at this stage. The tubers will undergo a logarithmic growth pattern which is characterized by an initial gradual growth increase, then a near doubling in size and weight and ending with a gradual slowing down of growth to a plateau level. Crop growth rate is defined as the rate of dry matter production per unit area. Potato is a vegetable crop with a relatively high growth rate. This facilitates a high yield in a relatively short growing period.

Partitioning dry matter to the tubers

Tuber yield can be defined in terms of the rate of assimilation and the proportion of assimilates which are partitioned to the tubers. The production and partitioning of dry matter are two characteristics of the potato crop, which can be altered both by agronomy and the environment.

The dry matter produced in the leaves is used for growth of stems, leaves, roots and tubers and it is the excess that is actually stored in the tubers. Prior to tuber initiation, all the available dry matter is used for canopy and root growth. After tuber initiation, the tubers compete for available dry matter. Their success in obtaining it is related directly to the strength of competition from the canopy.

A detailed study of patterns of dry matter partitioning in the cultivar "Rooster" was conducted at Oak Park, Ireland. The percentage of accumulated dry matter partitioned to the plant parts during three intervals in the growing season is illustrated in (Table 1). It should be noted that stems continue to compete for dry matter over much of the growing season.

Table 1.

Seasonal patterns of assimilate (dry matter) partitioning in cv. 'Rooster': % DM allocated to plant parts

Interval – (Days after planting)	Stems	Leaves	Roots	Tubers
48-55	39	34	13	14
82-91	9	0	0	91
122-131	0	0	0	100

The duration of the phase between tuber initiation and when all assimilated dry matter is allocated exclusively to the tuber is influenced by temperature and this duration is at a maximum for temperatures between 16^0 and 18 ^{0}C. The haulm to tuber ratio, which is a measure of assimilate partitioning, was shown to decrease as the temperature increased. A study, which followed the pattern of change in the rate of photosynthesis over the life span of the canopy, recorded a high rate during canopy expansion, a decline to a minimum coinciding with tuber initiation and then a resumption of high rates during the linear phase of tuber bulking. It can be seen therefore that partitioning of assimilates is influenced by the development stage of the plant, and by environmental factors. When plants of Maris Piper were fed with radiolabeled $^{14}CO_2$ at six stages during tuber bulking it was noted that two weeks after tuber initiation, the relationship between tuber fresh weight and ^{14}C content was almost linear, but the correlation declined at later harvests. In addition, no relationship was found between the node from which a tuber originated and the amount of ^{14}C which entered it, but within a node the tubers on primary stolons contained more ^{14}C than those on secondary stolons. In a further study using $^{14}CO_2$, it was shown that 90% of the carbon exported from leaf number 3 was translocated to the tubers but the percentage was lower from young expanding leaves.

Some care must be taken when interpreting these experiments using radioactive-labeled carbon since the proportion of label in a tuber was highly dependent on the vascular connections between the source leaf and the subtending tuber.

Tuber bulking phase

The phase of partitioning dry matter to tubers is often referred to as the tuber bulking phase or as the phase of linear tuber growth. It is a critical growth period for both tuber yield and quality. Under optimal growing conditions, tuber growth rates remain relatively constant during this period. Research has shown that two major factors influence tuber yield:

1. The photosynthetic activity and duration of the leaf canopy, and
2. The length of the linear tuber growth phase.

The duration during which a canopy can produce photosynthate at a relatively high rate, and the longer tubers are bulking at their maximum rate, the higher the yield.

After tuber initiation, tuber growth receives preference for partitioned dry matter compared with allocation to stems and branches. It is important to notice that environmental and cultural factors may reduce tuber sink strength, altering partitioning of dry matter to this plant part and reducing tuber yield.

The phrase 'sink strength' is widely quoted in discussions of potato yield physiology. In the case of the tubers, sink strength can be defined as the ability to compete with other organs on the plant and attract assimilates. It is considered that sink size and activity are the driving factors but sink age must also be included. The potential growth rates of tubers are not static but undergo constant change.

Any condition that limits growth of healthy foliage disrupts tuber growth, or shifts dry matter partitioning from the tubers to the foliage decreases yield potential. Therefore the bulking rate is a function of the physiology of the plant and it's environment

The rate of tuber bulking is determined early in the growing season from both environmental and physiological factors. Environmental factors include planting date, temperatures at planting (both soil and air temperatures) nutrient fertiliser application, weather extremes (such as frost or hail), irrigation and pest management. Physiological factors include cultivar, seed tuber size, the resulting number of tubers produced per unit land area and physiological age of the seed.

Rate of tuber bulking

Several workers have plotted the increase in tuber yield over time and observed a near linear relationship for a considerable portion of this phase in the plant growth cycle when growing conditions remained constant. The relationship is referred to as the 'tuber bulking rate'. Factors increasing or decreasing the rate of tuber bulking will increase or decrease the slope of the regression line. Tuber bulking rate is dependent upon the amount of PAR, the area of leaf absorbing the radiation, the rate of photosynthesis per unit leaf area, the concentration of CO_2 in the leaves, the proportion of assimilates being transported to the tubers and the rate of respiration of the crop. The numerical values ascribed to tuber bulking rate reflect the conditions under which the crop was grown. A value 14.3g of dry matter m^{-2} d^{-1} is considered as representative of crops grown in temperate latitudes.

Final yield of tubers is determined by the bulking rate and the duration of the bulking period. Some of the determinants of bulking rate are outside the growers control; others can be manipulated by agronomic practices. While the grower can eliminate inter-season variations in cultural practice, the environmental variables will continue to exert influence on bulking rate and hence tuber yields.

Tuber growth rate can be expressed as increase in the number of tubers per plant or as an increase in tuber mass. Tuber initiation is often defined as the date when 50% of the stolons have tubers greater than 10mm in diameter. Not all of the tubers formed at this stage will grow on to maturity. Depending on the sink strength of the established tubers some late-formed tubers may have their contents resorbed and translocated to more actively growing tubers. Tuber number generally peaks at about 60 days after planting and declines thereafter. Similarly the size hierarchy of individual tubers changes during the tuber bulking phase and the largest tuber at the start of tuber bulking may not be the largest at the end. This may result from the early death of the leaf supplying assimilate to that tuber.

Environmental Factors Affecting Tuber Bulking

The effect of radiation on tuber bulking rate.

The amount of PAR to which the canopy is exposed can be considered in terms of day length and light intensity. While day length has been shown to influence tuber bulking, its effects can be discounted in the current discussion since the cultivars are selected to perform under the day length regimes encountered between emergence and senescence. Radiation intensity, while also outside the control of the grower, has a controlling influence on the rate of tuber bulking through its direct effects on rate of photosynthesis and indirectly through its effect on temperature. An experiment succeeded in disassociating the relationship between radiation and temperature by growing seven clones at a range of elevations in Hawaii where the temperature varied considerably but the differences in irradiance were small. Clones demonstrated striking differences in the number of tubers set and the proportion of assimilate allocated to the tubers.

A trial to investigate the effect of increasing light intensity on the rate of photosynthesis in the potato crop showed, that the rate declined as the leaves became progressively older. A hyperbolic relationship in potatoes between light intensity and photosynthesis and that saturation occurred at about half of full sunlight. Typical values for gross assimilation rate of carbohydrate can be calculated for a crop growing at Carlow, Ireland (Lat. 52.8 ^{0}N) on a clear and overcast day (Table 2.)

Table 2.

Calculated daily gross assimilation (kg CH_2O ha^{-1} day^{-1})
for a typical potato crop at Carlow, Ireland.

Date	June 15	July 15	Aug. 15	Sept. 15	Oct. 15
Clear day	532	513	437	324	210
Overcast day	244	235	197	139	82

The effect of overcast days was simulated by shading the crop for 12 days during the early stages of rapid tuber bulking and noted that bulking rate was temporarily reduced, which led to a reduction in final yield. While the quantity of PAR intercepted by the plant has been shown to influence the rate of photosynthate production, the spectral balance of light influences the distribution of assimilate within the crop. This has been illustrated for potatoes where plants grown over white coloured straw mulches gave a 15% increase in marketable yield compared with unpainted straw mulch.

Effect of temperature on tuber bulking

Different stages of the potato crop growth cycle have different temperature optima. Potatoes are often described as a cool temperature crop and tuber growth is favored by temperatures around 15-16 ^{0}C. Soil temps above this restrict tuber growth. By contrast, the canopy can function and grow effectively (measured as percentage increase in leaf area) at temperatures of around 25 ^{0}C. In an environment of high air temperature values, the temperature in the root zone can be sustained at near optimum levels due to shading by the canopy. This combination high shoot temperature and low root temperature increases haulm longevity, but haulm longevity is greatly decreased when high shoot temperature is combined with high root temperature. Because high temperatures promote haulm growth, more of the pool of starch available for growth is directed towards the haulm at the expense of tuber growth. Heat stress occurring early in the growth cycle has a greater impact on tuber yield and tuber quality, whether expressed as a reduction in specific gravity or as in increase in misshapen tubers.

Tuber yield was found to decrease at 29 ^{0}C while tuber specific gravity and tuber shape were also negatively affected. As the temperature increases, the rate of respiration increases, while the rate of photosynthesis decreases. This means that starch is being respired to sustain plant growth rather than stored in tubers.

Temperature has been shown to influence dry matter allocation during the tuber bulking phase. High temperatures (around 30 ^{0}C) reduced the growth rate and carbohydrate metabolism, lowered the ratio of tuber to both leaf and stem dry matter and prevented further growth at 34 ^{0}C. High temperatures increase leaf senescence rate and therefore indirectly affect the rate of tuber bulking. However, it has been demonstrated that while senescence commenced earlier at 27^0 than at either 16^0 or 22 ^{0}C, the plants lived longer at the high temperature because new leaves were formed over a longer period. Low temperatures (below 10 ^{0}C) also affect dry matter allocation. These findings led to the proposal of an optimal bulking temperature, with values of 13 ^{0}C or 18 ^{0}C or 21 ^{0}C being suggested by different researchers.

Radiation use efficiency, which describes the amount of dry matter produced per unit of intercepted PAR, is significantly related to mean daily temperature. Values of 2.2 to 2.8 g MJ^{-1} were calculated for crops at different altitudes in Hawaii, while values of 2.49 to 3.42 g MJ^{-1} were calculated for crops in England.

In the absence of a strategy to uncouple the effect of light and temperature such as that employed in the study at Hawaii, it might be expected that the combination would produce additive effects. But when the effects of light and temperature on the growth of the cultivar 'Norland' were modeled, it was found that for an increase in tuber weight, temperature appeared to act independently of CO_2 levels and light.

The effect of CO_2 levels on tuber bulking rate

The carbon dioxide concentration in the atmosphere surrounding the leaves is not regarded as a factor, which limits photosynthesis and consequently tuber growth. There is however a considerable volume of evidence showing the effect of internal CO_2 concentrations on the rates of photosynthesis. The stomata permits water vapour to diffuse out of the leaf and CO_2 to enter and when there is an insufficient water supply to the leaves to maintain full transpiration rate the stomata begin to close. Because potatoes require such large quantities of water to permit optimum growth, the relationship between stomatal closure, internal CO_2 concentration, photosynthesis and yield increase have been widely investigated. When potato plants were water stressed, a reduction in photosynthesis was observed and furthermore, drought stress reduced the growth of tops significantly more than the growth of tubers and roots. A reduction in both net photosynthesis and transpiration due to water stress has been shown and furthermore that photosynthesis was less sensitive to drought than transpiration.

When five cultivars, with varying levels of field drought tolerance were exposed to water stress in a controlled environment, a drop was recorded in both the rates of photosynthesis and transpiration. While the initial reduction in photosynthesis was shown to have been induced by stomatal closure, subsequent declines in photosynthesis were due to inhibition of the photosynthetic capacity through influences on the mesophyll. However in another study, differences in stomatal conductance did not adequately explain differences in rates of photosynthesis between four potato clones. In a trial conducted during a dry growing season, with intense interplant competition from closely spaced plants, leaf area decreased in mid-summer and induced a near complete cessation of tuber bulking.

Effect of weather extremes on tuber bulking

Hail can damage crops, but potatoes are remarkably resilient to its damages compared to other crops such as maize and beans. Factors such as the amount and size of the hail, the variety, the growth stage of the plants and the weather immediately following the hail, will all contribute to the severity of the hail damage.

Tuber yield is most sensitive to hail damage, which occurs two to three weeks after tuber initiation or during early tuber bulking. Many varieties will be at his stage in about two to four weeks after flowering.

The physical manifestation of hail damage is torn leaves, a tattered appearance, and also leaves having holes through the blades where small hail penetrated. Stems may be partially completely defoliated (Fig. 1a). If 25% or less defoliation occurs early or late in the season, or 10% or less during mid-season (bulking), there may be little effect on yield if the subsequent weather is favourable for crop growth. Research has shown that if canopy dry matter is reduced by 50% one week after a severe hail-storm this effect was sufficient to arrest crop development. Fertilisation or irrigation of crops damaged to this extent is unlikely to be beneficial in terms of reversing the reduction in potential yield.

Stem injury is the main reason for crop loss due to hail. At the point of impact, hail can break the stem at worst, can go deep enough to cut the vascular tissue and expose it, and, at the least, form a whitish, papery, oval-shaped bruise on the surface (Fig. 1b) All of these open a portal for pathogens such as aerial black leg. Haulm maturity may be delayed due to the recovery period after hail. Fungicides

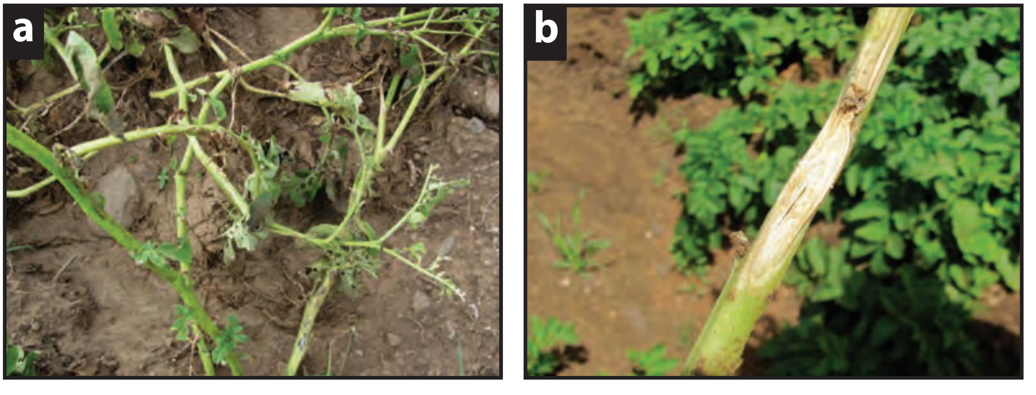

Figure 1.
Potato plants with leaves shredded by hail (a). Hail bruise damage to stem (Photos © Author).

application, as a protection is recommended as early blight (Caused by *Alternaria solani*) and alternata blight (Caused by *Alternaria alternate*) can invade.

Tubers are not directly affected, but misshaping of tubers may occur due to erratic growth as the haulm tries to recover. Late-season hail may reduce tubers solids (i.e. lower specific gravity).

Effect of soil moisture availability on tuber bulking

Potatoes require a continuous supply of soil water along with adequate soil aeration. Yields are greatest when soil moisture is maintained above 65% of the available soil water capacity. Any degree of moisture stress will impact on the linear phase of tuber bulking. Canopy and tuber growth are stopped during a period of stress and continuing for several days thereafter when soil moisture stress is allowed to drop below a critical level. A direct consequence of moisture stress is an effective shortening of the tuber bulking period and even further, it can induce a variety of tuber defects, both internal and external.

Note: *Exercise caution because excessive irrigation can restrict physiological activity in the plant, inhibit nutrient uptake and increase disease susceptibility. An excess of moisture may also lead to enlarged lenticels (Fig. 2), which are openings of the epidermis. This detracts from their appearance and allows entry of disease organisms, causing tuber rot in storage.*

Figure 2.

Tuber showing erupted lenticels, due to excess moisture in the soil surrounding the tuber. (Photo © Author)

Effect of pest management on tuber bulking

If an insect or disease can induce damage to leaves it can reduce the amount of light intercepted by the canopy and through this route, limit tuber growth. Among the most serious of these insect pests are aphids, while diseases such as late blight, early blight, and Verticillium wilt will reduce tuber bulking rate

Physiological Factors Affecting Tuber Bulking

Effect of cultivar on tuber bulking

Dry matter partitioning is also influenced by the choice of cultivar. Early maturing cultivars initiate tubers when the canopy is small and then proceed to divert the greater proportion of assimilate to the tubers - ensuring a commercial yield at early harvest. Another group of cultivars initiate tubers at moderate leaf areas and tuber growth proceeds simultaneously with canopy growth. In late maturing (usually indeterminate) cultivars tuber initiation does not commence until ground cover is achieved and such varieties will only provide full yield at delayed harvest.

When the differences in the duration of tuber bulking rate is discussed, there is a tacit acknowledgement that variations in the genetic makeup influence all aspects of growth and development yet efforts to quantify these differences have hardly extended beyond visual assessments of canopy development and tuber yield determination. Differences between cultivars in relation to root growth and stolon development are rarely quantified.

Cultivars differ in leaf area duration and cv. 'Cara' is typical of a group defined as indeterminate where sympodial branch formation sustains a continuing supply of young leaves. A study compared cv. 'Wilja', a second early, with 'Cara'. Tuber dry matter accumulation in 'Wilja' ceased after the canopy had intercepted approximately 1000 MJ m^{-2} while 'Cara' continued to intercept radiation and acquired approximately 1600 MJ m^{-2}.

An attempt was made to explain the mechanisms underlying increases in yield and improved rates of carbon assimilation per unit leaf area for three clones, which produced higher yield than the standard cultivar, 'Russet Burbank'. Neither stomatal conductance, number of stomata per unit area, total area of stomatal apparatus nor chlorophyll content appeared to provide the basis for the observed increase in carbon assimilation.

Effect of seed tuber physiological age on tuber bulking

Physiologically aged seed tubers tend to produce potato plants with numerous stems. A consequence of high stem numbers is normally a high number of tubers per plant. This has the effect of reducing average tuber size due to increased competition for the amount of carbohydrate available to each tuber during bulking. This is a desirable outcome when growing crops for seed, but is less desirable when the crop is being grown for the ware market.

Crops grown from seed with a high physiological age will have a shorter growing period and therefore reduced yield potential. Older seed is more suited to regions with a short growing season (restricted by early frost, virus incidence or early markets). High levels of physiological age also shorten canopy duration and advance the onset of senescence. A consequence of this early senescence is truncating the bulking duration and limiting overall productivity.

By comparison, when potato plants are grown from physiologically young seed they begin to bulk later, enjoy a longer growing period and possess a higher yield potential than plants raised from physiologically aged seed. This may shorten the linear tuber growth phase in areas with a short growing season, but will produce a higher tuber yield if the crop can grow to maturity in a long growing season.

Growth analysis was used to investigate the basis of increased early yield associated with physiological ageing of seed tubers. The response is explained by faster emergence, faster leaf-area establishment, and tuberisation earlier in the growing season compared with that from physiologically younger seed-tubers.

Effect of leaf longevity on the rate of tuber bulking

In order to maintain a linear rate of increase in tuber yield, the leaves must either retain their photosynthetic capacity for an extended period or the canopy must be constantly replenished, by new leaves. Leaves can be described as young, adult or senescent on a physiological basis and the photosynthetic efficiency of adult leaves was highest. Whereas young leaves attained values of 60-80% of those achieved by adult leaves, senescent leaves only attained values of 40-60%. In a study on the effect of leaf age on photosynthesis and stomatal conductance on leaf numbers 10, 14 and 18, it was observed that conductance initially declined faster than photosynthesis during ageing, but that leaves at the three insertion sites behaved similarly.

A decline in photosynthesis with leaf age is also associated with a corresponding decline in leaf nitrogen content. When plants were grown with adequate nitrogen the longevity of leaf number 12 on the mainstem was about 105 days while the life span of leaves on apical lateral branches varied from 30 to 100 days. In addition to the remobilization of nitrogen at leaf senescence, the remobilization of carbon during senescence has been demonstrated by recording a greater gain in tuber dry matter than in dry matter for the whole plant

The pattern of early tuber initiation, competition with new leaves for assimilate and the consequent reduction in canopy size are well recognised. When sensitivity analysis was used to compare the effects of tuber initiation, leaf longevity and relative tuber growth rate on assimilate allocation it was found that when conditions for tuber growth were not limiting, leaf longevity was the factor making the greatest contribution to tuber bulking.

Effect of rate of respiration on tuber bulking

In early studies, plant growth was analysed in terms of the size of the leaf surface in relation to the area of ground (LAI) and the increase in dry weight per unit area per unit time or the net assimilation rate. The finding that net assimilation rate - the increase in weight due to photosynthesis less the loss due to respiration - was not independent of internal plant processes led to the search for a more effective measure with which to quantify plant growth. Whole plant respiration studies must encompass the canopy, the roots and the tubers. But while respiration in the tubers post harvest has been studied intensively, the growing plant has received less attention.

The full compliment of carbon fixed during the assimilation process is not available to the tubers for an increase in yield since a portion of it is respired to provide energy for metabolic functioning. Respiration can be considered in terms of the energy required for growth and maintenance. The carbohydrates remaining after the maintenance requirements of the plant is satisfied are available for growth. A value of 0.04g g^{-1} dry weight is accepted as appropriate for growth respiration of leaves and 0.03g g^{-1} for stems tubers and roots. Maintenance respiration values must take account of organ dry weight and temperature. A further study also developed a model to simulate potato growth and regarded that the maintenance requirements of leaves, stems, roots and tubers were satisfied at 0.03, 0.015, 0.01 and 0.005g g^{-1} respectively of glucose.

Bulking of individual tubers in relation to overall bulking rate

The number of tubers, which develop to a marketable size, is often considerably less than the number initiated. Differences in tuber size at final harvest have led several workers to investigate the factors affecting individual tuber growth rates. Four stages have been recognised in tuber formation: induction, initiation, set and growth. The greater proportion of tubers that attain maturity are initiated over a short period and some of these commence rapid growth leading to the familiar distribution in tuber size. It was initially regarded the largest tubers were these which were formed first and remained the largest until maturity. Subsequent workers, who demonstrated that the hierarchy of tuber size is in a constant state of flux, refuted this concept.

Tuber growth is achieved through cell division, cell enlargement and storage of starch. While all three processes occur simultaneously in the early stages, increases in cell volume provide the increase in tuber volume after it has attained a fresh weight of 30 to 40g. Daily changes in tuber volume have been measured for the cultivar 'Bintje', where a periodicity was observed in which the greatest increase occurred at the beginning of the dark phase and the lowest after the resumption of the light phase. During the early stages of tuber development, the increases were greatest during daytime, while approaching maturity the greatest increases were observed at night. The impact on the increase in volume of individual tubers and the volume response to a 50% decrease in leaf area or of cooling the tubers to 8 ^{0}C was investigated. The result showed that growth of potato tubers during the linear phase of bulking is limited only by the capacity of the plant canopy to supply assimilates.

There is no agreement in the literature on whether increases in tuber volume are predicated through the amount of assimilate supplied to a tuber or as a result of the sink strength of the tuber *i.e.* its ability to compete with surrounding tubers for the available supply. Differences in sink strength have been shown to exist among stolon tips even before visible swelling occurs. There is some evidence that this difference in sink strength may be related to differences in the activity of the enzyme, sucrose synthase, responsible for the conversion of sucrose to starch.

Effect of Agronomic Factors on Tuber Bulking

Three distinct phases have been recognised in the idealised curve relating tuber yield to time: a period of exponential growth following tuber initiation, a long period when the relationship is linear and a final phase when growth rate of tubers declines coinciding with the onset of canopy senescence. Final yield is therefore the cumulative result of factors, which influence the rate and duration of each facet of the tuber-bulking phase. It follows therefore that factors, which shorten the duration of tuber bulking, can be expected to reduce yield.

Effect of foliar diseases on the duration of tuber bulking

The degree of defoliation of a potato crop by the fungal pathogen *Phytophthora infestans* depend on the severity of the infestation and therefore the timing of onset will restrict the duration of tuber bulking. The primary objective in a fungicide application strategy is to provide complete protection for the crop while a secondary objective will be to delay the onset of defoliation in the event of an outbreak. Current formulations of contact, translaminar and systemic fungicides provide a high degree of protection. A relationship has been demonstrated between the amount of intercepted PAR and the yield of potatoes where the canopy size has been reduced by late blight (*Phytophthora infestans*). While in the plants treated with fungicide, fungal spread was limited, ground cover was increased but radiation use efficiency was not affected by fungicide application or *P. infestans* infection

A study to simulate the defoliating effects of *P. infestans* examined the effect of defoliation by hand-removal of either 0, 25 or 50% of new leaf growth. Final tuber yields were 19% and 22% lower following 25 and 50% defoliation respectively. Differences in the duration of tuber bulking between the cultivars 'King Edward' and 'Majestic' were observed and it was considered that the difference was due to greater blight resistance in Majestic.

Effect of seed tuber size and plant spacing on tuber bulking

The number of stems produced by a potato plant is influenced both by seed tuber size and physiological age. Since each eye on a seed tuber has the potential to produce at least one stem, the larger the seed tuber, the more eyes, the more potential stems. Additionally, as seed acquires physiological age, the number of stems produced by each eye increases.

Seed size and spacing combinations must be selected to match the expected end use of the crop. In potatoes, the seed tuber provides both meristematic potential and substrate reserves. It has long been recognised that the size and quantity of seed tubers planted will influence the subsequent growth of the crop. Most of the research in this area has been directed towards determining an appropriate population at which a given seed size will produce optimum or maximum yield. These types of trials represent an oblique approach to the problem since it is reasonably well accepted that the mainstem represents the unit of potato yield. What is in fact required therefore is a procedure whereby a given population of mainstems could be established and modified to suit individual crop end-use requirements. Attempts at using set characters like weight, surface area, number of eyes and number of 'sproutlets' to predict mainstem emergence have only enjoyed limited success. However, even if the number of mainstems likely to emerge could be predicted with some certainty, then similar precision in predicting the number of tubers produced by each mainstem would be required before any assumptions on tuber size distribution could be attempted. At the level of farm practice therefore, adjusting the plant population relative to the set size still represents the only practical approach.

The number of stems produced by a potato plant influences the number of tubers that the plant will set. Because each stem tends to produce a certain number of tubers, the higher the number of stems, the more tubers that will be produced by each plant. Having more tubers per plant can be advantageous for cultivars that set few tubers with many of them oversized or more importantly, when crops are grown for seed production.

As seed tubers are spaced closer together, tuber numbers per plant typically decreases due to interstem competition. However, because the seed tubers are spaced closer together, the resulting total plant population per hectare increases, and the overall tuber number per hectare will also likely increase.

Both closer than optimal plant spacing and physiological ageing have similar effects on tuber growth, in that both increases tuber density relative to canopy size. This constrains the photosynthetic capacity to bulk each tuber. Although total yields may not be reduced, bulking rates of individual tubers decrease, which results in smaller tubers and lower marketable yields of ware size tubers. When wider than optimal spacing is employed it can lengthen the time it takes to reach full canopy, which restricts carbohydrate supply to the tubers.

The effect of seed size on mean bulking rate per week for large seed (45-51 mm) and small seed (32-38 mm) was investigated and no difference was observed in one growing season, while in the subsequent season the small seed provided the higher bulking rate. It is likely that this is an indirect effect, being moderated by the difference in the number of mainstems per seed tuber since the small seed had somewhat fewer mainstems in the first growing season and considerably fewer in the second season.

A further study also examined the effect of seed spacing on mean bulking rate and found that plants at a 30.5 cm spacing had higher bulking rates in both growing seasons than plants spaced at 45.7 cm or 61.0 cm. This result can be explained in terms of radiation interception where it is likely that plants at the wide spacing's were failing to intercept all the available radiation with consequent slower bulking rate until they achieved ground cover. Data on LAI from the trial would support this interpretation since the 30.5 cm spacing displayed the highest rate of LAI development.

Harvested tuber size profile is a function of the number of tubers set per plant, as well as the length of time tubers bulk during the season. Environmental and management factors can influence both of these characteristics.

Effect of nutrient fertiliser on tuber bulking

Nitrogen application rate constitutes the agronomic practice, which has the greatest single impact on crop growth. It is not surprising therefore that the influence of nitrogen on tuber bulking has been intensively investigated. The majority of nitrogen application studies have sought to identify the level of nitrogen, which should be applied to ensure the development of a canopy capable of sustaining the maximum rate of tuber bulking. High levels of nitrogen have been shown to produce vigorous growth of stems and leaves and induce a delay in tuber yield development

A common feature of nitrogen level studies relates to concern regarding the effect of high levels on rates of tuber bulking. Some confusion in earlier studies regarding the effect of nitrogen on tuber bulking resulted from the practice of extrapolating the date of tuber initiation from the linear phase of tuber bulking. This led to the suggestion that high nitrogen levels delayed tuber initiation. In reality, initiation was not affected, but the length of the exponential phase was increased. A study investigating the effect of nitrogen on tuber yield concluded that the yield increase achieved from increasing levels of nitrogen resulted from higher tuber bulking rates rather than from an increase in the duration of tuber bulking.

It was regarded that delaying the date of tuber initiation and thus ensuring that the crop had attained a larger leaf area at tuber initiation, would result in a higher yield. High nitrogen levels appeared to provide the high yields through mimicking this strategy.

Maximum tuber growth rate requires a healthy canopy, supplied with essential nutrients at optimal rates. Tuber bulking rates can be reduced by either deficit or excess fertiliser applications. Canopy growth is limited and canopy duration is shortened by nutrient deficiency, this results in reduced carbohydrate production and consequent tuber growth rates. By contrast, excessive fertilizer applications can cause nutrient imbalances that delay or slow tuber growth rates.

Nitrogen has been shown to produce a dramatic influence on dry matter partitioning. Nitrogen is essential to produce canopy growth and sustain leaf area duration. Excess nitrogen application increases the size of the canopy during the early growth phase and diverts dry matter into the production of excess leaf and stem at the expense of tubers. The investment of dry matter in these components will only be recovered by the maintenance of leaf area duration until late into the growing season. But by this time, radiation receipts are declining as outlined above, so that it is possible that the full value of the applied nitrogen will never be realised. A balanced supply of all the plant nutrients is required throughout the growth cycle, but especially during tuber bulking when the whole plant is functioning at its physiological limit.

A ranking of needs within the growing crop determines the partitioning of nitrogen. With the commencement of tuber growth, the first priority for N goes to tubers, to maintain their minimum nitrogen requirement of 0.8% by mass. With such a high demand from tubers, premature canopy senescence can be induced as N is remobilized to satisfy tuber demand. The next priority for N is to maintain the canopy structure and this value is assumed to be 0.5% by mass. After this comes the N requirement for leaf expansion at 20g m^{-2}. Excess N, beyond these requirements, goes into a labile pool that consists of NO_3 stored in leaves (up to 0.4g m^{-2}) and nitrogenous compounds in stems (up to 4% by mass). Demands are filled by uptake from the soil while nitrogen is available. When this source is depleted, nitrogen is removed from the lowest organ in the plant hierarchy to the step one below the current organ that is demanding nitrogen. Following the attainment of maximum green leaf area, the canopy becomes a net source of N. This is because the structural N in the canopy is fixed and mobile canopy N is remobilized to the tubers.

Magnesium assumes a greater importance at the later stages of growth, particularly during bulking, where it has a major role to play in maintaining tuber quality. Mg achieves this response due to its role as the central atom in the chlorophyll molecule, where adequate chlorophyll is required to sustain canopy longevity and contribute dry matter to the developing tubers. Increasing the dry matter intake will improve the specific gravity, a major quality attribute, of potato tubers.

Effect of irrigation on tuber bulking

After nitrogen, the next agronomic factor likely to influence the linear rate of tuber bulking is irrigation or it's converse, drought stress. Drought stress is considered as the main abiotic limiting constraint on world potato production. Drought imposes limitations on potato productivity by affecting photosynthetic processes either directly at the canopy, leaf or chloroplast level, or indirectly by limiting transport of photoassimilates to sink organs. Just as nitrogen studies seek to determine an optimum application level, irrigation studies seek to determine the soil moisture deficit below which growth is adversely affected.

In a study to investigate the effect of water deficit on the photosynthetic capacity of potatoes a significant increase in stomatal resistance with an increase in moisture stress was observed, but also that a water deficit influenced photosynthesis through mesophyllic factors. Gas exchange parameters are regarded as being more sensitive to moisture stress in potatoes than the more widely used measurement of leaf water potential. It has long been recognised that photosynthetic rates in leaves are reduced by plant water deficits. However, the cause of the water stress induced decrease in photosynthesis has not been completely elucidated. The low CO_2 assimilation rates induced by moisture stress are considered to be mediated by factors such as low intercellular CO_2, the accumulation of assimilates, localized low-water potentials in the mesophyll and decreased activity of the enzyme ribulose-1,5-bisphosphate carboxylase. Stomatal closure is also considered to be partly responsible for reductions in the photosynthetic rate, due to a decrease in stomatal conductance, in response to turgor loss when roots encounter low soil-water potentials and the shoot is exposed to low atmospheric humidity.

Potatoes have a high demand for water throughout their field growth phase, which must be met from soil storage, rainfall or irrigation. Using theoretical values for water vapour diffusion, leaf area and vapour pressure deficit, it has been calculated that under typical field conditions in northern Europe during August, a potato plant loses 250g of water for every gram of CO_2 assimilated.

(The effect of irrigation on potato growth will be discussed further in **Section 16**).

Summary

- The duration and efficiency of the tuber-bulking period is a major determinant of crop yield. While most of the bulking occurs early in the season, producers need to pay particular attention to the linear bulking period and even end-of-season bulking.
- Growers must understand how to manipulate the growth of the leaf and root system of the potato crop so that radiation interception can be maximised and efficiency maintained.
- Tuber yields vary between seasons and between fields within seasons. By understanding the fundamental principles of crop growth, growers can rationalise this variation.
- By knowing how any management activity will affect the plant, growers can make proper decisions that result in maximum harvest yield and highest quality tubers.

Sources accessed in the preparation of this section.

Carlos Alberto Da Silva, Olivera. (2000). Potato crop growth as affected by nitrogen and plant density. *Pesq. agropec. bras*., Brasília , **35:** 940-950

Fleisher, D. H. and Timlin, D. (2006). Modeling expansion of individual leaves in the potato canopy. *Agricultural and Forest Meteorology* **139:** 84–93.

Li W, Xiong B, Wang S, Deng X, Yin L, Li H. (2016). Regulation Effects of Water and Nitrogen on the Source-Sink Relationship in Potato during the Tuber Bulking Stage. Balestrini R, ed. PLoS ONE.;**11**(1):

Mihovilovich, E., Carli, C., de Mendiburu, F., Hualla, V., and Bonierbale, M., (2014). Protocol Tuber bulking maturity assessment of elite and advanced potato clones. CIP Lima Peru. 43p.

Radley, R.W., Taha, M.A., and Bremner, P.M. (1961). Tuber bulking in the potato crop. *Nature.* **191:** 782-783

Shah, S. F. A., McKenzie, B. A., Gaunt, R. E., Marshall John W. & Frampton, C. M. (2004) Effect of production environments on radiation interception and radiation use efficiency of potato (*Solanum tuberosum*) grown in Canterbury, New Zealand, *New Zealand J. of Crop and Hort. Sci.,* 32:1, 113-119,

Vos, J., Biemond, H., (1992). Effects of nitrogen on the development and growth of the potato plant. 1. Leaf appearance, expansion growth, life spans of leaves and stem branching. *Ann. Bot.* **70:** 27–35.

Section 11.

Potato crop: pathogens, pests and protection.

Introduction

The potato has been successfully cultivated for about 400 years, in a wide range of environments, outside of its center of origin. Despite its widespread adaptability to a vast range of growing conditions, the potato suffers huge losses wherever it is grown around the world, representing billions of dollars in wasted yield or lost sales. Potato is vegetatively propagated through seed tubers and they can act as an entry point and a carry over mechanism to dissipate many diseases and pests. Lack of access to good quality seed tubers is a major constraint in successful production of potatoes. The crop is infected by bacterial, fungal, viral and viroid diseases and infested by parasitic nematodes. The yield potential of the potato crop can only be realised if diseases and pests can be controlled.

Fungal diseases of the potato crop

Fungi are complex microorganisms, many of whose members cause plant diseases. One of the defining characteristics of fungi is the possession of a threadlike vegetative growth (mycelium). They reproduce by means of structures known as spores. These can be asexual or sexual forms and are variously referred to as chlamydospores, conidiospores, sporangiospores, swarmspores or zoospores; as- basidiospores, and oospores. The fungi that attack potato display a range of survival approaches; some live in the soil; others overwinter in or on potato tubers and in plant debris. They gain entry to the plant or tubers through wounds or through natural openings, such as lenticels, or by direct penetration of the epidermis. Direct penetration is effected by a germ tube or peg. Having gained entry to a leaf or tuber, the mycelial strands of the fungus either directly enter a cell and proliferate, or grow between the cells.

Examples of major fungal diseases are late blight, early blight, black scurf, Verticillium wilt/dry rot, wart, and powdery scab. Diseases such as late blight, early blight, Verticillium wilt and black leg primarily affect the crop/foliage whereas diseases such as black scurf, wart, powdery scab and common scab disfigure the tubers and reduce their market value. Some tuber diseases such as dry rots appear mostly in storage while others such as soft rot affect potato tubers at every stage i.e. in field, storage and in the transit and may cause substantial loss under certain conditions.

A partial list of potato fungal pathogens is presented in Table 1.

Table 1. Fungal diseases of potato plants

Black dot	*Colletotrichum coccodes = Colletotrichum atramentarium*
Brown spot and Black pit	*Alternaria alternata = Alternaria tenuis*
Cercospora leaf blotch	*Mycovellosiella concors = Cercospora concors* *Cercospora solani* *Cercospora solani-tuberosi*
Charcoal rot	*Macrophomina phaseolina = Sclerotium bataticola*
Early blight	*Alternaria solani*
Fusarium dry rot	*Fusarium solani* Other *Fusarium* spp. include: *Fusarium avenaceum* *Fusarium oxysporum* *Fusarium culmorum*
Fusarium wilt	*Fusarium spp.* *Fusarium avenaceum* *Fusarium oxysporum* *Fusarium solani f.sp. eumartii*
Gangrene	*Phoma solanicola f. foveata* *Phoma foveata*
Gray mold	*Botrytis cinerea* *Botryotinia fuckeliana* [teleomorph]
Late blight (not a fungus but oomycete)	*Phytophthora infestans*[2]
Leak	*Pythium* spp.
Phoma leaf spot	*Phoma andigena var. andina*
Pink rot (an oomycete)	*Phytophthora* spp. *Phytophthora erythroseptica*
Powdery mildew	*Erysiphe cichoracearum*
Powdery scab (not a fungus but Rhizaria)	*Spongospora subterranea f.sp. subterranea*
Rhizoctonia canker and black scurf	*Rhizoctonia solani* *Thanatephorus cucumeris* [teleomorph]
Rosellinia black rot	*Rosellinia* sp. *Dematophora sp.* [anamorph]
Septoria leaf spot	*Septoria lycopersici var. malagutii*
Silver scurf	*Helminthosporium solani*
Skin spot	*Polyscytalum pustulans*
Stem rot (southern blight)	*Sclerotium rolfsii* *Athelia rolfsii* [teleomorph]
Verticillium wilt	*Verticillium albo-atrum* *Verticillium dahliae*
Wart	*Synchytrium endobioticum*
White mold	*Sclerotinia sclerotiorum*

Late blight

Phytophthora infestans is an oomycete that induces one of the most serious potato diseases known as "late blight" or potato blight. Oomycetes are no longer classified as members of the Kingdom Fungi, despite sharing many biological, ecological, and epidemiological characteristics with fungal plant pathogens. Potato late blight is considered the most economically destructive disease of potato crops worldwide. Late blight has earned a significant reputation as the disease that triggered the Irish potato famine of the 1840s, resulting in the death by starvation of one million people, with another million forced to emigrate. Since it was the first plant disease for which a microorganism was proved to be the causal agent, some regard this as the first step in establishment of the discipline of Plant Pathology. Late blight continues to represent one of the most devastating diseases of potato and losses up to 85% have been reported if the crop (being a susceptible cultivar) remains unprotected.

The late blight pathogen (*Phytophthora infestans*) generally survives between seasons in latently infected (no visible symptoms) potato tubers. When these seed tubers commence growth, the fungus spreads from the tuber into the new haulm. Late blight affects all plant parts viz. leaves, stem and tubers (Figure 1). On the foliage, it appears as black/brown lesions on leaves that may be small at first and appear water-soaked or have chlorotic borders, but with moist weather, soon expand rapidly and become necrotic. On the lower (abaxial) side of the leaf, a white mildew (cottony growth) ring forms around the dead areas (Fig. 1b). This white growth is due to the presence of sporangia and sporangiophores on the surface of infected tissue. The pathogen sporulates on the primary lesions and the sporangia are carried over by wind currents/rain splashes to other plants/fields, where the infection cycle recommences and dispersal continues.

Light brown elongate lesions develop on stems and petioles often encircling the tissue and killing it (Fig. 1 c & d). Under favourable conditions, the disease spreads rapidly killing the vine and even on to killing the whole crop over just a few days. In dry weather the water soaked areas may dry up and turn brown.

The infected stems and leaves serve as the primary source of inoculum. Fungal sporangia are also washed down to the soil by rain water or dew and infect the new tubers. Tubers are readily infected while in soil, especially tubers formed near the surface or even when partly exposed. The first visible sign on the tubers is a shallow, reddish brown dry rot that spreads irregularly from the surface through the flesh.

Despite its existence being recognised for over 150 years then vast energy and expense being directed towards control, late blight continues to decimate potato crops worldwide. In many regions potato production is only feasible with the assistance of copious applications of fungicide. The search for a potato cultivar, resistant to the fungus, continues. This blight-resistant potato would

- Allow millions of subsistence farmers to grow the potato;
- Reduce the costs of production;
- Provide security against sudden losses and
- Reduce environmental hazards from the use of agricultural chemicals.

We can but hope for success!

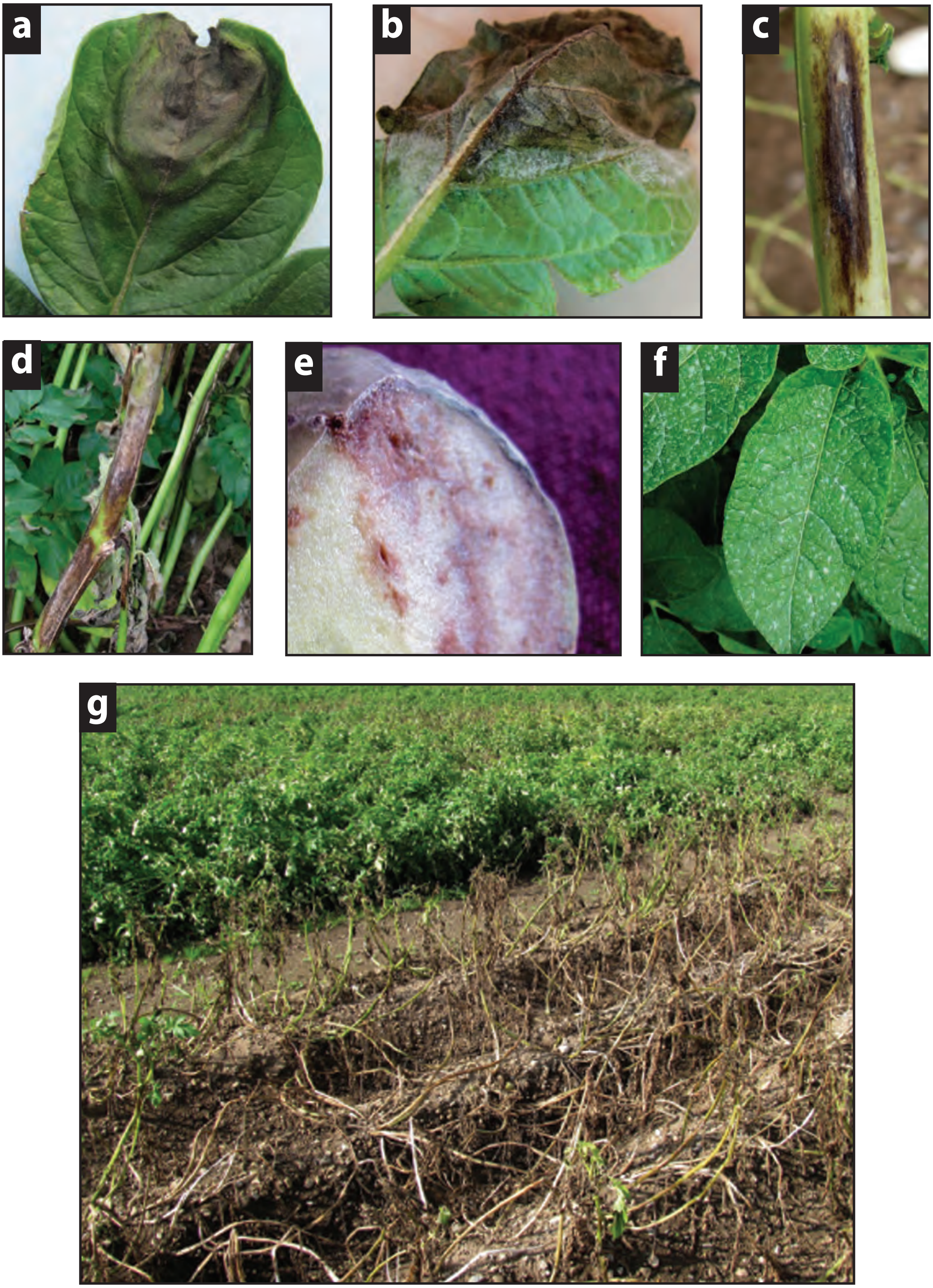

Figure 1.
Late blight on leaf upper surface (a), on leaf lower surface (b), on stem (c,d) and on a tuber (e). Fungicide droplets on a potato leaf (f). Crop devastated by late blight, foreground; protected by fungicide background (g) (Photos © Author)

Early blight

Early blight is a disease caused by the fungal pathogen, *Alternaria solani*, which is mainly a soil borne pathogen. The pathogen produces distinctive "Target spot" (or "bulls eye") patterned leaf spots (Figure 2a) that is helpful to distinguish between leaf lesions caused by late blight and early blight. A feature that distinguishes the disease from late blight is the absence of a distinctive milky ring of sporulation around the lesion on the underside of the leaf.

A. solani exerts its major damage in potato crops due to premature defoliation of plants, which can cause a tuber yield reduction of up to 30%. Initial infection appears on the older leaves, with concentric dark brown spots developing mainly in the area between leaf veins and the major veins often limit progression. The disease progresses during the log phase of canopy growth. With further progression, infected leaves turn yellow and either dry out or fall off the stem.

On stems, (Figure 2c) spots are gaunt with no clear contours (as compared to leaf spots). Tuber lesions are dry, dark and with the surface sunken into the tuber, with the underlying flesh turning dry, leathery and a brown discoloration. As the lesions are dry, they are generally not invaded by other spp.

Despite its common name, early blight is principally a disease of aging plant tissue. Normally lesions appear rapidly on older foliage when warm, moist conditions prevail and are usually visible within 5-7 days after infection. Factors such as environmental conditions, leaf age, and cultivar susceptibility will determine the duration from initial infection to appearance of foliar symptoms.

Sporulation usually requires a long wet period but it can also occur under conditions of alternating wet and dry periods. Conidiophores are produced during wet nights and then, during the following day, light and dryness induce them to produce spores, which emerge on the second wet night. Warm, humid (24-29°C) environmental conditions promote infection. In the presence of free moisture and at an optimum temperature of 28-30°C, conidia will germinate in approximately 40 min.

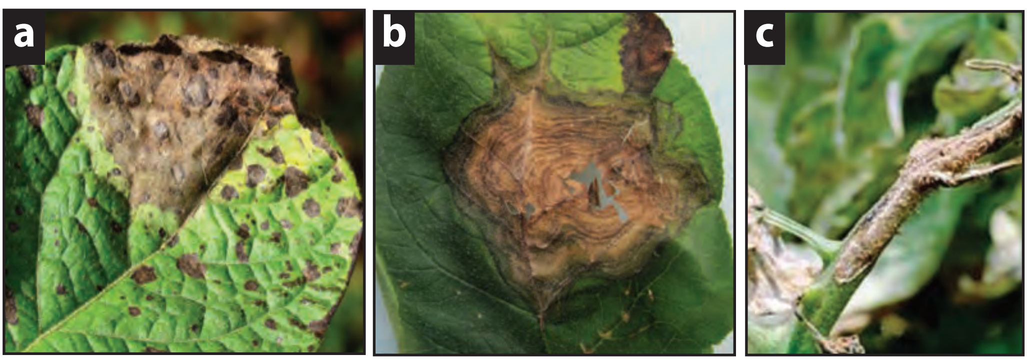

Figure 2.
Early blight on leaf (a) Lesion showing "Target" rings (b) and on stem (c).
(Photo (a, b)© Author (c) Wikipedia)

Secondary spread of the disease results from conidia being dispersed mainly by wind and occasionally by splashing rain or overhead irrigation. Early blight is considered polycyclic with repeating cycles of new infection. Under favourable conditions the disease can spread rapidly and build up to damaging levels of leaf infection, with severe levels causing defoliation in the crop.

Cultural control strategies for early blight:

- Plant pathogen-free seed.
- Maintain plant vigor through adequate irrigation and fertilization. This will increase disease resistance.
- Minimise plant injury through adequate insect control. This will mitigate against entry of the pathogen and spread of the fungus
- Practice field sanitation by removing and destroying crop residue after harvest. If this is not practical, plowing the residue into the soil will promote breakdown by soil microorganisms and it will remove the spore source from the soil surface.
- Practice crop rotation to non-susceptible crops (3 years). Control volunteer potatoes and Solanaceous weeds.
- Be aware of the crop microclimate and promote effective air circulation through appropriate plant spacing
- If possible, orient rows in the direction of prevailing winds, avoid shaded areas, and avoid wind barriers.
- Plant resistant or tolerant varieties.

Verticillium wilt

Verticillium wilt of potatoes can induce serious yield loss, with economic consequences and is caused by two different soil-borne fungi, *Verticillium albo-atrum* or *Verticillium dahliae*. Both species occur in the soil and invade xylem elements, where they disrupt water transport in plants and cause vascular wilt. The earliest symptoms of the disease are premature yellowing or other discoloration of the leaves, while the stems and leaf petioles remain green. A yellow colour develops on lower leaves of infected plants; these leaves also wilt. Leaf tissue between veins turns yellow then brown. The wilting and yellowing of foliage progresses up the stems of affected plants. In severely diseased plants, vascular tissue in stems (Figure 3a) and tubers often develops a brown discoloration. (The vascular discolouration of tubers is often more pronounced following Fusarium infection.) Wilt symptoms are induced when the water-conducting xylem tissue becomes blocked by the infection; it is more severe when temperatures are high and plants are stressed for water. Laboratory analysis of diseased plant tissue usually is necessary to determine whether Fusarium or Verticillium is the causal agent. In most areas Verticillium wilt is more common than Fusarium wilt.

To determine if wilt symptoms are caused by Verticillium infection, take the base of the stem near the ground, slice it diagonally and look for brown streaking as illustrated in Fig 3a.

Infected potato tubers may also show similar vascular discoloration occurring in rings, especially near the stem end (Figure 3b).

Do not confuse Verticillium wilt with water stress. Diseased plants generally occur in patches and even 1or 2 stems on a plant may be infected. Drought stress generally affects the whole crop

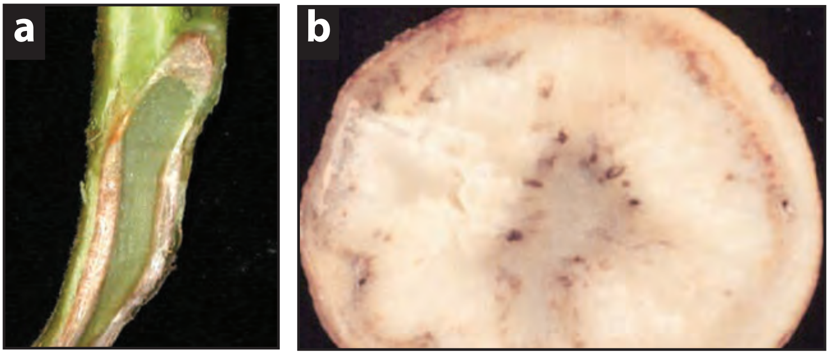

Figure 3.
Verticillium wilt symptoms on a potato stem (a) and a tuber (b) (Photos courtesy Univ. Minnesota Ext.)

Cultural control
Cultural control of Verticillium wilt is difficult as the pathogen can survive in the soil and infect many species. The most useful approach is to remove and destroy infected haulm to prevent the fungi from surviving on the infected material and infecting following crops

Black scurf
Rhizoctonia solani is a fungal disease causing black scurf on tubers and stem also stolon canker on underground stems and stolons and occurs wherever potatoes are grown. It is a disease associated with cool wet soils. Black scurf can be soil and seed borne and survives in soil and also on volunteer potatoes or crop debris. It does not proliferate significantly during storage. Infection severely impacts on the value of tubers destined for the washing trade.

The phase of the disease known as black scurf is observed on tubers. The irregular, black to brown hard masses on the surface of the tuber are sclerotia, or resting bodies, of the fungus (Figure 4a). While these structures adhere tightly to the tuber skin, they are superficial and do not cause damage, even in storage. These are readily rubbed or scraped off. Brown strands of fungal material called mycelium can sometimes be seen around the black scurf with the aid of a magnifying glass. The scurfs are compact masses of mycelium and they serve to perpetuate the disease and inhibit the establishment of a new plant from the tuber by infecting the emerging sprout.

When roots, stems and stolons are infected they show reddish brown necrotic patches called cankers. Rhizoctonia infections can significantly reduce seed tuber emergence. The sprout tips may be infected and killed before they emerge (Fig 4b). Sometimes a branch may form at a node on the sprout and a weak stem may emerge.

After emergence, brown, slightly sunken lesions with distinct edges develop on the stem base (Figure 4c). If severe, the lesions can merge to girdle the stem, interfering with water and carbohydrate movement. Later a white collar (a symptom of the sexual stage) can develop on the stems at soil level. The resulting pruning of the stem can lead to uneven emergence and gaps in crops. Poor stands may be mistaken for seed tuber decay, caused by *Fusarium* species or soft rot bacteria, unless the plants are excavated and examined. Symptoms caused by stem canker may resemble those of blackleg, in that plants are stunted and develop a rolling of the upper leaves. *Rhizoctonia* does not cause seed decay; its damage is limited to sprouts and stolons.

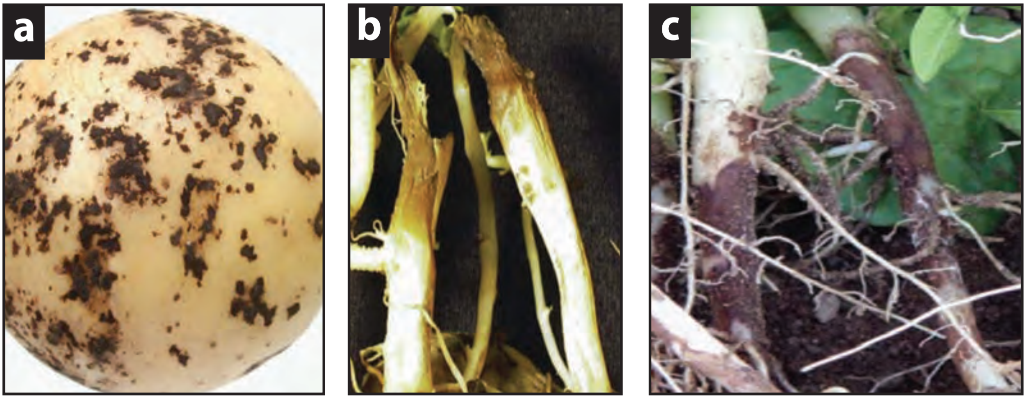

Figure 4.
Black scurf on tuber (a), *Rhizoctonia* on emerging sprout (b), stem bases (b).
(Photo (a) © AHDB. (b & c) © MSU Extension. With permission)

Cultural control
It is difficult to achieve complete control of Rhizoctonia, since the sclerotia can survive in the soil for several years. However a combination of cultural and crop protection interventions will help. The primary step is to only plant seed tubers, which are free from sclerotia, since tuber inoculum is more important than soil inoculum. At harvest time, the interval between haulm death and tuber lifting should be kept to a minimum as sclerotia increase as this interval increases.

In managing incidence levels of Rhizoctonia, nitrogen form is also important. It is best to use a balance of ammonium and nitrate at planting but too much ammonium nitrogen is a disadvantage; it reduces root zone pH and thereby promotes Rhizoctonia.

Research with potassium fertilizer also demonstrated that fertilizer rate and source impacted disease incidence. Applications of potassium sulfate increased overall yields, but potassium chloride fertilizers decreased *Rhizoctonia solani* incidence. Therefore, fertilizer applications can significantly impact both foliar and tuber disease.

Powdery scab

Powdery scab (*Spongospora subterranea*) is a fungal disease of potatoes causing a tuber blemish effect and occurs world wide in potato growing areas. Symptoms of powdery scab include small purple/brown lesions in the early stages of the disease, progressing to raised pustules containing a powdery mass. The “powder” effect is comprised of spore balls (cystosori) that are released into the soil and can survive up to ten years. These release motile zoospores that infect root hairs. Multiple generation of zoospore release and infection may occur during the growing season. In addition to the effect on tubers, Powdery scab is also a vector of Potato Mop Top Virus, a cause of the disease known as spraing.

The foliage of infected plants displays no symptoms. Light coloured irregularly lobed galls develop on roots. Infection occurs at tuber initiation. On the tuber, powdery scabs first show as small raised pimples beneath the skin. As they expand, the skin breaks open to expose a dark brown powdery mass of cystosori (Figure 5a). The lesions are usually shallow depressions surrounded by raised torn edges of ruptured skin (Figure 5b). They are generally small, dark and round. Cystosori under the skin can give the scab a dark margin.

During storage the disease does not spread but lesions may become more prominent. Non-erupting scabs may be confused with skin spot pustules. Powdery scab is not associated with direct yield loss but infected tubers will loose weight in store, resulting in loss due to shrinkage. Powdery scab is considered a cosmetic defect on tubers, and the financial penalty associated with infection will incur due to rejection of these potatoes, if the crops is destined for the washing trade. Infected tubers can be peeled to remove the infected skin and the remaining inside of the potato can be cooked and eaten. Do not confuse Powdery scab with Common scab, since these scabs tend to be larger, more angular and merge to form giant scabs.

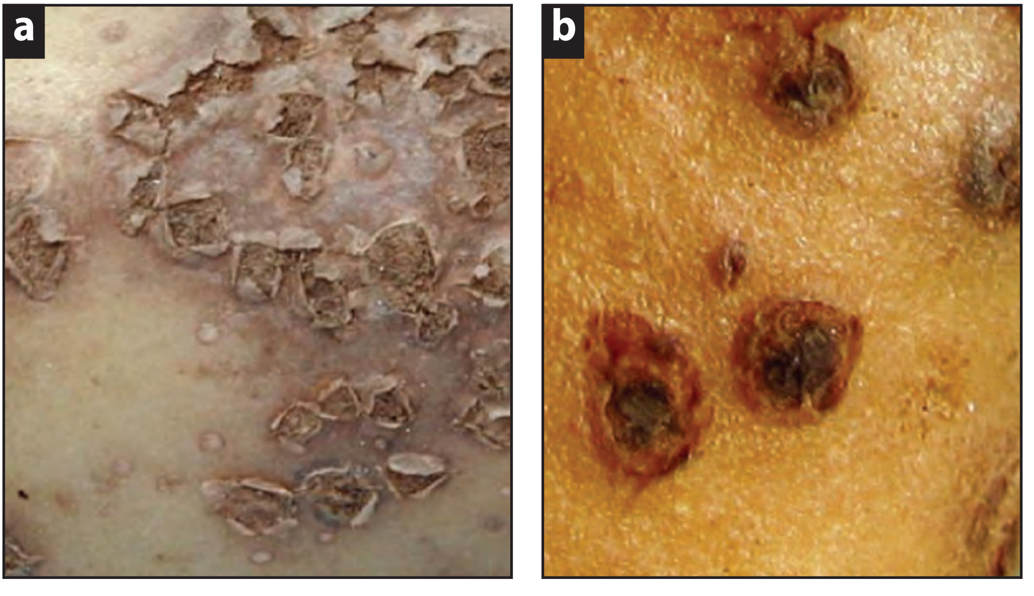

Figure 5.
Tuber covered with powdery scab (a); close-up of lesions (b). (Photo (a) © AHDB, With permission (b), Author)

Cultural control

The spores may be disseminated on seed or by soil and water movement, so only plant clean seed. These resting spores can survive in the soil for up to 6 years and are highly resistant to environmental stress.

Powdery scab is facilitated by cool, moist conditions and heavy soils, so avoid over irrigation. The disease is triggered by wet soil conditions at tuber initiation with infection through lenticels and occasionally through eyes or wounds

Controlling fungal pathogens in the potato crop.

Introduction

Effective disease management is critical to the successful production of the potato crop. The potato plant is susceptible to several fungal diseases, many of which consistently cause yield losses in potato production areas. Successful management of fungal potato diseases can be achieved mainly by integrated disease management, using resistant potato varieties, following the proper cultural practices (clean seed, crop rotation, planting of resistant cultivars) and by chemical treatment of the crop with fungicides and sometimes, of the seed. Fungicides have been used widely in order to control fungal diseases and increase crop production.

Fungi constitute the largest number of plant pathogens and are responsible for a range of serious plant diseases. Fungi cause several potato diseases. They damage plants by killing cells and/or causing plant stress. Sources of fungal infections are infected seed, soil, crop debris, nearby crops and weeds. Fungi are dispersed by wind and water splash, and through the movement of contaminated soil, animals, workers, machinery, tools, seedlings and other plant material. They gain entry to plants through natural openings such as stomata and through wounds caused by harvesting, hail, insects, other diseases, and mechanical damage.

Fungicide mode of action

About 40 different classes of fungicides used for plant protection. Classes are based on target site and biochemical mode of action.

A fungicide's mode of action can be described in general or specific terms. A fungicide with broad-spectrum activity is effective against a large variety of pathogenic fungi. Examples of broad-spectrum fungicides include captan, sulfur, and mancozeb. Some fungicides have a very narrow spectrum of activity; for example, mefenoxam is effective only against oomycetes like *Phytophthora*. Alternatively, a fungicide may affect a broad range of fungi but by only a specific mode of action. For example, Thiophanate-methyl is useful to control many fungal diseases; it acts by binding to tubulin, thereby blocking mitosis.

Another means of classifying fungicide's mode of action is to describe is use for protection or as a curative, or as an eradicant.

Protectants are applied to healthy plants to prevent fungal spores from germinating or penetrating host tissue. They must be applied before the fungal spore has the opportunity to infect the plant. New plant tissue, developing after application generally is unprotected. Protectants generally are not effective once the fungus gains entry to the plant tissues. Examples of protectants include mancozeb, fungicides based on copper, and chlorothalonil.

Note: Some formulations of chlorothalonil, such as "Bravo", can protect newly developed plant tissues because rain action redistributes the fungicide to other plant parts.

Curative materials generally act within the plant and are effective against fungi shortly after penetration. "Kickback activity" and "curative" are interchangeable terms. These materials must be applied within a certain time after infection starts. Materials such as dodine, triflumizole, or myclobutanil have 36-, 72-, and 96-hour curative activity, respectively, against the apple scab fungus.

Eradicants can be of two types. Lime sulfur is an eradicant that acts by killing fungi on contact. Eradicants such as triadimefon and myclobutanil have been developed that not only kill powdery mildew colonies but prevent sporulation as well. Many of these compounds also are active against rusts and various leaf-spotting fungi.

Another fungicide classification system describes the movement of the active ingredient, following application an uptake into the target tissue.

Contact fungicides remain on the outside of the plant and protect the plant from new infection. These fungicides do not have curative activity and new growth is not protected. The length of activity is short due to exposure to the environment (rain, traffic, ultraviolet light).

Localized penetrants form a protective barrier on the plant surfaces and permeate into the plant leaf in the area in which it was deposited. These fungicides have some curative activity, but do not move upward or downward in the plant.

Acropetal penetrants form a protective barrier on the plant, permeate into the plant, and move upward in the plant's xylem. These fungicides have protective activity including new growth, and have good curative activity.

Systemic penetrants form a protective barrier on the plant, permeate into the plant, move upward in the plant's xylem, and move downward in the plant's phloem. These fungicides have protective activity including new growth, and have good curative activity

Many newer fungicides have systemic properties, which means they are absorbed and translocated by certain plant parts. Most of these fungicides are locally systemic. Green plant tissues such as leaves or shoots absorb the materials and move them short distances within the transpiration stream (generally toward the leaf margin) or between plant cells. The QoI or strobilurin compounds have a slightly different distribution. These compounds move into and through the leaf but do not move as readily in the transpiration stream. This activity has been termed translaminar.

Long drying times and warmer temperatures after application favor the uptake of all of these materials.

Mefenoxam is a fungicide that can be absorbed by plant roots and translocated throughout the plant. Translocation, however, is only acropetally (upward), with the transpiration stream. The phosphonate fungicides are truly systemic compounds and are translocated both basipetally (downward) and acropetally whether applied to roots or leaves.

Some fungicides only inhibit fungi (are fungistatic) rather than kill them (fungicidal). Fungistats must be applied continually over the life of the plant to suppress disease development. For example, mefenoxam will prevent zoospores from penetrating roots but only inhibits an established *Phytophthora* infection

Fungicides are most effective when they are applied to foliage:

- Before infection occurs or
- When the disease is in very early stages of development and cannot be detected yet by the human eye and
- When they are applied at the correct dosage rate, dissolved in sufficient water to ensure an even application to the haulm [Fig. 1(e)].

Later applications are helpful in reducing the rate in which the disease spreads but are not nearly as effective as early applications. Late blight is very difficult to manage once infections become established. Total crop and canopy coverage with fungicides is essential for late blight management. The late blight organism, *Phytophthora infestans*, will most likely find and infect any plants or plant surfaces skipped during application.

Fungicides work against late blight by inhibiting one or more of the following:

- Germination of spores (and as a result, reduced infection of plants),
- Growth of the fungus within the plant,
- Production of spores (sporulation), and
- Formation or development of lesions.

Spore suppression. Some combinations of fungicides, such as [Acrobat (dimethomorph) plus an EBDC (ethylene bisdithiocarbamates)]; [Curzate (cymoxanil) plus an EBDC]; [Previcur (propamocarb hydrochloride) plus an EBDC or chlorothalonil] have post-infection activity that inhibits sporulation and/or restricts lesion expansion. These products may help reduce tuber infection when applied during and after tuber bulking. Their use at times can be very beneficial, but they should never be used as a predetermined management tool rather be used only as a "rescue" if plants in a field become infected. Proper use of protectant fungicides will ensure good protection.

Essential steps towards controlling late blight are:

- The correct scheduling of the first fungicide application and the making the correct choice of the appropriate product and its proper application rate. The aim of the first fungicide treatment is to reduce the growth of the fungus from the infected tuber up through the stem.
- Avoid extending intervals between applications during high blight risk. One day early is better than one day late.

- During the phase of rapid growth, good coverage of the growing point is essential.
- Recognise that every fungicide against late blight has strengths and weaknesses. Therefore it is important to choose the most effective product depending on the current conditions.
- It is important to wet plants completely. Many farmers underestimate the influence of the water volume rate on control results
- It is essential to prevent damage from foliar pathogens because tuber bulking relies on canopy health and duration to extend the period of maximum interception of PAR, leading to the attainment of optimum yield.

Fungicide Choice

Note. *The choice of fungicide will be dictated either by Government Regulations or commercial availability in individual countries. It is therefore outside the scope of this document to present specific advice as to the compound that might be applied to control a particular infection. However general principles guiding fungicide choice are presented.*

Table 2.

A list of fungicides designed to control fungal pathogens in potato crops (Contents © The Potato Review. With Permission)

Product	Active Ingredients	Max Individual Dose (Lha or kg/ha)	Mode of Action	Movement in plant
Carial Flex	180 g/kg cymoxanil + 250 g/kg mandipropimid WDG	0.6 kg/ha	Protectant and curative	Translaminar
Consento	75 g/l fenamidone + 375 g/l propamocarb	2 l/ha	Protectant and curative	Contact, systemic and translaminar Alternaria label recommendation
Curzate M WG	4.5% w/w cymoxanil + 68% w/w mancozeb WG	2 kg/ha	Protectant and curative	Translaminar and contact
Sipcam C 50	500g/kg cymoxanil WG	0.24 kg/ha in mix	Limited protectant and curative	Translaminar
Cymbal 45	450g/kg cymoxanil WDG	0.2 kg/ha	Curative	Translaminar
Dithane NT	75% w/w mancozeb	WG1.7 or 2 kg/ha	Protectant	Contact plus Alternaria label recommendation
Dithane 945	80% mancozeb	WP1.7 or 2 kg/ha	Protectant	Contact plus Alternaria label recommendation

Product	Active Ingredients	Max Individual Dose (Lha or kg/ha)	Mode of Action	Movement in plant
Electis/Roxam	8.3% w/w zoxamide (zoxium) + 66.7% w/w mancozeb	1.8 kg/ha	Protectant	Contact
Kunshi	250 g/kg cymoxanil + 375 g/kg fluazinam	0.5 kg	Curative and protectant	Translaminar and contact
Grecale	200g/l cymoxanil +300 g/l fluazinam	0.5 l/ha (0.4 l/ha in low blight pressure	Protectant	Contact and curative
Hubble	200g/l dimethomorph + 200 g/l fluazinam	0.75 l/ha	Protectan antisporulant; some curative	Translaminar, locally systemic and contact
Infinito	62.5 g/l fluopicolide + 625 g/l propamocarb	1.6 l/ha	Protectant anti-sporulant and curative	Translaminar and systemic and tuber protection
Invader	75 g/kg dimethomorph + 667 g/kg mancozeb	2.4 kg/ha *(New high dose rate)*	Protectan anti-sporulant with some curative	Translaminar, locally systemic and contact
Lieto	330 g/kg zoxamide and 330 g/kg cymoxanil	0.45 kg/ha	Protectant and curative	Contact and translaminar
Morph	500 g/l dimethomorph	0.3 l/ha	Protectant with some curative	Locally systemic and contact
Option	600g/kg cymoxanil WDG	0.15 kg/ha in mix	Curative	Translaminar
Percos and Zampro DM	300 g/l amectoctradin + 225 g/l dimethomorph systemic	0.8 l/ha	Protectant and locally	Translaminar and tuber blight recommendation
Presidium	180 g/l dimethomorph + 180 g/l zoxamide	1 L/ha	Protectant and locally systemic	Locally systemic and contact
Profilux	45 g/kg cymoxyanil + 680 g/kg mancozeb	2.5 kg/ha	Curative and protectant	Contact and translaminar
Ranman Top	160 g/l cyazofamid SC	0.5 l/ha	Protectant	Contact
Revus	250 g/l mandipropamid SC	0.6 l/ha	Protectant+ some curative	Contact and translaminar
Shirlan	500 g/l fluazinam SC	0.3 or 0.4 l/ha	Protectant	Contact
Shinkon	200 g/ha amisulbrom	0.5 l/ha	Protectant	Contact
Tanos	25% w/w famoxadone +25% w/w cymoxanil WG	0.5-0.7 kg/ha	Protectant and curative	Contact and translaminar
Valbon	17.5% benthia-valicarb + 70% mancozeb WDG + ZinZan in high pressure years	1.6 kg/ha (ZinZan at 150 ml/ha)	Protectant with some curative with ZinZan	Contact with translaminar

Management of fungicide resistance in potatoes

Pathogens respond to the continuous use of a particular fungicides by evolving resistance to the active ingredient. In the field several mechanisms of resistance have been identified. The evolution of fungicide resistance can be gradual or sudden. The fungus *Phytophthora infestans* is an example of a pathogen, which can quickly become resistant (unsusceptible) to fungicides. The risk of a fungus developing a resistance is increased considerably through frequent applications or applications at incorrect timings to control the fungus. Once resistance develops to a fungicide all formulations with the same biochemical mode of action are affected. "Cross-resistance *class*" is defined as a class of fungicides that share the same biochemical mode of action and mechanism of resistance. That is the basis for the advice to alternate a group of active substances after two applications – especially if the applied fungicide is classified as belonging to a group with a likelihood of inducing a resistance. Another strategy is to tank-mix fungicides with different modes of action to prevent or delay the buildup of resistant fungi.

Resistance management strategies

As many strategies as possible should be used

- Avoid repetitive and sole use
- Tank mix or alternate with an appropriate fungicide
- Limit number of treatments
- Apply protective sprays early in the epidemic
- Avoid eradicant use
- Maintain recommended dose rate
- Integrate with non-chemical methods

How fungi fight back (fungicide resistance modes)

- Modification of sensitive site. A fungicide has a specific target site where it acts to disrupt a particular biochemical process or function. This mechanism in particular acts as a defence against single site of action fungicides. If this target site is somewhat altered, it is presumed that this disrupts the binding of the fungicide to the protein, rendering the fungicide ineffective. This is the most common mechanism that fungi use to become resistant.
- Exclusion of fungicide. A fungal cell may rapidly export the fungicide before it can reach the target site of action.
- Detoxifying the fungicide. Metabolism within the fungal cell is one mechanism a disease pathogen uses to detoxify a foreign compound such as a fungicide. A fungus with the ability to quickly degrade a fungicide can potentially inactivate it before it can reach its site of action.
- Reduced uptake of fungicide. The resistant pathogen simply absorbs the fungicide much more slowly than the susceptible type

There is no risk of pathogen developing resistance to the classical contact fungicides (Mancozeb, Maneb, Metiram, Copper).

Bacterial diseases of the potato crop

Potatoes are particularly susceptible to diseases caused by bacteria, since the tubers comprise nearly 80% water. The bacteria that invade tubers causing soft rot are referred to as pectolytic bacteria; they secrete enzymes that decompose the pectin in plant cell walls, leading to tissue deterioration. Soft rot bacteria either affect potato tubers following harvest, or some can also cause black leg, a bacterial disease occurring on potato stems in the field. Bacterial disease can spread 'vertically' and 'horizontally'– Vertical route: seed crop to daughter crop to granddaughter crop, etc. - Horizontal route: environmental or by direct contact or by contact with tools, machinery or storage.

A partial list of bacterial diseases infecting the potato crop is presented in Table 3.

Table 3. Bacterial Diseases of Potatoes

Common Name	**Causal Organism**
Blackleg and bacterial soft rot	P*ectobacterium carotovorum* subsp. *atrosepticum* = *Erwinia carotovora* subsp. *atroseptica* *Pectobacterium carotovorum* subsp. *carotovorum* = *E. carotovora* subsp. *carotovora* *Pectobacterium chrysanthemi* = *E. chrysanthemi*
Dickeya solani	*Dickeya solani*
Pink eye	Pseudomonas fluorescens
Ring rot	Clavibacter michiganensis subsp. *sepedonicus* = *Corynebacterium* sepedonicum
Common scab	*Streptomyces scabiei* = *S. scabies*
Bacterial wilt = brown rot	*Ralstonia solanacearum*

Soft rot diseases of potato

Soft rot diseases of potatoes are caused by a range of bacteria around the world such as *Pectobacterium carotovorum* subspecies *carotovorum, Pectobacterium atrosepticum* and Dickeya species. Previously, these bacteria were classified as belonging to the genus Erwinia.

Soft rot infection produces a typical water-soaked area of soft tissue. Initially, the healthy part of a tuber is clearly distinguishable from the macerated, creamy infected part but eventually the whole tuber becomes infected. There may be a foul smelling odour as the tuber tissue is decomposed by the bacteria; after which, secondary invaders proliferate.

Non-emergence of plants, wilting, browning of tissues, haulm desiccation and plant death have all been linked to infection of seed tubers by soft rot bacteria. These symptoms are favoured by cool (10-15°C), wet soils at planting and temperatures above 20°C after emergence. These conditions can promote the development of black leg, where the bacteria invade the internal vascular system of the plant and cause wilt.

Soft rot (*Pectobacterium carotovorum)*

Potato soft rot is caused by the bacterium *Pectobacterium carotovorum* (synonym: *Erwinia carotovora*), a common soil resident. This bacterium can grow between the temperatures of 0 and 32 ^{0}C, with optimal growth between 21 and 27 ^{0}C. Bacterial soft rot occurs on a wide range of crops and is one of the most severe postharvest diseases of potatoes worldwide. Loss may occur during storage, transit or marketing. All potatoes varieties are susceptible.

These bacteria can live in soil, in decaying plant debris, and in seed tubers. Bacteria either enter seed potatoes and lower stems through wounds and injuries, or move directly from contaminated seed tubers to lower stems. Contamination of potato tubers occurs anytime they come into contact with the bacterium, most commonly during harvest, handling or washing. The bacteria can be splashed on to plants by rain or irrigation causing aerial stem rot, and if present in surface irrigation water, can cause infections of leaf petioles and plant stems. Many weedy plants act as hosts for the bacteria.

The Pectobacterium pathogen invades the potato tuber generally through wounds. Soft rot infections progress rapidly in tissues that have been weakened, invaded or killed by pathogens or by mechanical means. The development of soft rot in tubers is favored by immaturity, wounding, invasion by other pathogens, warm tuber and storage temperatures, free water and low oxygen conditions. Harvesting tubers at temperatures above 27 ^{0}C can predispose them to soft rot. The rate of decay can be retarded by store temperatures less that 10 ^{0}C, the lower the temperature, the better. Immature tubers are susceptible to harvester-related injury; then predisposed to bacterial infection. Suberizing cut seed and treatment of the cut surfaces with fungicide, helps to reduce the risk of other seed infections that could lead to soft rot breakdown of the seed.

The initial appearance of soft rot on tubers is as small, tannish, water-soaked spots on the surface. These spots rapidly enlarge and the tissue decomposes in a soft, blister-like area on the surface of the tuber. Often, a slimy or watery substance oozes from breaks in the blister. Soft rot often follows bruising and in its early stages of infection, it is white to cream-colored. After exposure to air, it becomes brown to black (Fig. 6a). The boundary between the disintegrated and the sound tissue is sharp. It is nearly odorless at the stage. As secondary rot occurs, the rot becomes very foul smelling. The rot typically progresses to the point of a chalky-white, foul-smelling mass.

Soft rot bacteria reside in potato lenticels, but can invade the tuber through the lenticels when they are swollen, which happens with exposure to wet soils or soaking in water (Fig. 6b). Flesh under the infected lenticel appears water soaked and can be a yellow to cream color. The depth of the infection varies from 6 to 12mm deep. When exposed to high temperatures, these infected lenticels may develop into soft rot. Under low temperatures, these lenticel infections can dry out, leaving a shallow spot with a chalky-white deposit under a normal skin color. Fresh, non-suberized wounds can also serve as entry points for the soft rot bacterium.

Soft rot symptoms on the foliage include weak, chlorotic (yellowed) plants with

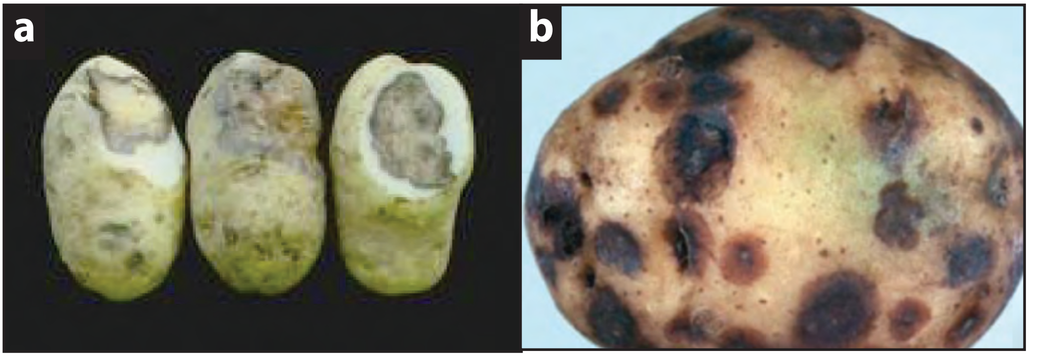

Figure 6.
Tubers infected with soft rot bacteria (a). Soft rot infection of lenticels (b).
(Photos Crown copyright FERA, UK. With permission)

margins of leaflets curled upwards. Stem lesions are usually light brown, but can be colorless, but not black. Stems will rot and become very mushy. Tuber rot will occur as localized infections often on an eye, but can be generalized on the tuber. The tuber rot is colorless and extremely wet and mushy.

The bacteria that cause soft rot can reside in both potato plants and tubers without any obvious symptoms — latent infection; only displaying symptoms when the potato's natural resistance is damaged and an entry port is provided.

Wounds or damage constitute the main route of spread to the potato. Harvesting and grading provide opportunities for wounding, which allows the bacteria to invade the tuber. The combination of damage and water on the surface of the tuber permits the bacteria to defeat the tuber's natural defences and initiate the tuber rot.

Blackleg (*Pectobacterium atrosepticum*)

Blackleg is caused by the bacterium *Pectobacterium atrosepticum* (Synonym: *Erwinia carotovora* subsp. *atroseptica*). The name of the disease is derived from the black lesions produced on infected stems (Fig. 7a). The disease affects both stems and tubers. Stems of infected plants typically have inky black symptoms, which usually commence at the decaying seed piece and may extend up the entire length of the stem. Stem pith can be decayed above the black discoloration, and vascular tissues can be discolored. When black leg develops early, plants are stunted and leaves turn yellow and leaflets tend to roll upwards at the margins. Young plants with severe infections may die.

With blackleg in mature plants, it appears as a black discoloration of previously healthy stems, accompanied by a rapid wilting, and sometimes yellowing, of the leaves. Black discoloration of the stems always starts below ground and moves up the stem, often until the entire stem is black and wilted. Leaflets, and later entire plants, may wilt and eventually decline.

In wet weather, decay is wet and slimy and may spread to most of the plant. Under dry conditions, infected tissue becomes dry and shriveled, and the disease is often restricted to the underground portions of the stem.

Disease is favored by moist conditions with temperatures less than 18 ^{0}C. It can be spread rapidly by wind-blown rain. Cool, wet soils at planting followed by high temperatures after plants emerge favor post emergence blackleg. Higher soil temperatures at planting favor seed tuber decay and pre emergence death of shoots. Reduced stands can result from blackleg-infected seed lots.

Tubers of infected plants may show symptoms ranging from slight vascular discoloration at the stolon end to wet breakdown of the entire pith, extending inwards from the stem end (Fig. 7b). The bacterium can gain entry to the tubers through stolons and produce various symptoms; inky-black, slightly sunken lesions develop at the stem end of the tuber. The flesh of the tubers is initially cream colored, gradually turning to grayish and finally black. Irregular cavities with blackened walls may extend through the center of the potato tuber. The blackleg organism may also infect lenticels, causing them to be slightly sunken and brownish to black in color. Spread in storage is minimal.

Several factors affect disease severity: the degree of seed lot contamination, seed-handling techniques, soil moisture and temperature at planting, environmental conditions during the growing season and exposure to external sources of the bacterium, such as irrigation.

Most of the serious blackleg outbreaks are from seed-borne blackleg. The pathogen is spread from seed tuber to seed tuber by physical handling and by machinery, such as cutting knives and planting equipment. Insects can spread the bacterium in a field by feeding on an infected potato stem. These feeding wounds provide a site of entry for the bacterium.

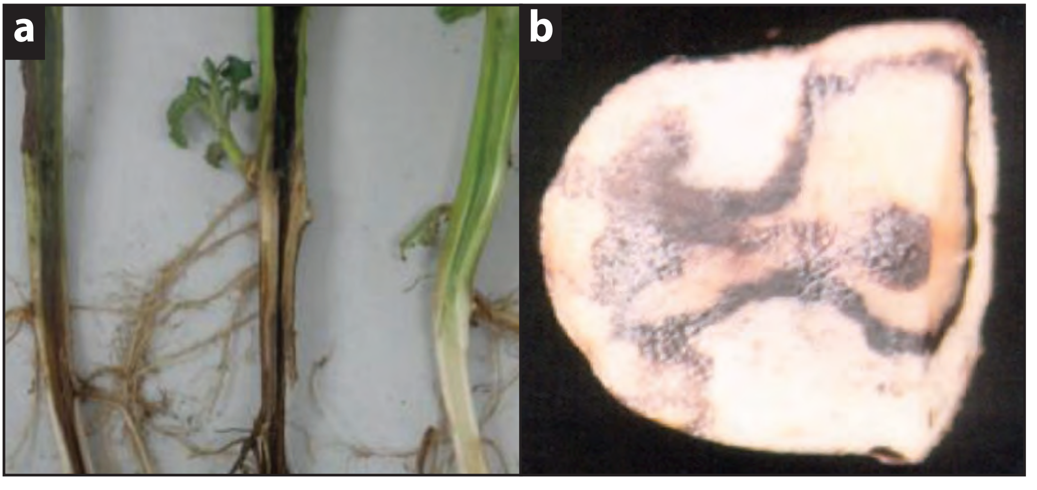

Figure 7.
Blackleg infection stem bases (a). Tuber symptoms blackleg infection (b).
(Photo (a) © Dept. of Ag. & Food, WA. (b) U. Maine Ext. With permission)

Dickeya species

Pectinolytic bacteria, members of the genus Dickeya have been recently isolated from diseased potato plants exhibiting blackleg and slow wilt symptoms. These bacteria are now considered as belonging to the genus Dickeya, previously the *Pectobacterium chrysanthemi* complex (*Erwinia chrysanthemi*). This pathogen thrives under higher temperatures than the *Pectobacterium* species; it is favoured by warm, wet seasons. *Dickeya dianthicola* causes a 'slow wilt' of the haulm, similar to those of blackleg but usually does not display the soft, black decay of the outer stem base. A newly emerging Dickeya species (proposed as *Dickeya 'solani'*) is more aggressive; inducing faster wilting and soft rotting of the stem. The primary source of the pathogen is contaminated seed tubers. Tuber rot symptoms are very similar to those caused by *Pectobacterium*, including heel-end rots (Fig. 8).

Although disease symptoms are often indistinguishable from those of the more established blackleg pathogen Pectobacterium spp., the new species appears to be able to rapidly induce blackleg symptoms and also to rot developing progeny tubers, even when inoculum levels are low. *Dickeya* spp., have a greater ability to spread through the plant's vascular tissue, are considerably more aggressive, and their optimal temperatures for disease development is higher.

The new *Dickeya* pathogen appears to assume additional aggressiveness when exposed to higher temperatures. This implies that it could assume increased importance in the light of temperature increase due to global warming. Since the pathogen is newly described, there is little substantiated practical information on the biology of this strain in relation to its host range, its ability to survive, establish and spread in the environment or its pathogenicity on stored potato tubers.

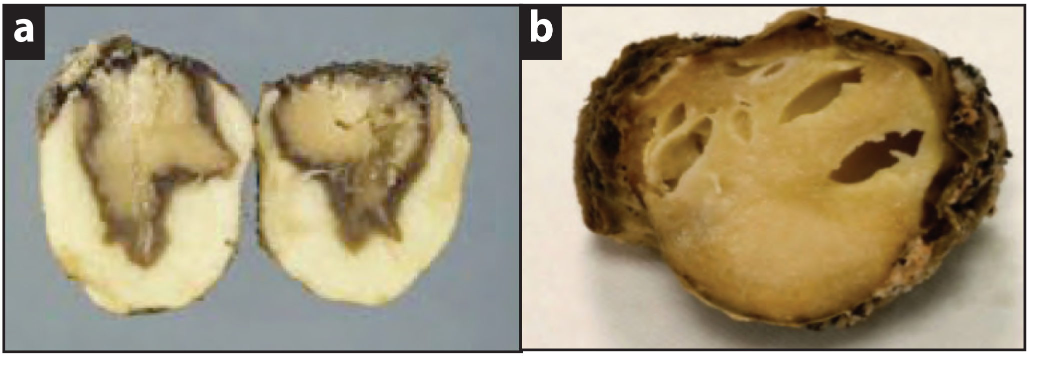

Figure 8.
Tubers infected with Dickeya (Photos Crown copyright – FERA, With permission)

Pink eye (*Pseudomonas marginalia*,)

Infection of tubers by the pathogen *Pseudomonas marginalia* produces pink to brown blotches on the skin, usually around the eyes at the apical (bud) end of tubers (hence the name Pink eye) but the area of the periderm between the eyes can also be affected. With a severe infestation a shallow, reddish brown rot occurs beneath the discolored areas. Pink eye is often prevalent on varieties, which are highly susceptible to Verticillium wilt, and commonly occurs during and after a wet harvest season. As a rule, the disease is not commercially serious in table-stock or seed potatoes that are stored under cool, relatively dry conditions. Tuber appearance may be somewhat impaired, but this improves as the affected skin and superficial rot usually dry up. The pinkish brown blotching mentioned above shows up readily on moist, freshly dug tubers, but is usually difficult to notice on dry, unwashed potatoes. In severe cases, a reddish brown decay extends a few millimeters (2-3) into the flesh. When the infection penetrates deeper, the rot may be confused with that caused by late blight (See Fig. 1d), but unlike late blight, it is not granular and is more superficial than the latter. If tubers are kept cool and dry, the only symptom commonly encountered is scaly, flaky skin over the affected areas. However, in the case of tubers destined for frying as chips then held at warm temperatures (approx. 8 ^{0}C) and high relative humidity, pink eye facilitates the entry of secondary soft rotting bacteria, which frequently cause extremely heavy losses. The end result is often the slimy, foul-smelling decay typical of bacterial soft rot.

The pathogen considered most likely responsible for Pink eye is thought to be the bacterium, *Pseudomonas marginalia*, which lives in the soil on dead organic matter. However there is not universal agreement among plant pathologists that it is the primary agent. Some have even proposed that the phenomenon described as pink disorder includes a physiological basis. One theory suggests that when moist conditions prevail at harvesting, the bacterium invades tubers, which show symptoms after they are harvested. The condition appears to be facilitated by crop stress that occurs early in the season (high temperatures) and wet soil conditions later in the season. There is no substantial evidence that *Pseudomonas marginalia* is seed-borne. Long rotational breaks between potato crops are advised, as land with many potato crops in a rotation can also be associated with promoting pink eye infection.

Ring rot (*Clavibacter michiganensis*)

Potato ring rot is caused by the bacterium *Clavibacter michiganensis* subsp. *sepedonicus.* The symptoms shown by infected plants are variable and can sometimes be mistaken for potato blight, wilt or stem canker. Symptom expression occurs at different rates in different cultivars and is affected by temperature and other environmental conditions. Some cultivars may only rarely express symptoms. The first symptoms are wilting in the lower leaves, either all around the plant or on one side of the plant. The margins of the leaves roll inwards and upwards and the leaf surface appearance changes from a light shiny appearance to dull. Leaves acquire a dull light green, then grey- green with occasional mottling, then yellow and finally brown and necrotic (Fig. 9a). Symptoms are enhanced by hot, dry weather conditions. Foliar symptoms resemble those induced by vascular wilt and generally occur late in the season. Areas between the leaf veins eventually become chlorotic and the leaf margins necrotic. Symptoms can be difficult to distinguish from those of other diseases and other crop damage, symptoms can also be masked by the natural senescence of the crop.

Expression of the wilt symptoms in the canopy varies, but the tubers display symptoms of infection. Tuber infection occurs through the stolon. “Ring rot” derives its name from a characteristic breakdown of the vascular ring within the tuber. This often appears as a creamy-yellow to light-brown, cheesy rot. Symptoms are somewhat similar to those of brown rot, but the initial discoloration of the vascular ring is usually glassy and water-soaked rather than brown, and the ooze from the ring is cheese- or cream-like (Fig. 9b). In severe cases the vascular ring rots completely and the skin of the potato may crack. External symptoms may consist of reddish brown blotches around the eyes, or irregular shaped cracks on the skin. The bacterium is thought to be unable to over-winter in the soil, but it can certainly do so in volunteer plants or ground-keepers (un-harvested potatoes from a previous crop) and debris from infected crops. Infected ground-keepers lifted at the same time as an otherwise clean seed crop can infect that crop. Bacteria can also survive and remain infectious for a long period on potato bags, barn walls, and other equipment that have been contaminated by rotting ooze and, although this is not the main means of disease transmission, it can make eradication of the disease very difficult. The primary source of infection is infected seed potato lots.

Control
Currently there is no method of direct chemical or biological control available. Breeding for resistance has produced some (mainly) tolerant cultivars The most important methods of control are production of disease-free seed following strict certification and testing schemes.

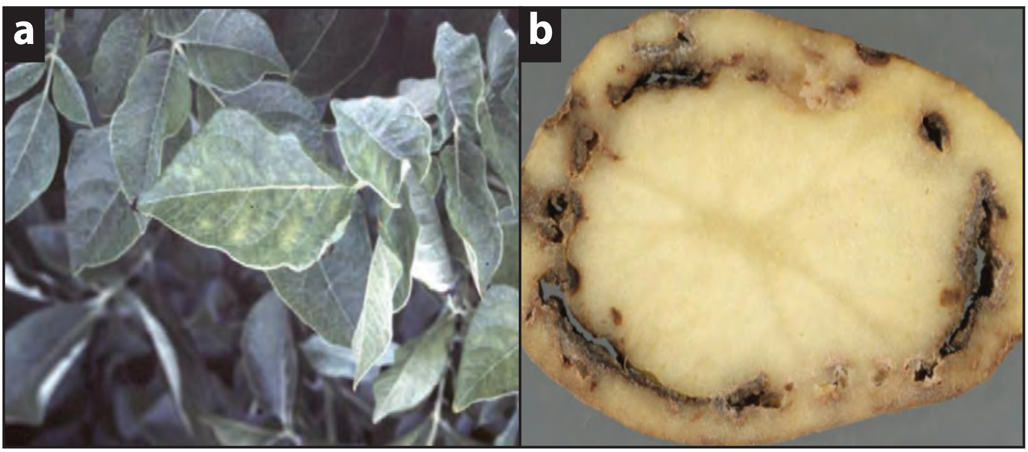

Figure 9.
Foliage showing early occurring symptoms of bacterial ring rot on potato: shortened internodes and interveinal chlorosis (a). Symptoms of bacterial Ring Rot, showing the cheesy discolouration of the vascular tissue (b). (Photos (a) (b) Crown copyright, FERA. With permission)

Common Scab (*Streptomyces scabies*)

A commonly occurring tuber skin disease that infects potatoes wherever they are grown. Potato scab appears as superficial dark brown, patches that may be raised, with a wart-like appearance. When the infection is light, the lesions may affect just a small portion of the tuber surface, but severe infections completely cover it. Sometimes the ridged portions form broken concentric rings.

Common scab is not caused by fungus as often stated; rather the causal agent may be several soil dwelling plant pathogenic bacterial species in the genus *Streptomyces*, including *S. scabies* and *S. turgidiscabies* that can exist in the soil, either free-living or as spores. In particular, S. scabies has been well documented as the causal agent of scab lesions. These are members of a large grouping of bacteria known as actinobacteria (sometimes also referred to as actinomycetes). *S. scabies* infects young developing tubers through pores (lenticels) in stems, through wounds and directly through the skin. It invades the surfaces of potato tubers and the plant responds by growing corky scabs, which actually limit the spread.

Common scab is often characterized by this corkiness of the tuber periderm, but symptoms are extremely variable. Lesions may be very superficial or may penetrate up to several peridermal cell layers deep into the tuber surface and have been described as russetted, slightly raised, slightly pitted, or deeply pitted. At severe infection, 100 percent of the tuber surface may be affected by the light brown to dark brown lesions. Leakage from the affected tissue attracts insects and these may enlarge the lesions. This disease usually occurs in soils with pH values higher than 5.2 and is favoured by dry soil during tuberisation. There are over 400 members of the Streptomyces genus, so not surprisingly acid–tolerant *Streptomyces spp.* exist that cause symptoms indistinguishable from *S. scabies*.

Common potato scab is an efficient saprophyte that can survive either on the surface of tubers and on crop residues. *S. scabies* survives in the field between potato crops on volunteers, in fallen leaves and in the soil. The organism can survive for very extended periods in slightly alkaline soil but is rarely a problem in highly acid soils. Several transmission routes exist; infected seed tubers, wind and water. Fresh, un-composted manure will also spread the organism, since it can survive passage through the digestive tract of animals. Common scab does not spread tuber-to-tuber in store. Most spread is through infected seed that can lead to infection of daughter tubers and contamination of soil.

The symptoms of common potato scab are quite variable and are manifested on the surface of the potato tuber. The disease induces the formation of several types of cork-like lesions including surface raised and pitted lesions (Fig. 10a). Individual scab lesions are circular but may coalesce into large scabby areas (Fig. 10b). Lesions may be shallow and easily removed during peeling or deeply embedded in the surface tissue (Fig. 11)

Streptomyces scabies infects a number of root-grown crops including radish (Raphanus sativus), parsnip (Pastinaca sativa), beet (Beta vulgaris), carrot (Daucus carota), as well as potato. The disease occurs worldwide wherever potatoes are grown. Although scab does not usually affect total yields, increasingly the marketplace for potatoes requires quality as represented by skin finish. In this situation, the presence of scab lesions, especially those that are pitted, ruin the appearance and significantly lessen the marketability for both table stock and processing varieties.

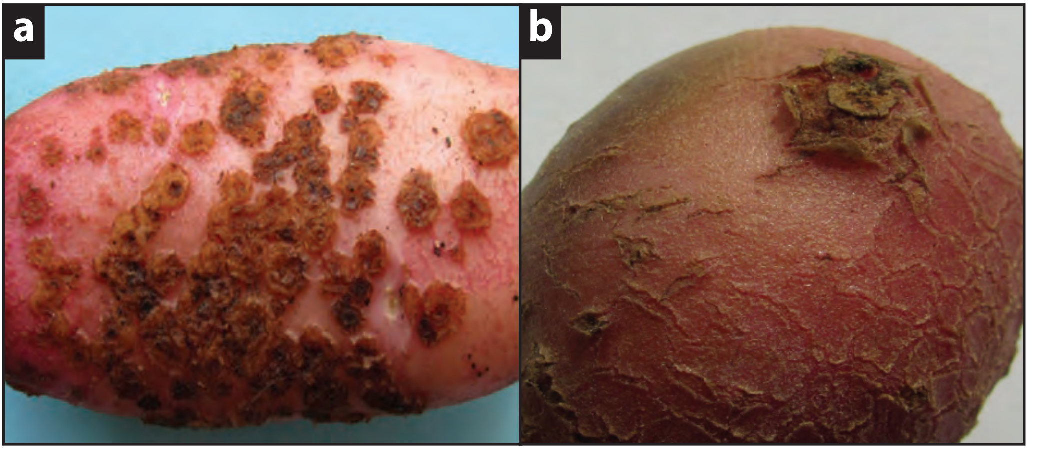

Figure 10.
Common scab lesions on tubers. (Photos © Author)

Figure 11.
Tuber displaying severe infection with common scab

Bacterial wilt (Potato Brown rot - Ralstonia solanacearum)

Bacterial wilt or brown rot is caused by *Ralstonia solanacearum.* Its one of the most damaging pathogens on potato worldwide and has been estimated to affect potato crop in 1.6 million hectares in approximately 80 countries with global damage estimates exceeding $1billion per year. This disease poses no risk to human or animal health. Worldwide, *Ralstonia solanacearum* has an extremely wide host range. However, the bacterium which affects potatoes, has a limited host range, but also affects tomatoes (*Lycopersicon spp.)* and the weeds *Solanum dulcamara* (Bittersweet) and *Solanum nigrum* (Black nightshade).

The disease first manifests in potato crops as wilting of the leaves at the ends of the branches during hot days, with recovery at night.

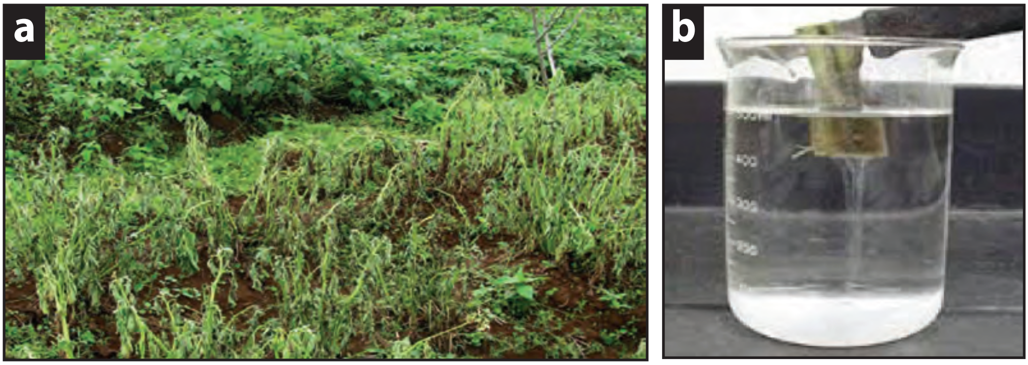

Figure 12.
Potato foliage showing wilt symptoms, foreground (a).
Infected stem showing bacterial ooze (b) (Photo (a) © Author. (b) © Cgiar)

The leaves assume a drooping habit, due to loss of turgidity, followed by total unrecoverable wilt (Fig 12a). In advanced stages of wilt, cut end of base of the stem may show dull white ooze on squeezing.

Note: *Bacterial wilt in the field can be distinguished from a fungal wilt by conducting a simple test. Obtain 3 to 6 cm long stem pieces from base of the stem showing wilt symptoms, dip the base end in clean water in glass tumbler, and allow it remain undisturbed for about one to two minutes. Observe for whitish thread like substance emerging from cut end into the water (Fig 12b). If wilt is due to bacteria, water in tumbler will soon become cloudy and turbid. The same test can also be carried out to visualise infection in the tuber.*

Potato seed tubers carry the bacterium in the vascular tissue, lenticels, and on the surface.

Under field conditions, plant infection usually occurs through the root system, especially through wounds. The pathogen can also enter through stem wounds or stomata.

As the disease develops, a streaky brown discolouration of the stem, 25mm or more above the soil line may be observed and the leaves have a bronze tint. Disease development rates is influenced by variety, but is favoured by warm temperatures (above 15^{0}C with optimum of 27^{0}C) and high soil moisture levels.

Once established in the xylem vessels, the bacteria can enter the intercellular spaces of the parenchyma cells in the cortex and pith in various areas of the plant. This impairs water flow throughout the plant; result in browning of the xylem and lethal generalized wilting of the plant

A cross-section of infected tubers often reveals a grey-brown discoloration of the vascular tissue, commonly referred to as the 'vascular ring'. As infection progresses, the discoloration may extend into the pith or cortex of the tuber. A milky-white sticky exudate or ooze, consisting of bacterial cells and their extracellular polysaccharides, are usually noticeable in freshly cut-sections of infected tubers.

Note. *This is best illustrated by: cutting the tuber in half, holding the cut pieces in their original position for a few minutes and then slowly moving them apart. Infected tubers will have fine, white, thread-like filaments extending between the cut surfaces*

R. solanacearum is primarily a soil borne and waterborne pathogen. No aerial spread of the pathogen has been reported. The bacterium can survive for days to years in infested water, wet soils or deep soil layers (> 75 cm), forming a reservoir of inoculum from which it can disperse. Because host resistance to R. solanacearum is limited, bacterial wilt is very difficult to control.

External symptoms may or may not be visible on tubers, depending on the state of development of the disease. Bacterial ooze often emerges from the eyes and stem end attachment of infected tubers (Fig. 13a). When the ooze dries, soil adheres to the tubers at the eyes.

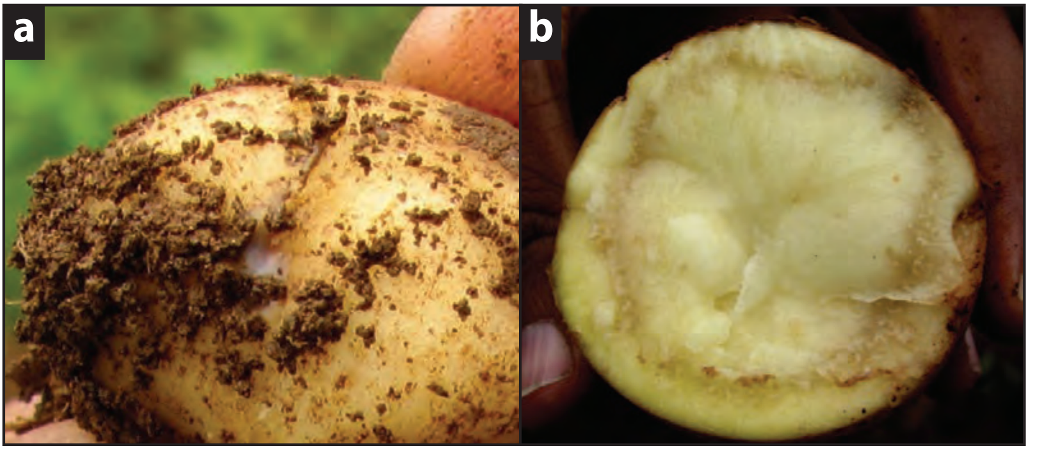

Figure 13.
Grey bacterial ooze emerging from a tuber eye (a). Bacterial ooze emerging from the vascular tissue of an infected tuber (Photos © Author)

In tubers, two types of symptoms are produced; they are vascular rot and pitted lesion on surface. In vascular rot, the vascular tissues of transversely cut tuber show water soaked brown circles and in about 2-3 minutes, dirty white sticky drops appear in the circle (Fig. 13b).

A second type of symptom is represented by lesions on the tuber. The lesions are produced due to infection through lenticels (skin pore). Initially, water soaked spot develop which enlarges in the form of pitted lesion. The tubers may not rot in storage and also may not show vascular browning.

Bacterial wilt is primarily spread by the planting of infected seed potatoes, but can also spread in soil and in irrigation water. The disease causes damage at two stages; (i) killing the standing plants by causing wilt and (ii) causing rot of infected tubers in storage and transit. Another indirect loss is spread of the disease through planting of healthy looking tubers harvested from infested fields. Bacterial wilt poses a serious restriction to seed and processing potato production.

Note: *The main risk associated with bacterial wilt infection is through contamination of the soil. There is no definitive evidence to state the duration of pathogen survival, once introduced to a field. Estimates vary widely – 3 to 5 to 10 years. Where insufficient land is available for extended rotation without potato, the disease causes extreme hardship, due to crop failure. Any effort, to implement strategies that will avoid soil contamination, is justified.*

Control of bacterial diseases in potato

Unlike fungal pathogens, there is no chemical control compounds for bacterial disease in potato. Control therefore relies on the four classical general disease control principles, exclusion, eradication, protection and resistance.

Exclusion: This principle is defined as any measure that prevents the introduction of a disease-causing agent (pathogen) into a region, farm, or planting. The basic strategy assumes that most pathogens can travel only short distances without the aid of some other agent such as humans or other vector, and that natural barriers like oceans, deserts, and mountains create obstacles to their natural spread. Unfortunately, exclusion measures usually only delay the entry of a pathogen, although exclusion may provide time to plan how to manage the pathogen when it ultimately arrives

Eradication: This principle aims at eliminating a pathogen after it is introduced into an area but before it has become well established or widely spread. It can be applied to individual plants, seed lots, fields or regions but generally is not effective over large geographic areas. Eradication can also be on a modest scale such as the removal of infected plants from the growing crop. Or, it can be the sorting and removal of diseased tubers after harvest.

Protection: This principle depends on establishing a barrier between the pathogen and the host plant or the susceptible part of the host plant. It is usually thought of as a chemical barrier, e.g., a fungicide, bactericide or nematicide, but it can also be a physical, spatial, or temporal barrier. The specific strategies employed assume that pathogens are present and that infection will occur without the intervention of protective measures. Protection often involves some cultural practice that modifies the environment, such as tillage, drainage, irrigation, or altering soil pH.

Resistance: Use of disease-resistant plants is the ideal method to manage plant diseases, if plants of satisfactory quality and adapted to the growing region with adequate levels of durable resistance are available. The use of disease-resistant plants eliminates the need for additional efforts to reduce disease losses unless other diseases are additionally present. Resistant plants are usually derived by standard breeding procedures of selection and/or hybridization. Selection of resistant plants involves subjecting plants to high levels of disease pressure and using the surviving plants as sources of disease resistance

Virus disease of potatoes

Introduction

Viruses are extremely small subcellular, (submicroscopic) infectious particles (virions). Plant viruses are obligate intercellular parasites, surviving in the symplast of their host and composed of nucleic acid core, within a protein coat that uses the host cellular machinery to replicate itself. Their genetic information is encoded in their nucleic acid, which typically specifies two or more proteins. Translation of the genome (to produce proteins) or transcription and replication (to produce more nucleic acid) takes place within the host cell and uses some of the host's biochemical "machinery". Since viruses do not capture or store free energy, functional activity outside their host is impossible. They are therefore parasites (and usually pathogens) but are not usually regarded as genuine microorganisms. Viruses can infect all types of living organisms including animals, plants, fungi, and bacteria, but most viruses infect only one type of host. Viruses cause many important plant diseases and are responsible for losses in crop yield and quality in all parts of the world. Viruses may cause latent infection, change in leaf colour, leaf deformations, stunting, death of foliage tissue, tuber necrosis and deformation

Potatoes are subject to infection by more than 30 virus diseases. All potato viruses contain a single-stranded RNA. Viruses are obligate parasites and infection of new hosts depends on assisted transmission. Different virus species can be transmitted by mechanical or biological means. Aphids transmit some 13 potato virus diseases. Virus may cause loss of yield, latent infection, change in leaf colour, leaf deformations, stunting, death of foliage tissue, tuber necrosis and deformation. There is no chemical capable of direct control of potato virus disease; various methods of indirect control must be employed. Developing a disease management strategy requires knowledge about the nature of viruses, sources of infection, means of transmission and detection and ways to avoid losses.

Table 4. A short list of major potato viruses

Virus	Transmission method	Type
Potato virus A	Aphid	Non-persistent
Potato virus M	Aphid	Non-persistent
Potato virus S	Mechanical and aphid	Non-persistent
Potato virus X	Mechanical	
Potato virus Y	Aphid	Non-persistent
Potato Leaf roll virus	Aphid	Persistent

Virus classification

The main viruses causing commercial loss in potato crops are presented in Table 4 and classified according to transmission method and persistence

Virus classification – method of transmission

Aphids cause greater economic damage to potato crops worldwide than defoliators or tuber pests. The primary importance of aphids is as virus vectors but at high population densities, they can cause direct plant injury and significant yield loss. Since potato viruses such as PVY are incapable of movement on their own, they require aphid vectors and mechanical transmission.

Mechanical transmission (also called sap transmission), allows PVY to spread by contact between infected and healthy plants resulting in short-distance spread of the virus. In order for this transmission to become effective a wound or other entry point is required. This can be caused by plant-to-plant contact resulting from wind movement-induced abrasion or human activity.

The most important method of transmission of PVY is the spread that occurs with the assistance of a mobile agent called a "vector." Here, the vector is an aphid. This can give rise to two methods of transmission.

Non-persistent virus transmission

- Feeding for several seconds on infected plant infecting its mouthparts.
- Aphid moves to a new plant and feeds on it, spreading virus
- The aphid remains infective for only a short time; approximately two hours

Persistent (circulative) transmission by aphids

- Aphid feeds on infected plant material for up to 30 minutes
- Incubation period of several hours once the virus has entered the aphid's body
- During this initial time the aphid cannot infect any plants
- The virus remains in the aphid's body for the rest of its life (e.g. Potato Leafroll Virus) and will infect subsequent plants that it feeds on.

Potato virus Y

PVY is an extremely damaging pathogen of potato crops worldwide. The causal agent of potato virus Y is a filamentous virus [genus Potyvirus and family Potyviridae]. The monopartite genome is composed of a single-stranded, positive-sense RNA molecule. Potential sources of the virus are infected seed tubers, volunteer plants and some weeds. The virus is transmitted mainly by winged aphid vector, but some mechanical transmission is also possible.

Details of PVY strains:

PVY^{O} is the original wild strain of PVY. The O stands for "ordinary."

PVY^{N}. The N stands for "necrotic," which means "dead." These strains cause a necrotic reaction on tobacco leaves but not on potato foliage. In fact, these strains of PVY usually cause milder symptoms in potato than those caused by PVY^{O}.

PVY^{NTN} is a PVY^{N} type that causes necrosis on tobacco but can also cause necrotic flecking and ringspot symptoms in the tubers of some potato varieties. The NTN stands for "n - tuber necrotic."

$PVY^{N:O}$ These strains are thought to be "recombinants," which means that they have some characteristics of both PVYO and PVYN.

PVY is a yield-limiting pathogen that can cause as much as 50 to 80% yield loss in heavily infected potato crops. The virus may also introduce post-harvest losses, resulting from tuber necrosis and reduced storage quality. Some potato varieties, once infected, can express symptoms in as few as 10 days. PVY infection induces symptoms that are variable and range from mild (foliar mottling, streaking, and mosaic) (Fig. 14a), to severe (leaf necrosis, leaf drop, and stunting). Factors such as cultivar, environmental conditions, and the strain of PVY infecting the plant will influence the severity of the symptoms. When infected with certain strains of PVY, tubers of some varieties are prone to develop the sunken necrotic lesions of potato tuber necrotic ringspot disease (Fig. 14b)

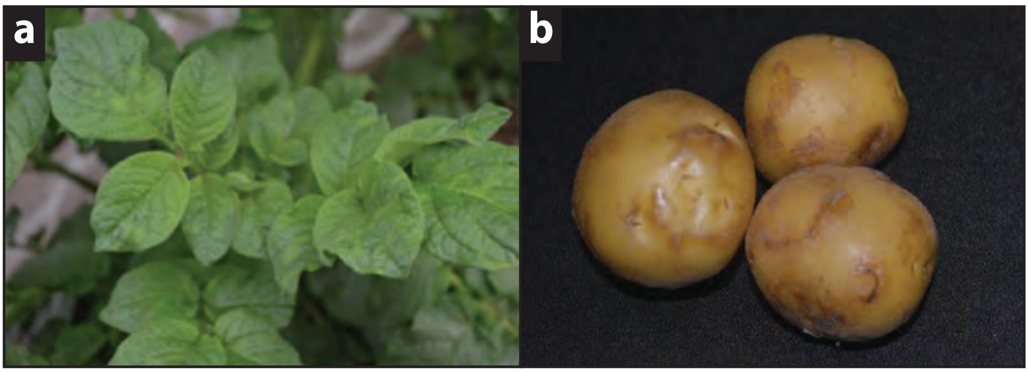

Figure 14.
Potato foliage showing symptoms of PVY $^{N:O}$ infection (a). Tubers from a PVY infected plant, showing lesions of potato tuber necrotic ringspot disease (b).
(Photos Courtesy F. Hutton, Teagasc)

PVY can currently be spread by many of more than 50 aphid species. With continuing research, this list is ever- growing.

A typical infection scenario – a winged aphid, free from virus, arrives on an infected plant; within minutes of starting to feed, the PVY particles become stuck on the aphid's mouthpart called a 'stylet'. If the aphid then moves to a healthy plant and soon starts to feed, the virus particles are transmitted to the healthy plant. This process is termed "stylet borne" or "non-persistent" transmission. This manner of transmission requires that the virus is present in high concentrations in the outer cell layers within the leaf. This method of transmission is referred to as "nonpersistent", because the virus only remains viable on the aphid's mouthparts for a relatively short time, usually less than

2 hours. To reacquire the virus, the aphid must repeat the feeding activity on another infected plant.

As the infected aphid moves to probe the leaves on a healthy plant and infects it with the virus particles, there is no latent period between acquisition and inoculation; the entire transmission process takes just minutes. Since the aphid may loose its infectivity after several probes, growing a non-host plant such as maize growing near potatoes can attract aphids and while probing the maize leaves the virus particles will be removed.

This non-persistent mode of transmission favors aphids, which probe frequently and move quickly from plant to plant, alate (winged) individuals of species that sample many plants including potato. A small number of aphids can spread the virus to a large number of plants quickly as they search for a suitable host plant to colonise.

When PVY infects the potato plant, it replicates by assuming control of some of the plant's proteins and enzymes (its cellular processes) to produce further copies of itself.

In potato and its wild relatives, two types of resistance genes against PVY have been identified; Ry genes that confer symptomless extreme resistance and Ny genes. The Ny genes induce a hypersensitive response, visible as local necrosis that may also be able to prevent the virus from spreading under certain environmental conditions. The potato cultivar Sárpo Mira originates from Hungary and is highly resistant to PVY, although the source of this resistance remains unknown

Potato Virus X

Potato Virus X (PVX) is a plant pathogenic virus [family Alphaflexiviridae; genus Potexvirus], and is the most common cause of mild mosaic. PVX is found mainly in potatoes; it is readily sap-transmissible, which ensures that it is transmitted mainly by mechanical contact. PVX has no insect or fungal vectors. This virus causes mild or no symptoms in most potato varieties, but the virus can cause symptoms of chlorosis, mosaic, decreased leaf size, and necrotic lesions in tubers. PVX can interact with PVY and PVA and synergy between these two viruses causes more severe symptoms and yield loss than either virus alone. The source of this virus is infected tubers. Tobacco, pepper, and tomato can also serve as hosts of PVX.

Spread occurs through either direct contact (between plants) or indirect contact (by man or machinery) when passing through the crop. It can remain infective on clothing and machinery for several weeks if kept damp. Sanitize all tools, rogue infected plants, and limit within-field movement.

While some varieties are more resistant to PVX than others, planting certified seed is the most important way to limit infection by this virus. Virus X occurs widely in many potato varieties and is cause many of the uncertainties and difficulties encountered in field inspections, because the production of leaf symptoms by many strains depends on the weather. Also, the predominating virus strain in a stock may change from season to season.

Figure 15.
Potato leaves showing symptoms of virus X infection. (Photo courtesy F. Hutton, Teagasc)

Potato Virus M

Potato virus M (PVM), [family Flexviridae; genus Carlavirus]. PVM is considered to be one of the most common potato viruses distributed worldwide and an economically important pathogen of potato. PVM can cause a yield reduction in potatoes between 15% and 45%. Infection in some regions is severe and in some cultivars may attain 100% infection. Transmission is by aphids in a non- persistent manner and also by mechanical inoculation with sap from young leaves. PVM infection manifests as, mottle, mosaic, crinkling and rolling of leaves and stunting of shoots; it may induce symptoms referred to as paracrinkle. These viruses are considered most important when they occur as mixed infections with other viruses.

PVM infection of potato plants induces symptoms that are similar to those caused by several other common potato viruses including Potato virus S (PVS, Carlavirus), Potato virus X (PVX, Potexvirus) and the common strain of Potato virus Y (PVYO, Potyvirus). Factors such as potato cultivar and PVM isolate will greatly influence the severity of the symptoms. Planting PVM-free potato seed tubers is a practical and important way to limit the spread of PVM and to control the disease caused by the virus.

Ideally seed potatoes would be screened for various viruses including PVM and the total virus incidence must be lower than an acceptable level (e.g. 5%). The predominant method employed for large-scale screening and the detection of PVM in potato samples is enzyme-linked immunosorbent assay (ELISA).

(**Note:** *when using ELISA, to screen for the presence of PVM, tuber dormancy must be broken and the sprouts used to detect PVM. This is to avoid false negative results, associated with the low PMV titre, detected in dormant potato tubers.*)

Potato Virus S

Potato virus S (PVS); [family Betaflexiviridae; genus Carlavirus] is a widely distributed latent virus and one of the most common potato viruses found infecting production worldwide. Two strains of PVS have been recognised PVS^O (ordinary) and PVS^A (Andean). Whereas PVS^O occurs world wide, there is no evidence of spread of PVS^A outside the Andean region. Susceptible species belong mainly to the families *Solanaceae* and *Chenopodiaceae.* PVS is transmissible by inoculation with sap from young fully expanded potato leaves but not from older leaves. Symptoms observed on infected potato leaves include slight chlorosis, roughness of the surface and undulation of the margin.

Potato plants infected with PVS do not always display symptoms but nonspecific symptoms have been described, including chlorotic mottling of the leaves and rugosity on the lower leaf surface.

A range of aphid species, including *Myzus persicae*, *Rhopalosiphum padi*, *Aphis fabae,* and *A. nasturtii* are considered to be capable of transmitting the virus in a nonpersistent manner; but mechanical transmission and vegetative propagation have also been associated with virus spread.

The presence of PVS and Potato virus X has been reported to produce a synergistic effect and to reduce potato yields by up to 20%. There is research evidence to show that leaves of potato varieties, resistant to late blight (*Phytophthora infestans*) loose this resistance if they are already infected with PVS.

Potato virus A

Potato Virus A (PVA) is a plant pathogenic virus [family Potyviridae; genus Potyvirus], which causes a mild mosaic on potato plants. PVA shares a number of characteristics with PVY and they both belong to the same virus group. PVA only infects potatoes and is one of the most widespread potato viruses being found in most potato growing areas. Aphids transmit the virus, in a non-persistent manner. Infection with PVA may lower yield only slightly.

Symptoms show a mild pattern of yellowish or light green patches alternating with patches of very dark green on most potato cultivars. The patches vary in size and can cross veins. The leaf surface is usually rougher than normal. These symptoms may be accompanied with slight crinkling on potato plants with mild mosaic. Edges of infected leaflets may be slightly crinkled or wavy. Infected leaves usually look shiny. Margins of affected leaves may be wavy, and leaves may appear slightly rugose (i.e., rough) where veins are sunken and interveinal areas are raised. The stems of the plant bend outward, giving the plants an open look.

Severity of symptom expression depends on environmental factors such as the potato cultivar, and the strain of PVA, weather conditions; the most pronounced symptoms appear in cloudy weather.

Viruses X, A and Y all may induce symptoms of light yellow mottling or mosaic. The presence of more than one of the viruses in a plant usually affects the types of symptoms and increases symptom severity. Symptoms caused by different viruses can be similar, so the type of virus usually cannot be identified by symptoms alone. Field diagnosis is often limited to mosaic virus. Positive identification requires the use of indicator plants or serological techniques

Tubers are usually unaffected, except for a slight decrease in size. Many varieties reportedly react to infection with hypersensitivity (field resistance) as mentioned under PVY. Control of this aphid-transmitted virus disease is through the use of disease-free seed, insecticides, and resistant varieties.

Potato Leaf Roll Virus

Potato leafroll virus (PLRV), is a phloem-limited virus [family Luteoviridae; genus Polerovirus] induces huge losses in potato crops worldwide. The virus is transmitted by aphids, in a persistent and circulative manner. PLRV is restricted to the vascular tissues of the plant, and only aphids are capable of transmitting this virus.

PLRV transmission is termed persistent, i.e., acquisition and inoculation take hours, and is favored by deep feeding in the phloem tissue. An aphid feeding on an infected plant, for a long period, will ingest the virus along with the phloem sap. After ingestion, the virus is actively transported through the epithelial cells to the hemocoel by receptor-mediated endocytosis and exocytosis. The virus particles are retained in an infective form in the hemolymph of the aphid. When the virus particles contact the basal lamina of the accessory salivary gland, they may be transported through the underlying plasmalemma into the salivary canal. From here, they are excreted with the saliva, while the aphid feeds on another (healthy) plant.

PLRV is a persistent virus, which means that an aphid acquires it from an infected plant, only after a feeding for at least 30 minutes and it may take a period of several hours. Transmission by the aphid is then delayed for several hours because the virus has to pass through the digestive system of the aphid and replicate in its salivary glands before transmission may occur. When an aphid acquires the PLR virus it will remain infective throughout its life.

Relatively few aphid species transmit PLRV; the major vector is *Myzus persicae*, the peach-potato aphid. The symptoms of ***primary infections***, which can occur in the season of virus transmission, but which are not regularly observed, are an upward and inward rolling of the young leaves (Fig. 15a). Sometime a purple tint, starting at the margins, is evident on the leaves. The virus then moves, with assimilates, to the developing daughter tubers. Plants infected close to harvesting may show no symptoms.

When seed tubers infected with PLRV are planted and the shoots emerge, the ***Secondary infection*** (seed tuber-borne) symptoms of infection are readily visible on young plants. The symptoms appear first as a rolling of the older, lower leaves, (*not the upper leaves as with primary infection)*. The leaves become stiff, dry and leathery, through abnormal accumulation of starch (Fig. 15b). Infected plants are stunted, and produce fewer leaves and smaller tubers.

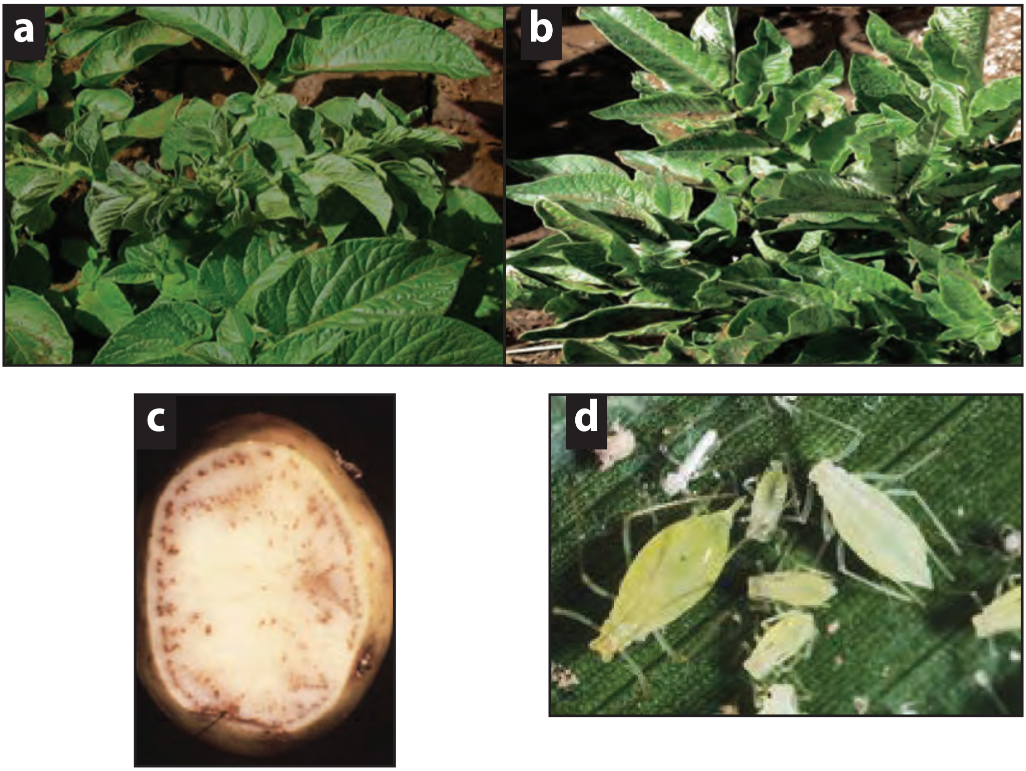

Figure 16.
Potato plant showing symptoms of primary PLRV infection, rolling of young leaves (a). Secondary infection – rolling of older leaves (b). Infected tuber showing net necrosis symptoms (c). Potato aphid, wingless adults and nymphs (d). (Photos (a, b) © Author (d) © Regents of the Univ. Calif. With permission)

Symptoms of PLRV include a characteristic upright character and rolling of the leaves, chlorosis (yellowing) or reddening, leaves with a leathery feel, phloem necrosis (dead spots along the leaf veins), stunting (reduced height) of the plant, and net necrosis in tubers (Fig. 16c).

Management of the Potato Leafroll Virus can be achieved with insecticide applications because this virus transmission process is much more complex and requires a great deal more time than PVY transmission.

In contrast to aphid acquisition of virus Y where they merely need to probe the outermost leaf cells, to acquire the PLR virus, aphids must probe deeply enough to feed on the plant's vascular tissues. Then after the virus has been acquired, another 24 to 48 hours are required to permit it to circulate through the aphid's body before it can transmit the virus. Because of the long feeding time required to ingest the virus, the aphid can also ingest a lethal dose of an insecticide, which has been applied to the foliage. Eliminating the aphids can be an effective method to prevent the spread of PLRV.

Containment and control of potato virus spread

Note: ***Plant viruses cannot be directly controlled by chemical application.***

The major means of control (depending on the disease) include:

Chemical or biological control of the vector (the organism transmitting the disease, often an insect): this can be very effective where the vectors need to feed for some time on a crop before the virus is transmitted (e.g. PLRV above). Insecticides are much less effective where transmission occurs very rapidly (e.g. PVY above) and may already have taken place before the vector succumbs to the pesticide.

Growing resistant crop varieties: whereas for some crops, plant breeders have been able to exploit sources of natural resistance to certain viruses, for many other crops, no such resistance has been discovered. Recently researchers have found that incorporation of part of the virus genome into the host plant may confer a substantial degree of resistance. While this transgenic resistance has shown considerable promise, the technology is controversial, and there is no certainty that it will be adopted widely.

Use of virus-free planting material: in vegetatively propagated crops (e.g. potatoes) where viruses are transmitted through seed, it is possible through tissue culture-derived clean seed and rigorous implementation of seed certification schemes, to ensure that the planting material is virus-free. Planting seed tubers with more than 10% level of infection can result in yield and quality loss in the progeny crop. Tuber yield is rarely affected by current season inoculation of PLRV by aphids (defined as primary infection), whereas primary infection with PVY can increase the number of undersized tubers. Potatoes are least susceptible to virus infection when plants are senescing and most susceptible during the vegetative stage before flowering.

Exclusion: the prevention of disease establishment in areas where it does not yet occur. This is the *raison d'etre* of plant quarantine protocols both local and worldwide

Aphids are regarded as pests both because they transmit plant viruses and also cause direct feeding damage. Like all living organisms, they have survived over millions of years though their capacity to adapt to changes in their environment. A recent example of such adaptation is their acquired ability to cope with insecticides, which hitherto were effective in controlling them

Insecticide Resistance

What causes insecticide resistance? Resistance mechanisms can be divided into two main categories:

Metabolic

Pests, which have acquired this type of resistance, synthesise increased amounts of certain enzymes that break down or detoxify insecticide molecules before they reach their target sites (which are primarily located in the insect nervous system). Resistance to the organophosphate group of insecticides in *Myzus persicae* is achieved through overproduction of enzymes called esterases. The effectiveness of the carbamates and pyrethroids are also reduced by this mechanism, but not as effectively. The amount of esterase synthesised by individual aphids can vary considerably. This leads to a classification of aphids as being either **S** (susceptible), **R1** (moderately resistant), **R2** (highly resistant) or **R3** (extremely resistant).

Target site

Pests acquired this type of resistance, through developing a mutation in the protein that insecticides normally bind to and inactivate; rendering them no longer sensitive to the insecticidal effect of the chemical.

Three target site resistance mechanisms are known to exist in *Myzus persicae*:

MACE (Modified Acetyl Choline Esterase): confers strong resistance specifically to some dimethyl-carbamates. Pirimicarb is the only insecticide approved in some countries that is affected by MACE resistance. Aphids are categorised as either MACE or non-MACE.

Knockdown resistance or kdr: this can arise through one of two genetic mutations, usually denoted as 'kdr' and 'super kdr'. They are associated specifically with resistance to pyrethroids. Aphids are categorised as either kdr or non-kdr (kds, knockdown susceptible).

Neonicotinoid Resistance (Nic-R++): Aphids possessing this characteristic will have strong resistance specifically to the Neonicotinoid group of insecticides.

Insecticide Choice

(Note. *The choice of insecticide will be dictated either by Government Regulations or commercial availability in individual countries. It is therefore outside the scope of this document to present specific advice as to the compound that might be applied. However general principles guiding insecticide choice are presented. Application advice is not provided and should not be inferred.)*

The choice of insecticide to control *Myzus persicae* will be dictated by the resistance mechanism in the aphid. From the list of active compounds (Table 5) and formulations it should be possible to select a product to provide effective control of aphids. Because individual *Myzus persicae* have now acquired all three resistance mechanisms outlined above, the OPs, carbamates and pyrethroids are now ineffective. However, the compounds employing the newer chemistry are still effective. This benefit will not persist, unless the compounds are used with care and the guidelines designed to avoid the development of resistance, rigorously adhered to.

Table 5.
A list of insecticides for possible use to control aphids in potato crops

Active Compounds	Group	Product examples	Mainly resisted by
Chlorpyrifos	Organo- phosphorous (OP)	Dursban WG & generic equivalents	Carboxylesterase R_1, R_2. R_3
Cypermethrin	Pyrethroid	Various products	kdr
Zetacypermethrin	Pyrethroid	Fury 10 EW; Minuet EW; Symphony	kdr
Lambda cyhalothrin	Pyrethroid	Hallmark and similar generics	kdr
Pirimicarb	Dimethyl carbamate	e.g. Aphox & similar generics	MACE +Carboxylesterase R3
Pirimicarb + Lambda-cyhalothrin	Dimethyl carbamate + Pyrethroid	Dovetail & similar generics	MACE +kdr
Pymetrozine	Pyridine azomethine	Plenum WG	None
Nicotine	Nicotine	No-Fid	None
Acetamiprid	Neonicotinoid	InSyst	None
Thiacloprid	Neonicotinoid	Biscaya	None
Thiamethoxam	Neonicotinoid	Actara	None
Flonicamid	Selective feeding blocker	Teppeki	None

General advice on application of insecticides:

- In order to prevent the development of resistance, which will result in control failure, growers should follow best practice and keep insecticide applications to the minimum necessary for preventing economic loss.
- Growers should always follow label advice on resistance management, including any restrictions on use and alternation with other chemical or non-chemical control methods.
- Over-use of Neonicotinoid, pymetrozine or Flonicamid is likely to lead to development of resistance to these products. Because of this, never exceed the specific restrictions on the number of applications.
- To prevent or delay resistance to insecticides, potato growers must rotate the use of insecticide having different mode of action. Insecticides are classified by their mode of action to assist growers determine what product employs what mode of action. This information is contained in the list above.
- Do not make repeat applications of any insecticide if it appears not to work at full rate and it has been applied correctly; use an alternative, which has a different mode of action. If necessary, seek guidance from your advisor or crop expert.
- Do not apply insecticides at less than the recommended rates; this can lead ultimately to an increase in resistance problems.
- Follow any label guidance (or other technical literature) on resistance management strategies.

Summary

- Since the potato crop is infected by bacterial, fungal and viral diseases also infested by parasitic nematodes, the yield potential of the potato crop can only be realised if diseases and pests can be controlled.
- Because fungal pathogens are equipped with long-term survival structures that persist in the soil, the due to the difficulties in reducing inoculum and lack of good sources of resistance, all serve to frustrate attempts to improve control of these pathogens.
- Several soil-borne fungal pathogens continue to cause problems in potato production worldwide, examples being Verticillium dahliae, Rhizoctonia solani, and Spongospora subterranea
- A further group normally considered as tuber-borne, including Colletotrichum coccodes, Helminthosporium solani and Fusarium species also induce losses.

Various bacterial pathogens attack potato plants and tubers. These pathogens include Erwinia, Corynebacterium, Pseudomonas, Ralstonia and Streptomyces.

- While there have been significant advances in the molecular biological strategies to help understand the major aspects of virulence mechanisms, the information is not sufficiently useful to allow us to intervene rationally in these bacterial potato diseases.
- Currently the only defence against bacterial pathogens is the application of standard husbandry practices.
- Because potatoes are a vegetatively propagated crop, several viruses are disseminated in tubers.
- While infection is rarely lethal, viruses generally reduce plant vigour; yield and tuber quality and they affect the current, as well as future, generations of the plant.
- The method of virus transmission will determine the effectiveness of insecticides to control the vectors.
- The control of M. persicae on many crops has relied almost exclusively on the use of chemical insecticides, and their intensive use over many years has led to populations, which have developed widespread and multiple forms of resistance.

Summary Continued

- Some 10 different chemical classes of insecticides utilizing six different modes of action can potentially be used to control M. persicae infestations, but half of these modes of action can be overcome by known metabolic and/or target-site resistance mechanisms.
- To ensure effective and sustainable control of this pest it is important to identify and exploit simultaneously all the insecticide classes that are approved and known to be effective.
- Unless the new insecticides are used intelligently, insect resistance will also develop and render them ineffective

Sources accessed in the preparation of this section.

Johnson, D. A. and Dung, J. K. S.(2010) 'Verticillium wilt of potato - the pathogen, disease and management', *Canadian Journal of Plant Pathology*, **32:** 58 — 67

Merz, U. & Falloon, R.E. (2009), Review: Powdery Scab of Potato—Increased Knowledge of Pathogen Biology and Disease Epidemiology for Effective Disease Management. *Potato Res.* **52:** 17.

Nolte, P., Alvarez, J.M. and Whitworth, J.L. (2009). Potato Virus Y Management for the Seed Potato Producer. Publ. Univ. Idaho, Ext. Service. https://www.cals.uidaho.edu/edcomm/pdf/CIS/CIS1165.pdf

Pérombelon, M.C.M. (2002) Potato diseases caused by soft rot Erwinias: an overview of pathogenesis. *Plant Pathology,* **51**: 1–12.

Tsedaley, B. (2015). A Review Paper on Potato Virus Y (PVY) Biology, Economic Importance and its Managements. *Journal of Biology, Agriculture and Healthcare*. **5:** 110-126

Section 12.

Canopy senescence.

Introduction

In the literature, various workers have divided the life cycle of the potato into a range of growth phases. In the following example the growth cycle of the potato crop has been divided into four phases:

Phase 0 – between planting and emergence- sprout growth depends completely on soil temperature (**Sections 5 and 7**).

Phase 1 extends over the period from emergence (taken as the time of 50% emergence) to tuber initiation (**Section 9**). The duration depends on plant development rate.

Phase 2 encompasses the period between tuber initiation and the period when 90 to 100% of daily assimilates are partitioned to tubers – this phase is often referred to as the tuber bulking phase (**Section 10**). The duration depends on relative tuber growth rate; the factor that determines partitioning of assimilates between tubers and the other plant constituents.

Phase 3 – maturity, the duration depends on the rate of leaf senescence and the cessation of crop growth

Defining potato senescence

A definition of potato senescence is not readily available as different sections of the potato production and processing sectors have different viewpoints and different requirements.

The grower accepts senescence as the onset of canopy yellowing and cessation of tuber growth. The processor might look to declining levels of sucrose and reducing sugars in the tuber and other processors might require increasing levels of dry matter, reflected in higher specific gravity values.

Canopy senescence

During senescence, potato leaves undergo changes in colour as a result of changes in the content and proportions between individual pigments. The change in colour in senescing leaves is related to the preferential degradation of chlorophyll over carotenoids, which results in yellowing (Fig. 1).

Figure 1.
The progress of senescence on a potato leaf. (Photo © Author).

At canopy senescence the vines turn yellow and lose leaves, photosynthesis gradually decreases, tuber growth rate slows and the vines die. This stage may not occur when growing a long season variety in a production area with a short growing season as early frost may defoliate the plants while the leaves are still green. When a variety has the opportunity to complete this stage and there will be almost nothing left of the plant but decayed stems and leaves when it is time to harvest the potatoes.

Over the course of their lifespan, potato leaves undergo a series of developmental, physiological and metabolic transitions that culminate in senescence and death.

Three broad phases of development are recognised in the life of a leaf. Initially, it undergoes a phase of rapid expansion. It is a net ***importer*** or sink - importing carbon and nitrogen and undergoing rapid protein synthesis until its full capacity for photosynthesis is reached.

Next the mature leaf becomes a ***donor*** - contributing a supply of assimilates to the tubers and other plant parts. During this stage, protein turnover is minimal. This stable condition persists until either internal signals or unfavourable external conditions initiate the onset of senescence.

In the final stage of development the leaf becomes a ***source*** - leaf senescence is defined by the structured mobilisation of nitrogen, carbon and minerals from the mature leaf to other parts of the plant. It is now recognised that leaf senescence is a genetically programmed step, highly complex and tightly controlled by multiple layers of regulation.

Senescence involves coordinated action at the cellular, tissue, organ, and organism levels under the control of a highly regulated genetic program. It follows an ordered sequence of events, involving decline and cessation of photosynthesis, disintegration of chloroplasts, degradation of chlorophyll, catabolism of leaf proteins, and removal of amino acids.

Leaf senescence however is not a 'wasteful death', since it allows for the degradation of macromolecules and the conservation of the valuable cellular building blocks that are produced during the growth phase of the leaf followed by their redistribution to augment the requirement of stems leaves, roots or tubers.

Senescence has a vital role in the potato plant because of the associated remobilization of nutrients, especially nitrogen, and, to a lesser extent, phosphorus, sulfur, and other elements. Senescence is one step in a program that specifies cell fate. It is activated by different stimuli in tissues and organs. We should not confuse senescing and dead tissue - senescing tissue continues to function, whereas dead tissue does not, and there is a stepwise progression between the two states.

Effect of leaf age

If it is accepted that there is a relationship between the amount of radiation intercepted and tuber yield, it follows that this relationship will be influenced by the duration of maintenance of an intact canopy. The canopy is composed of individual leaves and studies have examined the life span of leaves. It has been observed that the middle leaves on the mainstem had the longest life span and typical life spans varied between 30 and 100 days, with leaf position and nitrogen treatment having major influence on duration.

The change, during age, in the capacity of leaves to assimilate carbon has also been investigated with the highest photosynthetic rates occurring in newly matured leaves and that the rates declined as the leaves aged. However the potato crop, in common with other vegetative crops is largely indeterminate and in all but a few highly determinate cultivars, new leaves are produced throughout the growing season, thus maintaining canopy integrity despite the loss of individual leaves. This feature enabled the demonstration of a significant correlation between percent ground cover and intercepted radiation. Studies have sought to explain yield responses due to nitrogen application levels and considered that the yield differences were due to variations in canopy longevity resulting in different amounts of radiation being intercepted. Furthermore, the yield response to nitrogen was mediated in terms of an increase in the length of the period of full ground cover

The effect of low and supra-optimal levels of nitrogen on canopy expansion and duration was examined. It was found that under a high nitrogen regime, apical and basal lateral branch formation was stimulated by values from 5 to 20-fold and nitrogen redistribution towards the end of the season allowed growth to continue in these branches, thus maintaining a photosynthetically active canopy for longer than in the N-deficient plants. In another study where no nitrogen fertiliser was applied, it was observed that the nitrogen requirements of the tubers was met by translocation from the tops and the roots, resulting in premature senescence, with consequent reduced tuber growth rates. Late season growth, primarily from translocation out of the vines and into the tubers, can account for 10-15 percent of the final yield of the crop.

The potato mainstem typically forms 15 - 18 leaves. The number is increased by increasing nitrogen levels and reduced by increasing mainstem density, due to competition for assimilates and light. Leaf duration or life span increases with increase in leaf insertion until leaves 12-13 on the mainstem and then slowly declines. The leaves in the middle order of the main stem have the largest area and live the longest. When a potato crop was grown under three nitrogen regimes, leaves of the highest (N3) treatment showed systematically longer life spans than leaves of the NI and N2 treatment in the order of 3 weeks.

Potato leaf senescence is considered the final stage of leaf development and is a genetically programmed process, with the leaf cells dying in an organized, predetermined way controlled by the nucleus. Since senescence is under genetic control it requires differential expression of specific genes. Senescence is highly regulated, with recycling of reserves from leaves to other organs. The initial steps involve nutrient salvage while the process ends with cell death. Molecular studies show that primary steps towards senescence are taken when leaves are fully expanded. Leaf cells then commence a genetically programmed self destruction process that involves protein degradation, and altered rates of turnover, nucleic acid degradation, lipid degradation, membrane disruption and leaf pigment breakdown. The process is visible, with necrosis of leaf cells or discolouration caused by chlorophyll degradation, and the process is terminated with the death of leaf cells.

Leaf senescence can be considered a conservation step since the degradation products are transported out of the leaves to other parts of the plant. The senescing leaf now assumes the role of nutrient source for the whole plant, but at the expense of its own ability to survive.

Onset of canopy senescence

For the potato leaf the active life span is the period of time between leaf appearance and yellowing of the leaf. Leaf duration is measured on the time axis by the difference between active and senescent leaves. A leveling off in growth rate starts when

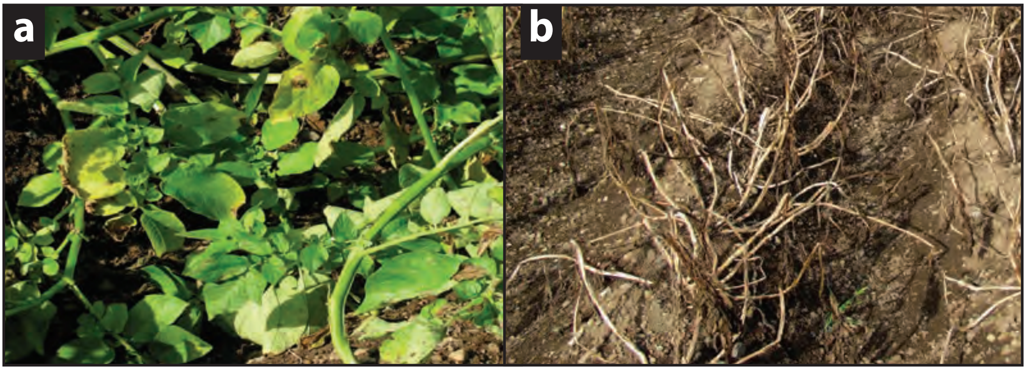

Figure 2.
Onset of canopy senescence – leaves pale green to yellow (a).
Complete canopy senescence – no green tissue surviving, (b). (Photos © Author)

senescence of leaves proceeds to the upper layers of the crop canopy. Vegetative crops, like potatoes, can maintain a photosynthetically active canopy by replacement of older leaves by new ones.

Potato leaves have a potential lifetime of 70 days, this represents about half of the lifetime of the crop. When leaf longevity is expressed as thermal time, the average leaf, well supplied with minerals and water, will accumulate about 1000 day-degrees. In early maturing cultivars, where the tubers compete aggressively for assimilates and nitrogen, leaf life span is reduced.

In monocotyledonous plants, after full expansion of the last leaf, only senescence occurs. Whereas wheat grains only grow during canopy senescence, potato tubers grow during canopy expansion and senescence. Senescence may follow a synchronous pattern or a progressive pattern.

Synchronous or progressive senescence

Simultaneous or synchronous senescence is more commonly associated with deciduous trees – where all the leaves turn yellow and fall almost simultaneously. It is not a common phenomenon in potato unless when the crop is subjected to severe stress, such as extended water logging around the roots. The normal response in potato is progressive or sequential senescence where the tips of main shoot and branches remain in a meristematic state and carry on to generate new buds and leaves while the older leaves at the base of the stem begin to yellow – often due to shading as new layers of leaves are formed above (Fig 1).

The senescence process has many advantages for the plant – the old, functionally inefficient leaves are discarded, while new functionally efficient leaves are created. Senescence ensures recovery and reutilization of mineral elements due to remobilization of mineral nutrients and organic substances from older senescing leaves to the newly formed growing leaves. The falling leaves add to the humus content in the upper layers of the soil.

Progressive senescence

The senescence process starts right after canopy closure from bottom to upper leaves. Initially this has no impact on plant growth. Experiments to measure the impact of environmental constraints on the onset of senescence observed little effect of treatments at the beginning, but increased considerably late in the season.

Leaf senescence and nitrogen supply

It is axiomatic that maintaining a green canopy and delaying the onset of senescence will permit an extension in the duration of tuber bulking with a concomitant increase in tuber yield. A study conducted to investigate the effect of large applications of N on patterns of canopy growth, observed stimulation of growth of leaves at the top of the stem, particularly lateral branches, for longer during the season. However this strategy accelerated the decline of leaves at the base of the canopy due to shading by the dense upper layers.

N deficiency can substantially reduce tuber yield, whereas excessive N application can extend canopy duration, delay tuber maturity at early harvest, lower tuber quality. Growing tubers have minimum demand for N and they will take this even if it is at the expense of green leaf area expansion or the acceleration of senescence. Available nitrogen is partitioned within the growing crop according to a ranking of requirements. With the commencement of tuber growth, the first priority for N goes to tubers, to maintain their minimum nitrogen requirement of 0.8% by mass. With such a high demand from tubers, premature canopy senescence can be induced as N is remobilized to satisfy tuber demand.

In a study, nitrogen fertiliser was applied either at zero rate or at rates in excess of normal plant requirements. In the plants receiving excess N, the N contents of leaves, stems and tuber were increased. When the potato plant took up the excess N from the soil it was stored in the leaves at the majority of positions on the stem, in the reduced (NH_2) form but in the oxidised form as nitrate (NO_3^-) in the lowermost leaves. The stems also acted as a storage site for substantial quantities of N in the NO_3^- form During the phase of maximum growth, this excess N was treated like a storage pool but then as growth declined towards season end, the stored N was redistributed, with lateral branches becoming major recipients. By contrast, very little N was redistributed from the leaves of N-deficient plants.

The mechanism of redistributing N from the areas of the canopy, which contain adequate to excess N, towards areas such as lateral branches extends their growth and maintains photosynthetically active leaves for longer than N-deficient plants. But this strategy must be adopted with caution since an optimal nitrogen supply ensures unrestricted growth by maintaining the ability of the canopy to intercept PAR, while an excess delays, maturity and increases the risk of infection by pathogens. A yield of tubers that is close to potential and the best quality tubers are produced when the nitrogen supply matches the requirement of the crop over the duration of the growing season.

In a fertiliser response trial, nitrogen applications increased the LAI through increased size and number of leaves. The LAI remained below the critical leaf area, 4.0 in the low nitrogen treatments throughout the growing season, and the crop reached maturity 2 weeks and 1 week before the high and medium nitrogen treatments respectively. By contrast, LAI in the medium and high nitrogen treatments remained well above the critical LAI during most of the tuber-filling period. Nitrogen application delayed canopy senescence.

The role of endogenous plant hormones in leaf senescence

The endogenous plant hormones, cytokinin and ethylene play important roles in the regulation of the onset of senescence. Exogenous application of cytokinins or an increase of the endogenous concentration delays senescence and facilitates nutrient mobilization. Therefore while increasing cytokinin production could delay leaf senescence, reductions in endogenous cytokinin levels resulted in accelerated senescence.

Ethylene is a plant hormone frequently associated with senescence. Plants produce ethylene in response to many stresses, such as wounding, radiation, temperature, water, CO, insect infestation, pathogen attack, toxic metals, herbicides, and air pollution. This would appear to implicate ethylene in signal transduction pathways that initiate stress responses in plants. While the relationship between ethylene and senescence is well understood, ethylene alone may not be sufficient to induce senescence. Ethylene (C_2H_4) activity is not confined to the senescent stage of plant development but rather regulates many diverse plant processes during all the development stages. Ethylene content is high during the first phases of leaf development, declines when the leaf reaches full expansion and increases again during leaf senescence.

Ethylene is well established as a dominant hormone in regulating the onset of leaf senescence and whereas ethylene promotes senescence, it is not an essential ingredient for the senescence syndrome induced by other factors (e.g. abscisic acid). Ethylene increases chlorophyll degradation by increasing chlorophyllase gene expression. Chloroplast membranes loose their integrity and allow chlorophyllase to come in contact with chlorophylls. The role of ethylene during leaf senescence is well understood and while blocking ethylene in sensitive plants delays leaf senescence, this is a temporary response. Once the senescence process commences, its progress is not reliant on an ethylene-dependent pathway.

Effect of canopy senescence on the duration of tuber bulking

Ultimately all potato canopies undergo senescence but premature senescence can result from an array of causes such as drought, nitrogen deficiency and soil borne nematodes. Senescence is an integral part of plant growth, with leaves senescing naturally at the end of their life cycle due to mutual shading, or inadequate supply of nutrients.

An agronomic strategy to maximise yield would therefore be dedicated to sustaining the duration of an optimum degree of ground cover. Within the literature there is a considerable debate regarding the magnitude of the value of LAI, which should be regarded as optimum. A linear relationship was observed between tuber dry matter yield and leaf area duration. It was also noted that when leaf area duration was increased from 10 to 20 weeks tuber yield was increased by 40% and 30% in consecutive growing seasons.

One of the commonest associations with premature canopy senescence and thus limitation in the duration of tuber growth is the link with the physiological age of the seed tubers. Canopy senescence in cv. 'Estima' was assessed after the seed tubers were subjected to three levels of physiological ageing (0, 125 and 250 Day^0). The results showed that physiological age exerted a greater influence on senescence than fertiliser application rates, since canopy assessment prior to harvesting showed 58.9% senescence from the zero Day^0 treatment and 84.2 and 85.6% from the remaining treatments.

A mathematical model of dry matter partitioning among plant organs was developed for the purpose of simulating potato growth. The simulated values were validated by comparing them with empirical values obtained from regular destructive harvests. Over two seasons and six sites, the only estimated parameter that showed a marked difference was that for 'ageing' (i.e. senescence) and they conclude that the 'ageing factor' is highly sensitive to cultivation practice.

The decline in canopy integrity and the associated decline in leaf area by senescence are followed after a short time by the cessation of tuber bulking. If however tubers are harvested to coincide with this event, they will be considered to be immature. Tuber maturation is characterised by suberisation and increase in dormancy and this state is more likely to occur some weeks after the onset of senescence.

Summary

- Leaf senescence is the final stage of leaf and canopy development.
- Orderly senescence ensures that nutrients invested in the leaf are remobilized to other parts of the plant.
- In potatoes, the major beneficiaries of senescence-induced remobilisation are newly formed leaves and the developing tubers.

Sources accessed in the preparation of this section.

Kleinkopf, G. E., Westermann, D. T. and Dwells, R. B. (1981). Dry Matter Production and Nitrogen Utilization by Six Potato Cultivars. *Agronomy Journal* **73:** 799-802.

Maillard, A., Diquélou, S., Billard, V., Laîné, P., Garnica, M., Prudent, M., … Ourry, A. (2015). Leaf mineral nutrient remobilization during leaf senescence and modulation by nutrient deficiency. Frontiers in Plant Science, **6,** 317.

Millard, P. and MacKerron, D.K.L. (1986). The effects of nitrogen application on growth and nitrogen distribution within the potato canopy. *Ann. App. Biol.* 109: 427-437.

Oliveara, Carlos Alberto Da Silva. (2000). Potato crop growth as affected by nitrogen and plant density. *Pesq. agropec. bras*. [online]., **35:**.940-950.

Section 13.

Harvesting and tuber yield

Introduction

Harvesting the potato crop is a critical part of the entire potato production and marketing operation. Crop yield and quality cannot be increased during harvest, but they can be decreased, sometimes drastically by inappropriate or untimely activity. The results of many studies have indicated how tuber quality can be reduced by improper harvesting techniques. The principal cause of quality loss, as these studies have pointed out, occurs through failure to observe proper procedures both proceeding and during harvest.

Crop Maturity

As the potato crop matures, biochemical changes occur in both the canopy and the tubers. In the canopy, chlorophyll levels in the leaves decline and the rate of photosynthesis decreases. Phloem mobile metabolites, including carbohydrates, are remobilsed from senescent foliage to the tubers and tuber dry matter reaches a maximum. The senescing leaves turn yellow and fall from the stems, which in turn, also senesce.

During this time changes are also taking place in the tuber. The periderm (skin) thickens and becomes stronger, resisting abrasion during harvesting and biochemical changes occur within the tuber.

Pre harvest operations:

Haulm removal

It is accepted that after canopy integrity has declined by 50%, very little increase in tuber yield is possible as respiration utilises the diminishing amount of dry matter being produced. The grower must now decide when to destroy the canopy. Haulm can cause mechanical difficulties during digging. They can also harbor certain insects and diseases which, if not removed, will come in contact with the tubers during harvest If the canopy is infected with *Phytophthora infestans* there is a severe risk that rainfall will wash the spores from the leaves onto the soil and then down thorough the soil layer to the surface of the tuber. Given the appropriate environmental conditions they will germinate and infect the tuber.

Whether the canopy had died due to desiccation by chemical means, frost, or natural senescence it is worthwhile to eliminate the stems from the ridges. The stems can be removed by pulling or by cutting. Removal by cutting can be completed earlier that by pulling. If the attachment of the tuber to the stolon is still intact pulling will result in tubers being dragged to the surface and exposed to the light. Whether the crop is harvested by traditional means or by machine, haulm removal prior to harvesting reduces mechanical damage to the tubers.

Prevention of a late virus spread on seed crops and reducing late/ tuber blight infection

Two critical steps in seed potato production are prevention of late virus infection and controlling tuber size distribution. Once seed crops have bulked to the appropriate size and have been found free of virus it is important to prevent virus spread by a late aphid migration. Aphids will seek to feed on residual green material on senescing haulms. This renders virus control necessary right up to the point of complete haulm death.

Because new races of late potato blight have shorter latent periods, the risk of infection is minimised by rapid foliage removal and the prevention of regrowth.

A desiccation protocol that prolongs the duration from functioning canopy to complete desiccation can expose the tubers to risk of tuber blight, especially in a season of high blight pressure. Therefore growers should select a desiccant chemical or haulm destruction practice that provides rapid death and furthermore reduces the risk of regrowth. In a high blight pressure situation a final fungicide application may be required. A compound that provides anti sporulant activity would be appropriate. Because of the risk of tuber contamination by spores surviving in the soil layers, heavily blighted crops should not be lifted earlier than 14 days after haulm destruction.

Controlling tuber size distribution

In earlier sections, topics such as the effect of physiological age, seed size, inter plant also interrow competition and nutrient application levels on tuber size distribution were discussed. In a crop grown for ware, all the tubers have a value. By contrast the tubers in a crop grown for seed must meet size criteria in addition to the normal quality attributes. Typical size specifications for seed are that tubers fall between 35 and 55mm. Tubers in size grades outside this specification must be directed towards the ware market.

Tuber size is an ever-evolving dynamic scenario. The largest tuber in the period following tuber initiation may not be the largest at final harvest; a tuber may undergo a period of sustained growth and then suddenly cease growing when the leaf supplying most of the assimilate senesces. The only way a grower can be aware of the size profile of the tubers in by digging samples on a regular basis and plotting the changes in tuber number and tuber weight. This will provide the information required to make the difficult decision regarding when to defoliate the crop so as to prevent too many of the tubers, which are approaching the upper limit of 55mm, from continuing to grow and exceed the size limit.

Tuber skin set

Do not harvest immature potatoes. Immature potatoes have very thin skins that rub off easily during harvest handling. Areas where skin is rubbed of turn brown and darken; this facilitates dehydration, and may become an entry point for decay. This results in greater dehydration during storage as well as skinning of fresh market tubers, which lowers their salability. Bruising of immature tubers is probably the single most important factor that reduces the financial returns to the grower due to shrinkage and susceptibility to pathogens. Tuber yield increases in line with plant maturity, also the tuber skin becomes thicker, tougher and attached more firmly.

The "skin" or periderm of the potato tuber has a structure and role that resembles the bark on the stem (trunk) of a tree. Similar to the tree bark the periderm is a tough coating that prevents moisture loss and solutes from interior tissues and also to protect the tuber from unfavorable environmental conditions and invasion by diseases, insects and other pests. Since the primary role of the periderm is to provide protection it must continue to do so during the entire tuber bulking process-a process characterized by dramatic daily increases in tuber size.

To carry out its role effectively, the development of the periderm must keep pace with increases in the tuber size. This is a dynamic situation where there is an expanding tuber and the requirement that the constantly increasing surface area must be continually covered and protected This task can only be achieved where the periderm is in a constant state of growth matching the tuber growth. To achieve constant coverage the periderm cannot be anchored to the underlying surface, rather it must be able to slip as the tuber increases in volume. It is this slipping facility that causes the problems when tubers are harvested without attaining maturity and skin set.

The slippage occurs in a specific region of the immature periderm, but first it is important to understand the process of periderm formation.

A representation of a cross sectional view of developing periderm is shown in Fig. 1. The periderm ha three zones as illustrated in the diagram.

The green zone represents a meristematic region (A meristematic region is an area with undifferentiated cells, found in regions where rapid cell division leading to growth can occur) called the "phellogen."

Above or outward of the phellogen are five to six layers of "phellem" (meaning 'cork') cells (Fig. 1, the yellow zone) that were produced by the phellogen meristem. This is the outermost corky layer and the structure of this phellem layer is often compared with the structure of a "brick wall," since it consists of a series of flattened, rectangular, brick-shaped cells stacked on top of each other. The cell layers are not offset like alternating courses of a brick wall would be (Fig. 1, yellow zone). Phellem (or tuber skin) is composed of cells that are dead at maturity, and their primary walls become covered from the inside by the secondary wall which consists of parallel suberin lamellae alternating with wax layers.

Inward from the phellogen is the "phelloderm" region. It draws the energy and biochemical metabolites required for the growth process from the meristematic phellogen. Evidence for this is the lack of starch granules because the granules have been sacrificed to provide the energy needed for periderm formation.

The meristematic activity of the phellogen layer provides a constant supply of cells to the corky phellem layer to replace the cells sloughed off as the tuber expands. This is the process by which the protective skin on the potato tuber is maintained. The layer of phellem cells formed is not permeable for water and gases, but its integrity is interrupted at certain points by lenticels, which function in a manner similar to stomata and permit gas diffusion.

Excessive mechanical pressure will cause the skin on an immature tuber "to slip" because the walls of the cells in the phellogen meristem (Fig. 1 green area) layer are necessarily soft and therefore easily damaged. It is this very characteristic that allows the periderm to continue expand in line with increase in tuber volume, but also leaves it vulnerable to shear or bruise damage

The skin set process commences when the tuber finally stops growing, due to cessation of supply of assimilates resulting from vine death and/or other factors. Production of new cells ceases in the meristematic zone, the cell walls lignify, and the cells in the zone from above the former meristematic area to the outside become heavily suberized (i.e. impregnated with suberin). At the same time, the periderm becomes tightly bound to the underlying tissues and in this way becomes very resistant to shear inflicted mechanical damage.

Note: *Skin set does not protect against severe bruise/impact damage.*

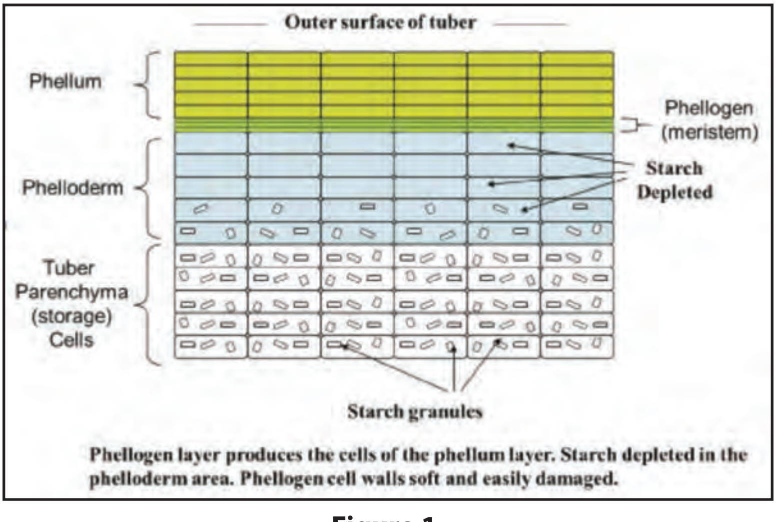

Figure 1.
Periderm formation on a potato tuber.
(Diagram © The Potato Grower, With permission.)

Then the question arises – how to promote skin set? The major factors that contribute to final skin set include:

- Variety,
- Soil type,
- Cultural and environmental conditions,
- Vine maturity and
- Duration from vine kill to harvest.

Varieties differ in their rate of skin set. While skin set is primarily under genetic control, it is also influenced by factors such as late season bulking rates and how the variety responds to the conditions in the field. Smooth-skinned varieties do not set a skin as rapidly as cultivars with russet skin. Since the tuber should have ceased bulking or expanding for skin set to begin, it is best to avoid having vigorous green haulm into the later part of the season. Not applying excess rates of nitrogen at planting or applying nitrogen top dressing at late stages in growth can prevent this.

Typically the haulm should be dead for 10-21 days prior to harvest depending on factors such as variety and haulm maturity or "greenness" at the time of haulm kill. But a word of caution - the longer tubers remain in the ground after vine kill, the greater the risk for black scurf (*Rhizoctonia*) and silver scurf development.

Soil conditions, both temperature and moisture, can influence periderm maturation. Available soil moisture should be managed for 60-65 percent at vine kill to promote skin set. Excessive soil moisture after haulm destruction can restart activity in the meristematic zone of the periderm layer and this renders the tubers vulnerable to skinning damage during harvest. The grower cannot influence soil temperature but it is important to recognise that cool and wet soil conditions can delay maturation, whereas warmer soil temperatures increase the number of cell layers and thickness of the periderm.

The grower must balance the requirement of proper skin set with desired yield, weather and market end-use of the potato. For example, proper skin set is very important for stored potatoes since an immature potato has 10 to 60 times greater weight loss compared to a mature potato. The requirement of early harvest to capture a price premium must be set against the implications for weight loss, bruise potential and disease susceptibility, when managing the risk of reduced skin set.

Harvesting before full maturity is a profitable procedure only when a premium price is paid for immature potatoes that are to be sold immediately.

Irrigation should cease 2 to 3 weeks before harvest. If frost does not kill the haulm or if rainfall is not a factor, this practice allows a slow decline of the haulm. This hastens and enhances skin set.

How to measure skin set

The most widely practiced test for skin set is widely referred to as the ‘thumb test’. Pressure is applied to the tuber with the thumb, which is then rotated through 90 degrees. Immature skin will slide under the pressure, whereas properly set skin will withstand the force applied. The criticism of this test is often made that it is not reproducible and the response is a function of the operators' ability to exert sufficient pressure. Notwithstanding these limitations, it is widely used to guide decision-making and helps to avoid storage losses.

HARVESTING THE TUBERS

A basic rule!

Do not take rotten and damaged potatoes into the store. Such potatoes have no economic value and can only cause further disease and damage to the other potatoes, if mixed together.

Tuber damage during harvesting.
What is generally termed harvest management is primarily aimed at minimizing tuber damage, so could essentially be called bruise management. Bruised tubers reduce yield and quality through increased shrinkage in storage, more disease, loss of product, less consumer appeal, and lower prices to the producer. While most of the tuber damage occurs during the harvesting operation, the bruise management practices aimed at minimizing bruise damage should not be confined to the harvest period. Some damage to the tubers will inevitably occur during harvesting, but the severity of damage can be altered to a point of insignificance by properly controlling harvesting operations and by modifying excessively damaging procedures. Tubers can be predisposed to damage through certain cultural practices, such as excess nitrogen, excess water, and poor soil aeration. This notwithstanding, most of the actual damage occurs during digging, loading, and transporting operations. Also, different potato cultivars show differing propensities to bruising and the type of bruising that occurs.

Tuber bruising: Types of Bruises

Blackspot Bruise: An impact does not break the skin of a tuber, but damages several cell layers beneath the skin causing a chemical reaction within the cells to form a dark gray to black pigment called melanin. The chemical reaction takes 24 to 48 hours to complete, and the damage is invisble unless the tuber skin is removed. Varieties differ in their susceptibility to this damage. It is useful to note that when tubers have been in the store for about 30 days, they can withstand 30% to 80% more impact without producing black spot bruising compared to the level of impact that would result in bruising at harvest.

Shatter Bruise: With type of bruise, the tuber skin and possibly several layers of cells underneath display a radial type crack or the tuber is broken by an impact.. It is often easier to see the cracks when the surface has dried.

Skinning: In contrast to impact type damage, skinning is induced by rough handling of tubers with immature skins, which may cause the skin to be scuffed off exposing the tuber flesh. Exposed flesh turns dark when subjected to oxygen in the atmosphere.

Pressure Bruise: This damage is not directly associated with harvest, but potatoes that were dehydrated at harvest or become dehydrated in storage will, after several months in storage, become flattened and the area beneath the skin discolors as a result of cell damage.

One of the most critical bruise management practices is to harvest tubers at the correct pulp temperature. However, the amount of tuber bruise damage is also associated with tuber hydration level. At any given temperature, shatter bruise will increase and blackspot bruise—if the variety is susceptible to this defect—will decrease as tubers become more hydrated. Therefore, the least total amount of tuber bruising occurs at a point midway between dehydrated and fully hydrated. Unfortunately, there is not a reliable, repeatable test that can ascertain the level of tuber hydration.

The effect of temperature and tuber hydration level on total tuber bruising is fairly straightforward when tubers are either very dehydrated or completely hydrated. As tuber pulp temperature becomes colder, total bruise potential increases at the extremes of tuber hydration level. However, for tuber hydration levels between these two extremes, the effect of tuber pulp temperature is less clear. There is a fairly wide range of temperatures that will result in the least amount of total tuber bruising when tubers are midway between dehydrated and hydrated. Ideally, tuber pulp temperature while harvesting should be 7 °C to 18 °C. Although warmer pulp temperatures generally result in less bruise, there is an increased risk of tubers rotting in storage. If harvesting at temperatures above 18 °C, be sure the storage facility has the capability to rapidly cool the tubers to less than 18 °C.

Several factors affect susceptibility to bruising during harvest. While the physical condition of the soil such as type is important, the grower cannot control it; but the key factor that the grower can control is the soil moisture. To ensure minimum risk of bruising, it is important to maintain the soil moisture at between 60 and 80% of field capacity (FC) during harvesting. Tuber hydration and maturity are the most critical factors controlling the tendency to bruise and type of bruising that the tubers will incur. Hydrated tubers (turgid) are firm and less susceptible to black spot; however they are more susceptible to shatter and cracking. By contrast, dehydrated tubers (flaccid) are less susceptible to shatter bruising and cracking.

Potato tubers are damaged when they strike an object harder than a tuber, but tubers striking other tubers will generally not be damaged. All potato harvesting or handling equipment has the potential to bruise tubers, so care must be exercised at all times. Remember is is easier to protect the tuber from damage than for the tuber to heal/repair the damage

How to minimise tuber injury

Three key conditions should be met in order to minimize harvest injury:

- Destroy the haulm at least two weeks before harvest,
- Harvest when soil conditions are dry, digging gently and carefully not to puncture the tubers and
- Avoid harvesting when soil and air temperatures are below 7°C.

Removing haulm before harvest allows them to dry thoroughly and allows time for pathogens to die, reducing the chances of transporting them into storage. It also allows for tuber skin maturation, reducing skinning and bruising. Harvesting when soils are dry, decreases bruising due to soil clods and transport of soil into storage, where it can block air circulation through the potato pile. Harvesting at temperatures below 7°C will injure potatoes more than at higher temperatures. Avoid harvesting when soil temperatures are above 16°C to minimize water loss and shrinkage.

It is important to consider temperature and tuber condition if potatoes are to be harvested with minimum damage. There is an increase in total damage as temperature decreases and especially the type of damage resulting from impact is influenced by temperature and tuber condition. Research data indicates that at a given tuber turgidity level, total damage susceptibility level is minimal for a given tuber temperature. Furthermore, the turgidity level at which maximum damage occurs, changes as temperature changes. A tuber hydration level, which produces little damage when bruised at a flesh temperature of 18-21°C results in severe damage (shatter bruise) when subjected to the same force at 7-10°C. Conversely, a hydration level, which results in severe blackspot at 18-21°C may result in slight to moderate total damage when subjected to the same impact at 10-13°C.

Harvesting under high temperatures

Do not harvest in extremely hot weather. The coolest part of the day is from early morning to early afternoon. Harvesting during the combination of hot soil and warm air temperatures can result in surface browning, black heart, soft rot, and/or greening. If harvesting must proceed, it is essential to cover the tubers as soon as possible. It is most critical in hot weather to prevent drying, surface browning, greening, and other heat induced disorders. Sacks or boxes filled with freshly harvested tubers should be placed in a shaded area to reduce the possibility of heat damage. At any temperature, however, wind damage and drying occur if the tubers are not protected.

Wound Healing

At least two consequences arise from a break in the tuber skin; it allows tubers to loose water or dehydrate, and facilitates the entry of pathogens into the tuber causing storage rots. The tuber however has a defence mechanism – known a wound healing. The wound healing is achieved by the formation and cross-linking of lignin and pectin between the cells in the area immediately below the damage. This slows water loss. The next step involves suberization in cell walls thereby inhibiting bacterial rots. The final step involves the formation of a new skin, the phellogen layer. That layer is formed via cell division, as discussed above, and it inhibits fungal rots and controls movement through the skin. The process of wound healing is highly affected by temperature, and additionally affected by relative humidity and air quality. It is speeded up by regular air changes in the store, which ensures the CO_2 levels are kept low and that high concentrations of O_2 are maintained.

Skin wounds provide an entry point to the tuber for Fusarium spp., which are present in all soils. Effective wound healing and the formation of a suberised layer is essential to reduce infection by Fusarium; the healing process is speeded up by holding the tubers at 10° to 14°C with good ventilation and a relative humidity of at least 95% for the first 2 to 3 weeks of storage.

Note: *The topic of tuber bruising is teated in greater depth in* **Section 14**.

Tuber Yield

Potato productivity is influenced by broad range of factors. The potential yield of a crop is determined by a variety's genetic traits including field growth; tuber formation and consequent partitioning of assimilate to the developing tubers. Potential yield is also influenced by how the variety responds to environmental conditions, which the crop encounters such as day length, temperature, soil fertility and soil structure, also availability of water.

Abiotic factors such as drought and heat influence actual productivity. In addition, biotic factors including infestation by insect pests and infection by fungal, bacterial and viral pathogens that can affect yields directly or by reducing seed quality.

Research has shown that the two major factors which influence tuber yield are:

(1) the photosynthetic activity and duration of the leaf canopy, and

(2) the length of the linear tuber growth phase.

The ingredients that promote a high yield are an extended duration when the canopy is producing photosynthate at a relatively high rate, and a correspondingly long period when tubers are bulking at their maximum rate. The two key components that determine tuber yield of potato: tuber numbers per unit area, and tuber size or weight. Increased yields come from achieving the optimum tuber numbers because of their contribution to attaining the optimum sink size and through maintaining a green leaf canopy, because this ensures increasing tuber size and weight.

Tuber size distribution (i.e. tuber size and uniformity) is an increasingly important aspect of potato quality. As markets increase in sophistication, buyers whether merchants purchasing seed to end users either for fresh market or processing, now insist on tubers with a uniform and consistent size profile. Many purchasing contracts have implemented clauses with sizable economic incentives to reward growers who meet specific tuber size specifications. But of course the details in these same contracts are also used to penalize other growers who fail to supply tubers of the required dimensions and produce a potato crop with too many small or large tubers. Harvested tuber size profile is a function of the number of tubers set per plant, as well as the length of time tubers bulk during the season. Environmental and management factors can influence both of these characteristics. The grower must exercise all their attention on prolonging a healthy leaf canopy since this will increase the average tuber size.

Regression procedures indicate a strong positive relationship between stem number and tuber number but indicate a negative relationship between stem number and average tuber weight. Since tuber number exerts a greater influence on yield than average tuber weight, there is a positive relationship between the numbers of main stems and tuber yield. Consequently in potatoes, the main stem is often regarded as the unit of yield.

Considerable effort and expenditure have been invested in the quest to control tuber size distribution. But because it is regulated by diverse factors and interrelated metabolic systems, it is complex to understand and difficult to manipulate. The size distribution of the tubers in influenced by interrow and intrarow spacing, stem number per plant, number of tubers per stem and tuber yield, While seed size and plant density can be readily controlled, stem number per seed tuber is far more difficult to manipulate. Stem density is not the sole determinant of tuber-size distribution since interactions between different types of stems are also important.

Duration of tuber bulking and final yield

From the foregoing, final yield can be defined in terms of the average rate of tuber bulking and the duration over which that rate was maintained. If these are not curtailed by environmental or agronomic influences, the potential yield of the crop will be realised. The validity of discussing final yield in terms of rate and duration of tuber bulking has been questioned, citing as evidence both the existence of curvature relating yield with time and an interaction between agronomic treatments and time of harvest.

However the concept of duration of tuber bulking provides a framework where, factors which are known to influence final yield can be discussed and it is proposed that duration of tuber bulking was a more important determinant of tuber yield than rate of tuber bulking, since the rate varies over time of tuber bulking.

Factors affecting total tuber yield

Tuber yield represents the satisfactory culmination of three separate processes, stolon development, the proportion of stolons that form tubers and the subsequent growth of these tubers. Final tuber yield is defined by the rate and duration of tuber bulking. Increasingly however, growers intervene and prevent the crop attaining its full potential in order to ensure that harvesting is completed before soil conditions deteriorate excessively or to maximise yield in a specific grade. The factors affecting tuber yield at early harvest have been investigated intensively for early potatoes due to the financial premium associated with early yield. Maincrops with a longer growing season and produced from physiologically younger seed are generally harvested at maturity i.e. after the cessation of tuber bulking since there is no premium for earliness.

Factors affecting graded yield

While the relationship between the amounts of radiation intercepted by the canopy and the efficiency of its conversion to tuber dry matter provides a valuable tool to analyse total tuber yield responses, it provides little information regarding likely tuber size distributions. Average tuber size is a more reliable indicator of "marketable yield' than total tuber yield. The refinement of grading requirements to satisfy a range of market specifications ensures that profitability will be influenced more by yield within a specific grade than by total yield. Tuber size distribution is a function of total yield and number of tubers. Further, the distribution of tuber size is defined by two parameters μ (the mean), a measure of average tuber size and σ (the standard deviation) a measure of the spread of tuber sizes. But since σ increased in proportion to μ, a relative variability parameter R_v would define the ratio of σ to μ and furthermore that there were two sources of variation in R_v: genetic and agronomic. But since within a cultivar, R_v was observed to be constant, variation in graded yields could be ascribed to cultural practices.

If the objective were to increase tuber yield then the simplest strategy would be to increase average tuber weight. But since graded yield is the objective, the only means by which it can be increased is to increase the number of tubers in the required grade.

The number of tubers per mainstem is influenced by 'external' factors such as seed size and spacing, soil moisture, temperature, light intensity and by 'internal' factors such as cultivar, physiological age and the degree of tuberisation. The relationship between number of tubers, total yield and the yield of large tubers (60-80 mm) was examined. It was demonstrated that yield in this grade was a linear function of total yield and the number of tubers >1 cm. The influence of physiological age on tuber number has been researched extensively and the relationship between level of temperature accumulation by the seed tubers prior to planting and tuber number varies considerably.

When the effect of physiological ageing on maincrop cultivars is considered, the response is somewhat more complex. One study recorded a reduction in tuber number in only one cultivar from a range of cultivars subjected to increased physiological age. Another study observed a reduction from 16.1 to 14.6 tubers per plant for a seven-fold increase in physiological age, while a further study observed no significant difference in tuber numbers per stem, for a three-fold increase in physiological age. When two levels of physiological ageing on yield and size distribution of cv. 'Estima' were examined, it was noted that physiologically older seed gave a greater yield in all size fractions >55 mm and a lower yield in all size fractions <55 mm.

Factors other than physiological age influence tuber number. The effect of harvesting date on tuber size distribution was studied and the results demonstrated that delaying the date of harvest by 63 days, reduced the number of tubers from 559,000 to 526,000 ha^{-1} but increased mean tuber weight from 100 to 129g.

Nitrogen application at 150 kg ha^{-1} produced 517,000 tubers with a mean weight of 119g, while 250kg ha^{-1} produced 556,000 tubers with a mean weight of 117g.

When the researchers compared 75 day-degrees with 275 day-degrees physiological ageing, the number of tubers were reduced (560,000 to 512,000) while mean tuber weight was increased (110 to 126g). It is considered that within row competition acts as the major determinant of tuber number.

The reduction in tuber number during the growing season has been reported in the literature. The phenomenon is known as resorption and it has been observed that within the period of 30 days following the cessation of tuber initiation, the number of tubers in five cultivars had reduced by 50%.

In the discussion on tuber bulking above, only the effects on total tuber yield were considered. Studies show that for two cultivars, the grade over which yield is considered affected the bulking rate. For total yield, cv. 'Maris Piper' bulked faster than cv. 'Pentland Crown' but when yield greater than 44 mm is considered, Pentland Crown out yielded Maris Piper.

Graded yield categories

Average tuber size and its variation will determine the suitability of a potato crop for a desired market.

The potato market can be divided into two main categories – tubers grown for seed or for human consumption – typically known as ware potatoes. Within the ware trade two further subdivisions exist, fresh potatoes for immediate consumption or graded and stored for processing. Again the potatoes for processing can be subdivided into a those for processing as 'crisps' or 'chips' – thinly cut slices, deep fried in oil or further into square cut sections - 'French fries' - and also deep fried in oil.

Until there is a requirement for prepacking, very little emphasis is placed on size grading of potatoes destined for fresh consumption.

Seed Yield.

Tubers for seed are graded by size (generally 35-55mm) or by seed piece weight (generally the case only when seed tubers are cut).

A grower seeking to produce a crop for the seed market would aim to maximise yield in the 35-55mm fraction. Extensive research has been directed to optomising tuber size distribution in order to maximise yield in the target grade.

Tuber size distribution is influenced by the following parameters:

- The number of plants per unit area as determined by the number of seed tubers planted and the percentage emergence.
- The number of stems per plant, number of leaves per stem and the inter-stem competition.
- The number of tubers per stem, which attain the desired size and the total yield

These factors are then impacted by agronomy and by environmental influences.

The mainstem is now accepted as the unit of yield in the potato crop and again extensive research has been directed to accurately control both main stem density and the number of tubers per main stem.

For seed production, the objective is to provide maximum tuber numbers in the required size grade; therefore higher stem densities are necessary to maintain interstem competition and encourage the production of the target sized seed tubers. The simplest strategy that can be employed to increase stem density is to use closer in-row seed tuber spacing or a larger seed tuber size. Stem density is a more accurate predictor of tuber set compared with plant density.

Despite at least 40 years research and countless field trials attempting to obtain tuber size uniformity, success is still quite a way off! Factors affecting tuber size uniformity might be defined as managerial or environmental. These factors combine to introduce the variation in tuber number per plant observed between years, between fields and between plants within a field.

Post harvest seed handling

If the seed tubers are being harvested in fine weather, then it is desirable to spread them in a thin layer on the ground near the DLS. This will allow a time for wound healing and time to dry off the soil adhering to the tubers. A coating of soil will reduce airflow through the layers of tubers on the shelves.

Note: *Size grading should be carried out before the tubers are stacked on the shelves in the DLS. This will avoid the need for grading prior to planting and the attendant risk of breaking off the newly formed sprouts.*

Be rigorous in removing diseased, bruised or tubers showing mechanical damage acquired during the harvesting operation. The respiration rate in these tubers is considerably higher and they will increase the respiration of surrounding tubers. Diseased tubers pose a risk of infecting the surrounding healthy tubers.

Graded Ware Yield - Processing

Processors will seek to minimise losses due to wastage by purchasing only the tubers that will give them the maximum yield of product with minimal waste. This failure to meet precise size grade requirements for specific markets costs the potato industry millions of Euro each year.

With the arrival of sophistication in potato marketing it will no longer be profitable to produce a crop directed at general use. Failure to meet quality specifications targeted towards the end use of the tubers will attract a financial penalty, or at worst product rejection. Processors insert clauses in contracts, which apply penalties for losses due to blemishes, bruising, pest-damage, greening, growth cracks, etc. A standard contract will typically specify a maximum of 5% out grade potatoes by weight, out grades above that will attract a financial penalty.

The two major processing markets for graded ware potatoes are for chips (crisps) and French-fries

Before delivery to a chip processor, the grower will grade the tubers to remove those that are undersize and those that are oversized. It is important to remove small potatoes because: they are generally immature, they discolour easily during frying, they do not cook evenly and they produce waste as offcuts when sliced. Tubers that are too large are also rejected, as again they produce excess waste on slicing for chip manufacture. The chip trade requires that tubers are within the size 40 - 60 mm. Tubers for the chip trade may also be graded by weight where a typical target value is 70 to 110 tubers per 10kg.

The French-fry market has two components – frozen French-fries and freshly cooked French-fries.

Frozen French-fries are generally considered a lower quality product compared to the freshly prepared and freshly cooked French-fries. They are produced in vast quantities in high output processing plants and transported in temperature-controlled containers to markets around the world.

Freshly prepared French-fries fetch a premium price due to a crisp texture, superior mouth feel and attractive fry colour. One cultivar ‘Russet Burbank’ dominates this market worldwide – largely since is the cultivar of preference for a multinational fast food restaurant chain.

For the current discussion the focus is on maximising yield in the required grade – i.e. tubers greater that 113 gr. A major factor influencing yield this grade is planting density and the associated stem density. When planting density and the related stem density is high, yield in the small size grades will be enhanced. An optimum yield of the desired size tubers for French-fries – greater than 55mm – is facilitated by low stem density.

Fresh Market Tubers

To the consumer, tuber quality in terms of appearance and cooking quality is of prime importance. Choice of variety is highly significant, but also the way the potato is grown harvested and handled post harvest

The fresh market requires tubers that are consistent in shape and size (45 -85 mm), with good bright skins, free of any disease or blemish.

Further quality parameters such as dry matter (DM) content is also important as tubers with a DM above 18-20% are more susceptible to bruising and may disintegrate when boiled during cooking.

Fresh market tubers should be stored at 3.5 to 4.5°C with 90 to 95% relative humidity and adequate ventilation.

Summary

- Haulm destruction and removal protects the tubers from infection by pathogens, which may be present on the senescing haulm.
- Tuber yield increase is minimal after the haulm attains 50% senescence.
- Allow sufficient time between haulm destruction and harvesting to facilitate tuber skin set.
- Be cognizant of soil temperature and tuber hydration level so as to minimise bruise damage.
- Tubers destined for the seed trade require careful handling and storage to minimise loss and improve the field performance of the daughter crop.

Sources accessed in the preparation of this section.

Bohl, W.H., Nolte, P., Kleinkopf, G.E. and Thornton, M.K. Potato Seed Management: Seed Size and Age. Univ. Idaho Extension Service. https://www.cals.uidaho.edu/edcomm/pdf/CIS/CIS1031.pdf

Gastelo, M., Kleinwechter, U. and Bonierbale, M. (2014). Global Potato Research for a Changing World. *International Potato Center* (CIP), Lima, Peru. Working Paper 2014-1. 43p.

Pereira, André Belmont., Villa Nova, Nilson Augusto., Ramos, Valdir Josué, & Pereira, Antonio Roberto. (2008). Potato potential yield based on climatic elements and cultivar characteristics. Bragantia, **67**:327-334.

Section 14.

Crop Quality

Introduction

A definition of the word quality, in relation to potato, might be – the suitability of the tubers for the intended end use. As the market for potatoes becomes more sophisticated – the quality criteria have become correspondingly sophisticated. Since potatoes are primarily a foodstuff, nutritional quality is of prime importance. As the demand for processed product grows, processing quality assumes greater importance. Tuber quality is influenced by the fact that the potato is maintained in a fresh state throughout its existence, constantly respiring and exposed to physiological and environmental influences during both the field growth stage and during storage.

Tuber quality of potatoes for domestic consumption

Nutritional quality of potatoes

Potatoes produce more edible energy and protein per unit area of land than any other crop. With world population increasing and starvation in developing countries, improving yield performance of the potato crop could help alleviate starvation as well as increase the disposable income of farmers. The crop has a high consumer acceptance by all socio-economic classes. As the standard of living in developing countries increases, it is expected that this increase will be paralleled by a rise in demand for processed potatoes

Potatoes are considered a nutritious and wholesome food that supplies many important nutrients to the diet. Potatoes contain approximately 78% water, 22% dry matter (specific gravity) and less than 1% fat. Some 82% of the dry matter is composed of carbohydrate, mainly starch, with some dietary fibre and small amounts of various simple sugars. On a dry weight basis, the protein content of potato is similar to that of cereals and is very high in comparison with other roots and tubers. In addition, the potato is low in fat. Potatoes contain at least 12 essential vitamins and minerals.

There is a widespread availability of tables listing the nutritional quality of potatoes. The values presented below are typical:

Potatoes – *their nutritional value*
Nutritive value per 100 g.
(Source: USDA National Nutrient data base)

Principle	**Nutrient Value**	**Percentage of RDA**
Energy	70 Kcal	3.5%
Carbohydrates	15.90 g	12%
Protein	1.89 g	3%
Total Fat	0.10 g	0.5%
Cholesterol	0 mg	0%
Dietary Fiber	2.5 g	7%
Vitamins		
Folates	18mcg	4.5%
Niacin (B3)	1.149 mg	7%
Pantothenic acid (B5)	0.279 mg	6%
Pyridoxine (B6)	0.239 mg	18%
Riboflavin (B2)	0.038 mg	3%
Thiamin (B1)	0.081 mg	7%
Vitamin A	7 IU	<1%
Vitamin C	11.4 mg	20%
Vitamin K	2.9 mcg	2.5%
Electrolytes		
Sodium	6 mg	0.4%
Potassium	455 mg	10%
Minerals		
Calcium	10 mg	1%
Iron	0.73 mg	9%
Magnesium	22mg	5.5%
Manganese	0.141mg	6%
Phosphorus	61 mg	9%
Zinc	0.33 mg	3%
Phyto-nutrients		
Carotene-ß	4 mcg	--
Crypto-xanthin-ß	0 mcg	--
Lutein-zeaxanthin	21 mcg	--

Potatoes are rich in several micronutrients, especially vitamin C; eaten with its skin, a single medium-sized potato of 150 g provides nearly half the daily adult requirement (100 mg). The potato is a moderate source of iron, and its high vitamin C content promotes iron absorption. It is a good source of vitamins.

Vitamin B6

Potatoes represent a very good source of vitamin B6 and a good source of many essential minerals such as potassium, copper, manganese, phosphorus, niacin, dietary fiber, and pantothenic acid. Potatoes also contain a variety of compounds referred to as phytonutrients; they are deemed to possess antioxidant activity. Among these phytonutrients are compounds, which the plant uses to protect itself against pests and pathogens – examples are, carotenoids, flavonoids, and caffeic acid, as well as unique tuber storage proteins, such as patatin, which has the capacity to scavenge free radicals.

Vitamin B6 is a nutrient that plays an important role in carbohydrate and protein metabolism where it helps convert the energy from food into energy the body can utilise. Vitamin B6 is one of the B vitamins complex required for the proper production of neurotransmitters (messaging molecules) in our nervous system and brain. Three key neurotransmitters—namely Gamma-Amino Butyric acid, dopamine, and serotonin, all require vitamin B6 for synthesis.

Patatin

Patatin is the major glycoprotein in potato tubers. It is considered as the major storage protein in potato tubers and is a group of immunological identical glycoproteins that have highly homologous NH_2-terminal amino acid sequences. Patatin is present in all potato cultivars and comprises some 20 to 40% of the soluble tuber protein. Using EM-immunocytochemistry reveals that patatin occurs largely in the vacuoles of potato tuber cells. It is not found in leaves and stems.

Due to the high starch content and the existence of other non-nitrogenous constituents of potatoes, it is not possible, when using whole potato is, to prepare a potato diet having more than 7 to 8 per cent of crude protein. The significance of the low levels of nitrogen becomes apparent when it is considered that only about 63 per cent of potato nitrogen is present as protein.

The physiological role of patatin has yet to be clarified. The presence of large amounts of this glycoprotein in tubers suggests a major role as a storage protein. Unlike the majority of storage proteins, patatin is considered rather stable, since metabolic constituents are detected when tuber storage compounds are degraded during tuber sprouting. In recent observations, biochemical and genetic studies reveal that patatin encodes a lipid acyl hydrolase and wax synthase. This suggests an expanded role for patatin beyond that of storage protein. It is now considered part of the tuber defense mechanism, since it increases dramatically on cell disruption.

Total protein content

Several factors, such as the cultivar, degree of tuber development, storage duration and influence of agro-ecological conditions will influence both the total content of protein in potato tubers and patatin relative abundance in extractable tuber protein. There is considerable variation in the content of crude protein in dry matter of processing potato tubers with values ranging from 6 to 11%. Nitrogen application rates of 100 kg N ha^{-1} and 200 kg N ha^{-1} significantly ($P<0.05$), altered the crude protein content from 7.5 to 8.4% of dry matter of potato tubers, respectively. Cultivar produced the greatest variability (34.3%): growing season accounted for 24.1%; while the interaction of growing season and the site accounted for 41.5% of the variability.

Vitamin C

Vitamin C is a water-soluble vitamin. Its major role is to act as an antioxidant, scavenging free radicals and therefore helping prevent cellular damage. Additional roles have been ascribed to Vitamin C, such as to aid in collagen production; promote iron absorption; helps with wound healing and maintain healthy gums. It is suggested that Vitamin C may help enhance the body's immune system.

Influence of field growth on tuber quality

Several factors affect tuber quality, but the most important ones are, the agroecology of the production site, variety, cultural practices employed, irrigation, fertilisation and the use of other agrochemicals such as fungicides. Tuber quality and nutritional value at harvest are moderated by cultural and environmental factors during growth of the crop.

Tuber dry matter

Tuber dry matter content (specific gravity) is an important quality characteristic whether potatoes are consumed in the home or following commercial processing. Starch is the predominant part of tuber dry matter accounting for between 60 and 80% of the dry matter. There is a strong correlation between the percentage of starch in the dry matter and dry matter in the tubers. This means that tubers that have a low dry matter also have a low amount of starch in the dry matter. Factors that affect the storage or accumulation of starch alter the proportion of starch in dry matter.

Generally the seasonal increase in yield is paralleled by an increase in dry matter. Occasionally a negative correlation between yield and specific gravity is recorded. This may result from choice of cultivar, crop nutritional status or environmental factors. Several environmental factors have the potential to cause differential performance in tuber quality and this is the resolution of the genotype environment interaction in potatoes.

Air and soil temperatures are the primary environmental factors affecting tuber dry matter (specific gravity). Warm days and cool nights provide optimal conditions for producing high specific gravity tubers. High soil temperatures have a direct effect on tuber physiology and inhibit starch deposition.

Tuber yield increased with increased temperature to 22.2^{0}C and then decreased at 29^{0}C. At 29^{0}C specific gravity of tuber was lower than at the other temperatures studied. Tuber shape was also affected by high soil temperature. This may have significant impact on a crop grown for chip production where a round shape is preferred. In a further study, the dry matter content of the tubers was reduced when the crop was grown at elevated soil temperature. When the soil temperature was 18^{o}C the dry matter content was 21.56%, whereas when the soil temperature was maintained at 28°C, a dry matter content of 18.99% was recorded. Cultural factors such as variety will also influence tuber dry matter. The *raison d'etre* underlying the activity of generations of plant breeders has been to improve yield and also increase dry matter content, a major quality criteria. Dry matter content is genetically controlled and significant differences exist between cultivars for this parameter. While some cultivars consistently produce high dry matter values and others produce low values, there is no absolute value for any cultivar, as dry matter content can be modified by cultural and environmental factors.

A cultural factor, widely recognised to influence dry matter content, is the application of fertilisers. The main nutrients concerned are nitrogen, phosphorus and potassium. The major role ascribed to nitrogen is the production and maintenance of a green canopy, which will intercept the maximum amount of photosynthetically active radiation (PAR) and facilitate its conversion to dry matter. Either low N availability or over-fertilization with N will reduce tuber quality. Excessive application of nitrogen fertiliser will promote growth of canopy and roots at the expense of dry matter being partitioned to the tubers, unless a long growing season and the canopy is kept free from defoliating diseases such as Phytophthora infestans. When scheduling N application it is important that site-specific nitrogen management practices are developed. Several factors must be considered such as cultivar physiological responses to total nitrogen application as well as to the developmental stage when the nitrogen is applied so as to maximize yields, tuber quality, and economic returns, while at the same time, reducing N losses to the environment.

Phosphorus is important for early root and shoot development, providing energy for plant processes such as ion uptake and transport. When developing a fertilisation strategy to optimize yield and quality, it is important to understand the influence of phosphorus on the pattern of production and partitioning of dry matter and nutrients to potato tubers. Because potato has a short field growth phase and a high yield potential it is highly responsive to soil-applied nutrients, especially to phosphorus. Through its role as a constituent of ATP (Adenosine Tri-Phosphate) phosphorus is essential for plants, as a key factor in the metabolic processes related to energy uptake. Low soil levels of P delay early growth of potato roots and stolons. To optimise tuber yield, dry matter and starch levels, P should be available in adequate quantities from the early growth stages. While excess applications of nitrogen and potassium have been demonstrated to reduce dry matter content, by contrast, elevated P levels have increased it.

As an essential nutrient, potassium has a major effect upon yield and quality of potatoes, as well as promoting the general health and vigour of the crop. It regulates the amount of water in the plant; when there is insufficient potassium the potato crop does not use water efficiently. Potassium is recognised for promoting synthesis of photoassimilates in potato leaves, then their transport to the tubers and for enhancing their conversion into starch, protein and vitamins. This promotes the rate and duration of tuber bulking and improves tuber quality composition. When potassium is applied to potatoes, it increases leaf expansion particularly at early stages of growth, and extends leaf area duration through retaining leaves and by delaying leaf shedding towards maturity. Through increasing both the rate and duration of tuber bulking, it increases the yield through increasing tuber size not tuber number and in this way increases the number and yield of large size tubers – a significant quality attribute

These positive effects of potassium application are associated with optimum levels. But by contrast there is ample research evidence to demonstrate that excess application of potassium, through its effect of water balance in the plant, will decrease tuber dry matter and starch content. Potatoes are recognised for their high requirement for potassium; potatoes require K at roughly twice the application rate of N. Field experiments indicated that K application improved the dry matter content of tubers, which is highly essential for processing into chips and French fries.

The chemical form of potassium has an effect on dry matter. Sulphate of potash (SOP) has long been recognised as providing higher dry matter compared to muriate of potash (MOP). Therefore it is frequently the form, which is applied to potato crops grown for processing. The chloride in the muriate of potash has a negative effect on tuber dry matter content; the major quality attribute in potatoes.

Field trials also indicated that K application, through SOP, improved specific gravity, chip colour score and decreased the reducing sugars content of 4 processing grade potato varieties. Plants treated with K_2SO_4 translocated more photoassimilates from the leaves and stems to the tubers compared with plants treated with KCl.

While high levels of K are required to produce an optimum yield of tubers, such a high yielding potato crop may remove 250kg of K per hectare from the soil as the tubers are harvested.

Irrigation is another cultural factor that has been shown to influence dry matter content of tubers through the application of water. The sensitivity of potato to drought or water stress is well recognised. Compared to other crops, potato leaves close their stomata at relatively low soil moisture deficits. Water stress (too much or too little) during tuber growth tends to decrease specific gravity, particularly when accompanied by high temperatures. To promote high specific gravity, available soil water content should be maintained above 65 percent throughout the tuber growth period until just before vine kill. Water and nitrogen are regarded as two important factors, which the grower can modify, to influence tuber growth and quality.

The impact of radiation interception and dry-matter accumulation on tuber yield were measured in potato crops grown either with irrigation or droughted from plant emergence. Moisture stress decreased total yield through reductions in both dry-matter accumulation and tuber water content. In droughted crops the reduction in dry-matter accumulation was attributed primarily to diminished interception of radiation consequent on reduced leaf expansion and the suppression of branching.

The effects of irrigation on dry matter content or specific gravity of tubers is an important quality criterion and the relationship is complex. Irrigation affects tuber size and maturity and both affect tuber dry matter content. Where high soil temperatures have been reduced by irrigation, then positive effects on tuber dry matter have been recorded. However, increasing uptake of the soil nutrients, nitrogen and potassium to above optimum levels by irrigation, might be expected to depress dry matter content, especially if irrigation is applied late in the growing season. The timing of the drought episode, or its corollary, the timing of the irrigation event on the development stages of the crop, is known to differentially influence tuber yield and quality. This response is linked to the scarcity of nitrogen in the root zone under drought, or the supra optimal supply following an irrigation event. Research on the interactions of irrigation and nitrogen management on total yield and yield of large tubers show different responses. As soil moisture stress increased total yield, yield of large tubers and tuber dry matter declined. While yield of large tubers and tuber quality is particularly sensitive to short periods of drought during tuber initiation, total yield appears most sensitive to short periods of irrigation deficit during tuber bulking. Irrigation during the tuber-bulking phase of growth promotes yield of large tubers and high dry matter content.

However water deficit during tuber bulking, followed by late season irrigation leads to tubers having reduced starch content and high levels of reducing sugars. During seasons when water supply is limited longer-term irrigation deficits should be either:

- Scheduled to coincide with peak rate of tuber bulking, or
- Distributed uniformly over the entire tuber bulking growth period.

There is a relationship between soil nitrogen and irrigation deficit. Under deficit irrigation, tuber yield increases with higher total available soil nitrogen but the yield response diminishes with decreases in the amount of total seasonal water.

A further cultural factor that will influence tuber dry matter is the application of fungicides to control defoliating diseases such as *Phytophthora infestans* or *Alternaria solani*. These pathogens reduce the duration of tuber bulking by destroying leaf tissue and reducing the amount of PAR that the canopy can intercept.

A severe infestation occurring mid-season will halt tuber bulking and leave a crop of small tubers with very low dry matter. By applying the appropriate fungicide at the correct rate, the infestation can be halted, the green canopy sustained and both tuber bulking and the associated increase in dry matter content can proceed to crop maturity.

Tuber quality of potatoes for processing

Introduction

By far the greatest quantity of potatoes grown worldwide is consumed within the home. This is helpful to the grower as the housewife is generally more tolerant of tuber defects. When preparing the potatoes, damaged or defective areas on the tuber can be cut away and the viable part of the tuber added to the cooking pot. As the market becomes more sophisticated and a greater proportion of the crop is directed towards the processing industry, tuber quality assumes a new significance. This places a new onus on the grower to exercise greater care during the field growth, harvesting, post harvest handling and storage stages.

Two major aspects define tuber quality in potatoes, suitability for processing and consumer acceptability. The major factors determining suitability for processing are tuber size and dry-matter content. Tuber dry-matter content varies between seasons and within a season it may be influenced by cultivar, desiccation date, and the tuber size under consideration. Dry matter concentration can vary within and between tubers. Starch is the major constituent of dry matter in potatoes. In addition there are small quantities of sugars, fibre, protein and ash. While the dry matter content of immature tubers can be as low as 16%, for mature tubers the value can range form 18 to 28%. Maximum dry matter content can be attained at different times but can fluctuate widely especially towards the end of crop growth.

For the processor, high dry-matter in tubers is desirable since it is associated with a high yield of product and low oil uptake on frying. Consumer acceptability may also be influenced by tuber dry-matter content through its association with the texture of the fried product, but light fry colour is regarded as the dominant factor influencing consumer acceptability. Fry colour results from non-enzymatic browning induced by the Maillard reaction between reducing sugars and α-amino groups during frying. The resultant dark fry colour and the associated bitter taste are unacceptable.

The potato grower's role is to maximise the amount of starch that is stored in the tuber, as this will produce the greatest yield. The emphasis now shifts to tuber storage; where the requirement is to store the potatoes correctly to ensure that the starch does not break down into glucose and fructose, the simple sugars that produce dark fry colours.

Tuber quality required by the processing industry.

The potato processing industry is dominated by a single processing technique – frying at a high temperature in oil. The two major products are French fries or chips (Figures 1 and 2). Chips are produced by peeling the tubers and then slicing longitudinally, to provide slices 0.12–0.15 cm thick. Slices are washed in cold water for 45 s, stirring continuously and then cooked in high oleic sunflower oil for 3 min at a starting temperature of 177 °C. Fryers are in fact drying systems, reducing the moisture in the potato slices from around 76% down to around 1.6%. This cooks the potato slices to give chips having a good flavour and golden colour. Colour influences consumer acceptability and is therefore one of the key appearance attributes of food materials. Regardless of the food item, the consumer preference is for product with a light colour and they discriminate against the darker product and its associated bitter taste. When a food is presented the consumer initially reacts to the colour and this is a critical parameter determining acceptance of rejection. For the consumer, colour is associated with flavor, safety, nutrition, and level of satisfaction.

The processing industry uses a colour scale to grade fry colour (Figure 2). The lightest coloured French fries receive a score of 000 while the darkest are ascribed a score of 4. When French fries are producing dark fry colours, the situation can be rescued somewhat by blanching, (A process whereby the strips are treated in hot water at 85 °C for 3.5 min.) which reduces glucose and asparagine content by average 76 and 68%, respectively in potatoes.

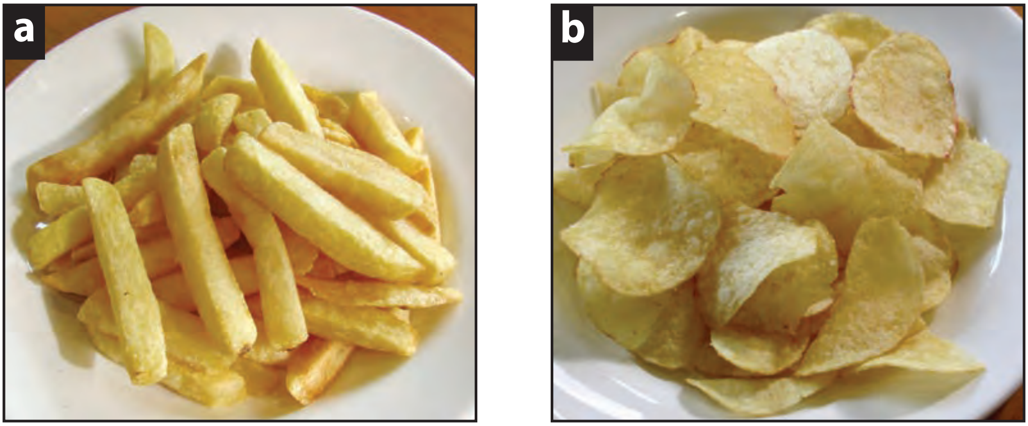

Figure 1.
French fries (left) and potato chips (right) (Photos © Author)

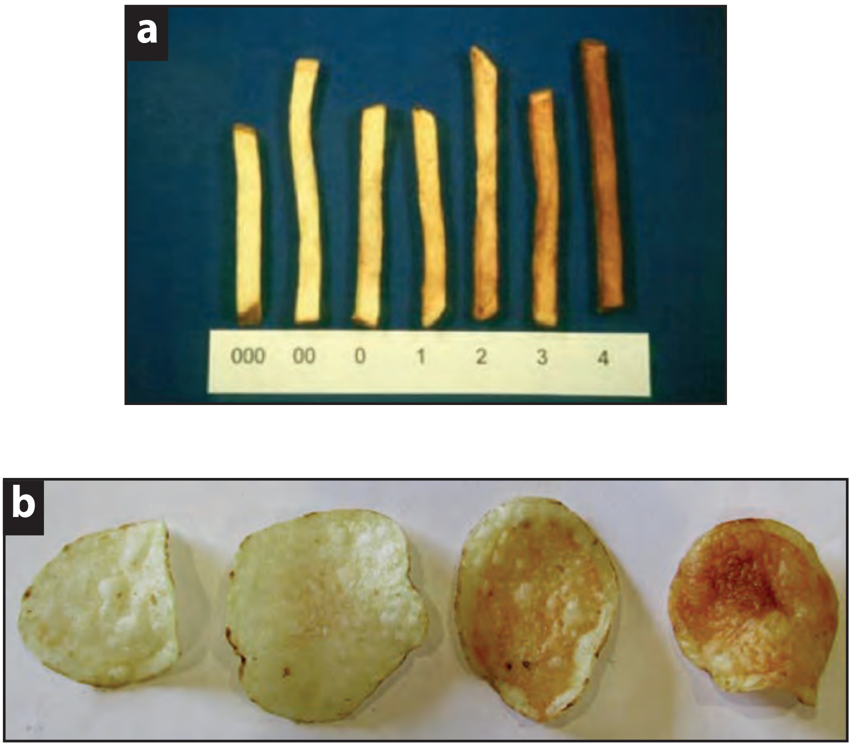

Figure 2.
An illustration of a French fries colour comparison chart (a).
Maillard reaction-induced darkening of potato chips (b).
(Photo (b) © Author)

Effect of cultivar on tuber processing quality

Even when the effects of cultivation, soil type and weather are eliminated, the percentage dry matter will be consistently high or low in certain cultivars since the character is under partial genetic control. This feature is acknowledged by growers and informs their choice of cultivar for a required end use, but other quality parameters such as fry colour must additionally be considered. Cultivars acceptable to the processing industry are expected to provide dry matter values in excess of 20%, which is regarded as the industry minimum for French fry production.

Effect of tuber size on tuber processing quality

Since tuber size minima (and sometimes maxima) are specified for French fry and chip manufacture, it is of interest to investigate the relationship between dry matter and tuber size. Small tubers have the lowest mean specific gravity values and the widest range whereas large tubers have the highest mean and the widest internal variation between regions such as the cortex, the vascular system and the pith. Dry matter concentration has been shown to increase with increases in tuber size and these differences could extend to 6 percentage points between tubers <32 mm and those >51 mm.

When the effect of tuber size on dry matter concentration in up to 20 cultivars, classified as early, second early and early maincrop was examined, it was observed that dry matter in particular tuber sizes varied according to cultivar and time of harvest and additionally that a negative quadratic relationship existed between dry matter percentage and tuber size. Early in the growing season tubers in the grade 40-50 mm had the highest percentage dry matter at harvest, but by the latter stages of the growth cycle, the tubers >60 mm had the highest values. Furthermore a negative quadratic relationship between dry matter content and increasing tuber size was observed at three dates of defoliation and it is proposed that since both the direction of change in tuber dry matter content and the tuber size giving the maximum dry matter content can change during growth, there is considerable implications for processing quality.

The relationship between specific gravity and dry matter

Percentage dry matter is an important component in tubers for processing but is time consuming to measure and therefore unsuitable for decision making at intake points. In these situations it is usual to estimate dry matter content from specific gravity determinations. Whereas in the European literature, dry matter values are cited as the quality parameter, in the literature from the USA, specific gravity is most often cited for the same purpose. The relationship between dry matter and specific gravity has been investigated and a high correlation recorded between the two values. It was further demonstrated that the weight of the tubers in water was unaffected by the water in the potatoes but was reduced by air in the intercellular spaces, which is affected by cultivar, growing season and storage.

Factors affecting fry colour

Fry colour is one of the primary quality attributes of French fries or chips. Consumer preference discriminates against product with excessively dark fry colour. The colour development, known as a Maillard reaction, is produced during the frying stage through sugar-amine condensation with subsequent Amadori rearrangement; followed by sugar and amino acid degradation, aldol condensation and aldehyde-amine polymerisation. The carbon compounds chiefly associated with fry colour are the reducing sugars fructose and glucose while the amides glutamine and asparagine provide the greater portion of the nitrogenous components.

Lighter fry colours are highly desirable for frying potatoes and this quality aspect can be improved by applying adequate potash. When the soil is treated with muriate of potash the resultant fry colour of the tubers appears to be marginally lighter than when sulphate of potash is used. However sulphate of potash is known to improve tuber dry matter and this will reduce the quantity of fat absorbed on frying, which has important cost implications for the processor.

The carbon components of fry colour

In potatoes, the carbon pathway from the formation of triglycerides in the chloroplast through the mobile intermediates to the ultimate storage as starch in the tuber has been researched extensively. While detailed discussion of the biochemistry of carbon metabolism is outside the scope of this document, the impact of environmental influences and agronomic practices on starch metabolites can be demonstrated to have a determining effect on fry colour.

Sucrose is regarded as the dominant form in which carbon is translocated from the site of production in the shoot to the storage site in the tuber. The fate of this sucrose is determined by the development stage of the tuber. At tuber initiation, sucrose accumulates at the stolon tip, but subsequently declines throughout tuber bulking. Reducing sugar concentrations parallel these changes in sucrose. A reducing sugar/sucrose ratio of 48:1 at the stolon tip during tuberisation, declining to 0.7:1 as tubers developed, has been recorded. Thus the concept of tuber maturity has become associated with low concentrations of sucrose and reducing sugars.

Some 25% of the sucrose arriving from the shoot is utilised for respiratory metabolism, organic acid and amino acid biosynthesis while most of the remainder is converted to starch, catalysed by the enzyme, sucrose synthase. When the tuber becomes detached from its stolon (or even during the final stages of growth) sucrose synthase activity declines while alkaline invertase activity resumes and the sucrose not incorporated into starch now become available for breakdown to glucose and fructose. The starch represents the greatest potential pool of reducing sugars and while there is cycling of carbon through the starch / sucrose /reducing sugars complex during storage; there is a net flux of carbon to soluble sugars as storage progresses.

The nitrogenous components of fry colour

Soluble protein and amino acid levels in potato tubers have been measured and there is general agreement that the storage amides, glutamine and asparagine together with glutamate and aspartate can account for from 50 to 90% of the amino acid pool. During tuber storage, this pool can be augmented by the degradation of soluble protein but the relative levels of glutamine and asparagine remain constant throughout.

The predominant free amino acid in potato tubers is asparagine. Free amino acids react with reducing sugars at high temperatures in the Maillard reaction. Therefore the concentration of these compounds is an important quality determinant for potato tubers. The Maillard reaction produces melanoidin pigments and a large group of aroma and flavour volatiles. Not all of the asparagine is incorporated into protein and some free asparagine can participates in the temperature-induced reactions during cooking. When this happens acrylamide, is formed. There is concern about excessive levels of acrylamide consumption in human diet.

This poses a question, whether it is imported from the leaves or synthesised in the tuber. Carbon dioxide labeled with C^{14} was supplied to a leaf or leaves of potato plants (cv. Saturna) in the light. The leaves, stems, stolons and tubers were investigated for the presence of incorporated radioactivity. It was detected in free amino acids, including asparagine in all tissues. However higher amounts were detected in glutamate, glutamine, serine and alanine than the amount incorporated into the asparagine transported to the stolons and tubers. This demonstrated that free asparagine is not a major contributor when nitrogen is transported from leaves to potato tubers. The inference therefore is that the potato tuber is the synthesis site of the high concentrations of free asparagine.

A model system was used to isolate the tuber nitrogenous constituents responsible for the dark colours on frying and it was observed that purified potato protein was not involved in the reaction but that amino-N was required to induce the colour response. Nitrogen application in potato production is intrinsically linked with the attainment of high yields and an associated delay in maturity (i.e. delay in yellowing and die-down of haulm). It was found that the rate of nitrogen application had a greater effect on fry colour, than its effect on maturity. This was achieved because the total amino-N content of the tubers was increased when the application of nitrogen at planting was increased.

High levels of free amino acids produce dark fry colours. While the free amino acid content of tubers increased with increases in nitrogen application, the levels also increased during the storage period, particularly the first few weeks, but no changes occurred in the relative proportions of amino acids.

The relationship between Maillard reaction substrates and fry colour

Glucose is regarded as the main carbon ingredient of the browning reaction in potatoes. Despite recognition of the fact that both reducing sugars and amino acids are required to induce the dark fry colours many studies have attempted to explain fry colour changes simply in terms of glucose levels. It was demonstrated that for similar reducing sugar levels of about 3-4 mg ml^{-1}, the intensity of the fry colour was related to the level of nitrogen applied to the crop. It was further shown that variation in sugars could explain 90% of the variation in fry colour; but that 98% could be accounted for when amino acids were included in the regression analysis.

By contrast, another study noted that fry colour trends paralleled those of reducing sugars and the relationship was not improved by the inclusion of amino acids. In addition to the work with glucose and fructose there has been some interest also in sucrose and its relation to fry colour and it was observed that sucrose levels in a poor chipping cultivar were three-fold higher than in cultivars that produced light fry colours.

Freshly harvested immature potatoes contain significant amounts of sucrose as the major free sugar. Sucrose is a 12-carbon, non-reducing di-saccharide that plays a crucial role in the development of potato tubers. Synthesised in the leaves and translocated to the tubers, sucrose is the major source of carbons and energy for starch synthesis and potato growth. In immature tubers the rate of translocation to the tuber exceeds its rate of metabolism in the tuber. This explains the high sucrose concentration. Potatoes cultivars differ in the amount of sucrose they accumulate during the growing season.

Although not strictly a Maillard reaction substrate, sucrose has received considerable attention as a marker or possible indicator of future likelihood for frying success. The theory underlying this concept suggests that the sucrose, not incorporated into starch, is hydrolysed subsequently to glucose and fructose. This concept was extended to the development of a 'sucrose rating' or a measure of the sucrose content of the tuber from which the likelihood of it's frying suitability could be predicted. While the system appears to successfully predict frying potential after extended storage, it is a poor predictor of fry colour when used with short-term storage.

Two well-recognised conditions associated with high sucrose levels in tubers are 'Sugar-end' and 'Stem end discolouration'. Such disorders result in French fries, which are dark at the stem end of the fried piece. These defects are often induced when heavy frost or a quick acting haulm desiccant suddenly kills haulm that is actively photosynthesising. Other stresses such as water shortage and especially when combined with heat stress will aggravate the problem. Several factors affect fry colour, quality and flavour of French fries; among them sugar concentration, cell size, and starch content. A cultivar, widely used for French fry production "Russet Burbank", is susceptible to sugar end, a condition in which excessive sugar collects in the ends of potatoes, resulting in unattractively dark fries due to carmelisation

The difficulty in attempting to predict fry colour from parameters such as dry matter, reducing sugars, sucrose and tuber weight is compounded by the reliance of each factor upon tuber age, cultivar and the conditions of growth and storage.

Tuber sweetening

Sucrose, glucose, and fructose are the major sugars, which accumulate in potato tubers. The reducing sugars (glucose and fructose) lower the suitability of tubers for processing, when they are present at high concentrations. Excess sugars in stored tubers commonly arise from two situations: when tubers are stored for more than 7 months, this can induce 'senescent sweetening', when tubers are stored at temperatures below 7°C, this can result in 'cold-induced sweetening'. Both defects result from the breakdown of starch to sugar. The progressive loss of membrane integrity, due to lipid peroxidation, during storage induces senescent sweetening. The development is correlated with an increase in saturation of membrane lipids. In low-temperature sweetening, in which the low temperature stress induces changes in the amyloplast membrane structure, this produces the same effects on amyloplast membranes as those induced by ageing. In potato tubers, ageing increases lipid peroxidation, which is induced by the build-up of free radicals and results in the loss of membrane integrity.

While low temperature storage induces negative responses for tuber destined for processing, in crops destined for 'fresh consumption' such as boiling in the home, or for seed production, low temperature storage of potato tubers may provide beneficial responses. Chief among these are a lowered respiration rate, slowed physiological aging, inhibition of sprout growth, reduction in loss of water due to evaporation, and the possibility of microbial pathogenesis is minimised. When potato tubers attain stability in storage there is a relationship between starch degradation, starch synthesis, and respiration of carbohydrate. Sugars accumulate when there is an imbalance between these relationships.

Factors affecting the concentration of fry colour components in tubers

Effect of cultivar

Since cultivars differ in their content of reducing sugar at maturity and because it is a factor over which the grower exerts primary control, the selection of cultivars suitable for processing has long been a major objective for potato breeders. Considerable success has been achieved in selecting cultivars with desirable chipping qualities using empirical methods and while heritability values for total sugars and chip colours are high, dedicated crossing programmes for fry colour have been less successful because of the associated requirement for high yields. When genotype environment interactions were investigated it was noted that while heritability for yield components was low, chip colour, specific gravity and haulm maturity were far more heritable. It is proposed that chip colour is influenced by two genetically independent systems and their interaction with storage environments. These independent systems are referred to as "chipping stability" and "overall chipping quality". The standard deviation of crosses over the storage environments defines a relationship, which is referred to as "chipping stability" or the ability to produce light colours from cold store, while the phrase "overall chipping quality" is used to define the additive and genetic interactions of the cross, which are involved in determining the ability to chip.

When 12 cultivars were compared over two seasons it was found that reducing sugar levels were reproducible from year to year, with approximately the same values being measured and close agreement between the cultivars accumulating high and low levels. Another study observed that cultivars exhibited a close relationship between sugar levels at maturity over growing seasons. However, processing cultivars differ in their capacity to produce tubers with low reducing sugars over a wide range of environmental conditions and storage regimes.

Empirical breeding methods have provided cultivars capable of producing tubers with acceptable fry colours either following harvest or short term storage. Sprout growth interferes with fry colour after extended storage unless this growth is curtailed. To date this has been achieved using chemical suppressants since the available cultivars will not produce satisfactory fry colours after storage at temperatures low enough to suppress sprout growth.

Effect of tuber maturity on fry colour

The concept of 'maturity' has been discussed in relation to canopy senescence and dry matter, but the term is also used in connection with suitability for processing and fry colour development where it is more easily understood than defined. The concept of 'chemical maturity', has been defined as the condition when a crop attains minimum sugar content, before or as it ceases growth. Changes in both reducing sugars and sucrose have been observed. Tubers contained up to 6% sucrose at early harvest and the levels declined to <1% after eight subsequent weekly harvests. A rapid decline in sucrose levels was recorded over the first four harvest dates while the reducing sugar levels were considerably lower and remained unchanged throughout. Individual reducing sugars appear to behave differently at maturity, with glucose being less responsive to maturity than fructose.

It was sought to further extend this concept by measuring the maturity of the canopy at intervals and a decline in total sugar concentration in petiole sap was recorded from maximum values at 125 days to minimum values at 180 days after planting.

The physiological status of the potato plant at harvest can significantly affect tuber processing quality parameters. The form and the amount of sugar in the tuber are indicative of haulm photosynthetic activity, with significant implications regarding tuber acceptability for processing. Processors require tubers, which have low levels of the reducing sugars, glucose and fructose and the non-reducing sugar sucrose. Furthermore they want fully "mature" tubers in which these sugars will not rise when stored at temperatures of 8-10 ^{0}C for up to six months. This type of maturity is often referred to as 'Chemical maturity'. A consignment of potatoes are said to reach chemical maturity when the concentration of free sugars drop to minimum level acceptable for processing.

When the concept of maturity is defined as the degree of die down of tops, this will introduce the topic of harvest date. When fry colour was examined in a range of cultivars at harvest from 85 to 160 days after planting, some cultivars produced optimal fry colour after growing for 87 days, but others required 115 days growth.

Tuber size has also been suggested as a measure of maturity. It has been proposed that a tuber was mature when it had attained 97% of its final size, but the predictive value of this observation is obviously somewhat limited.

The relationship between crop/tuber maturity, harvest date and 'storability' has significant implications for successful production of potato crops for processing. If an interaction between cultural practices and carbohydrate metabolism could be demonstrated it would enhance the possibility of producing tubers with consistent and predictable fry colour performance.

Effect of environmental conditions during growth

There is a general recognition that the environment can influence processing quality during crop growth. But in describing the effects of environmental conditions, it is difficult to discriminate between specific responses and the general responses arising from location at which the crop is grown. Whereas 'location' may be used as a global phrase to encompass aspects as diverse as soil type, elevation, aspect and their associated husbandry constraints, there is evidence that environmental conditions influence fry colour. Soil temperatures during the growing season have been shown to influence fry colour and when increasing the frequency of irrigation reduced the temperature, there was a consequent improvement in quality.

A decline in fry colour was observed to coincide with cold wet weather prevailing before harvest but that glucose levels were not as responsive to cold temperatures as fructose. However it is the soil temperature before harvest that has received the greatest attention in regard to influencing fry colour and provides the basis for the emphasis, which has been placed on early maturity, which will permit an early harvest without excessive yield penalty. Despite recognising the contribution of low soil temperature to dark fry colour many studies do not cite the soil temperature prevailing at harvest.

Whilst seasonal effects on fry colour are recognised, consistency in fry colour is difficult to achieve since the processing quality between two seasons can be very different, even when the crop is planted at similar dates and experiences a similar length of growing season. Agronomic factors, which could be controlled, such as water supply and fertiliser rates, may even be the same in both years. Despite this, the differences in fry colour between seasons can be greater than the differences resulting from field treatments.

Factors that could have contributed to these seasonal differences include:

- Accumulated temperature
- Solar radiation
- Field location/aspect
- Previous cropping
- Soil condition.

The effects of these cannot be viewed in isolation as they are confounded by and interact with each other. Therefore, the causes of seasonal differences cannot be attributed to specific factors.

Effect of handling

In recent years there has been a steady improvement in the understanding by growers of the importance of careful handling to minimise tuber damage. Most of the effort is directed towards the elimination of loss due to bruising but the contribution of improper handling to changes in fry colour has received less attention. Careless handling will result in tuber bruising and this condition will be aggravated where the supply of potash to the crop is restricted. Supraoptimal supply of potash beyond that required to produce full yield will not compensate and protect the tubers from poor handling induced damage.

Lack of maturity causes dehydration and risk of microbial infection in store. It is also associated with 'skinning' – that is the disruption and partial removal of the skin layer. This will impact negatively on the visual appearance of the tubers and lower their saleability. Farmers traditionally determine skin set by applying thumb pressure and lateral force to the skin. In addition to the physiology of skin maturation, there are other requirements that should be considered when discussing tuber maturity.

Effect of storage temperature

Since fried potato products are consumed all year round, the industry depends on the availability of suitable quality tubers from store. This gives rise to two problems - the suitability of potatoes for storage and for frying following storage. The first aspect has been addressed in relation to harvest date, maturity and freedom from disease, but the response of cultivars to storage temperature will determine fry colour following storage. The general principles underlying the selection of storage conditions to provide tubers suitable for frying are well understood. The low temperatures (4^0C), which would prevent water loss, rotting and sprout growth will produce tubers giving chips with unacceptably dark fry colours due to low temperature sweetening, while high temperatures (10^0C) which avoid these responses, will promote senescent sweetening. The general compromise therefore is to store tubers at 10^0C for short duration storage and at 7-8 ^{0}C for prolonged storage.

Storage temperature has a determining effect on fry colour and the response has been investigated at different temperatures. The fry performance of two cultivars was assessed at storage temperatures of 2, 5 and 10^0C and concluded that 10^0C was necessary for the maintenance of acceptable fry colour values.

Storage temperature cannot be considered in isolation as it has been shown that the effect of temperature is modified by a genetic component and clones with the lowest accumulation of reducing sugars from 4^0C storage also contained the lowest concentration of these sugars following storage at 10^0C. A poor association has been recorded between the colour produced by a genotype after storage and the colour after harvesting or reconditioning.

Other quality related constituents of potatoes

Acrylamide

Scientists in Sweden accidentally discovered acrylamide in food in 2002. They detected the chemical in starchy foods, such as potato chips, French fries and bread and coffee that had been heated higher than 120 °C (production of acrylamide in the heating process was shown to be temperature-dependent). Food that had been prepared by boiling or foods that were not heated were free from acrylamide.

Acrylamide is a chemical that can form in some foods during high-temperature cooking processes, such as frying, roasting, and baking. Acrylamide in deep fried potatoes is formed via the Maillard type reaction between the free amino acid asparagine and a carbonyl source such as the reducing sugars glucose and fructose that are naturally present in the potato; it comes from the food and not the environment and is not an artifact of packaging. Potato varieties differ widely in their concentration of water-soluble components, including acrylamide, which provide the quality markers for processed potato products.

There is considerable variation in the free amino acid content of potato tubers. Results show that it varies over the range 73 to 137 mmol/kg dry weight. Asparagine may contribute from 14% to 29% of the total free amino acids. Sugars showed much greater. The variation on sugar content was considerable greater, with values ranging from 3.7 to 520 mmol/kg. As a result of health concerns relating to acrylamide consumption there was modification of cooking practices and improved management of tuber storage. This resulted in a 53% decrease in acrylamide levels in potato chips produced in Europe between the years 2002 and 2011. Even so, there will be a continuing need for a further reduction in acrylamide levels in chips, to permit manufacturers keep up with an evolving regulatory situation. The current best practice recommends the use of the ALARA (As Low As Reasonably Achievable) concept, where food manufacturers use mitigation strategies to reduce acrylamide levels in their products.

It is clear from published literature that levels of reducing sugars in tubers are affected by variety, storage (temperature, use of sprout inhibitors, atmosphere), and growing conditions (rainfall, temperature and mineral content), with effects often being variety-dependent.

Even though there is a strong correlation between acrylamide formation and reducing sugar content, it is difficult to make predictions of acrylamide formation in chips. A strategy might be to choose a variety that has been shown to produce chips consistently with low levels of acrylamide. The European Commission has suggested an indicative value of less than 1000 μg/kg.

Glycoalkaloids

These are naturally occurring, nitrogen containing, potentially toxic compounds, synthesised in the plants of the genus Solanaceae. Potatoes and tomatoes have been found to contain at least 20 structurally different alkaloids, while about 300 have been recorded in other Solanaceae species. Two major glycoalkaloids are found in regular potato cultivars, α-chaconine and α-solanine, with α-solanine ($C_{45}H_{73}NO_{15}$) being the more toxic of the two. They are both glycosylated derivatives of the aglycone solanidine (Aglycone: the non-sugar component of a glycoside molecule, left over after hydrolysis). Glycoalkaloids exist in all parts of the potato plants but the highest concentration is in flowers (See Table 1) and sprouts on tubers.

They are referred to as bioactive compounds; are active as pesticides and fungicides and are produced by the plants as a natural defense against animals, insects and fungi that might attack them. When present at low concentration, glycoalkaloids enhance flavour but higher concentration causes bitter taste. Consumption of glycoalkaloids causes gastroenteritis and the safe limit is 150mg/kg fresh tuber weight. In general, glycoalkaloids offer resistance to Colorado potato beetle and potato leafhopper. In breeding programmes there can be a conflict between the requirement of pest- and disease-resistant potatoes and those with low levels of glycoalkaloids.

Peeling tubers decreases glycoalkaloid content. The conditions, which favour glycoalkaloid content of tubers, are immature tubers, small tubers, exposure to sunlight immediately after the harvest, short storage in light, damage, microbial infection etc. Breeding programmes screen promising lines for glycoalkaloid values. For this reason therefore they are usually present at low levels in commercial cultivars. However, when tubers greened, stored incorrectly or damaged values can accumulate to high levels. Because they have defensive role the tuber will respond to injury or damage by the accumulation of glycoalkaloids. Furthermore they are synthesised in response to disease, insect attack or rough handling, during or after harvest,

In humans, the potato alkaloids exert their toxic effects on the nervous system. The mechanism is through interfering with the body's ability to regulate acetylcholine, a chemical responsible for transmitting nerve impulses. Acetylcholine acts as the neurotransmitter and functions at neuromuscular junctions, at synapses (or gaps) in the ganglia of the visceral motor system.

Potato glycoalkaloids also act by general disruption of membranes, and symptoms reported for solanine toxicity include headache, nausea, fatigue, vomiting, abdominal pain and diarrhea.

Note: *It is important to understand that cooking potatoes does not destroy the solanine.*

Table 1. Levels of glycoalkaloids (GA) in various parts of the potato plant

Plant part	**Glycoalkaloid concentration (mg/kg fresh weight)**
Flowers	2150 - 5000
Leaves	230 - 1000
Stems	23 - 33
Roots	180 - 400
Bitter tasting tuber	250 - 800
Whole tuber	10 - 150
Skin (2-3% of tuber)	300 - 640
Peel (10- 12% of tuber)	150 - 1068
Flesh	12 - 100
Cortex	125
Pith	Not detectable
Sprouts	2000 - 7300

Internal disorders and tuber quality

Non-enzymatic after cooking darkening

One of the most widespread, undesirable characteristics of cultivated potato is after-cooking darkening (ACD). It is a non-enzymatic oxidation reaction, originating from the oxidation of a ferric-diphenol complex. The grey discolouration observed after cooking comprises a grey pigment consisting of ferrous iron and chlorogenic acid known as ferri-dichlorogenic. The intensity of darkening depends on the concentration ratio of iron, chlorogenate and citrate and this ratio varies between tubers and even between areas within tubers.

Blackening after cooking (greying of the flesh) appears especially when tubers are cooked in water or steam, and are then peeled or cut and left exposed to the air.

The first step in the reaction is the formation of a colourless complex of ferrous iron and chlorogenic acid. When it is exposed to the air it is oxidized to a ferric complex. Two factors influence the discolouration; pH and the ratio of citric acid to chlorogenic acid. An increase in pH (up to 8) stimulates discolouration and since the pH at the heel end is normally higher than at the rose end, the degree of discolouration is normally greater here. The level of discolouration after cooking would be reduced by a higher ratio of citric acid to chlorogenic acid because citric acid binds the iron in the tuber; which renders it unavailable to react with chlorogenic acid. Elevated concentrations of citric acid lowers the tissue pH, and reduces the intensity of colouration.

The factors that contribute to tubers susceptibility to ACD (i.e. the concentration of chlorogenic and citric acids) are genetically controlled and influenced by environment. There is a complex relationship with soil nutrients: K increases citric acid while chlorides decrease it; nitrogen increases the chlorogenic acid but potassium decreases it. The soil type in which the crop is grown influences the response, with tubers growing on peat soils being more prone to discolouration than those from silt or loam soil.

The formation of ACD differs between varieties with those having more chlorogenic acid blackening most, whilst the intensity is less in those having low chlorogenic acid.

Tuber Bruising

There are three types of bruises in potato tubers shatter bruise and black spot bruise and pressure bruising (Fig. 3), and each type causes losses.

The first two bruise types, occur during harvest and handling while the third category is associated with improper storage. A less serious type of damage is know as skinning, where small sections of the outer skin are broken.

Internal blackening / Blackspot

A potato tuber develops blackspot bruise when the impact against an object damages cells in the tissue just beneath the skin, but the impact is not sufficient to break the skin. After a period of 24 to 48 hours a dark grey to black colour develops in the damaged tissue but is only visible after peeling the potato.

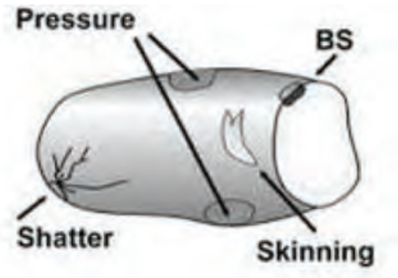

Figure 3.
Summary diagram illustrating 4 main categories of tuber bruising
(Image © Onions-potatoes.com. With permission)

Blackspot bruise results from oxidation of phenolic compounds (such as tyrosine and chlorogenic acid) to melanin by polyphenol oxidase after bruising. Within the damaged cells, a substrate, primarily tyrosine, mixes with an enzyme, polyphenol oxidase, to turn normally white tissue dark gray to black in color. Not all potato varieties are susceptible to blackspot bruising, and there are varying degrees of susceptibility among varieties exhibiting this damage.

Bruise damage occurs during harvest and handling, but the question was raised whether there were conditions prior to harvest that would increase the potential for blackspot bruising. And, if so, what management practices could be used to minimize this damage?

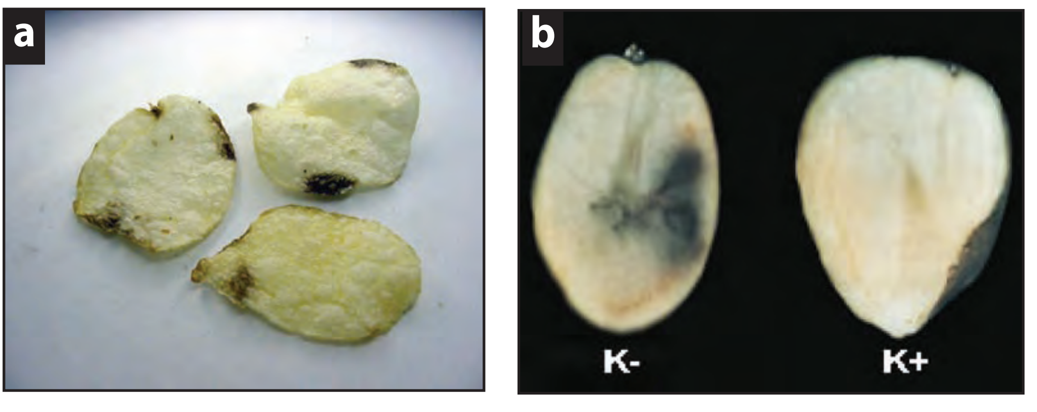

Figure 4.
Blackspot bruise on potato chips (left). Tubers from crops with sufficient and deficient levels of potassium (right).
(Photo (a) Uni. Nebr. Extension (b) © PDA, UK with permission)

A comprehensive review of the several factors affecting bruising confirms that there are many reports highlighting a reduction in bruising when potassium application was increased. But the usefulness of the reports is queried, as there was no consistency in aspects of the methodology such as the mechanism for inflicting the damage and the damage assessment methods.

The link between bruising and potassium has been investigated and while some reports have described no effect of potassium on bruising, others have recorded effects only on soils where potassium is deficient. The broad consensus view concluded that there was sufficient evidence to indicate that potassium nutrition plays a role in the bruising response. If potassium is making a contribution to alleviating bruising, the response is achieved through its effect on dry matter content (starch concentration), high cell turgor and elevated concentrations of organic acid.

Two theories around potassium and bruising exist. One proposal suggests that applying potassium at supraoptimal rates will alleviate bruising. However, they support the contention that the degree of bruising alleviation and the economic return from applying this strategy, even on potassium-deficient soil, would be so small, it would not be warranted. The other proposal is that application at rates for maximum yield is adequate.

Some workers have reported a response to the form of potash (muriate or sulphate) and considered that muriate is better at alleviating the problem, but ultimately it is the rate of K application that is more important.

Tubers with higher specific gravity generally were more susceptible to blackspot bruising. Cultivars producing tubers with a specific gravity above 1.080 were more susceptible to blackspot bruising than tubers with lower specific gravities.

Additionally, available soil moisture affected the amount of blackspot bruising. Fields with lower available soil moisture at harvest tended to have more blackspot bruising. Growers are advised to maintain at least 50% of available soil moisture until harvest.

Soil type is also known to influence incidence of black spot bruise. Fields with sandy or loamy sand soil generally had lower available soil moisture at harvest resulting in tubers with a higher amount of blackspot bruising.

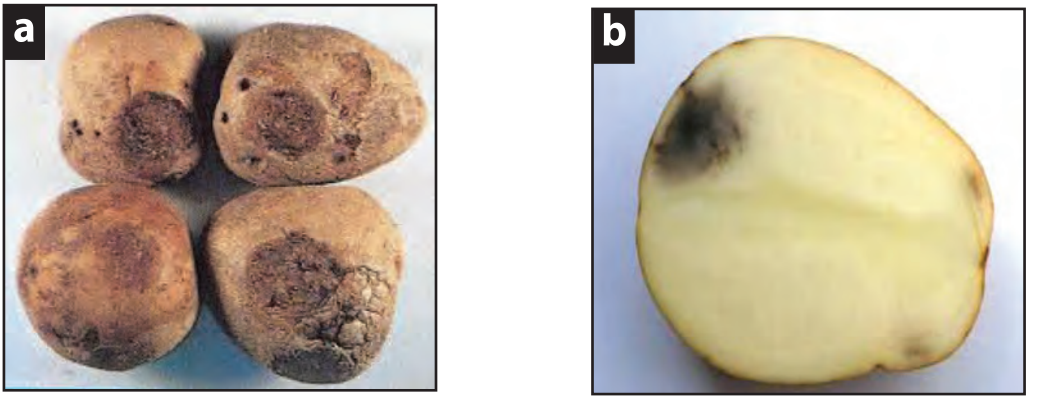

Figure 5.
Bruise damage on potato tubers, external and internal responses.
(Photo (a) © Uni, Nebr. Extension. (b) © AHDB, UK With permission)

Research evidence indicates that environment affects the susceptibility of tubers to blackspot bruising. Remember, however, tubers are blackspot or shatter bruised only after sustaining an impact of sufficient force to cause damage. A potato crop harvested from fields with the least potential for blackspot bruising can still be damaged if the tubers are subjected to improper handling.

Pressure bruising

A flattened or depressed area on a potato tuber, called a pressure bruise, often develops in storage. This is caused by tuber dehydration (water loss) resulting from low soil moisture before harvest and/or by low humidity ventilation air in storage. Pressure bruise typically manifests on tubers in the lower layers of the pile. Affected tubers acquire a flattened look to the tuber outer surface that is often accompanied by a gray/black colored internal defect. Two factors contribute; weight loss from the potato combined with pressure or force from tubers or structure surfaces.

Several factors predispose potato tubers to pressure bruise. The state of the potato, at store filling time, has a significant effect on subsequent behavior in storage.

First, the state of the potato going into storage will influence how the potato responds to the storage environment. Potatoes can be predisposed to pressure bruising if they are flaccid, if there is already wound damage, if the tubers are immature, or if harvesting takes place when the tubers have high pulp temperatures then they are more prone to weight loss and thus pressure bruise. As a general rule, mature potatoes are 10-60 times less likely to lose weight compared to immature potatoes. Water loss from a wounded potato is up to 1000 times more than a non-wounded potato prior to completion of wound healing and suberisation.

Even the fresh market may discriminate against potatoes with pressure bruises. Minimising pressure bruising requires an integrated approach; harvest when tubers reach maturity, harvest when soil moisture and temperatures are near ideal, handle the tubers with care and store them in a manner designed to minimise the risk of pressure bruising by controlling stack height.

Potato breeders have long factored in quality aspects into their selection criteria. Fortunately potatoes are also being bred having properties to help meet new challenges. For example, tubers with a regular size and shape are more resistant to bruising; this permits digging by machine.

Shatter bruising

Shatter bruise, as its name suggests, is caused when impacts induce cracks or splits in the tuber skin. If severe, the cracks may extend deep into the underlying tissue. Shatter bruise facilitates the entry of pathogens such as those causing Fusarium dry rot, early blight, and bacterial soft rot.

As ever, a prerequisite to avoiding bruising at harvest is to ensure a high degree of tuber maturity and skin set. This can be achieved by an effective haulm kill, waiting to allow tubers to set skin long enough and avoiding late applications of nitrogen. Once again, these factors will vary depending on variety and combined with appropriate plant potassium levels.

Figure 6.
Shatter bruise on potato (Photo © Onions-potatoes.com, With permission)

Bruise testing during harvest is an effective tool to illustrate the cause and degreed of damage. Bruise testing involves soaking tubers in a catechol solution (20 g. catechol in 14 L water) for 1 minute, allow the tubers to rest for 3 minutes and then peel them. If there is bruising it will show up as red cracks and marks. Noting the amount of peel that must be removed will provide an indication of the depth of the bruise.

Blackheart

This defect is induced by low oxygen levels in the interior of the tuber. It is reasonably simple to diagnose, since the center of affected tubers display an irregular pattern with black to blue-black border. A cavity may form in the center of the tuber due to shrinkage of the tissue. It can be distinguished from Pythium leak, as the darkened areas in Blackheart-affected tubers are firm, in contrast to the sponginess associated with the Pythium infection. Furthermore, Blackheart affected tissue does not smell and the condition is induced when tubers are held in a low-oxygen environment due to inadequate ventilation of the tuber clamp. Temperature extremes will facilitate the development of Blackheart, since extremely cold (0 °C) or warm (36°– 40 °C) temperatures, slow down the rate of gas diffusion through the tubers. This means that the larger tubers are more likely to develop the condition. Field conditions, where the soil is flooded, or store conditions where there is poor aeration, will promote the development of Blackheart

Figure 7.
Blackheart and the internal cracking. (Photo © AHDB, UK. With permission)

External disorders

The external disorders of tubers have often been dismissed as cosmetic conditions when the potato crop is sold from the field to the market and directly onto the consumer. However with increasing sophistication in presentation and marketing, such as washing and packaging in clear plastic bags, these external disorders assume commercial importance.

(**Note**: Two diseases, Silver scurf and Black dot are discussed here, rather than in **Section 11**, since they are considered as blemish inducing rather than yield reducing disorders)

Silver Scurf

Silver scurf is caused when the fungus *Helminthosporium solani*, attacks the periderm of the potato tuber causing blemishes. While it is primarily a blemish disease it has commercial significance; small lesion might be ignored but large lesions may coalesce and ruin the appearance of the tubers. Two phases of the disease exist; a field phase and a storage phase.

Primary infection occurs in the field because *H. solani is* seed borne and these mother tubers provide the major source of inoculum for infection of daughter tubers. The infection cycle commences when the pathogen produces reproductive structures, called conidia, on the surface of the seed tuber. The exact mechanism of infection transfer from mother to daughter tubers is not known, but it is supposed that conidia are washed off the seed tuber and through the soil by rain or irrigation. When conidia are deposited on or close to the surface of daughter tubers, they are induced to germinate by free water and then go on to infect these tubers through lenticels or periderm and next they colonise the periderm.

Symptoms of infection are visible following harvest but the disease makes real progress in potato stores. High temperature and relative humidity favours the spread and increase of silver scurf in potato stores. RH values greater than 90% in combination with temperatures greater than 3 or 4 ^{0}C will promote spread and infection. Furthermore, high humidity following washing of potatoes destined for market is conducive to sporulation of *H. solani* on infected tubers.

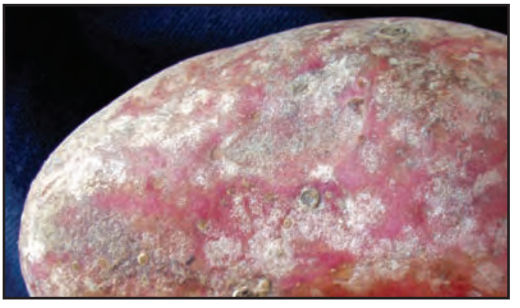

Figure 8.
Silver scurf lesions on tubers (Photo © Author)

Silver scurf is a difficult disease to control, whether by chemical or cultural practices. Initially the fungicide thiabendazole (TBZ) gave good control of infection but now *H. solani* isolates resistant to the fungicide have developed.

Traditionally only tubers destined for the washing trade were discriminated against when they were infected with silver scurf. Now the processing industry is rejecting them due to peeling losses when mechanical peeling as the extra periderm material is removed and due to blackening of the edges in potato crisp slices from infected tubers.

Black dot

Black dot disease of potato is caused by the fungus *Colletotrichum coccodes*. While it can affect all parts of the plant, it is most often observed on tubers. The condition acquires its name from the numerous dot-like, black microsclerotia that can appear on tubers. The infection is not confined to tubers but can colonise stolons, roots, and stems both above and below ground level. On the foliage, the symptoms closely resemble early blight. The disease in particularly easy to see on stems after they have been chemically desiccated. The roots are also attacked producing a brown to black colour and growth is reduced.

The disease cycle for black dot is straightforward. The fungus survives between potato crops as microsclerotia, either on volunteer tuber surfaces or on plant debris in the field (potato, tomato, and other hosts) and manages to survive there for long periods. In the next potato crop, sclerotia on tubers develop into acervuli and then progress to producing spores. Because black dot has both soil-borne and tuber-borne phases, it has a long infection cycle control can only be achieved through the use of long rotations (extending beyond 3-4 years) and by planting clean seed tubers.

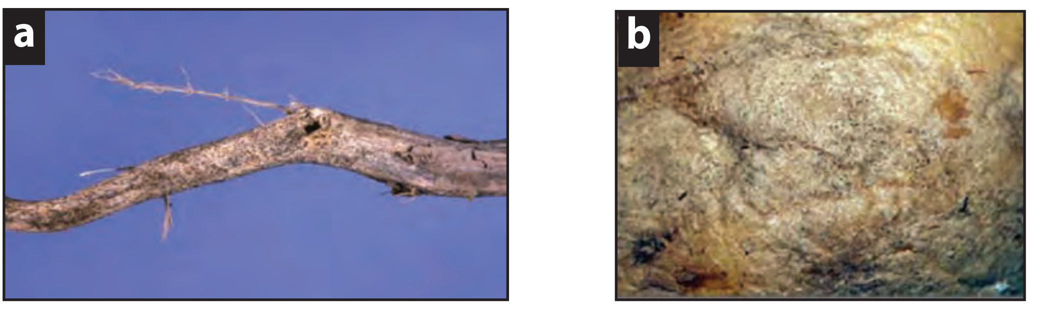

Figure 9.
Black dot infection of potato stem and tuber
(Photo b © Univ. Idaho Extension Service, With permission.

Summary

- One of the most important aspects of the potato tuber is its quality.
- Quality parameters of tubers change according to the specific market utilization types.
- "External quality" aspects comprise skin colour, tuber size and shape, eye depth. These traits are deemed very important for fresh consumption where external traits are most likely to influence consumer's choice.
- "Internal quality" aspects include nutritional properties, culinary value, after-cooking properties or processing quality. Internal quality is defined by traits such as dry matter content, flavour, sugar and protein content, starch quality, type and amount of glycoalkaloids. These factors determine suitability for processing
- Several factors affect tuber quality. They include the genetic make up of the cultivar, crop maturity, agronomic practices, environmental conditions, storage temperatures, the presence of pests and diseases.

Sources accessed in the preparation of this section.

Corsini, D., J. Stark, and M Thornton. (1999). Factors contributing to the black spot bruise potential of Idaho potato fields. *Amer J of Potato Res* **76:** 221-226.

Elfnesh, F., Tekalign, T. and Solomon, W. (2011). Processing quality of improved potato (Solanum tuberosum L.) cultivars as influenced by growing environment and blanching. *African Journal of Food Science* **5:** 324 – 332.

Errampallia, D., Saundersa, J. M. and Holley, J. D. (2001). Emergence of silver scurf (Helminthosporium solani) as an economically important disease of potato. A Review. *Plant Pathology* **50**: 141-153.

Fernandes, A.M., Soratto, R.P. & Pilon, C. (2015). Soil Phosphorus Increases Dry Matter and Nutrient Accumulation and Allocation in Potato Cultivars. *Am. J. Potato Res.* **92:** 117-127.

Genet, R. A. (1992). Potatoes - the quest for processing quality. Proc. Agron. Soc. N.Z. **22:** 1-7.

Harper, S. (2004). Potato tuber quality management in relation to environmental and nutritional stress. Publ. Horticulture Australia. 80p.

Leeman, M., Ostman, E. and Bjorck, I. (2008). Glycaemic and satiating properties of potato products. *Eur. J. Clin. Nutr.* **62**: 87-95.

Sonnewald, U., Studer, D., Rocha-Sosa, M., and Willmitzer, L. (1989). Immunocytochemical localization of patatin, the major glycoprotein in potato (*Solanum tuberosum L.*) tubers. *Planta,* **178:** 176-183.

Section 15.

Climate Change and Potato Growth

Introduction

Before engaging in a discussion on climate change, it is important to define the word climate and ask how the concept of climate differs from weather. Weather and climate are often discussed as if they were similar, but in fact, they are in fact two very different concepts. Weather describes the current meteorological conditions at a specific time and location. Climate encompasses a broader timespan and looks at the weather conditions the have prevailed in a region during a 30-40 year timespan.

Climate change is defined as a significant change in the climate of a given region. Evaluating climate change requires examining the change in the statistical properties of the climate (principally its mean and spread) when considered over a long timespan, regardless of cause of these changes. This permits discounting fluctuations over short periods, such as the "El Nino effect".

Two broad factors are associated with climate change; the Earth's natural processes and human activity.

Natural phenomena such as variations in solar intensity or volcanic eruptions can induce climate change. But it is human activity-induced change that attracts the greatest amount of comment, particularly in relation to the build up of greenhouse gases (GHGs) in the atmosphere. It is important to state however, that without the so called 'greenhouse gasses' and the associated 'greenhouse effect' life in this planet would not be possible. The ability of the atmosphere to capture and recycle energy, emitted by Earth's surface, is the basis of the greenhouse effect (Fig. 1). (The analogy of the greenhouse has gained popularity, but it is incorrect. A green house retains heat by restricting airflow and retaining the warm air inside the structure). The GHG's ensure that the average temperature of 14^0C facilitates plant and animal life. Concern therefore focuses, not on the GHG'S *per se* but on the continuing increase in their concentration.

Human activities, such as burning fossil fuels for energy to power transport, heating and manufacturing, and also methane emissions from agriculture are proposed as contributing to GHG build up. GHGs permit the short wave sunlight energy to pass

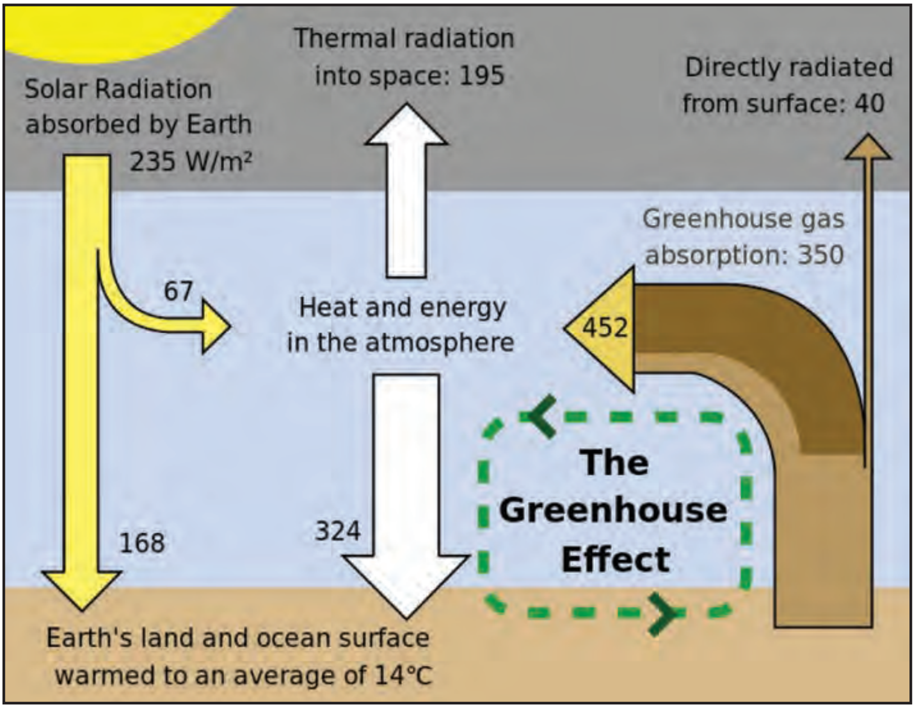

Figure 1.
A representation of the exchanges of energy between the sun, the earth's surface, the earth's atmosphere, and outer space.
(Source: Environment Change Canada. © With Permission)

through the atmosphere to reach the earth. But these gasses then act like a blanket and trap the outgoing longer wave energy from the heated surface of the earth. While this phenomenon explains the general warming of the global atmosphere, it does not provide a guide to the effect on climate at regional level.

(Note: *Global warming, or the rise in the earth's average temperature over recent decades is not disputed. However, the cause of this increase is hotly disputed, by groups with contrasting political points of view; the cause of global warming will not be discussed in this publication*.)

Background

Over the next two decades, the world's population is expected to grow on average by more than 100 million people a year. World population is expected to reach 9.2 $\times 10^9$ people by 2050. Population experts suggest that more than 95 percent of that increase will occur in the developing countries. Since pressure on land and water resources is already intense, the expanding population presents a challenge to ensure food security for present and future generations. At the same time it is vital to protect the natural resource base on which we all depend. The potato will be a key contributor to efforts designed to meet those challenges.

A relatively stable climate has persisted since the last ice age, which ended around ten thousand years ago. Human societies have adapted to this stability. The current challenge now is to adapt to a warming climate. The new scenario will affect water supplies, agriculture, power and transportation systems, the natural environment, and even human health and safety. Once produced, carbon dioxide can remain in the atmosphere for nearly a century, so it can be expected that Earth will continue to warm in the coming decades. Increasing temperatures increases the risk of inducing more severe changes to the climate and Earth's system. Attempting to predict the exact impacts of climate change is notoriously difficult, but what's clear is that the climate we are accustomed to, can not be considered a reliable guide to conditions we can expect in the future.

Earth's average temperature has risen by 1.0^0C over the past half-century, and is projected to rise between 1.4 and 5.8^0C over the next hundred years. But even small changes in the average temperature of the planet can translate to large and potentially serious shifts in climate and weather. When the increase in temperature is combined with the buildup of greenhouse gases this can amplify the change in Earth's climate with potentially serious effects on human welfare and the natural ecosystems.

Influence of Climate on Human Progress

Food crop domestication that began approximately 10,000 years ago marked one of the most dramatic evolutionary events in human history. When a large proportion of the population was liberated from food production they could transfer to performing diverse social activities, which subsequently evolved into todays civilizations. The great proportionof the food crops we rely on today were domesticated from wild grasses, including wheat, rice, maize, barley, sorghum, oats, and millets, collectively known as cereals. It is remarkable that domestication of our essential cereal crops started in different continents within a relatively short period of time: wheat and barley in Middle East ~10,000 years ago, rice in China ~8,000 years ago, and maize in Central America ~7,000–9,000 ago.

The exact rationale driving these independent domestications is not known, but climate change following the last ice age has been suggested. Then either the change in prevailing climate altered the vegetation or provided an opportunity to exploit the expanding grassland. Another theory proposes that the requirement of feeding an expanding population forced them to develop a more reliable food source than that provided by hunting and gathering.

Procedures to study climate change

It is expected that the increase in atmospheric carbon dioxide concentration (CO_2) will have major effects on plant growth and the nutritive value. Trying to modify the open air to replicate the effect of elevated CO_2 on plants under field conditions is extremely difficult. The most widely used and most efficient solution is the open-top chamber (OTC) system where the effects of elevated temperature, CO_2 and other atmospheric gases on vegetation can be assessed (Fig. 2). They are simple enclosures, with an open top, constructed of an aluminum frame covered by panels of polyvinyl chloride plastic film. Air is introduced at the base of the chamber, enriched with CO_2, and then allowed to escape through the open top of the chamber. They are relatively inexpensive to construct and maintain. A typical arrangement is eight OTCs, each with 1.2 m^2 of ground area (four with elevated CO_2 and four with ambient CO_2) and four control plots of the same dimension to assess the chamber effects on plant responses to CO_2.

Figure 2.
A typical open top chamber.
(Image courtesy ASDA, ARS)

Growing potatoes in a changing climate

Because plants have evolved against the background of a changing environment, they possess such flexibility in their development capacity they can react to ever-changing environmental conditions. Climate change is predicted to have significant effects on global potato production. It is to be expected that potatoes are likely to be affected by increases in atmospheric carbon dioxide, temperature and precipitation, as well as interactions between these factors. In addition to affecting potatoes directly, the distributions and populations of many potato diseases and pests will be modified by climate change.

Potato response to change in atmospheric CO_2

Research has shown that elevated CO_2 enhances photosynthetic rates in the leaves of almost all C3 species that are well supplied with nutrients. It could be expected that potato crop growth and therefore tuber yields will benefit from increased carbon dioxide concentrations in the atmosphere. This increase would be achieved through an increase in their photosynthetic rates, which can increase their growth rates. Again research has shown that the efficiency of carbon flux to yield components depends on coordination between the activities of source organs, transport and sink activity. Potato crop yields are also predicted to benefit because potatoes partition more starch to the tubers under elevated carbon dioxide levels and the tubers are not limited in their capacity to take in the additional fixed carbon, under conditions of elevated CO_2.

Higher levels of atmospheric carbon dioxide also results in potatoes having to open their stomata less to take up an equal amount of carbon dioxide for photosynthesis, which means that this will result in less water being lost through transpiration from stomata. An upside to this development would be an increase in water use efficiency (the amount of carbon assimilated per unit of water lost) of potato plants.

The ratio of leaf surface area to unit ground cover is called leaf area index (LAI, m^2 m^{-2}). Variations in soil moisture, soil fertility and atmospheric CO_2 influence LAI and it is likely therefore to be co-limited by a number of resources, including water, nitrogen and light. LAI is regarded as an integrative measure of carbon and water balance in plants because it describes the potential surface area available for leaf gas exchange (CO_2, O_2 and H_2O).

Atmospheric CO_2 exerts a significant influence on LAI. When CO_2 supply is available at relatively low concentrations is strongly limiting to gross primary production. Under these circumstances LAI is strongly correlated with CO_2. But when CO_2 is abundant, the sensitivity of LAI to CO_2 decreases considerably. The nonlinear relationship between leaf area production and atmospheric CO_2 has the capacity to introduce a potential bias in mathematical models simulating low-density vegetation, such as potato canopy, which can significantly increase canopy size without inducing self-shading.

Variation in the amount of intercepted radiation (largely determined by LAI) can expalain variation in growth and productivity. Elevated CO_2 levels affect growth through stimulation of leaf photosynthesis. LAI is prone to considerable variation and the variability can be induced by climatic and growing conditions including CO_2 concentration, seasonal climate, water and nitrogen availability.

In open top chamber studies, tuber yield (expressed as dry matter) increases ranging from 0-60%, were recorded when plants were grown under CO_2 concentrations of double the ambient. In these studies, the yield increase was achieved by an increase in either the total yield or the yield of marketable tubers (>35mm). In other studies, an increase in yield under elevated CO_2 resulted from an increase in tuber number. This latter response is explained by the large increase in photosynthetic capacity of the young potato plants, resulting from increased leaf area and the availability of potential sites to facilitate tuber formation. This elevated CO_2-induced formation of increased leaf area provides the foundation for tuber yield increase, either through increase in tuber number or through increase in mean tuber size.

Potato response to change in atmospheric temperature

Care must be taken when considering these results above. Any increase in atmospheric CO_2 will obviously be accompanied by increase in ambient temperature. Elevated temperatures hasten the onset of leaf senescence and reduce the length of the growing period. Without the benefit of a full growing season, the yield bonus that might be derived from the initial investment in increased leaf area will not be realised. Furthermore, elevated temperatures increase the potential for drought stress. Since drought stress limits stomatal opening and CO_2 uptake, the hoped for benefits from increased CO_2 levels may not be forthcoming.
Research, using growth modeling, has shown that potato leaf area expansion was influenced by air temperature and CO_2. Cooler temperatures and elevated CO_2 provided maximum individual leaf area values. The time interval between leaf appearance and when 99% of final area is attained, defines growth duration. This period was negatively correlated with increasing temperature.

Potato response to change in precipitation patterns

A reduction in the reliability of rainfall and the availability of soil-water and the consequent limitation to plant production are all being induced by global climate change. Even though it is well recognised that drought stress can seriously affect tuberisation, yield and quality of potato plant there is a poor understanding of the precise molecular mechanisms dictating the potato stolon's response to drought stress and water supply.

Stem growth and development underpin potato canopy development. Water stress has been found to reduce elongation rate and final stem length. There is a consistent pattern to the effects of water stress duration – it intensifies with time; the initial effect is on LAI and as the stress becomes more severe, stomatal and other physiological parameters become affected

As drought stress increases, and more so in plants growing under elevated $CO_{2,}$ apical branch elongation and duration are reduced. This effect is replicated in the development of other lateral branches, to the extent that continuing water stress reduces both lateral branch length and branching order. The foregoing responses result in a decrease in dry matter partitioned to the canopy and also reduce the relative contribution of secondary stem mass to the canopy particularly under increasing drought stress. Potato is considered a drought sensitive crop, where even mild levels of moisture stress will limit canopy formation. This results in a reduction in net assimilation rate throughout the season. Seasonal net assimilation and total biomass production in potatoes is enhanced with CO_2 enrichment. This response has also been recorded in other crops relying on the C3 biochemical pathway.

The response of potato plants to water stress can be partially alleviated when the plants are exposed to atmospheric conditions where CO_2 is elevated. Potato canopy formation is influenced by the interaction of CO_2 and water stress, but the mechanism driving the interaction will require greater elucidation

Crop production by small farmers is being severely compromised by disruption in traditional rainfall patterns. These farmers rely on rain fed agriculture and some climate scientists have predicted that yields from this type of agriculture will decline by up to 50% by 2020.

Impact of climate change on potato tuber quality

Tuber quality defines the suitability of potatoes for processing, but the effects of elevated CO_2 on tuber quality are not well understood.

A study to investigate the effects of elevated CO_2 concentrations on tuber quality of potato over two full growing seasons under 380, 550 or 680 µmol mol^{-1} CO_2 in open-top chambers (OTCs). When results were combined over two years, tuber malformation was increased by 62.8% as CO_2 levels raised from 380 to 550 µmol mol^{-1}, thereby downgrading tuber quality. However, tuber greening was lower when the plants were grown under elevated CO_2 and this increased their market value. There was also a positive relationship between CO_2 and dry matter content, which produced tubers having superior processing quality.

Chemical quality characteristics were also influenced by CO_2 concentrations. There was a positive relationship between CO_2 levels and concentrations of glucose, fructose and total reducing carbohydrates. These compounds reduce tuber quality because they induce an elevated risk of browning and the concomitant generation of acrylamide in the fried product. **(See Section 14)** By contrast, CO_2 enrichment produced a negative relationship between the concentrations of protein, potassium and calcium This response would imply a negative effect on tuber quality, especially with regard to nutritional and sensory quality of processed product.

Significant negative relationships were demonstrated between elevated CO_2 treatments and concentrations of leucine, phenylalanine and methionine. This reduction in the levels of physiologically valuable amino acids may also decrease nutritional quality of potatoes. By contrast the CO_2-induced decrease in glycoalkaloids lowers the toxicological potential and this would help to improve the quality.

CO_2 enrichment produces a mixed response, with both positive and negative impacts on potato tuber quality. These quality attributes have implications for tuber commercial value, processing quality and consumer nutrition

There is considerable work remaining to determine whether CO_2-induced changes will induce beneficial of adverse changes in tuber quality

Impact of climate change on disease and pest survival and development

As well as affecting potatoes directly, climate change is predicted to affect the fecundity, dispersal and distribution of many potato diseases and pests. These include insect pests such as the potato tuber moth (*Phthorimaea operculella*) and Colorado potato beetle (*Leptinotarsa decemlineata*) (Fig. 3), which are predicted to spread into areas currently too cold for them. Since arthropods are exothermic organisms they cannot internally regulate their own temperature. Because of this, their development is subject to the temperature of the environment to which they are exposed. Of all the abiotic factors associated with climate-change, temperature is the one most directly affecting herbivorous insects.

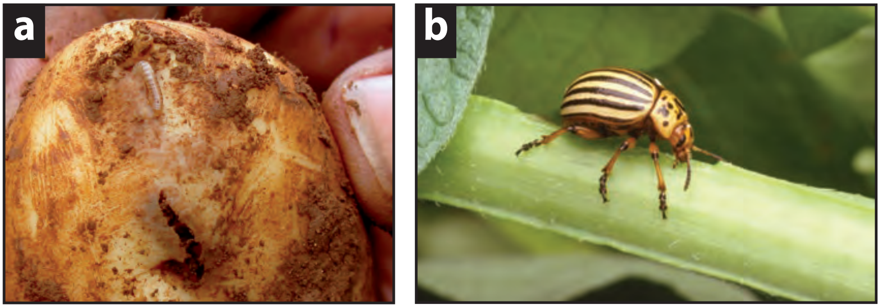

Figure 3.
Potato tuber moth damage (a). Colorado Potato beetle.
Photo (a) © Author. (b) Courtesy Wikipedia)

Aphids, which act as vectors for many potato viruses, will also be able to spread under increased temperatures. This will likely impact the seed potato industry. Currently seed potatoes are grown at cooler high altitude locations to avoid virus infection spread by aphids. Higher temperatures will mean that those high altitude locations would now become accessible to aphids.

Increasing temperatures will likely facilitate the development of increased cycles of nematodes. Potato cyst nematodes are responsible for yield losses of around 10% each year. In addition to the direct effect they are also associated with the wilt inducing fungus *Verticillium*. The root knot nematodes (*Meloidogyne spp.*) thrive under the temperature regimes of the tropics and will likely assume increasing importance.

Rising temperatures mean that migratory pests are expected to arrive earlier, infestation levels are worse and they reproduce faster.

Currently, it is estimated that disease outbreaks destroy between 10% and 16% of the world's crops and rising global temperatures could exacerbate this problem.

Higher temperatures facilitate the growth and reproduction of pathogens that cause blackleg, ensuring that it becomes a bigger problem. The main cause of tuber decay in store and blackleg or stem rot in the field are the soft rot coliforms, *Erwinia carotovora* ssp. carotovora (Ecc), *E. carotovora ssp. atroseptica* (Eca) and *E. chrysanthemi* (Ech). While all three of the bacteria can cause tuber soft rot, only Eca and Ech appear to cause blackleg symptoms, but all three can cause tuber soft rot. Their ability to colonise a host is temperature-dependent: Eca tends to cause blackleg at temperatures < 25°C, and Ech, regardless of biovar, at higher temperatures. Recently strains have been isolated that can also cause blackleg in cool temperate areas.

Higher temperatures will facilitate the spread of Bacterial infections such as *Ralstonia solanacearum*. Under conditions of increased rainfall, flash flooding would facilitate the spread of the pathogen.

Late blight, (causal agent, *Phytophthora infestans*), is often regarded as the most important disease of potatoes globally and benefits from higher temperatures and wetter conditions. The optimum temperature for late blight occurrence is considered to lie between 18 and 21^{0}C, while temperatures above 25.5 and below 7.5 are considered unfavourable. It is predicted that late blight will arrive earlier in some potato growing regions; in some areas the threat of infection will increase while in other areas still, the threat will diminish. More frequent rainfall events will increase the cost of fungicides to control late blight, due to wash off.

The impact of elevated CO_2 on growth and competitiveness of C3 and C4 crops and weeds

A weed is defined as "a plant growing in the wrong location". Weeds are undesirable because they interfere in growth, yield and production of cropping systems. They achieve this response through competition with crops for soil and water resources. Furthermore, land value is diminished and farmers spend money and expend labour attempting to minimise the weed damage. Currently, a significant portion of production expenditure is absorbed by the cost of weed control. For example it is reported that world wide, weeds caused 12 percent reduction in crop production and their control costs some 35 billion dollars. Developing countries spend relatively larger amounts. In addition to their effect on crop productivity through competition, weeds can also act as a host for pests and diseases and this will further increase the complexity of their control.

Recognising the characteristics that play a role in weed competition ability are important in weed management, since environmental factors significantly alter weed competitive ability.

The current most active environmental topic is climate change. CO_2 concentration has risen from 285 ppm in 1950 to above 400 (approx. 30 percent increase). Increases in CO_2 have also caused the temperature to change; hence the importance of understanding the effects of elevated CO_2 on plant growth and metabolism. It's reported that elevated CO_2 promoted growth and development of more than 100 plant species. Agriculturalists are concerned about the effects this increase is having on weed-crop competition.

When the ambient CO_2 is increased there is an initial and transient response, where photosynthesis rate is increased and transpiration rate is reduced. The increase in CO_2 fixation, achieved through a decrease in photorespiration, is related to stomatal closure. These effects are transitory since permanent effects of CO_2 on growth and physiology of plants has rarely been detected.

Environmental conditions affect the dynamics of this crop and weed competition – where increasing CO_2 concentration modify the environmental parameters. Since C3 and C4 plants are likely to respond differently to increasing CO_2 and temperature, this might change their competitive ability. Since most of the major world crops are C3 and often the noxious weeds are C4, the increase in CO_2 concentrations would acquire increased significance. Several studies have shown that C3 plant growth would be promoted by elevated CO_2 concentration. However it was observed that there is considerable interspecific variation in the manner in which plants might respond to CO_2, for example, growth of C4 plants also could be promoted by CO_2 at lower concentration rates.

When atmospheric concentration of CO_2 was doubled, the average growth of 156 species was increased by 37%; with C3 plant growth (41%) was higher than C4 (22%). The responses of CAM plants were lower.

(Note: *Crassulacean acid metabolism, also known as CAM photosynthesis, is an alternative carbon fixation pathway. It is an adaptation that evolved in some plants and it permits those plants to grow under arid conditions. Plants using full CAM metabolism achieve their success by having the stomata in the leaves remain shut during the day to reduce evapotranspiration, but open at night to collect carbon dioxide. Pineapple is one of the best-known commercial CAM plants.*)

A study examined the competitive ability of sorghum, under normal and elevated CO_2 concentrations, against *Xanthium strumarium* (a weed containing significant concentrations of the extremely toxic chemical carboxyatratyloside). The study revealed that the competitive ability of sorghum decreased under increasing CO_2 concentration.

Some researchers demonstrated that C4 plants responded better to elevated CO_2. For example, a study observed a higher response to CO_2 in C4 wheatgrass (*Agropyron elongatum*) than C3 plants. This variation in plant response can be related to different temperate, soil, water and nutrient ability.

When atmospheric CO_2 concentration was increased, the photosynthesis, growth and competitive ability of C3 plants was also found to increase. In order to achieve the same level of control of weeds using the herbicide glyphosate, it was necessary to adjust both the timing of application and the dosage rate. Similar levels of effectiveness the herbicide were only achieved when it applied earlier and at higher concentrations. This response was confined to C3 plants, as these changes had not been observed in C4 plants.

To ensure success in controlling weeds, it is necessary to understand the effect of elevated CO_2 concentrations on the interactions of crops and weeds, the competing responses of C3 and C4 crops and also C3 and C4 weed species.

How might potato cultivation react to climate change

Any major factor likely to have a significant impact on climate change will have to be adopted at a global level. In the meantime smaller local initiatives can be employed to combat local problems.

Many of the experiments investigating the optimum seed size and spacing were conducted in the 1950's and 1960's, when the CO_2 levels in the atmosphere were 285ppm. Today the values are approaching 400 ppm. The conclusions arrived at then were valid for the prevailing environmental conditions and remained valid for several decades subsequently. A new set of environmental conditions now prevail - higher mean average temperature and elevated levels of CO_2. Perhaps it is timely to carry out a new series of trial to determine if revised plant densities are required to reflect the new reality in current environmental conditions

Adjusting the planting date, planting different potato varieties and improving soil water supply, especially in dry regions, might be useful – to reduce the expected decrease in global yields. But, in practice, adaptation options may not be so simple to implement. Several factors such as the preceding crop, water availability, pests and diseases, and markets affect the planting date. While there are cultivars available, which are adapted to climate change, farmers in some regions may not be able to access them. Tuberisation is the critical developmental step in the potato crop. This process is temperature sensitive and the search has already begun for cultivars that will set tubers at elevated soil temperatures.

At lower latitudes it will be less feasible to shift planting date or location, and in these regions global warming could have a strong negative effect on potato production. There is an urgency to develop heat-tolerant potato cultivars that could be used to mitigate effects of global warming in (sub) tropical regions.

Two strategies to combat the effects of climate change have been proposed, introducing potato into areas where there is currently no potato production or moving production to areas more favourable for growth. Neither of these can be achieved without some risk. Potatoes are bulky and expansive to transport. Moving the production site away from the consumption area will inevitably force a price increase. This would pose a serious threat to less affluent consumers. There may be an opportunity to expand production into higher altitudes especially in the tropical highland regions. But again, there is a risk here however, because planting potatoes at higher altitudes will necessitate using steeper areas, with the difficulty of access or the increased risk of soil erosion.

Summary

- Climate change describes the meteorological conditions that prevail in a particular region over a period of time, typically 30 years.
- While climate change can be caused by natural factors, it is now generally associated with changes in our climate due to the build up of greenhouse gases in the atmosphere,
- Elevated CO_2 enhances photosynthetic rates in the leaves of potato plants that are well supplied with nutrients.
- Potato tuber quality is important with regard to food and industrial processing, but the consequences of future atmospheric carbon dioxide CO_2 enrichment on quality attributes are still unclear.
- An important agricultural aspects arising from CO_2 elevation is weed-crop competition.

Sources accessed in the preparation of this section.

Anon. (2011). Insect phenology modeling and climate change. International Potato Center, Lima, Peru

Bita, C. E., & Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science*, **4,** 273.

Cowling, S. A., and Field, C. B. (2003). Environmental control of leaf area production: Implications for vegetation and land-surface modeling, *Global Biogeochem. Cycles,* **17**: 1007

Hijmans, R. J. (2003). The effect of climate change on global potato production. *Am. J. Potato Res.* 80, 271–279.

Högy, P. and Fangmeier, A. (2009). Atmospheric CO_2 enrichment affects potatoes: 2. Tuber quality traits. *Europ. J. Agronomy* **30 :** 85–94.

Miri, H. R., Rastegar, A. and Bagheri, A. R. (2012). The impact of elevated CO_2 on growth and competitiveness of C_3 and C_4 crops and weeds. *European Journal of Experimental Biology*, **2:** 1144-1150

Pérombelon, M. C. M. (2002). Potato diseases caused by soft rot Erwinias: an overview of pathogenesis. *Plant Pathology* **51:** 1-12.

Section 16.

Irrigating the potato crop

Introduction

Water is crucial to all life – including plant growth. The plant absorbs this water from the soil through its roots, so adequate water must be available in the soil.

More than 97% of the water absorbed by plants from the soil is utilised for transpiration. It is the most important factor sustaining the movement of water in plants. Only about 3% of the absorbed water is used during photosynthesis, the process that produces the carbohydrates necessary for plant growth. Two factors influence the rate of transpiration: water availability within the plant (and soil) and the availability of sufficient energy to vaporize water. Some 80 – 95% of the mass of growing plant tissues is composed of water. When soil water reserves are depleted by plant uptake and by evaporation, they must be replenished either by rainfall or by irrigation.

Drought is regarded as one of the major abiotic stresses experienced by crops. Irrigation is the controlled application of water to arable lands in order to supply crops with the water requirements not satisfied by natural precipitation. Irrigation facilitates the growing of crops in regions where there is inadequate rainfall to sustain plant growth. But water is becoming less freely available for agricultural communities. The list of factors influencing this problem include inadequate rainfall, excessive levels of salts in the soil solution or the increasing diversion of limited fresh-water resources to competing urban and industrial uses

Background

In around 9000 BCE, a wide expanse of land existed along the Tigris and Euphrates rivers. It stretched from the Persian Gulf to the Mediterranean Sea, and even according to some definitions, extended into the Nile River Valley. These river valleys, known as the Fertile Crescent and referred to by historians as the "cradle of civilization," had rich soils in which crops flourished.

Archeological evidence shows that around 5500 BCE, irrigation channels were dug by farmers in Mesopotamia, in the land between the two rivers. Farming required irrigation and a simple system evolved. This relied on channeling water from streams onto their fields, and this simple strategy permitted farmers to settle in areas once regarded as unsuited to agriculture. Farmers could now sow barley in areas where the natural rainfall would not be adequate to supply the crop's demand.

The technology was improved upon in places like Mesopotamia, and later in Egypt and China, where large groups of people organized themselves and worked cooperatively to build and maintain more sophisticated irrigation systems. In hitherto dry areas, crop irrigation provided considerably increased yields. This led to an increase in population, ensuring that more labour was available to undertake more complex irrigation projects.

In Mesopotamia, the simple irrigation that had began, led to increased agricultural production. As farm output expanded and surplus food became available, it was no longer necessary for the whole population to engage in agriculture. This change of roles and the freedom to pursue other activities, eventually contributed to the rise of cities and the development of civilisations.

When crops are grown with the assistance of irrigation they are much more productive than rain fed cropland. Irrigation systems are currently used to grow crops in about 280×10^6 ha. of arable land; this represents just under 20% of the total cultivated land, but produces more than 40% of world food supplies. In theory therefore, a significant increase in food production could be achieved by and increase in the area of irrigated arable land. Unfortunately, the supply of water for irrigation is severely constrained by applications competing for fresh water.

One of the great historical advances in food production was the cultivation of land using the plough. Turning over the sod in ploughing returned the soil nutrients to the surface layer. Harnessing animal labour to pull the plough produced a significant increase in the productivity of both labor and the land.

World population is expected to reach 9.2×10^9 people by 2050. Feeding a population of this size them will require the adoption of innovative approaches to boost crop productivity. Significant amounts of agrochemical inputs underpin current agricultural production but water availability is a major limiting factor.

Moisture stress is the environmental factor, which causes the most devastating consequences for agriculture. The amount of available water in the soil is seriously depleted by lack of rainfall. This affects plant growth and development and reduces crop yield, it prolongs periods of drought which result in premature plant death, complete crop loss and ultimately, the land becomes abandoned. Almost 50% of the earth's land surface is rated as arid or semiarid. While the cropland in these regions in highly productive, the output is constrained by the lack of water for irrigation.

Soil - Plant – Water Relationships

Soil- plant – water relationships are illustrated diagrammatically in Fig. 1. Precipitation, mainly in the form of rainfall, makes liquid water available to plants. Three storage systems are replenished, surface water, soil moisture, and groundwater

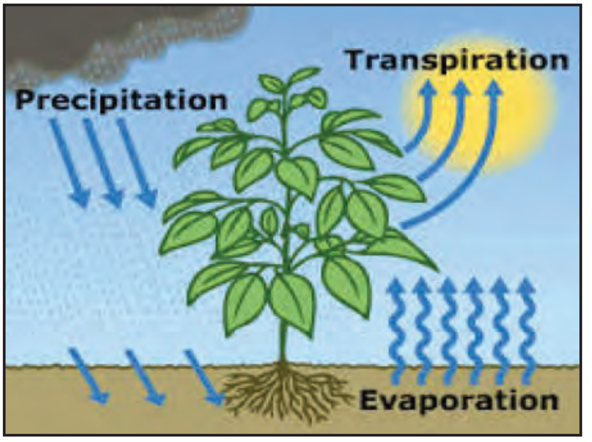

Figure 1.
Diagrammatic representation of soil plant water relationships (Image courtesy Salinity management guide)

The phrase Soil-Plant-Water relationships describes how water is transported through the soil to the plant and through the plant. It takes account of the role of all three in sustaining plant growth.

The soil acts as a storehouse for plant nutrients, it provides a habitat for microbial life, it anchors plant roots, and a reservoir that retains the water, which is essential for plant growth. The physical properties of a soil determine the amount of water it can hold in a form available for plant uptake. The amount of water held in this available form, determines how long a plant can survive between additions of water. The water retention properties of a soil can be used to measure irrigation frequency and to calculate the size of the irrigation system required to sustain uninterrupted crop growth.

Crushing dry soil by hand reveals its particulate composition and it will be evident that the mineral particles are derived from the weathering of rocks. Other particles – referred to as organic particles – are derived from residues of plants and animals. All these particles appear to be in intimate contact, but there are actually spaces between the particles, referred to as pores. When the soil is 'dry', the pores are mainly filled with air, but after irrigation or rainfall, the pores are mainly filled with water.

Living material also inhabits the soil; examples are plant roots as well as living creatures such as beetles, worms, larvae, fungi, bacteria etc. They assist with the decomposition of organic matter in addition to aerating the soil and improving growth conditions around the roots.

Water adheres to the soil particles. This results water being drawn into the soil – the soil is in fact acting like blotting paper. When the soil moisture is depleted and the soil is dry, the soil is holding the water to itself and making it more difficult for the roots to acquire it. In water-logged soil, when all of the air space between soil particles is full of water, then the force of gravity is greater and can overcome the soil's hold on the water. This permits the excess water to drain down to the lower soil zones. One metric for expressing soil water content is to define it as a percent of total volume. The greatest amount of water that the soil can hold against the force of gravity is referred to as the 'Field Capacity' (FC). Clay and loam soils with their very small particles can hold far greater amounts of water that sandy soil, with its large particle size.

When there is adequate water in the soil, the roots take it up readily. In order to extract the water from the soil, take it into the roots, then up through the stems and out to the leaves, the plant must overcome the forces holding the water onto the soil particle surfaces. With soil water content diminishing, the plants must expend more energy and when this continues for a while, the plant growth rate slows and less metabolites are stored in the tubers. With reduced energy available, uptake of water slows further and beyond a certain point, the plant can no longer take up water and it dies. The soil water content at this point is known as the 'permanent wilting point' (PWP). Plants wilt as a defence mechanism if they cannot take up sufficient water to satisfy the climatic evapotranspiration demand. Even wilted plants are taking up water, but the uptake is not at a sufficient rate to reestablish turgor.

The Plant

Plant life in the absence of water is unsustainable. Water is an absolute requirement to perpetuate all living organisms, plant and animal and is involved either directly or indirectly in the metabolic processes.

Water is an important climatic factor in crop agriculture where it affects or determines plant growth and development. The continuum between availability, or scarcity, can provide either a successful harvest, or diminution in yield, or total failure. But plants differ in their response to water and the importance of water also differs depending on plant species. The majority of plants including potato, are mesophytes, that is, they will grow under conditions of moderate water supply.

The plant relies on water to perform the following list of tasks

- It is a solvent for mineral nutrients and the complex substances manufactured within the plant.
- It is both a transportation agent and the means whereby the equilibrium of salts and other dissolved products is maintained between the various plant parts.
- It is an ingredient for the process of photosynthesis - the basic process sustaining all life.
- It serves as a temperature regulator, whereby water vapor given off by leaves produces a cooling effect.
- It provides a structural component. When plant cells are replete with water they are turgid and the plant stands erect; when there is a moisture deficiency, the cells are flaccid and the plant droops and wilts

To understand the reaction of the potato plant to drought, we must consider the interaction between uptake of water by the roots below ground and loss of water from the shoot above ground. For the current discussion, the emphasis will be on the mechanism that the plant uses to acquire water from the soil surrounding its roots, how the acquired water is moved up through the stem and escapes to the atmosphere.

Transpiration

Water is lost from the soil to the atmosphere by two individual processes. In the first instance, water is lost by evaporation from the soil surface (Water can exist in 3 states, as a solid, as ice, a liquid and a gas as a vapour or steam. This is often referred to as the hydrology cycle. Evaporation defines the transition from water in the liquid form to water as a gas). The second mechanism of water loss is by transpiration

(The combination of the two separate processes evaporation and transpiration is referred to as evapotranspiration (ET)

Transpiration describes the process of water movement up through a plant against gravity. Water moves upward in tubes, made of dead xylem cells and evaporates from aerial parts, such as leaves stems and flowers. Water, forming on the surface of spongy and palisade cells (inside the leaf) evaporates and then diffuses out of the leaf. This process is called transpiration (Fig. 2). More water is drawn out of the xylem cells inside the leaf to replace what's lost. As the xylem cells make a continuous tube from the leaf, down the stem to the roots, this acts like a drinking straw, producing a flow of water and dissolved minerals from roots to leaves. Transpiration creates a negative pressure gradient that helps draw water and minerals up through the plant from its roots.

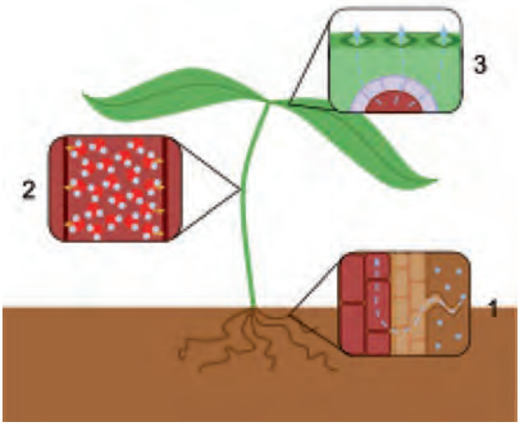

Figure 2.

Overview of transpiration.

1. Water enters the root hairs by osmosis and then into the xylem. 2. The forces of cohesion and adhesion cause the water molecules to form a column in the xylem. The transpiration stream pulls water up the stem 3.Water moves from the xylem into the mesophyll cells, some is used for photosynthesis; the remainder evaporates from their surfaces and leaves the plant by diffusion through the stomata (Diagram courtesy Wikipedia).

Water is an essential requirement for plant life but approximately 1% of the water taken up by roots is used for growth and metabolism. The remaining 97-99.5% is lost from the leaves to the atmosphere by transpiration. The stomata are bordered by guard cells and their stomatal accessory cells (together known as stomatal complex) that open and close the pore. Transpiration occurs through these stomatal apertures (Fig. 3), and can be thought of as a necessary "cost" associated with the opening of the stomata to allow the inward diffusion of carbon dioxide gas from the air for photosynthesis. Transpiration also cools plants, changes osmotic pressure of cells, and enables mass flow of mineral nutrients and water from roots to shoots.

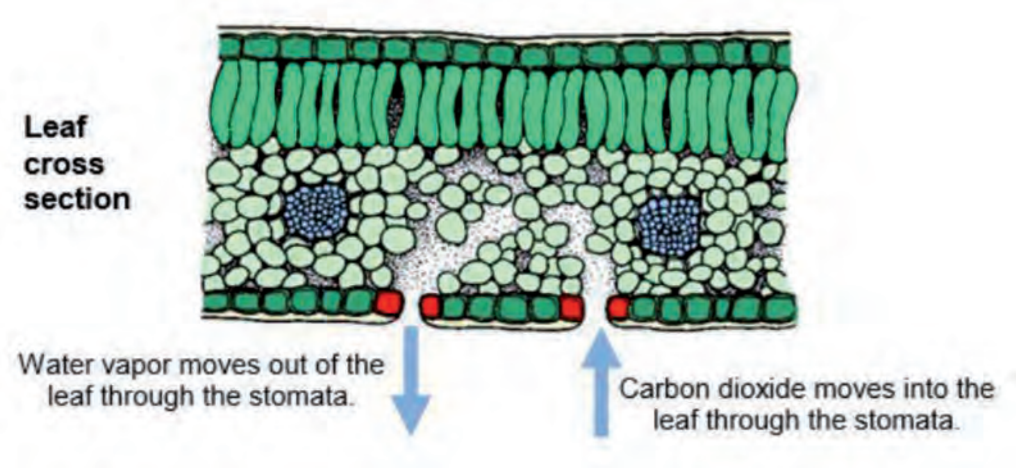

Figure 3.
Graphical illustration of carbon dioxide uptake and water vapour release through leaf stomata. (Diagram © Colorado State Univ. Ext. Service.)

When the rate of transpiration is speeded up, this will also increase the rate of water uptake from the soil. When water is scarce, or the roots are damaged, a plant's chance of survival is increased if the transpiration rate can be slowed down. This is the rationale behind the plants self protection mechanism, expressed as wilting

Factors Affecting Rates of Transpiration

The rate of transpiration is affected by both plant parameters and prevailing environmental conditions

PLANT PARAMETERS – These are the plant control mechanisms that limit the rates of transpiration by resisting water movement out of the plant.

Stomata – Stomata are pores in the leaf that permit gas exchange by allowing water vapor to leave the plant and carbon dioxide to enter. They act as hydraulically operated valves in the leaf surface, preventing excessive water loss. Opening and closing the stomata, either speeds up or decreases the transpiration rates. Movement is regulated by environmental conditions such as light intensity, CO_2 concentration and relative humidity. Guard cells respond to change in these environmental conditions and then act as motor cells to perform the opening and closing functions. The transport of K^+ salts across the guard cell membranes provides the stimulus for stomatal movement.

Boundary layer – The boundary layer is a thin layer of still air in close contact with the surface of the leaf. This layer of air is stationary. To facilitate transpiration, water vapor leaving the stomata must diffuse through this motionless layer to reach the atmosphere, where the water vapor will be removed by moving air. A larger boundary layer slows the rates of transpiration. Plants possess many structural features, which can alter the size of their boundary layers around leaves. Leaves that possess many hairs or pubescence will have larger boundary layers; the hairs serve as mini-wind breaks by increasing the layer of still air around the leaf surface and slowing transpiration rates. Some plants possess stomata that are sunken into the leaf surface, dramatically increasing the boundary layer and slowing transpiration. Boundary layers increase as leaf size increases, reducing rates of transpiration as well.

Cuticle – The cuticle is the waxy layer present on all aboveground tissue of a plant and serves as a barrier to water movement out of a leaf. Because the cuticle is made of wax, it is very hydrophobic or 'water-repelling'; therefore, water does not readily move through it. The thicker the cuticle layer on a leaf surface, the slower the transpiration rate. Cuticle thickness varies widely among plant species. In general, plants from hot, dry climates have thicker cuticles than plants from cool, moist climates. In addition, leaves that develop under direct sunlight will have much thicker cuticles than leaves that develop under shade conditions.

ENVIRONMENTAL CONDITIONS – Some environmental conditions create the driving force for movement of water out of the plant. Others alter the plant's ability to control water loss.

Relative humidity – Relative humidity (RH) is the amount of water vapor in the air expressed as a percentage of the maximum amount that the air could hold at the given temperature; the ratio of the actual water vapor pressure to the saturation vapor pressure. A hydrated leaf would have a RH near 100%, just as the atmosphere on a rainy day would have. Any reduction in water in the atmosphere creates a gradient for water to move from the leaf to the atmosphere. The lower the RH, the less moist the atmosphere and thus, the greater the driving force for transpiration. When RH is high, the atmosphere contains more moisture, reducing the driving force for transpiration.

Temperature – Temperature exerts a significant influence on the magnitude of the driving force for water movement out of a plant, rather than by having a direct effect on stomata. As temperature increases, the water holding capacity of that air increases sharply. The amount of water does not change, just the ability of that air mass to hold water. Because warmer air can hold more water, its relative humidity is less than the same air sample at a lower temperature, or it is 'drier air'. Because cooler air holds less water, its relative humidity increases or it is 'moister air'. Therefore, warmer air will increase the driving force for transpiration and cooler air will decrease the driving force for transpiration.

Soil water – The soil provides the source of water for transpiration out of the plant. Plants with access to adequate soil moisture will normally transpire at high rates because the soil provides sufficient water to move through the plant. If the soil is very dry, plants cannot continue to transpire without wilting, because there is insufficient soil water to replace the water in the xylem that has moved out through the leaves. This condition causes the leaf to lose turgor or firmness, and the stomata to close. In potatoes, this condition is generally manifest first in the upper, new leaves. If this loss of turgor continues throughout the plant, the plant will wilt.

Light – Stomata are triggered to open in the light so that carbon dioxide is available for the light-dependent process of photosynthesis. Stomata are closed in the dark in most plants (except CAM plants; see **Section 15**). Very low levels of light at dawn can cause stomata to open so they can access carbon dioxide for photosynthesis as soon as the sun hits their leaves. The guard cells of the stomata are most sensitive to blue light, the light predominating at sunrise.

Wind – Wind can alter rates of transpiration by removing the boundary layer, that still layer of water vapor in intimate contact with the surface of leaves. Wind increases the movement of water from the leaf surface when it reduces the boundary layer. This reduces the length of the path for water to reach the atmosphere.

The Soil

Soil is defined as a natural aggregation of mineral grains that can be detached by light mechanical methods such as crumbling between fingers or by gentle agitation in water. The soil can be considered a mixture of mineral particles, containing void space, which may be filled with air or water or both at same time. An agriculturalist might define soil as the material which nurishes and supports growing plants. In agriculture, we are concerned mainly with uppermost layer of the earth that may contain a three-phase complex of solids, liquid and gas in a ratio approximately, 50 : 25 : 25 as follows:

- Solid phase made of *mineral* and *organic matter* and various chemical compounds
- Liquid phase called the *soil moisture*
- Gaseous phase called the *soil air.*

The main components of the solid phase are the soil particles, the size and shape of which give rise to pore spaces of different geometry. These pore spaces are filled with water and air in varying proportions (Figure 4), depending on the amount of moisture present.

Minerals soils consist of 4 major components:

- Mineral materials,
- Organic matter (OM),
- Water and
- Air in various proportions.

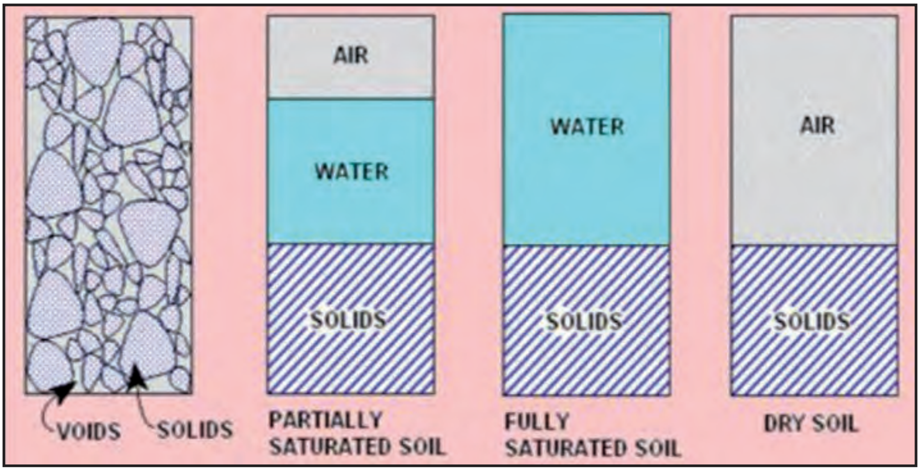

Figure 4.
A diagrammatic representation of the soil 3-phase complex
(Diagram courtesy Geotip)

Approximately 50% of the total volume of the surface horizon of many soils is made up of inorganic materials (mineral matter) and OM (5%) and the remaining volume is pore space between the soil particles. These pore spaces are occupied by water and air in various proportion; with the proportion of air and water varying from one season to another. At optimum moisture for plant growth, the 50% of pore space available is divided roughly in half 25% of water space and 25% of air.

As mentioned above, it is useful to consider the soil as a three-phase system: Soil-solid, liquid and gaseous phase.

1. Solid phase: Soil material with a particle size of less than 2 mm size constitutes the soil sample that is composed of inorganic and organic constituents. When soils have more than 20% of organic constituents they are arbitrarily designated organic soils. Where the dominant constituents are inorganic, such soils are described as mineral soils. Some 95% of the solid phase is made up of inorganic or mineral matter, the remaining 5% weight comprises of OM, which is mainly derived from decomposing and dead parts of the vegetation and organisms. The inorganic constituents consist of silicates, certain preparation of carbonates, soluble salts, and free oxides of iron, aluminium and silicon. The humus and humus-like fractions of the solid phase constitute the soil organic matter. Humus consists of decomposing plant and animal material. It no longer retains its original cell structure. An enormous number of living organisms like roots of higher plants (Soil Macro flora), bacteria, fungi, actinomycetes and algae (Soil Micro flora) reside in the soil. A gram of fertile soil will contain billions of these microorganisms. The live weight of the micro-organisms may be about 4000 kg/ha, and may constitute about 0.01 to 0.4% of the total soil mass. Soil may also contain protozoa and nematodes (Soil Micro Fauna).

2. Liquid phase: About 50% of the bulk volume of the soil body is generally occupied by spaces or soil pores; these may be completely or partially filled with water. The soil absorbs a considerable portion of the rain, which falls on it. It is absorbed by the soil and stored in it, awaiting return to the atmosphere by direct evaporation or by transpiration through plants. The soil acts as the reservoir ensuring a supply of water to plants for their growth. The soil water retains salts in solution, which act as plant nutrients. Thus, the liquid phase is an aqueous solution of salts, but when water drains from soil, the pores refill with air.

3. Gaseous phase: The gaseous phase of the soil system are the air filled pores. The volume of air in the soil is dependent on the volume of the liquid phase. The N and O_2 contents of soil air resemble that of the atmospheric air, but the concentration of CO_2 is much higher (8 – 10 times more), which may be toxic to plant roots. The gaseous phase supplies O_2 and thereby prevents CO_2 toxicity.

All three phases of the soil system have definite roles to play. The solid phase provides mechanical support for the roots and nutrients to the plants. The liquid phase supplies water and along with it, dissolved nutrients to plant roots. The gaseous phase satisfies the aeration i.e. the O_2 required for root respiration.

The Water

Water is considered the universal solvent simply because it dissolves so many substances. Through its role as a solvent, it also serves as a transport medium to move mineral nutrients from the soil to the plant roots, and additionally in the translocation of organic substances throughout the plant. Because it is a chemical reactant in photosynthesis, water is therefore essential for life.

Soil moisture can be defined simply as the amount of water contained in the soil. It is a key variable in controlling the exchange of water and heat energy between the land surface and the atmosphere. It achieves this response through evaporation and plant transpiration. It plays a major ecological role and influences several parameters

- It helps to maintain soil temperature
- It helps to maintain salt balance
- It reduces salinity and alkalinity
- It influences weed growth
- It influences atmospheric weather
- It helps the beneficial microbes
- It influences the pest and diseases
- It helps for land preparation like ploughing, tilling, etc.,
- It helps to increase the efficiency of cultural operations like weeding, fertilizer application etc., by providing optimum condition

Soil moisture is one of the most important ingredients of the soil and is also one of its most variable properties. Only water stored in the root zone of a crop can be utilized for transpiration (Fig. 5) and buildup of plant tissues. When ample water is present in the root zone, plants can obtain their daily water requirements for proper growth and development. As plants continue to use water, the soil supply diminishes, and unless water is added, the plants stop growing and finally die. When water is added to a dry soil following rain or irrigation, it is distributed around the soil particles. It displaces air in the pore spaces and eventually fills the pores.

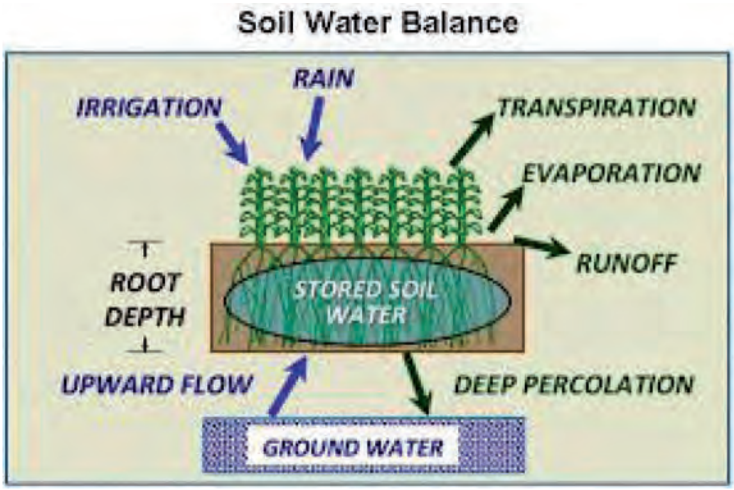

Figure 5.
Soil – plant – water system.
(Diagram © S. Melvin, D. Yonts. Univ. Neb. http://passel.unl.edu. With permission)

Classes of water

There are three basic types or forms of soil water. It is important to remember that all forms of soil water begin as free water deposited in the soil by rain. The final form depends on the moisture conditions of the soil and each water type is controlled by a different force and behaves differently in the soil.

Hygroscopic water. Water held tightly to the surface of soil particles by adhesion forces. This water forms very thin films around soil particles and is not available to the plant. The water is held so tightly by the soil that it cannot be taken up by roots. It is not held in the pores, but on the particle surface. This means clay will contain much more of this type of water than sands because of surface area differences. Forces of adhesion very tightly hold hygroscopic water, which is why this water is not available to the plant (Fig. 6).

Capillary water. Forces of surface tension hold water in continuous films around soil particles and in the capillary spaces. Capillary water is detained in the micro pores, considered as the soil solution. Most, but not all, of this water is available for plant growth (PAW - Plant Available Water). Capillary water is held in the soil against the pull of gravity. Micro pores exert more force on water than do macro pores. Capillary water is held by cohesion (attraction of water molecules to each other) and adhesion (attraction of water molecule to the soil particle). The amount of water held is a function of the pore size (cross-sectional diameter) and pore space (total volume of all pores). This means that the tension (measured in bars) increases as the soil dries out.

Gravitational water. Water that moves freely in response to gravity and drains out of the soil. Gravitational water is found in the macro pores. It moves rapidly out of well-drained soil and is not considered to be available to plants. It can cause upland plants to wilt and die because gravitational water occupies air space, which is necessary to supply oxygen to the roots. Gravitational water drains out of the soil in 2-3 days. Gravity is always acting to pull water down through the soil profile. However, the force of gravity is counteracted by forces of attraction between water molecules and soil particles and by the attraction of water molecules to each other.

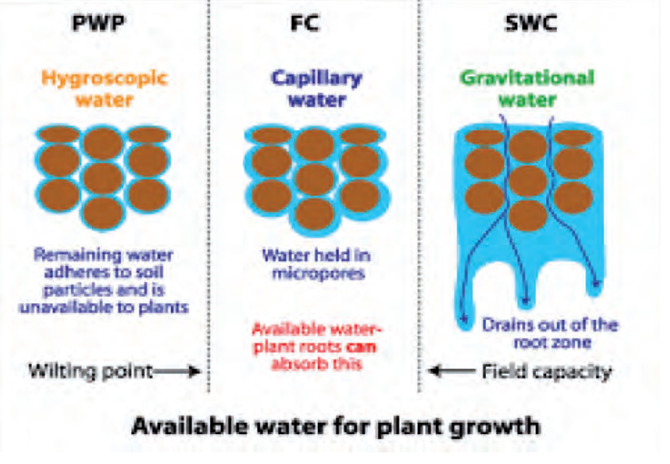

Figure 6.
Classes of soil water available for plant growth
(Image © Growflow Australia, with permission)

Soil Moisture Constants

The following terms are used when discussing soil water:

Saturation is the condition when all the soil pores are filled with water and this is the condition that usually prevails following heavy rain.

Available water is the amount of water in soil based on rainfall amount, the proportion of rain that infiltrates into the soil, and the soil's storage capacity. Available water capacity is the maximum amount of plant available water a soil can provide. It is an indicator of a soil's ability to retain water and make it sufficiently available for plant use. Available water is the difference between field capacity, which is the maximum amount of water the soil can hold and wilting point where the plant can no longer extract water from the soil.

Water holding capacity is the total amount of water a soil can hold at field capacity.
Field capacity is the water remaining in a soil after it has been thoroughly saturated and allowed to drain freely, usually for one to two days.
Permanent wilting point is the moisture content of a soil at which plants wilt and fail to recover when supplied with sufficient moisture. The term "wilting point" is now preferred, as plants will recover from a mild form of wilting
Water capacity is usually expressed as a volume fraction or percentage, or as a depth (in or cm).

Figure 7 shows the variation in FC and PWP water content by soil texture. The figure may be used as a general guide for estimating the AWC of soils based on texture until local curves can be developed

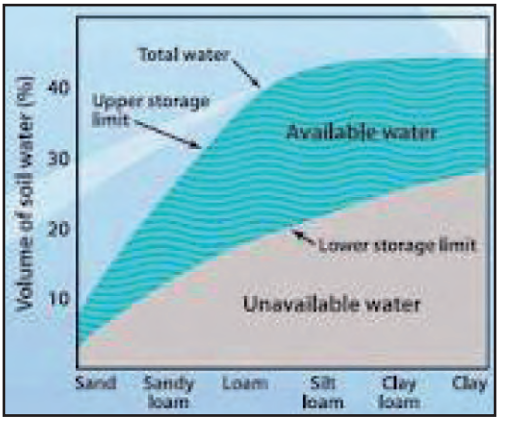

Figure 7.
The relative amounts of water available and unavailable for plant growth in soils, with textures from sand to clay. (Diagram © Nature Education. With permission)

Water movement in the soil.

The movement of water in the soil is complex due to the various states (liquid, gas, solid) and directions in which water moves and furthermore, because of the forces that cause it to move.

- Because of gravity, water moves downward (liquid).
- Because of adhesive and cohesive forces, it moves in small pores by capillarity (liquid).
- Because of heat, it vaporizes and diffuses through the soil air (gas/vapour).

Water moves in the soil-plant-atmosphere continuum in response to differences in the potential energy of water in the system.
The rate at which gravitational water percolates through the soil is determined

largely by the size and continuity of the pore spaces. While water usually moves freely through the large pores in coarse-textured soils, it moves less rapidly through fine-textured soils because of the resistance to flow in small pores. These small pores may also be blocked by swollen colloidal gels and trapped air. A slowly permeable layer such as a claypan or plowpan will retard percolation.

Movement of irrigation water down through the soil profile (Fig. 8) can be described as follows:

- It moves as a front--from a saturated soil layer to an un-saturated layer.
- Movement of the front is unsteady; water builds up behind the front until the large pores are filled and then moves to the next layer of large pores.
- Movement in moist soils is more uniform than in dry soils.
- The movement of capillary water is affected by soil texture. The forces that cause capillary movement in small pores result largely from the difference in tension between films of different thickness around soil particles; the movement is from thick films to thin films.

If the forces that cause water to move are expressed in terms of tension, it can be said that water moves from an area where tension is low to an area where tension is high. When a soil is saturated, capillary movement is most rapid in a sandy soil and slowest in a clay soil. But when capillary water is moving in dry or unsaturated soils, it moves slowly in sands and more rapidly in clays.

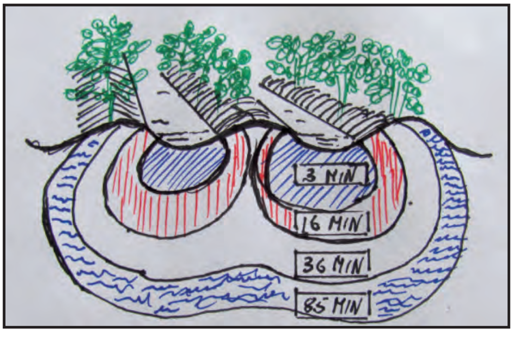

Figure 8.
llustration of furrow irrigation and rate of water penetration in a uniform soil
(Redrawn from Utah Univ. Irrigation)

How water is lost from the soil

Heat causes water to move as a vapor. Then when water vapor diffuses through the soil air near the surface, it either condenses in another part of the pore space or escapes into the atmosphere. When water evapourates from the surface, capillary water rises to the surface layers and replaces part of the evapourated water. This continues until the upper few cm. of the soil become dry and capillarity is broken. Water then leaves the soil only by vaporizing at the upper capillary fringe and diffusing through the over-lying dry soil.

Water movement to the root system

Transpiration causes a lower water potential in the plant shoot and root system than in the bulk soil; consequently, soil water moves into the root system along this potential gradient. Water first enters the root system through epidermal cells in contact with the moist soil, then in turn through cortical cells, the endodermis, pericycle cells, and finally to the xylem, that transports the water to the aerial plant parts. Central to the success of this process is the intensity of root development and physical contact between the root and soil. Rooting density plays a significant role in water uptake especially when the upper part of the root zone becomes comparatively dry and water is available only in the lower zone. Under these conditions, the uptake of water per unit volume of soil has been observed to be proportional to the rooting density. Thus, the distribution of roots that varies with crop species and soil physical properties becomes an important management concern.

Soil Moisture Measuring Techniques

Gravimetric Determination

Because the water content is determined by direct weighing, this method is referred to as gravimetric. It is the classical method of measuring the amount of water in a soil. The method involves taking a volume of soil, accurately weighing it, completely drying it out in an oven, re-weighing the dry sample and calculating soil moisture percentage from the weight loss. This is a time consuming and painstaking procedure. The mass of water lost on drying is a direct measure of the soil water content. This measure is normalized either by dividing by the oven-dry mass of the soil sample, in which case the units are Mg Mg^{-1}, or by converting the mass of water to a volume (by dividing the mass of water by the density of water) and dividing this volume of water by the volume of the sample, in which case the units are m^3 m^{-3}. This method is standard and reliable. It is the standard method against which all others are compared and calibrated.

Radioactive Technique

This method, which uses radioactivity, is called the Neutron Probe Technique. Because of the radioactive transmissions, these instruments are very expensive and measurements need to be taken by qualified personnel. Shafts are permanently installed at the measurement site, into which the Neutron Probes lowered each time the readings are taken.

The general principle underlying the measurement involves high energy (fast) neutrons emitted from the source (~10^9/s) which are either slowed through repeated collisions with the nuclei of atoms in the soil (scattering and thermalisation) or are absorbed by those nuclei. A small fraction of scattered neutrons are reflected back to the detector (Helium3). Of these, an even smaller fraction (~10^3/s) is slowed to thermal (room temperature) energy levels and can be detected. Two of the most common atoms in soil (aluminium and silicon) scatter neutrons with little energy loss because they have much greater mass than a neutron. However, if a neutron strikes a hydrogen nucleus, its energy is halved, on average, because the mass of the hydrogen nucleus is the same as that of the neutron. On average, 19 collisions with hydrogen are required to thermalize a neutron. Carbon, nitrogen and oxygen are also relatively efficient as neutron thermalizers (about 120, 140 and 150 collisions, respectively).

On the timescales of common interest in irrigation research and management, changes in soil carbon and nitrogen content are minor and have little effect on the concentration of thermal neutrons. Also, on these timescales, changes in soil hydrogen and oxygen content occur mainly due to changes in soil water content. Thus, the concentration of thermal neutrons is most affected by changes in water content; and volumetric water content can be accurately and precisely related to the count of thermal neutrons through empirical calibration. Soil density has a small but measurable effect on the concentration of thermalized neutrons around the detector. The effect is small enough to be ignored in most calibrations.

Note: *This method is expensive and inflexible. Measurement sites are not easily changed, and readings are infrequent. The equipment poses a serious threat to the users health unless they are highly trained and adhere rigidly to the operating protocols.*

Capacitive Technique

There are several instruments, which indicate the percentage of water in the soil, by measuring its capacitance. These instruments give instantaneous volumetric moisture contents quickly and easily by measuring the dielectric properties of the soil. Probes are inserted into the soil to the required measurement depth and the measurement can either be displayed on a meter or can be recorded using a data logger. However, the dielectric property of the soil not only depends on the amount of water present, but also on the type of soil, its porosity and its organic content. So for accurate volumetric soil water content readings, each measurement site should be individually calibrated.

Capacitive soil sensors are also made of two electrodes, but insulated (i.e. not exposed). The two electrodes, together with the soil as a dielectric material, form a capacitor. The higher the water content, the higher the capacitance. So by measuring the capacitance, we can infer the water content in soil.

There are many ways to measure capacitance, for example, by using the capacitor's reactance to form a voltage divider, similar to the resistor counterpart. Another way is to create an RC oscillator where the frequency is determined by the capacitance. By counting the oscillation frequency, we can calculate the capacitance. You can also measure the capacitance by charging the capacitor and detecting the charge time. The faster it charges, the smaller the capacitance, and vice versa. The higher the capacitance, the lower the peak voltage. Capacitive sensors are not too difficult to make, and are more reliable than resistive ones, so they are quite popular.

Capacitance or Frequency Domain Reflectometry Probes:
Capacitance probes utilise the fringing effect of two metal ring electrodes located one above the other on the probe to measure soil moisture. The fringing effect is the tendency for the electric field to flow or jump from one electrode to another - similar to arcing. So, these two metal rings form the plates of the capacitor with the soil acting as the dielectric or insulation in between. Capacitance measures the ability of this soil to hold an electrical charge when you apply a voltage to it. The ability to hold a charge is very dependent on the dielectric constant of the material between the electrodes or in this case the soil between the metal rings. Dry soil has a constant of between 2 and 5 whereas water has a constant of 80.

The sensor applies a voltage and creates a circuit (flow of electrical current). This current, which will oscillate or vibrate at a (resonant) frequency that is dependent on the amount of water in the soil. When water is added to the soil, its ability to hold charge (capacitance) changes, which then changes the vibration (resonant frequency) of the circuit. The probe measures this change in (resonant frequency), and uses it to determine the soil moisture content.

The best way to think of it, is like a row of glass bottles, each with a different level of water in it - the sound each one makes when you tap it tells you roughly how much water it contains.

Time Domain Reflectrometry:
Another example of a technique measuring the capacitance of soils is Time Domain Reflectometry (TDR). Although the metal probes themselves are inexpensive, generally the electronics to control and interpret the measurements are rather costly. These devices also make use of the dielectric constant to measure the soil moisture content. They employ microwave technology and send a high-frequency electrical pulse down two parallel probes embedded in the soil. The signal reaches the end of the probe and is reflected back along the probes to a sensor.

The time it takes for the signal to travel to the end of the probe and back again varies with the soil dielectric constant and therefore can be related back to the water content of the soil surrounding the probe. The more water content the slower the electric field will travel.

Theta Probes:
Theta Probes use an array or four rods pushed into the soil to enclose a well-defined cylinder of soil. Theta Probes send radio waves down the middle one of the steel rods. The radio wave is deformed as it travels dependent on the soil moisture that is present. The Theta Probe actually measures the change in the amplitude of the radio wave rather than the change in frequency of the signal (as per a capacitance probe) or the time taken for the signal to travel (as per TDR probe). The amplitude change is highly dependent on the soil dielectric permittivity and therefore can be used to work out the soil moisture content.

These are the most accurate soil moisture content sensors, working in all soil types.

Conductivity Technique

Generally, soil conductivity decreases with decreasing soil moisture. Resistance or gypsum block sensors measure soil conductivity and are quite inexpensive. Gypsum is a naturally occurring porous mineral. When shaped into a block and buried in the soil, water from the surrounding soil moves into and out of the gypsum block as though it were another piece of soil. A gypsum block sensor consists of two electrodes embedded in a block, 'tablet' or cylinder of gypsum. When water moves into the gypsum block some of that gypsum dissolves, allowing a current to move between the electrodes. As the amount of water in the block changes so does the resistance to current flow.

As the soil dries out, water leaves the gypsum block and the resistance between the electrodes increases. Conversely, as the soil wets, water is drawn back into the gypsum block and the resistance decreases. These resistance values are then translated into soil moisture tension readings, which have the units of kilo Pascals (kPa). However, conductivity of the soil water is different in different soil types (alkaline or acid soils) and can change according to the sprays or fertilisers applied. So resistance block sensors are generally used for trends in soil moisture changes only.

Soil Suction Technique - Ceramic Tensiometers

The soil suction technique measures water availability to plants, rather than actual percentage of water in the soil. This water availability measurement is more valuable in agriculture and irrigation of crops than is water percentage values. This measurement is also independent of soil type and gives a measurement of the plant or crop's actual water requirements. Inexpensive soil moisture tensiometers measure the availability or water potential of the soil. Readings are in units of pressure, or more exactly negative pressure or suction, expressed as centibars (cbar) or kilo Pascals (kPa).

The hollow ceramic tips of tensiometers are porous, allowing water to move into and out of a sealed water storage 'reservoir' or tube inside the tensiometer shaft.

As the soil dries out, water is sucked out of the tensiometer through the porous ceramic tip. This creates a partial vacuum inside of the tube, which is registered by a vacuum gauge. Tensiometers usually operate over the range 0kPa to -80kPa

The tensiometer is one of the oldest and most widely used instruments for irrigation scheduling around the world. Tensiometers do not measure soil water content. Tensiometers are sealed glass or polyvinyl chloride (PVC) tubes filled with degassed water, connected at one end to a porous ceramic cup and attached to a pressure gauge or sensor at the other. They are normally buried permanently in the soil at a specific depth. They measure the combined expression of matric and gravitational potentials in the field. Matric potential is the amount of energy with which water is held in the soil; it has zero or negative values. Tensiometers are not capable of measuring the osmotic potential due to salts in the soil water.

The total soil water potential, ΨT (kPa), is the energy contained in unit amount of soil water, relative to pure, free water at the soil surface.

It is the sum of the following components:

$$\psi_T = \psi_M + \psi_P + \psi_O + \psi_Z$$

where Ψ_M and Ψ_O are the most important components: the matric potential, related to the capillary and absorptive forces; Ψ_P is the pressure potential, related to variations in pressure; Ψ_O is the osmotic potential, related to variations in solute concentration; and Ψ_Z is the gravitational potential, related to position in the earth's gravitational field.

When the water potential of the soil is low (more negative) compared with that inside the tensiometer, water moves from the tensiometer to the soil, creating a vacuum within the tensiometer which is equivalent to the suction from the soil. The water flow continues until equilibrium is reached. The tensiometer registers the vacuum as a pressure reading: the drier the soil the higher the absolute value of the pressure reading. Thus, tensiometer readings are typically positive values that can be seen as suction or tension values (A soil suction of 10 kPa is equivalent to a matric potential of –10 kPa). When irrigation or rainfall occurs, water is drawn back into the tube, decreasing the vacuum.

Most commercially available tensiometers use a vacuum gauge with a scale from 0 to 100 kPa or 0 to 100 cbar. However, the practical operating range is from 0 to 75 kPa. A zero reading indicates saturated soil conditions. Readings of around 10 kPa correspond to field capacity for coarse textured soils, while field capacity of finer textured soils is around 30 kPa. The upper limit of 75 kPa corresponds to as much as 90% depletion of total available water for the coarse textured soils, but is only about 30% depletion for silt loam, clay loams and other fine textured soils. This limits the practical use of tensiometers to coarse textured soils or to high frequency irrigation where soil water content is maintained at high values.

Plant extraction of water from the soil must work against three forces: those signified by the matric potential, the osmotic potential and the gravitational potential. Tensiometers cannot measure the osmotic potential; and if the osmotic potential is large, a tensiometer reading will overestimate the availability of soil water to the plant. In most cases, tensiometer readings include the gravitational potential, the difference in elevation between the pressure gauge and the tensiometer cup, in addition to the matric potential. For example, a tensiometer installed at 1 m depth will need to subtract the gravitational component from its reading to obtain the actual matric potential. In this case, the gravitational potential would be the potential difference between the elevation of the pressure gauge and that of the ceramic cup (typically ~1.1 m when the pressure gage is 0.1 m above the soil surface). Dividing 1.1 m by 10.22 m per bar gives 0.108 bars, or 10.8 cbar. Subtracting 10.8 cbar from the tensiometer reading will give the matric potential at the tensiometer cup.

Irrigation scheduling

The shallow root system of the potato plant, limits water extraction from soil, ensuring that plants are sensitive to drought stress. Developmental parameters such as leaf size, photosynthesis rate, tuber number, yield and quality were all severely limited when grown under a drought stress condition. Irrigation management seeks to maximize potato yield and quality by ensuring that soil water content is maintained within specified limits throughout the growing season. This is achieved through timely and controlled water application to the crop. In order for an irrigation schedule to be effective, it has to tell us when to apply water and how much water to apply. When rainfall is insufficient or variable, which occurs to some degree in most regions of the world, some form of water management is required. In many regions, farmers use irrigation to supplement rainfall.

Irrigation management heavily influences the profitability of potato production. Unless proper scheduling is implemented, irrigation at best becomes hit and miss and at worst, both wasteful and crop damaging. The primary requirement of successful scheduling is the application of a method of measuring soil moisture deficit (SMD). Systems can be simple of complex – they can be based on manual balance sheets; computerised balance sheets or manual plans using direct soil moisture measurement as a baseline. Scheduling requires an estimate of likely evapo-transpiration in the period ahead (normally weekly), which may range from 1mm per day or less at around the time of emergence to 4.5 mm per day or more during hot dry weather. Schedules will vary according to the type of crop being grown (seed, ware or processing) and the quality criteria required, equipment and labour available, irrigation water available and soil type. As a consequence, there is no one magic schedule suitable for all crops. Potatoes are very sensitive to water stress with a substantial decline in tuber yields and quality when subjected to under- or over-watering. The plant has a shallow, fibrous root system, with most roots in the top 30 - 40 cm. Approximately 85 percent of the plant's water requirements are extracted from the top 25 cm of soil.

The sensitivity of potato yield to irrigation management is well documented. Potato yield is reduced by both over- and under-irrigation; for example yield may begin to decrease if there is a 10 percent deviation from optimum water application for the growing season. The potato crop is sensitive to water management and this is because the crop is extremely sensitive to water stress. Poor soil aeration can induce yield reductions due to over- irrigation. Incorrect irrigation can also facilitate increased disease problems, and leaching of nitrogen from the shallow crop-root zone. Among the many benefits from efficient irrigation management are: an increased marketable yield, reducing production costs by conserving water, energy, and nitrogen fertilizer, as well as reducing potential ground water contamination.

Relating water requirement to potato crop growth stage

Potato growth is dramatically affected by the timing and amount of water applied during crop production. Certain stages of plant growth are more sensitive to water stress than others.

The growth of a potato plant can be considered in several stages (Fig. 9):

- Sprout development,
- Plant establishment,
- Tuber initiation,
- Tuber bulking, and
- Tuber maturation.

The onset and duration of these growth stages varies depending upon environmental factors, such as elevation and temperature, soil type, availability of moisture, cultivar selected, and geographic location.

At northern latitudes, emergence of new plants (Growth Stage I) can occur as early as March or as late as June, and harvest (after completion of Growth Stage V) typically occurs between August for early-maturing cultivars and as late as October for late ones.

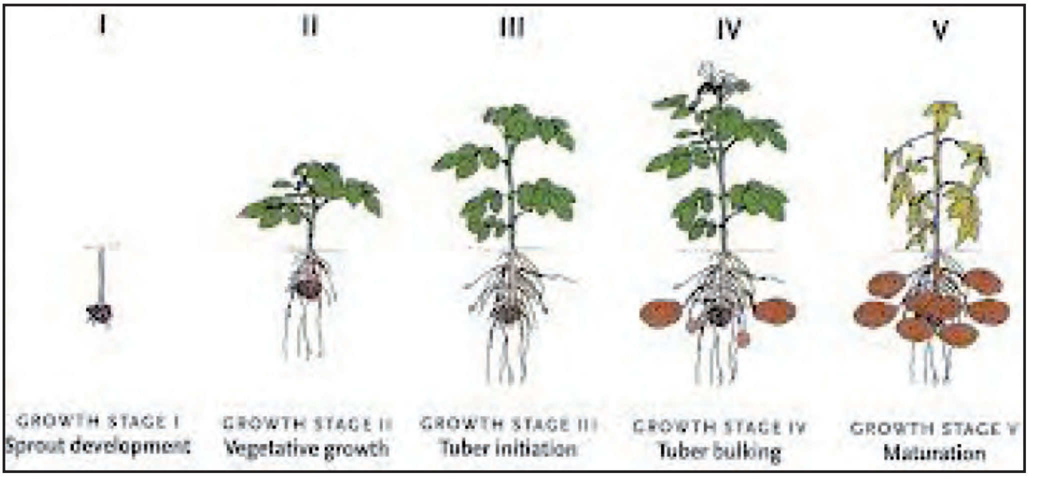

Figure 9.
Diagram illustrating potato growth stages
(Diagram Adapted with permission from Potato Health Management, 1993, Randal C. Rowe (Ed.), APS)

All plants vary in their water requirements according to their size and growth stage as well as the length of their maturity and time of year of maximum growth. The potato is regarded as the major agricultural crop, which varies in its sensitivity to water stress based on growth stage. Drought stress is considered as the main limiting constraint on world potato production. Developing drought-tolerant cultivars would maintain yields under climate change conditions and extend agriculture to sub-optimal cropping areas.

Growth Stage 1. Sprout Development and Irrigation
Seed tubers are capable of growth once they have broken dormancy and when exposed to favourable environmental conditions, sprout growth can commence. Since the mother tuber provides water and nutrients to sustain sprout growth from planting to emergence, irrigation in the immediate post planting period will not normally be required. Avoid excess soil water at planting since it promotes seed tuber decay and delays emergence due to decreased soil temperature. If irrigation was applied during this period, it would raise the soil moisture and lower soil aeration to a level that would support several pathogens, most notable bacterial soft rot or black leg (*Erwinia carotovora*), and stem and stolon canker (*Rhizoctonia solani*).

The metabolites required for sprout growth are provided from the breakdown of seed tuber storage products. Oxygen is required to drive this process and wet or overwatered soil restricts the amount of O_2 available around the respiring tuber. This excess water will also reduce the rate of tuber respiration, putting the seed-piece under metabolic stress. When the soil profile is saturated for more than 8-12 hours, this can cause damage to the young roots due to a lack of oxygen required for normal respiration

Growth Stage 2. Plant establishment and irrigation
Plant establishment defines the duration of the growth period from early sprouting until initiation of new tubers occurs. This period also includes development of roots and the "vegetative growth" of shoots. It is a period of rapid growth, often referred to as the log phase of canopy growth,

Drought early in the growing season restricts canopy expansion and therefore light interception and yield. The first physiological response is closure of the leaf stomata: the small pores in the leaf that control gas exchange between internal leaf cells and the environment. Evaporation of water from within the leaves serves to cool them. This ensures that the plant canopy temperature is below air temperature, under well-watered conditions. The plant responds to water deficit by closing the stomata and this acts as a further defence against water loss. The physical indication is an increase in canopy temperature as a result of reduced evaporative cooling of the leaves. Young, recently expanded leaves, display drought stress earlier that the more mature leaves toward the base of the stem (Fig. 10).

Figure 10.
Young leaves displaying drought symptoms, with older leaves still turgid (Photo © Author).

One of the first morphological manifestations of drought is a reduction in leaf size. This results in a reduction in light interception and leads to a reduction in dry matter accumulation in tubers. When a potato crop is affected by water deficit the primary physiological response is a reduction in the development of leaves stems and tubers. Water deficits exert their effect on growth by reducing the internal water pressure in plant cells (turgor pressure), which promotes expansion. When vine and leaf growth is reduced, this limits total photosynthetic capacity. This response is compounded when reduced root development limits the plant's ability to take up water and nutrients.

A study to investigate the effect of drought on potato plant architecture has shown a reduction in both dry matter production and the proportion of dry matter partitioned into tubers. However, drought increased the proportion of dry matter in shoots and roots. The root: shoot ratio increased under drought conditions implying that root growth was maintained to a greater extent than shoot growth.

Since the crop will not have reached its maximum rooting depth during canopy expansion, a smaller SMD will result in a yield penalty. Commencing irrigation at lower SMDs earlier in the season can offset this effect. It is important to achieve a well-established root system to support early growth and this also can allow for quick regrowth after early season defoliation from frost, hail, or insect damage.

Note: *Farmers often believe that dry soils encourage root activity while they search the soil profile for water. There is no research evidence to support this concept and in fact the opposite is true, moist soils encourage root growth (when the soil has been tilled properly). This constitutes further evidence that in a dry season, early irrigation is desirable to promote root growth.*

Growth Stage 3. Tuber initiation and irrigation

It is vital that potatoes receive the correct irrigation application during tuber initiation. If water stress occurs during initiation there will be fewer tubers set per plant and the longer the period of drought, the greater the reduction in tuber number, thus reducing total yield. Although tuber initiation takes place over a short period, it is most important to ensure adequate irrigation at this early growth stage. Water stress (inadequate water) will lead to earlier tuber initiation. The potato crop is particularly sensitive to water stress during tuber initiation and early tuber development. Water deficits at this time can substantially reduce yields in the size grade >50mm by increasing the proportion of rough, misshapen tubers. Early-season water stress can also reduce specific gravity and increase the proportion of tubers with the physiological disorder translucent end. Effect of drought on tuber number and size distribution has been investigated. It has been demonstrated that the number of tubers can be increased by irrigation at tuber initiation. Later irrigation maintains leaf area and functioning and decreases misshapen tubers. Several factors can impact on tuber number including nutrition, plant-to-plant competition and light intensity levels during the period of tuber initiation. Early irrigation therefore maximises tuber number, other things being equal.

Several studies have investigated the mechanism by which drought reduces tuber number. In one such study, a glasshouse experiment, potatoes were grown in containers. Water was withheld from emergence onward or from tuber initiation onward in some treatments. The number of stolons per stem was greatly reduced but the number of tubers + tuber initials per stolon remained unchanged (cv. "Radosa") or increased (cv. "Bintje") as a result of the earliest drought treatment.

Potato cultivars vary in their tolerance to drought. For a range of cultivars with varying tolerance to drought, the effect of drought and irrigation was assessed by measuring the distribution of yield and tuber number. Differences in the distributions of numbers of tubers in droughted and irrigated crops were statistically significant in four of the six cultivars examined. The main reason for lower ware yields in the droughted crops was that fewer tubers reached the minimum size (40 mm).

Common scab (*Streptomyces scabies*), a blemish disease, can be minimised by irrigation early in the growing season and this also encourages crop canopy growth. To achieve control of, common scab, irrigation needs to be applied well in advance of the onset of 50% soil moisture depletion. The objective behind irrigation scheduling and water application for maximum common scab control is to ensure that soil water reserves are maintained close to field capacity.

There is a relationship between the amount of common scab on tubers and the length of time that potatoes are deprived of irrigation. A five-day drought period caused the amount of scabby surface to increase from zero to over 20%, making tubers unmarketable. A 10-day drought period caused over 40% of the surface area to be scabby.

The timing of onset of a drought period, also affects the amount of surface that's scabby. Drought periods, started six weeks after planting, induced the largest amount of scabby surface on tubers. Unless the drought period started after tubers had more than 6 nodes (eye number) then the infected surface area was less than 5%.

Early drought periods induce scab on the first internodes of the tuber while drought at later periods affect the later formed internodes. It should be noted that earlier formed internodes are longer than later ones. This establishes a relationship between the amount of surface that's scabby and drought periods in relation to tuber growth and internode development.

By starting irrigation when tubers have less than three internodes, the scab-infected area will be small. Delaying the commencement of irrigation, until 4-5 internodes are present, will ensure that the first two internodes will be scabby. Delaying irrigation until seven are present, then the first four will be scabby. This means that over half of the tuber's surface area will be scabby

Growth Stage 4. Tuber bulking and irrigation

During this period, the canopy and roots attain full growth except for indeterminate varieties, which have the potential to add more levels of axillary branching. Tubers are in their log phase of growth and expanding rapidly. It is essential to remember that the tubers are 76 to 82% water and this water must be provided either by rain or irrigation. The duration of tuber bulking continues for about six weeks and the crop requirements for irrigation plus rain should be 50 to 65 mm per week or about 350

- 400 mm for the period. Soil moisture should be maintained at close to 80 - 90% FC. Plants have their highest demand for water and are the most sensitive to a deficit during this period. Water deficits occurring during tuber bulking will reduce tuber growth but will also increase the proportion of tubers with malformations.

Several environmental and cultural factors can influence tuber bulking rate and duration. Any factor that restricts healthy foliage growth, interrupts tuber growth, or redirects assimilates from the tubers to the foliage will decrease yield potential. Moisture availability/irrigation is a key factor affecting tuber bulking. A large photosynthetically-active leaf surface area is necessary to maintain high tuber bulking rates for extended periods. Maintenance of this large active leaf surface area requires continued development of new leaves to replace older, less efficient ones.

After nitrogen, the next agronomic factor likely to influence the linear rate of tuber bulking is irrigation or it's converse, drought stress. Just as nitrogen studies seek to determine an optimum application level, irrigation studies seek to determine the soil moisture deficit below which growth is adversely affected. In a study to investigate the effect of water deficit on the photosynthetic capacity of potatoes a significant increase in stomatal resistance with an increase in moisture stress was observed, but also that a water deficit influenced photosynthesis through mesophyllic factors. Gas exchange parameters are regarded as being more sensitive to moisture stress in potatoes than the more widely used measurement of leaf water potential.

When soil moisture content drops below critical levels, this reduces or stops canopy and tuber growth not only during the stress period but for several days thereafter. This results in a shortening of the tuber bulking period and can also induce a variety of defects, both internal and external.

By contrast, applying excess water can also reduce tuber growth through restricting plant physiological activity and nutrient uptake and through increasing disease susceptibility.

Tuber growth will resume following relief of plant water deficits, but because the normal tuber expansion rate was disrupted, the resumption of growth may

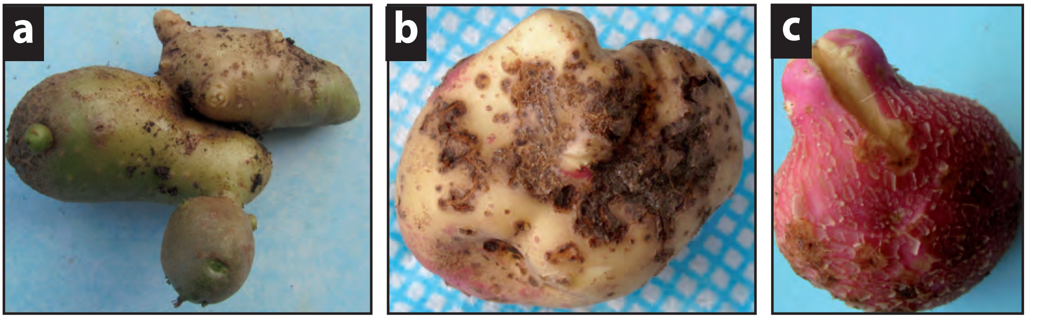

Figure 11.

Tuber malformations: Second growth (a), second growth and common scab (b). Growth crack (c) resulting from interruption and resumption of water supply during growth. (Photos © Author) result in tuber malformations such as pointed ends, dumb- bells, bottlenecks, and knobs (Fig. 11a). The greater the level of fluctuation in soil water contents the greater the opportunity for developing these tuber defects. Growth cracks are another manifestation of wide fluctuations in soil water availability coupled with corresponding changes in tuber turgidity and volume of internal tissues (Fig. 11c).

When water stress occurs during tuber bulking there is a greater effect on total tuber yield more than on tuber quality. Moisture deficits will reduce dry matter and specific gravity, whilst poor water management during tuber bulking can induce twin undesirable effects such as misshapen tubers infected with common scab (Fig. 11b) and also tubers displaying hollow heart (Fig. 11d). The conversion of sucrose to starch may be disrupted during periods of moisture stress, resulting in an increase of sugar content in the stem-end, affecting processing quality.

Figure 11

(d).Tuber displaying hollow heart (Photos © Author)

Growth Stage 5. Tuber maturation and irrigation.

The later stages of this period are characterized by leaf senescence; in the case of indeterminate cultivars, lower leaves are dying, tuber growth rate slows and eventually yield increase ceases. The term often used to describe this stage is "tuber maturation". Tubers attain their maximum content of dry matter and minimum content of reducing sugars, glucose and sucrose. Water stress coinciding with this stage hastens leaf senescence and interrupts new leaf formation and the outcome is an unrecoverable loss of tuber bulking.

The effect of drought/irrigation on total tuber yield has ben investigated in many studies. There is a general agreement that differences between cultivars in their response to drought could be ascribed to differences in the number of tubers produced. Since graded yield is defined by the mean tuber weight for the grade and the number of tubers in the grade, the economic value of a crop can be severely reduced by drought. A study examined the effect of drought and irrigation on graded yields in a range of cultivars and demonstrated that drought reduced the proportion of total yield that attained the minimum size specified for ware, whether 40 or 45 mm. Furthermore, the proportion of yield in the economically desirable grade 40 - 60 mm was lowered by drought to a greater extent than yield in the grades above or below this range.

While considerable information exists regarding yield increases due to irrigation, the underlying basis for this increase is not always forthcoming. A study examined the effect of drought on leaf expansion in 19 genotypes and demonstrated that in the droughted treatment, the reduction in final size was the result of reduced expansion rate rather than effects on the duration of expansion. When this work was extended, by seeking to partition the effects of drought in terms of crop development, the yield reduction due to drought was correlated with leaf area duration and additionally drought reduced canopy expansion and the maximum LAI achieved.

The high cost of energy associated with irrigation during the last two decades has encouraged studies on water use efficiency. These studies have been directed towards elucidating the effect of drought on primary development processes such as stolon formation and tuber initiation. A typical example is where drought stress was imposed on potatoes in containers at 50% emergence, tuber initiation and the small tuber stage. The study was concerned mainly with effect on tuber number and observed that drought, coinciding with 50% emergence, caused the greatest reduction in tuber number. Similar studies provide useful insights on the influence of timing and severity of drought stress on the numbers of tubers formed but do not address the effect of drought on tuber bulking. Nevertheless they provide support for the observations that irrigation before tuber initiation influences tuber number, whereas irrigation after this phase only increases mean tuber size.

Water is an essential requirement for potato production, as it ensures maximum yield and optimum quality. Soil moisture availability permits optimum tuber growth rate and at seasons end, facilitates harvesting with minimal crop damage. Low soil water content at harvest ensures that tubers are more susceptible to blackspot bruise. By contrast, tubers that are turgid as a result of high soil water content, are more susceptible to shatter bruise and thumbnail cracking.

Irrigation and Soil Salanisation

Irrigation permits farmers to grow crops in regions where rainfall level is inadequate to meet the plants' water needs. In many regions, irrigation ensures that crops to grow to marketable size. To achieve this result, water must be applied at the correct rate and at the correct time. Water is a valuable resource and should be scheduled to avoid waste and be in sympathy with the environment as a whole.

If the level of drought is so extreme that irrigation is needed to allow efficient crop growth, then prolonged irrigation often introduces another serious problem for agriculture: soil salinisation. Increasingly, salinisation is limiting crop productivity and reducing the pool of land available, with more than 20% (and up to 50% according to some estimates) of irrigated cropland being affected by salt, to a greater or lesser extent. All fresh water used for irrigating crops, regardless of source, contains salts. Even if only the minimum amount of water required to wet the soil is added, when most of that water evaporates from irrigation, the salts in the water are left behind to accumulate in the soil (e.g. like salt crystals seen after a glass of salt water evaporates). Over time, concentrations of those salts can accumulate to levels that make it more difficult for plants to take up water from the soil. At higher concentrations, the levels in the soil may become toxic, killing the crops. A concentration of salts in the soil of 0.5% to 1.0% can render that soil toxic to plant life. Soil may acquire salt from two sources; 'primary salination' due to salt blowing in the air from e.g. saline estuaries or 'secondary salination', accumulation in the soil due to human intervention.

Following prolonged periods of continuous irrigation, toxic ions dissolved in irrigation water (even if fresh, good-quality water is used) progressively accumulate in the soil, leading to this 'secondary salinisation' – of anthropic origin. This human induced salinisation renders more of than 1 million hectares of arable land unsuitable for crop growth every year. This problem is often more acute in areas with water is scarce, due to improper scheduling of irrigation. Furthermore, these losses of hitherto fertile land, are expected to increase in the years ahead, due to the effects of climate change.

In addition to the loss of agricultural land due to secondary salinization, there are large areas of the world's land surface amounting to about 6% are naturally saline and alkaline. Since all our major crops are salt-sensitive, these marginal lands have never been cultivated on account of their high soil salinity.

Summary

- Plants use up to 98% of the water absorbed from the soil for transpiration; some 1% is used during photosynthesis.
- The uptake of water per unit volume of soil has been observed to be proportional to the rooting density of the potato crop.
- Approximately 85 percent of the plant's water requirements are extracted from the top 25 cm of soil.
- There is a wide range of equipment available to measure soil moisture content
- The sensitivity to water management is attributable to the sensitivity of potato plants to water stress.
- Developing drought-tolerant cultivars would maintain yields under climate change conditions and extend agriculture to sub-optimal cropping areas.
- Dry soil does not encourage root growth – roots grow better in moist soil when the tilth is suitable.
- Water stress during tuber bulking usually affects total tuber yield more than quality.
- Irrigation scheduling prevents yield loss due to over or under application of water

Sources accessed in the preparation of this section.

Alva, A., Moore, A., and Collins, H. (2012). Impact of deficit irrigation on tuber yield and quality of potato cultivars. *J. Crop Improv*. **26,** 211–227.

Eldredge, E., Holmes, Z., Mosley, A., Shock, C., and Stieber, T. (1996). Effects of transitory water stress on potato tuber stem-end reducing sugar and fry color. *Am. Potato J.* **73,** 517–530.

Gregory, P., and Simmonds, L. (1992). "Water relations and growth of potatoes," in *The Potato Crop*, ed P. M. Harris (London: Springer), 214–246

Haverkort, A. J., Vandewaart, M., and Bodlaender, K. B. A. (1990). The effect of early drought stress on numbers of tubers and stolons of potato in controlled and field conditions. *Potato Res.* **33,** 89–96.

Hsiao, T. C. (1973). Plant responses to water stress. *Annu. Rev. Plant Physiol.* **24**, 519–570.

Jones, H. G., and Corlett, J. E. (1992). Current topics in drought physiology. *J. Agric. Sci.* **119,** 291–296.

Jefferies, R. A., and Mackerron, D. K. L. (1987). Aspects of the physiological-basis of cultivar differences in yield of potato under droughted and irrigated conditions. *Potato Res.* **30**, 201–217.

Jefferies, R. A., and Mackerron, D. K. L. (1989). Radiation interception and growth of irrigated and droughted potato (*Solanum tuberosum*). *Field Crops Res.* **22**, 101–112.

Obidiegwu, J. E., Bryan, G. J., Jones, H. G., & Prashar, A. (2015). Coping with drought: stress and adaptive responses in potato and perspectives for improvement. *Frontiers in Plant Science*, **6:** 542

van Loon, C.D. (1981). The effect of water stress on potato growth development and yield. *Am. Potato J.,* **58**, 51–69

Section 17.

Intercropping potatoes

Introduction

Intercropping is an all-encompassing term for the practice of growing two or more crops in close proximity: in the same row or bed, or in rows or strips that are close enough for biological interaction. It represents a strategy to increase agricultural productivity per unit land, underpinned by ecological mechanisms for improved resource capture. Intercropping aims to achieve a greater yield on a unit area of land by improving the efficiency of the available growth resources through using a mixture of crops having different rooting ability, canopy structure, height, and nutrient requirements where there is complementary utilization of growth resources by the component crops.

Crops use environmental resources in different ways. When intercropped they can complement each other, often utilising resources better than under monocropping. This complementarity can be regarded as *temporal,* deriving success due to the crops making their major demand on resources at different times, or *spatial*, due to differences in canopy and root architecture.

Mixed cropping, companion planting, relay cropping, interseeding, overseeding, underseeding, smother cropping, planting polycultures, and using living mulch are all forms of intercropping. The practice includes the growing of two or more cash crops together, or the growing of a cash crop with a cover crop or other non-cash crop that provides benefits to the primary crop or to the overall farm system. Cover crops can also be intercropped with one another.

For the future, agriculture must satisfy two requirements: meet higher food demands for a growing population, and achieve this objective while mitigating its ecological footprint. These conflicting demands must be addressed by sustainable intensification of agriculture. Intercropping can make a contribution to these objectives since by increasing crop biodiversity this improves resilience, food security and nutrition. The objective is achieved through improved resource capture and utilization due to differences in spatial and temporal distribution of component crops. Planting mixtures, particularly C3/C4 mixtures could lead to substantial improvements in land use efficiency in agriculture. Farmers will need to have a thorough knowledge of species combination, arrangements and proportions if they are to obtain maximum advantage from this system. Intercropping has not received the research input it deserves and most of the existing agronomic recommendations are tailored on monoculture practices. There is a need to enhance agricultural research on intercrop systems, combining conventional and modern research approaches.

Background

Food scarcity is one of the most important problems that our world is enduring nowadays, attributed to the exponentially growing numbers of population and limited potential expansion of land areas suitable for cultivation. This illustrates the immense need for more intensive research to accommodate the problem. Increasing agricultural output is the key to solve the problem of food scarcity. Extensive research being conducted around the globe has the expressed aim of increasing yield by many means and innovative cultivation techniques. Since new land resources are limited and diminishing, a strategy to increase productivity and labour utilization per unit area of available land is to intensify currently available land use. One such technique is intercropping, which has been practiced over centuries and achieved the goal of agriculture. It increases productivity per unit of land via better utilization of resources, minimizes the risks, reduces weed competition and stabilizes the yield.

The development history of intercropping has not been recorded so we do not know when the practice began nor why early civilizations fostered its use. It may never be known how the first "real" intercropped field appeared, but historians believe that intercropping probably existed early in agricultures' evolution. Whether by accident or design, intercropping dominated early agriculture and is still widely practiced in many areas of the world, making the practice quite possibly as old as settled agriculture. The evolution of intercropping is part of the process of species domestication.

With the adoption of mechanisation and specialisation as an integral part of "modern" agriculture, intercropping largely disappeared from many areas. However, despite pressure to abandon intercropping, it has survived and flourished in other areas. With the new focus on sustainability and environmental concerns, attention has shifted back to intercropping, as a means of better utilising resources, while preserving the environment. Farmers generally consider three factors: cost, risk and return calculation, before deciding to adopt a new technology. This is the reason why on small subsistence farms, the farmers raise multiple crops which minimise the risk of total crop failure and additionally, to harvest different products to provide the family's food, income, etc.

In many areas of the world, intercropping still dominates the cropping systems and this is particularly true of specific plant species. It has been estimated that 80% of the cultivated area of semi-arid West Africa is intercropped. In Latin America, it has been estimated that 60% of the maize and 80% of the field beans are intercropped. In India, the majority of pigeonpea is intercropped. In tropical Asia and the Pacific, multistorey intercropping is common with tree species dominating the upper canopy.

As our environmental and production concerns increase, it is likely that intercropping will provide some profitable alternatives, since it has the potential to improve rural livelihoods through better resource utilization.

The most important aspect of multiple cropping is the intensification of crop production in the dimensions of time and space; for example, when two crops share the same space at the same time.

Advantages of intercropping

Increasing production

One of the main reasons for the use of intercropping around the world is to produce a higher yield than would be produced in a pure cropping of same amount of land. The scientific literature is replete with examples of increased productivity under intercropping. This increased production can be attributed to the higher growth rate, reduction of weeds, reducing the pests and diseases and more effective use of resources due to differences in resource consumption. Several benefits have been ascribed to interspersing two crops, such as increased nutrient and soil organic carbon cycling, decreased soil erosion and increased carbon sequestration. In addition, interspecific interactions can provide either "complementary effects" or "competitive effects" between the components of intercropping. Production increases due to complimentary effects would result in yield increases. Intercropping is recognised as an economic method for higher production combined with lower levels of external inputs. This increasing use efficiency is important, especially for small-scale farmers and also in areas where the growing season is short.

Greater use of environmental resources

An intercrop may use resources of light, water, and nutrients more efficiently than single crops planted in separate areas, and this can improve yields and income. Intercropping achieves its advantage in crop production compared with pure cropping, through the interaction between components in intercrops and the difference in competition for the use of environmental resources. When the intercrop components do not compete with each other for the same environmental resource they are regarded as complementary in the use of this resource. This means that the resource is therefore used more effectively than in pure cropping, with resultant increased yield. This positive outcome means that intercrop components are not competing for the same ecological niche. Due to differences in morphological and physiological components, competition between species is lower than competition within the species.

Mixtures have certain advantages over pure stands, these include,

- When there are different rooting habits that may result in better use of soil moisture and nutrients from various soils depths
- Stabilise seasonal production,
- A variety of crop nutrients is more likely to improve plant productivity

- Crop mixtures may have greater longevity and
- When components of mixtures have the capacity to fix nitrogen, this may exert a favorable influences on other components

Reduction of pest, disease and weed damage

Intercropping has been demonstrated to possess the ability to reduce pest and disease damage. The strategies involved in reducing pest infestation and damage under intercropping may be divided into three groups:

First*: delimiter crop hypothesis:* here the second crop, degrades the ability of a pest to attack to its host, and is used more with proprietary pests.

Second*: trap crop hypothesis:* here there is a greater attraction for the pest or pathogen to the second crop than to the main crop and is used more in general pests and pathogenic agents.

Third*: natural enemies' hypothesis:* here intercropping provides a more favourable environment for predators and parasites than monocropping, and this has the effect of diminishing parasitized and prey.

Crop mixtures frequently have lower pest densities, especially of insect pests. It is considered that this occurs both because the mixture 'confuses' the insects and with a careful choice of components the crop mixture may attract beneficial predators. While intercropping does not always reduce pest or pathogen, there is considerable evidence in the scientific literature indicating reduced populations of pests and diseases under intercropping.

A review of the literature on intercropping found that in 53% of the experiments intercropping reduced the pest, whereas in 18%, pest numbers increased more than in pure cropping. Increased pests numbers can be due to several reasons, such as the second crop in intercropping is a host for pests, or increasing shade from the canopy, provides favorable conditions for pest and pathogen activity. In addition plant residues can be a source for pathogen inoculum. Additional species diversity in agricultural ecosystems can limit plant pathogenic spread. When intercropping systems increase biodiversity, similar to that recorded in natural ecosystems, the increase in diversity reduces pest damage and diseases.

It is well recognised that the weeds interfere with crops, causing serious impact, through either competition (for light, water, nutrients and space) or allelopathy. Intercropping patterns provide additional competition against weeds, but their effectiveness varies considerably. There are two mechanisms by which intercrops display weed control advantages over pure cropping: first, greater crop yield and greater suppression of weed growth may be achieved if intercrops more effectively usurp resources from weeds than under pure cropping or suppressing weed growth through allelopathy. Secondly, intercrops may provide a higher yield, without suppressing weed growth below levels observed in component pure cropping, if intercrops use resources that weeds cannot exploit, or if the crop combination converts resources into harvestable materials more efficiently than sole crops.

Due to the difficulty in quantifying the use of multiple resources by intercrop/

weed mixtures throughout the growing season, it has not been possible to identify the specific mechanisms of weed suppression and yield enhancement in intercrop systems. In monocropping systems, all the available natural resources, such as moisture, nutrients and light are rarely used by the plant, consequently the weeds capture resources released from the niche. If the use of resources by the plants in the intercropping system are complementary, then, the intercropping system with the more effective use of ecological resources, leads to better and more effective weed control than a monocropping system.

Stability and uniformity Yield

For farmers who have limited resources, stability both of income and yield of agricultural produce is very important. When several crops can be grown together, failure of one crop to produce an economic yield could be compensated for by another crop, thereby reducing the risk. This may result because growth conditions appropriate for one species may be inappropriate for other species.

Improve soil fertility and increase soil nitrogen

Conservation of soil fertility through intercropping is a form of rotation practiced each season on an area of land. *Rhizobium* bacteria can have a symbiotic relationship with plants of the Leguminosae family, and thereby can fix atmospheric nitrogen into a form of nitrogen available for plant uptake. The resulting nitrogen (as an essential element for soil fertility and plant growth) is added to the soil. There are several reports, which describe increasing the nitrogen content in non-leguminous plants, due to intercropping of these plants with plants of the Leguminosae family.

Economic impact

Success of an intercropping scheme can defined by the question; does it improve the overall economics of the farm? To minimise exposure to financial risk, a new intercropping strategy should be tested first on a relatively small area. This will permit evaluation of how successfully it fits into the overall management system and whether benefits accruing, outweigh extra costs, labor, or yield reduction. It is also important to consider that a single test year may not be sufficient to evaluate some consequences of intercropping—such as better or worse weed control, or difficulties in timing planting or harvest.

Potential problems with intercropping

Just as with any other farm practice that involves risk to continuing food supply and/or family income, adopting an intercropping system should not be attempted without careful consideration of all the possible advantages and disadvantages. The advantages of intercropping do not come for free:

- Intercropping systems require additional management as there is two crops to monitor
- It calls for careful timing of field operations, and they may necessitate special

interventions to maintain a balance in competition between the intercropped species.

- A crop mix that is successful in one season may fail the next, if weather favors one crop over another.
- When there is a mixture of crops with different growth forms or timing of development, this may render cultivation and use of mulches more difficult and less effective.
- Planting crops in alternate rows or strips greatly simplifies management and captures some of the benefits of intercropping for pest control. It may fail to achieve it objective to increase resource capture by the crops, unless alternating strips are close together.

Intercropping and crop rotation

Intercropping introduces an additional problem for crop rotation. A fundamental concept of crop rotation is the separation of plant families in time, which is critical for management of diseases and, to a lesser extent, insect pests. When mixing plants from two families in the same bed or field, it may be difficult to achieve a substantial time lag before replanting either of those families. This difficulty can be illustrated by the following example: a farmer grows separate plots each of potato, beans, barley, and legume. A simple rotation would put each of the crops in a different location each season, with a three-season interval before a crop is repeated on the same plot. If, however, the potato and beans were grown together, crops would be separated by only a two-season interval, which may be insufficient to keep some diseases under control. This illustrates why intercropping requires extra care and effort in planning so as to achieve a viable crop rotation.

Types of intercropping

Compared with pure cropping, where only one species is planted, intercropping consists of planting two or more crops. Intercropping can include: annual plants with annual plants intercrop; annual plants with perennial plants intercrop; and perennial plants with perennial plants intercrop. Iintercropping practice may be divided into four groups as follows:

1- **Row-intercropping:** Growing two or more crops simultaneously where one or more crops are planted in regular rows, and the intercrop or other crops may be grown simultaneously in row or randomly with the first crop.

2- **Mixed-intercropping:** Growing two or more crops simultaneously without a distinct row arrangement. This format can be suitable for grass-legume intercropping in pastures.

3- **Strip-intercropping:** Growing two or more crops simultaneously in different strips wide enough to permit independent cultivation but narrow enough for the crops to interact agronomically.

4- **Relay-intercropping:** Growing two or more crops simultaneously during part of the life cycle of each. A second crop is planted after the first crop has reached its reproductive stage but before it is ready for harvest.

Intercropping systems can be characterized according to the degree to which roots of different crop species interact in an intercrop setting. It is determined not only by the intercropping system but also by the root architecture of each of the crops in the mixture. Of course this does not mean that with intercropping, the plants must be planted at the same time, but that two or more crops are together in one place, during their growing season or at least part of the timeframe.

Competition indices to evaluate the performance of intercropping combinations

To describe the competition and possible economic advantage in intercropping, various indices such as land equivalent ratio (LER), relative crowding coefficient (K), competitive ratio (CR), aggressivity (A), and monetary advantage (MA), have been developed. Mathematical indices can provide a basis to permit researchers summarize, interpret, and display the results from plant competition. Indices can illustrate attributes of competition in plant communities, including competition intensity, competitive effects, and the outcome of competition.

Land equivalent ratio is the most commonly used for assessing competition, for intercrop versus sole crop comparisons. Indices such as land equivalent ratio and area time equivalent ratio facilitate assessment of the biological efficiency of an intercropping system. Competitive ratios seek to define a measure of intercrop competition in intercropping systems and monetary advantage index to evaluate economic advantage of each intercropping system as compared to sole cropping.

The following are a list of indices used to measure productivity in intercropping systems:

Land Equivalent Ratio (LER). Measuring productivity, using Land Equivalent Ratio (LER), permits an assessment of the benefits of growing two or more crops together. It is defined as the relative land area required from sole crops to produce the same yields as intercropping. The concept underpinning intercropping is to capitalize on the beneficial interactions between crops while avoiding negative interactions. The value of LER is that it measures the effect of both beneficial and negative interactions between crops.

To calculate the LER, divide the intercrop yield of one crop (e.g., corn) by the yield of the pure stand and add that to the intercrop yield of the next crop (e.g. beans) divided by the yield of the pure stand and so on. The equation goes like this:

intercrop1/pure crop1 + intercrop2/ pure crop2 + etc. = LER.

or

intercrop corn/pure corn + intercrop beans/pure beans + etc. = LER

The resulting number is a ratio that indicates the amount of land needed to grow both crops together compared to the amount of land needed to grow pure stands of each. LER values of more than 1, indicates yield advantage, equal to 1 indicates no gain or no gain or no loss and less than 1, indicates yield loss. For example, an LER of 1.15 means that an area planted as a pure stand, or monoculture, would require 15% more land to produce the same yield as the same area planted in an intercrop combination. An LER of 2.0 means the inter-cropped area would produce twice as much as the monoculture. On the other hand, an LER of 0.80 indicates the intercrop yield was only 80% of the yield of the pure stand.

Income Equivalent Ratio (IER): The ratio of the area required under sole cropping to produce a similar gross income as is obtained from 1 ha of intercropping while employing the same management level. The income equivalent ration represents the conversion of the LER into economic terms.

Relative Yield Total (RYT): The sum of the intercropped yields divided by yields of sole crops. The same concept as land equivalent ratios. "Yield" can be measured as dry matter production, grain yield, nutrient uptake, energy, or protein production, as well as by market value of the crops. It may be that each crop in the mixture yields slightly less than the monoculture, but the combined yield of the mixture on less total land area is the important aspect.

Area time equivalent ratio (ATER): Allows comparison of the yield advantage of intercropping over monocropping in terms of time taken by component crops in the intercropping systems. ATER is calculataed by the formula:

Area time equivalent ratio (ATER) = LER x Dc / Dt

Where LER is land equivalent ratio of crop,
Dc is time taken by crop,
Dt is time taken by whole system.

Published data often suggest a sizable gain in land-use efficiency by growing two or more crops in mixtures. The *land equivalency ratio* (LER) is the most-used convention for intercrop- vs. -monoculture comparisons, but LER is frequently inappropriate because cropping-system duration, i.e., time, is not included in its calculation. This becomes an issue when the duration of land occupancy by an intercrop is longer than production-cycle duration for one or more of the interplanted species. The *area-×-time equivalency ratio* (ATER) has been developed to correct this conceptual inadequacy in LER.

Relative crowding coefficient (RCC): Relative crowding coefficient (RCC) measures the relative dominance of one component crop over the other in an intercropping system. If a species i is in mixture with a species j in a 1:1 mixture of i and j, then an individual coefficient, termed the relative crowding coefficient k can be expressed as where,

$$K_{ij} = \frac{Y_{ij}}{Y_{ii} - Y_{ij}}$$

$$K_{ji} = \frac{Y_{ji}}{Y_{jj} - Y_{ji}}$$

K_{ij} and K_{ji} = relative crowding coefficients of crop i intercropped with crop j and crop j intercropped with i; Y_{ij} and Y_{ji} = yields per unit area of i intercropped with j and j intercropped with i; Y_{ii} and Y_{jj} = yields per unit area of sole crop i and sole crop j.

The crop component that had a higher coefficient was said to be dominant. If the coefficient of a particular crop species is less than, equal to or greater than 1, then that species has produced less yield, the same yield, or more than "expected", respectively.

Aggressivity (A): Aggressivity (A) is another index which represents a simple evaluation of the relative yield increase in crop 'a' over crop 'b' in an intercropping system and was calculated as:

$$Aab = (Yab / Yaa\ Xab) - (Yba/Ybb\ Xba)$$

If Aab=0, both crops are equally competitive, if Aab is positive, 'a' is dominant, whereas if Aab is negative, 'b' is the dominant crop. Competition ratio (CR) has been proposed instead of "aggressivity" to indicate the degree that one species competes with the other in an intercrop system.

Factors for consideration in selecting an intercropping system

To ensure successful intercropping, several factors must be considered before and during cultivation. Intercropping affects vegetative growth of component crops; therefore it is essential to consider the spatial, temporal and physical resources. To ensure economic viability, the adaptation of planting patterns and selection of compatible crops are critical for successful intercropping. When choosing crops which will provide a compatible intercropping system it is important to consider factors such as plant growth habit, land, light, water and fertilizer utilization. The objective in successful intercropping is to have different crop species in mixtures increase the capture of growth limiting resources while factors like staggering the planting times of the component crops helps improve the resource utilization and reduce the competition.

Compatible crops: Choosing an appropriate crop combination is central to the success of intercropping. Plant density, shading and nutrient competition between plants reduce the yield of the mono crop. Two possible mechanisms exist to minimise plant competition adjusting the spatial arrangement, also by choosing crops best able to exploit the available soil nutrients. For example, when maize is included in the intercrop mix; the companion crop should be tolerant of maize shade

Plant density: Since low plant population per unit area result in low yield, the seedling rate of each crop in the mixture should be adjusted below its full rate to optimize plant density. Planting full rates of each crop would reduce yield due to serious overcrowding. Reducing the seedling rates of each would offset this response and that will provide the crops with a chance to yield well within the mixture. The dilemma therefore is to choose the appropriate seedling rates, remembering that a reasonable Leaf Area Index (LAI) is critical to maintain high photosynthetic rates and yield

Time of planting: Maize has diverse uses and is capable of growth under a considerable diversity of environments and has high potential for carbohydrate accumulation per unit area per day. Maize has been recognized as a common component in most intercropping systems. In a potato-maize intercrop, selecting the appropriate planting date for the maize is crucial, so as to avoid excessive shading during the potato tuber bulking phase.

Intercropping potatoes

In Africa, South East Asia and South America, potatoes are commonly intercropped. Farmers in the tropics have long experience in intercropping of potato with other crop species. This combination is planted to take advantage of the complementary food values and the differing morphologies of the two species.

But a note of caution*: Improvement to indigenous systems that are successfully functioning should only be undertaken after careful consideration. To create a system, appropriate to future potato-production zones in hot areas, requires a clear understanding of their physical and biological interactions.*

This knowledge required to undertake this may obtained from research on temporal and spatial demands by intercrops. Central to the success of intercropping is the selection of compatible crops and the choice of compatible crops for an intercropping system depends on plant growth habit, land, light, water and fertilizer utilization. In addition it must take account of factors such as light interception, planting density and planting time

Intercropping Potato and Maize - Effect of reduction in irradiance

The benefits of intercropping potato with annual or perennial crops with respect to total resource use, particularly of solar energy have been investigated. Results showed that there was a negligible decline in yield of the potato crop in the tropics when the canopy was subjected to a 25% reduction in the receipt of irradiance for extended periods. If further reductions in irradiance receipts were experienced, potato genotypes possessing shade tolerance would be required in order to maintain output at the appropriate level.

Continuing to investigate the effect of shading on potato growth, intercropping of potato and maize was investigated in fourteen experiments at three hot tropical sites (5–12°S, 180–800 m.a.s.l.) within Peru over a 5-year period using artificial or natural shades. Shade was provided:

- Artificially throughout the potato crop,
- By a maize crop for a short (10–30-day) period following planting (relay cropping), or
- By a maize crop during the last 30 days of the potato crop (mixed cropping).

As shade was increased, there was a linear reduction of soil temperature (7-cm depth) and more rapid emergence in all artificial-shade and relay experiments but one. There was a more marked delay of emergence when the weighted daytime soil temperature exceeded 30°C. Shade treatments also resulted in conservation of soil moisture, improved emergence and plant height. However, results were not all positive as tuber

initiation was delayed by shade, despite the earlier emergence, while branching and dry-matter production were also reduced by shade, to a degree, depending upon shade intensity. Later-season shading in mixed-cropping experiments resulted in a reduction of up to 40% transmission of irradiance to understory potato plants.
Another study showed that when potato and maize were combined in an intercropping system, where there were differences in the growth pattern of potato and maize leaves, the light competition decreases the growth and affects leaf formation. Other results showed that root competition in the first stages of plant's life cycle leads into weak growth and decreases plant light interception.

Intercropping Potato and Maize – Controlling Water Loss

Where studies have shown an increased yield due to intercropping, the result is often achieved through controlling water loss. Potatoes in the tropics are often planted on sloping sites and there are few studies examining the effect of intercropping on controlling water loss on sloping land. Such a study, with maize and potato as experimental crops, was made of surface runoff, soil evaporation, soil moisture content, crop transpiration and crop yield between the intercropping and the sole crop on sloping land during 2012–2013.

The results suggested that on sloping land, the maize and potato intercropping could reduce both the water loss from the surface runoff and the soil evaporation. This increased the soil moisture content and contributed to the increase in transpiration and crop yield. Data also indicated that the lower runoff in maize and potato intercropping compared with sole maize is associated both with the higher leaf area index and also with the potato tubers.

Intercropping Potato, Maize and Beans - Effect of Irrigation

A field experiment was conducted to study the effects of different irrigation levels (irrigating at 65%, 75% and 85% of field capacity) on the yield of potatoes, faba beans and maize as they were grown under sole cropping and intercropping with two different row arrangements (2:2 and 2:1). The results of the experiment indicated that higher yields of potatoes, maize and faba beans were achieved under intercropping than under sole cropping, regardless of the soil moisture levels. However, the highest average yields of intercropped potatoes (70.4 ton ha^{-1}), and maize (5.54 ton ha^{-1}), were obtained when minimum soil moisture level was maintained through out the growing season under 0.75 of field capacity (FC), while the highest average yield of faba beans (5.6 ton ha^{-1}), was at 0.65 FC.

The highest yields of potatoes, maize and faba beans grown under sole cropping were obtained at a soil moisture level of 0.85 FC, 0,75FC and 0.65FC, respectively. Including a legume crop (faba beans) in the intercropping system, had a beneficial effect on the other crops (corn and potatoes) when associated with it, especially under 2:2 row arrangement. When the efficiency of intercropping was measured by the land equivalent ratio (LER), it was higher than 1.0 under all intercropping combinations and irrigation treatments, indicating that intercropping provided an advantage compared with sole cropping.

Intercropping Potato and Maize – Shoot and Root Competition – Effect on Growth and Yield

Greenhouse experiments were carried out to investigate interspecific competitive relationships and their effect on yield of potato and maize,

Three configurations were employed: (NC: no interspecific competition; FC: shoot and root interspecific competition; SC: shoot-only interspecific competition). While there were large variations between replicate experiments the study revealed consistent patterns of competition for above- and below-ground resources.

The potato dominated light interception in FC and SC (60%) during the first 45 days after planting while maize dominated thereafter (80%). Soil moisture was increased by 10% in the SC treatment due to the additional shading. Yield responses were complex; in potato, FC reduced tuber yield (number and size) by 4–26%, while SC increased tuber size (compared to NC) by 3–39%.

In maize, FC reduced LAI and plant height by up to 45%, shoot and root dry mass, nutrient content, yield, the weight of 100 grains and harvest index by ca. 30–100%, while SC affected all but LAI and plant height.

The potato root system achieved early rapid extension in contrast to the more progressive development of the maize roots and therefore the result of the root competition manifest the effect in competitive relationships in the shoots. The authors concluded that the competition effects on maize in the potato/maize intercropping could be explained by light availability in the mixed canopy.

Intercropping Potato and Maize – Effect of Spatial Arrangement

Successful crop production in intercropping system depends on many factors including variety used, plant density, planting arrangement, cropping seasons and agricultural practices like irrigation, fertilization etc. When potato and maize are grown in an intercropping system, the light competition decreases the growth and affects leaf formation, due to differences in the growth pattern of potato and maize leaves. As shown above this reduction in light interception is induced due to root competition in the early stage of plant growth.

While there is ample research data to indicate that land equivalent ratio was highest under intercropping system compared with sole cropping, fewer research studies answers the question, which maize-potato intercropping spatial arrangement is the best.

Potato Productivity: There is research evidence that intercropping maize-potato in different spatial arrangement significantly affect potato tuber yield. Sole cropping potato produced a significant increase in productivity (24.8 ton/ha) compared with the intercropped (8-23.4 t/ha). The spatial arrangement at 2 maize: 1 potato provided the lowest potato mean tuber yield due to low plant population per unit area. Other research has confirmed this result by indicating to the potato productivity was reduced by 61% and 53% when it was intercropped with maize plants, compared to the sole cropped potato. This reduction is related to the low solar radiation intercepted by potato plants and its small leaf area.

Maize productivity: Results from the foregoing study also indicated that intercropping, using different spatial arrangements significantly affected grain yield of maize. The highest mean maize grain yield was recorded in sole cropped compared with all intercropping systems, but this was similar to the yield from 1 maize: 1 potato arrangement. The planting arrangement, 1 maize: 2 potatoes provided the lowest mean maize grain yield due to low plant population per unit area.

However the intercropping arrangements, 1 maize: 1 potato arrangement gave significantly higher mean grain yield (4.1 ton/ha) as compared to other intercropping arrangements probably due to high plants density. The reduction of productivity of both crops under intercropping system, is possibly attributed to the more favourable competition feature of maize plants, which permits the interception of more light.

Intercropping Potato and Maize – Effect of Plant Density

An experiment was conducted to optimize the effective spatial arrangement for intercropping of maize and potato using different planting geometry and row proportions by comparing competition indices. The results of this research showed that in the case of equal plant densities of potato and maize (4.76 plant m^{-2}) resulted in an increase in the mean length of potato stems, which reached 27.45 cm. Moreover, intercropping of maize of 2.38 plant m^{-2} permitted the increase in the mean weight of potato shoots (fresh and dry) to 227 and 21.28 g $plant^{-1}$ for fresh and dry weight, respectively, in addition to the increase in the mean weight of potato tubers, which reached 101 g $tuber^{-1}$. Results also showed that intercropping did not affect either the number of potato stems or the number of tubers.

What was the effect on productivity? Results indicated that the total productivity per unit area from intercropping was higher than the productivity of the sole crop. Comparing the results using LER showed positive influence from intercropping compared with sole cropping, where LER values, were higher (1.43-1.55) in intercropping compared to (1.00) in the sole cropping.

Instead of concentrating on crop yield as a measure of success, another approach is to use financial gross margin as the criterion. An experiment was designed and conducted to find out the appropriate ratio of maize in potato maize intercropping practices for better economic return to farmers. Four different ratios (10%, 20%, 30% and 40%) of maize intercropped with potato were compared with potato as a monoculture. Intercropping potato with 40% maize plants produced the lowest yield of potato while all other combinations produced statistically identical yield. Growing potato under monoculture produced the highest yield of 20.66 t/ha. The optimum combination for intercropping, that provided maximum gross margin, LER and equivalent yield was recorded when potato was combined with 30% maize.

Intercropping Potato with Maize and Bean

Experiments evaluating potato-intercropping systems with maize and faba bean (*Vicia faba*) were conducted at two sites - (1900 and 2700m.a.s.l.). Intercropping reduced potato yields, ranged from 0–21 percent depending on year, and location. Potato yield reductions were not offset either by variation in planting geometry or maize planting date. L.E.R ratios ranged from 1.03–1.06 for faba bean and from 1.11 to 1.49 for maize intercropping systems. At one location, an increase in gross benefits of 12-15% was recorded when potato was intercropped with maize at 2.8 plants m^2, while at the other site no benefit accrued from intercropping. However, intercropping produced two positive outcomes, it reduced environmental risk and improved market out turn.

Intercropping Potato and Legume

A field trial to evaluate the effect different proportions of intercropping potato and pinto bean (*Phaseolus vulgaris* L.) compared with growing each crop under sole cropping. Two experiments were carried out, with proportions 2:1 and 3:1 of potato with pinto bean, (the densities of potato 4.7 and 5.3 plants per m^2 and those of pinto bean 45 and 55 plants per m^2). In addition, two sole cropping treatments of potato (4.7 and 5.3 plants per m^2) and two sole cropping treatments of pinto bean (with 45 and 55 plants per m^2) were planted.

Potatoes derived a benefit from intercropping: tuber yield per m^2 and per plant, number of leaves and branches and size of tuber per plant increased significantly as compared with plants raised under sole cropping. Pinto bean also derived a benefit from intercropping: grain yield per m^2 and per plant, number of pods per plant and number of leaves and branches per plant increased significantly as compared with plants produced under sole cropping.

An intercropping proportion of 2:1 (66% potato with density of 5.3 plants per m^2 + 34% pinto bean with the density of 55 plants per m^2) provided the highest amounts of LER in two years (1.25 and 1.27). This result suggests that these two crops have used more environmental resources in intercropping than sole cropping due to an increase in Resources Use Efficiency (RUE).

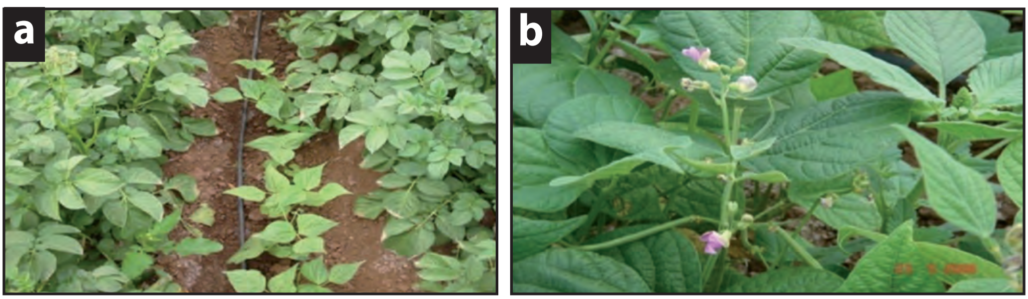

Figure 1. intercropping potato and bean, before (a) and after bean flowering (b) (Photo Ref. Rezig, et.al. 2013. With Permission)

Intercropping Potato with Bean – the Performance of Cultivars

This study, aimed to evaluate the varietal response of potato and bean as they are intercropped with corn and with each other. Three varieties of potato (Spunta, Agrico and Alaska), three varieties of bean (Bronco, Matadore and Lolita) and one variety of corn (Jubilee) were planted. Light interception and leaf area were measured in order to determine their effect on crops yield. The results revealed that only two potato varieties (Spunta and Agrico) produced significantly higher yields when they were intercropped with corn and with the three bean varieties as compared with growing as a sole crop. Yield of the potato variety 'Spunta" was improved when intercropped with beans, while yield of "Agrico" was enhanced in combination with corn.

Growing the potato cultivar "Alaska" with bean varieties produced an increase in yield of 17%- 32%, but when planted in combination with corn, yield was reduced by 61% as compared with its sole crop. This reduction was related to a significant decrease in light interception and leaf area values.

Intercropping Potato with Bean – Effects of Shading and Temperature

The success of intercropping relies on an improvement in the utilization of plant resources. But this depends on microclimate modification created by the two crops selected for intercropping, row arrangement, microclimate and soil type.

Despite the popularity of intercropping in some regions there is little available information in regard to the effect of plant resource utilization on intercropping yield production, especially for potato and bean grown in association under different row arrangements. However, certain reports indicated that lower light interception values, obtained when potato was grown with corn, produced a beneficial effect on potato yield. By contrast, the yield of potato per plant was reduced, as well as yields of faba bean under certain shaded treatments compared to that of un-shaded. Furthermore, different potato cultivars reacted differently to the effects of temperature in intercropping settings

The intercropping response is not totally negative since lower temperature associated with high irradiation under short photoperiod promotes tuber initiation and bulking at the expense of top growth. Intercropping faba bean with peas and lettuce increased both air and soil temperatures and thus increased faba bean yield as compared to its sole crop.

Furthermore it was found that higher yields of corn intercropped with potato were due to higher soil moisture available to the corn after the potato crop attained maturity. Moreover, it has been reported that water use efficiency was higher under intercropping system than sole cropping system. However, another study obtained opposite results, with reductions in land equivalent ratio, light interception and water use in annual intercrops in the presence or absence of in crop herbicides. These conflicting results imply that more research in this area is called for.

Intercropping Potato and Bean - Effects on Light Interception and Radiation Use Efficiency

An investigation was carried out during three crop-growing seasons to determine how potato and bean might grow and develop in an intercropping system compared with their performance under sole cropping. Total dry matter production was used to compare crop productivity of potato and bean intercropping systems. Percentage light interception and radiation use efficiency were calculated for plants under sole cropping and intercropping. Results showed that potatoes produced higher total dry matter production (TDM) in intercropping compared with sole cropping. This increase was recorded during the three experiments from, with values ranging 3.60 to 4.75% compared to the potato in sole cropping.

However, when beans were grown under intercropping the TDM was significantly lower than in sole cropping, with reductions varying from 48.9 to 63.1%. Radiation interception in both potato and beans was reduced when the two were intercropped, but radiation use efficiency for potato under intercropping was improved from 7.7 to 23.6%.

Intercropping Potato with Radish or Spinach

Intercropping potato might improve yield and profit for small-scale producers, if a suitable companion crop was available. In a study potato was intercropped with radish (*Raphanus sativus* L.) or spinach (*Spinacia oleracea* L.). The three crops were also grown in monocrop, in a field experiment under irrigation. Intercropping radish and spinach with potato increased potato equivalent yield over monocropped potato. Potato + spinach had a higher land equivalent ratio (1.78) and area time equivalent ratio (1.29) than the potato + radish intercrop, which had a higher relative net return (3.28) and benefit: cost ratio (6.38).

Intercropping potato with radish and spinach delivers efficient land use and higher economic return. Monocropping radish may be more profitable and energy efficient than sowing it under other crop combinations

Intercropping Potato with Brassica oleracea

Three experiments carried out to test the proposition that solar radiation falling on the soil is 'wasted' until the attainment of a complete crop canopy by potato crops and could be utilized by intercropping with cabbages without detriment to the potato yields. The cabbages were established by transplanting and harvested by the time the potato crop had achieved a ground cover between 40–80%. However, almost without exception, intercropping reduced the economic yields of both component crops. The land equivalent ratio (LER) varied between 1.01 and 1.78 and the partial LER of potatoes between 0.56 and 1.11, suggesting only in the latter case was there complete absence of competition between the component crops.

Intercropping Maize

Intercropping Maize and Cowpea - Effect on Water Status, Gas Exchange and Productivity

Cowpeas are one of the most important food legume crops. A drought-tolerant and warm-weather crop, it also has the useful ability to fix atmospheric nitrogen through its root nodules and it grows well in poor soils. The effect of intercropping on plant water status, gas exchange and productivity of maize (cv. Centralmex), and cowpea (*Vigna unguiculata* cv. 'Pitiuba') were evaluated.

The treatments were: maize and cowpea as sole crops, at a population of 40,000 plants ha^{-1}, and intercropped at a population of 20,000 plants ha^{-1}. The results obtained in this study may be explained by the degree of competition experienced by the components, mainly for water and light.

Intercropped maize had higher values of leaf water potential, stomatal conductance, transpiration and photosynthesis than when grown as a sole crop. Intercropped cowpea had higher values of leaf water potential but lower stomatal conductance, transpiration and photosynthesis than sole cowpea.

Maize productivity increased 18% in relation to sole crop whereas a 5% decrease was observed with cowpea. Despite these facts the Land Equivalent Ratio obtained was 1.13 indicating intercropping advantage over the sole system. The higher partial Land Equivalent Ratio observed for maize suggests that this species was the main component influencing the final productivity of the intercropping system studied.

Figure 2. Intercropping Maize and Beans
(Photo © Kevan Christensen /One Acre Fund, With permission)

Intercropping Maize and Bean – Effect of Plant Density

A field experiment was conducted to determine the optimum combination and efficiency of resource utilization in intercropping of maize (*Zea mays*) and faba bean (*Vicia faba*). Intercropped combinations of maize at densities (6, 7 and 8 plant/m^2) and faba bean densities (30, 40 and 50 plant/m^2) and 6 sole-cropped treatments were grown. Maize and faba bean densities significantly affected the biological and grain yields of maize and faba bean.

Maximum land equivalent ratio (1.97) was attained by 6 maize plants/m^2 with 40 and 50 plants/m^2 of faba bean intercropping combinations. This indicates that in order to achieve the same grain output under monoculture, an area of land double in size would have to be planted.

Intercropping 8 maize plants with 50 faba bean plants/m2 produced the highest standard land equivalent ratio. Maximum relative value total (1.31) was obtained in maize and faba bean intercropping with 8 maize and 50 faba bean plants/m^2. The monetary advantage of intercropping in comparison with mono cropping was 30%.

The authors propose that under their growing conditions, the combination of 8 maize and 50 faba bean plants/m^2 showed the highest profitability and could be introduced as best intercropping system.

Intercropping and weed control

When discussing weed control, intercropping can provide at least two advantages over monocropping. Firstly, crop yield is increased and weed growth is reduced if intercrops are more effective than sole crops in competing for resources with weeds or suppressing weed growth through allelopathy. Alternatively, the yield advantage accruing from intercropping can be achieved without suppressing weed growth below levels observed in component sole crops, if intercrops can exploit resources that are not accessible to weeds or convert resources to harvestable material more efficiently than sole crops.

Notwithstanding the visible effect of intercropping, it is extremely difficult to identify the specific mechanisms which produce the response of weed growth suppression and yield improvement. This should not be a barrier to the expansion of intercropping practice when it can be demonstrated to provide beneficial returns at farm level

A literature review sought to investigate the effect of crop rotation and intercropping on weed population density and weed biomass. It was noted that in intercropping systems where a main crop was intersown with a 'smother' crop species, weed biomass in the intercrop was lower in 47 cases and higher in 4 cases than in the main crop grown alone (as a sole crop); in 3 cases the response was inconclusive.

Furthermore, when intercrops were composed of two or more main crops, weed biomass in the intercrop was lower than in all of the component sole crops in 12 cases, intermediate between component sole crops in 10 cases, and higher than all sole crops in 2 cases.

It can be understood from the foregoing that weed competition represents a huge drain on agricultural output (**Section 7**). For this reason it is important that effort be expended to assemble information on factors such as weed seed longevity, weed seedling emergence, weed seed production and dormancy, agents of weed mortality, differential resource consumption by crops and weeds, and allelopathic interactions. Answers to these questions would assist in the planning and implementation of beneficial intercropping strategies

Intercropping and improving energy conversion efficiency

The maximum amount of energy that can be transformed into crop yield is defined by solar energy input. But two factors determine the actual yield of energy in food (Y): it depends on the product of the solar energy input (S) and the efficiency with which the solar energy is transformed into the harvested product. Since 100% of the solar energy will never be captured as harvested product, the efficiency is expressed as a number between 0 and 1. The size of the value shows what proportion of the

solar energy reaching the field is transformed into food.
The overall efficiency can be further subdivided as the product of:
- The efficiencies with which leaves intercept the sunlight energy (ε_i),
- The efficiency of conversion of intercepted energy to plant matter (ε_c) and
- The partitioning of this plant matter into structural and edible matter (ε_p)

$$\mathbf{Y=S + \varepsilon_i + \varepsilon_c + \varepsilon_p}$$

Whereas the last 50 years have witnessed large increases witnesses in crop yield largely due to improvements in ε_i and ε_p, whereas progress in improving (ε_c) have not kept pace. Conversion efficiency is dependent on the efficiency of the photosynthesis process, net of respiratory losses by the crop. Conversion efficiency remains at about 0.02, which is roughly one-fifth of the theoretical efficiency of 0.1 for C3 crops such as wheat and rice or 0.13 for C4 crops such as maize and sorghum. It is crucial that we achieve improvement in plant energy conversion efficiency (ε_c) if we are to meet the increasing demand for food and bioenergy crop production and yields.

Using a meta-analysis, the effects of factors such as greenhouse gases, weather-related stresses, management practices, including inputs, shading, and intercropping on ε_c were statistically quantified to identify where improvements could succeed in closing the current yield gaps. It is proposed that significant mean increases in ε_c might be induced by elevated [CO_2] (20%), shade (18%), and intercropping (15%). Nutrient fertiliser responses are interesting: ε_c increased curvilinearly up to 55% with nitrogen additions whereas phosphorus application was most beneficial at low levels.

The answer to improving ε_c may come from increasing tolerance to stress factors and taking greater advantage of elevated CO_2 levels as well as modified management practices to reap the benefits from intercropping, shade tolerance and pest control.

Glossary of Intercropping terms (Ref. Sustainable Agriculture, Research and Education)

Alley cropping: Growing annual crops in tilled strips between rows of a tree or shrub crop.

Biostrips: Permanent sod strips, usually of high botanical diversity, maintained to provide food and habitat for beneficial organisms and disrupt dispersal of pests.

Companion planting: A general term essentially synonymous with intercropping but often used to refer to the planting of non-crop or ornamental species with vegetables for attraction of beneficial insects.

Insectary planting: Planting strips or patches in a field with species that attract beneficial insects.

Interplanting: Intercropping.

Interseeding: Planting a direct-seeded crop into another crop, either at planting of the first crop or later, after it is established.

Living mulch: Permanent sod strips of perennial grasses or legumes between rows or beds.

Monoculture: A field with a single crop in it, or pertaining to such a field.

Nurse crop: A fast-growing crop that suppresses weeds while a slow-growing crop establishes.

Overseeding, oversowing: Planting a direct-seeded crop or cover crop into an already established crop, usually by surface sowing of the seeds.

Parasitoid: An insect that lays its eggs in or on another arthropod. The larvae develop inside the host, eventually killing it.

Polyculture: A field (or cropping system) with multiple, interacting crops, or pertaining to such a field or cropping system.

Relay (inter) cropping: Planting a second crop into an already established crop. Usually the first crop is harvested before the second matures.

Smother crop: An interseeded crop sown with the intent of smothering weeds; sometimes also applied to a weed-suppressive cover crop grown alone.

Underseeding, undersowing: Overseeding or oversowing.

Summary

- Intercropping, the practice of growing two or more crops in close proximity is a strategy for increasing agricultural productivity per unit land that is based on ecological mechanisms for improved resource capture.
- The main reason for the use of intercropping is to produce a higher yield than would be produced in a pure cropping of same amount of land.
- For an intercropping scheme to be useful, it should improve the overall economics of the farm. A new intercropping idea should be tested first on a relatively small area.
- Intercropping potatoes in the tropics show that the crop may tolerate reductions in the receipt of irradiance of up to 25% for extended periods without incurring a yield penalty.

References.

Rezig, M., Sahli, A., Hachicha, M., Ben Jeddi, F. and Harbaoui, Y. (2013). Potato (Solanum tuberosum L.) and Bean (Phaseolus vulgaris L.) in sole intercropping: Effects on light interception and radiation use efficiency. Can. Journal of Agric. Sci. 5: 65-77.

Sources accessed in the preparation of this section.

Bantie, Y.B., (2014). Determination of effective spatial arrangement for intercropping of maize and potato using competition indices at South Wollo, Ethiopia. *Intl. J. of Res. in Agric. and Food Sci.* **2:** 9-19.

Chimonyo, V.G. P., Modi, A.T. and Mabhaudi, T. (2014). Perspective on crop modelling in the management of intercropping systems. *Archives of Agronomy and Soil Science*. ***61:*** 1511-1529

Mohammed, S. A. A. (2012). Assessing the Land Equivalent Ratio (LER) of two leguminous pastures (Clitoria and Siratro) intercropping at various cultural practices and fencing at Zalengei –Western Darfur State – Sudan. *ARPN Journal of Science and Technology.* **2:** 10074-1080

Mousavi, S.R. and Eskandari, H. (2011). A general overview on intercropping and its advantages in sustainable agriculture. *J. Appl. Environ. Biol. Sci*., **1**:482-486.

Yu, Y.; Stomph, T.J.; Makowski, D.; Werf, W. van der. (2015). Temporal niche differentiation increases the land equivalent ratio of annual intercrops: A meta-analysis. *Field Crops Research* **184**:133 - 144

Section 18.

Crop Rotation

Comment

Topsoil describes the upper, outermost layer of soil, usually the top 25 cm. It is the storehouse for the greatest concentration of organic matter and microorganisms and it is also the site for most of the earth's biological activity. Plants concentrate the majority of their roots and acquire most of their nutrients from this layer.

The topsoil is the most valuable asset a farmer owns. It is a fragile entity, prone to contamination, erosion and degradation; it requires care. The topsoil feeds and sustains the family today and if it is preserved and protected from depletion, it will continue to sustain the generations yet unborn.

Introduction

Crop rotation is defined as the practice of growing different crops in succession on the same land, chiefly to save or increase the mineral and organic content of the soil. Crop rotation involves the implementation of a strategy to improve soil quality and preserve the productive capacity of the soil, rather than planting random crops to avail of market opportunities. Crop rotation is used as a system of growing successive crops that have different food requirements and which can exploit different rooting zones in the soil. It is a crop, soil management and conservation method, designed to prevent soil depletion and break up disease cycles. Different crops have different soil requirements and impart different benefits to the soil. This is why farmers change crops from year to year so as to minimise deficiencies and allows the soil to replenish; particularly where there is a regular occurrence of a pulse crop in the sequence, which returns nitrogen to the soil.

Crop rotation – the History

Throughout human history wherever people settled and established a civilisation, the farmers developed a crop rotation system appropriate to their cropping cycle, their agro ecological environment and their access to available land. When human populations were low and land was freely available, early farmers in South America and Africa followed a less orderly rotation system called 'slash and burn'. By cutting and burning the nutrient-rich tropical vegetation it enhanced a plot of nutrient-poor tropical soil; then after planting crops on the plot for several years they moved on. This has been described as a successful strategy provided the plots remain small in relation to the surrounding forest, and the plot has sufficient time to recover. Large-scale slash and burn agriculture destroys ecosystems, and leads to a complete loss of agricultural productivity on the deforested land.

Historic crop rotation methods such as that described by Cato the Elder are mentioned in Roman literature, and referred to by several civilizations in Asia and Africa. One system in central Africa employs a 36-year rotation; a single crop of finger millet is produced after a 35-year growth of woody shrubs and trees has been cut and burned. However, shorter rotations were more widely adopted.

A **Two-field rotation** was practiced by the ancient Greeks. This is the simplest form of crop rotation, where under a two-field rotation, half the land was planted in a year while the other half lay fallow. In the following year, the two fields were reversed. One of the few surviving examples of a two-field rotation still in use today is the corn (maize)-soybean practiced in the American mid-west. Here two high value crops are grown and still take advantage of rotation

A **Three-field rotation** was practiced by the Romans. For 2,000 years after the Romans spread their farming practices throughout the Roman Empire and European farmers adopted the Roman cropping system referred to as "food, feed, and fallow." Having divided their land into three sections, farmers each year planted a food grain such as wheat on one section, barley or oats as feed for livestock on another, and permitted the third section lie fallow. This rotation allowed each section to lay fallow, recover some of its nutrients and rebuild some organic matter every third year, before it was again sown with wheat and the cycle recommenced.

Figure 1. A diagrammatic representation of the 3-field crop rotation system (Image © Onions-potatoes.com. With Permission)

It was not a panacea, farmers following the "food, feed, fallow" system did not achieve bumper harvests, typically harvesting six to ten times the amount of seed as they had sown, plus, they had to save a sixth to a tenth of their harvest to plant as seed in the following year. Such low yields meant there was a small amount of grain for storage; crops failed and people often starved during years of flood, drought, or pest infestation. A graphical illustration of the food-feed-fallow system is presented in Fig. 1.

A **four-field rotation** was pioneered by the Dutch, in the late medieval ages. From the 15th century, the size of agricultural allotments began to increase, allowing farmers more space to experiment with different crop rotation schedules. By 1800, many European farmers had adopted the four-year rotation cycle developed in The Netherlands. This system rotated wheat, barley, a root crop such as turnips, and a nitrogen-fixing crop such as clover. Livestock grazed the clover and consumed the root crop in the plot.

Under the new system, plots were always planted with either food or feed, increasing yield and livestock productivity. Then by adding a nitrogen-fixing crop and allowing manure to accumulate directly on the surfaces improved soil fertility. Eliminating a fallow period protected the land from soil erosion by stabilising soil through maintaining vegetation cover throughout the cycle.

All of the crop rotations discussed above evolved in an empirical fashion, relying on experience or observation, but without any understanding of the chemistry or scientific principles underlying the concept. The underlying principles for planning effective cropping systems began to emerge in the middle years of the 19th century.

Early experiments, such as those at the Rothamsted Experimental Station in England in the 1850's, provided a scientific basis for crop selection in rotation cycles. They demonstrated the value of three classifications: cultivated row, close-growing grains, and sod-forming, or rest crops, which provided continuing soil protection and sustainable production.

Crop rotation use by farmers has gone through cycles of adoption and neglect throughout history. Crop rotation fell out of favour in developed nations in the 1950s. With the availability of chemical fertilisers, pesticides, and herbicides, farmers found they could maintain high-yield of monoculture crops by applying the new technology. Crop production was dominated by large-scale commercial agriculture requiring these chemical inputs. Now there is an increasing awareness that this approach is not sustainable. Crop rotation is again being considered as a route to allay concerns about the effect of agricultural chemicals on human health and damage to soil structure and fertility arising from continuing establishment of monoculture crops. Increasingly farmers realise the importance of using some modification of crop rotation to increase yields and reduce weed, disease and herbicide resistance.

A note of caution: *Some crops will only produce an economic yield when planted in a particular soil type.* ***Crop rotation seeks to promote the needs of the soil and not of the crop.*** *Planting a sensitive crop on an unsuitable soil will lead to a lower yield in a specific growing season.*

Crop rotation - the Rationale
Overall, three major advances in agriculture are recognised: domestication, irrigation and crop rotation.

Domestication involves the introduction of genetic change, through concious or unconcious human modification of a plant (animal), to such an extent that it now relies on human input to maintain a healthy, productive crop and for its continued survival. It describes the process whereby farmer ancestors took useful plants and by selection and crossing, developed the forerunners of todays' crops. One of the largest accomplishments in human history has been the domestication of plants. This process has ensured a continuous food supply, which has allowed the development of civilisations, population growth and promoted urban expansion. Examples of change induced by domestication include increased seed size and the elimination of undesirable traits such as bitterness in the edible plant portion. A variety of food crops, including wheat, rye, barley, lentils, chickpeas and peas were all domesticated in the Near East and South Asia about 11,000 to 9000 years before present. Domestication of plant species has substantially contributed to human wellbeing, but the tradeoff has been a strong decrease in the genetic diversity of modern crop cultivars. For example this may have affected the ability of domesticated plants to establish beneficial associations with rhizosphere microbes (Fig. 2).

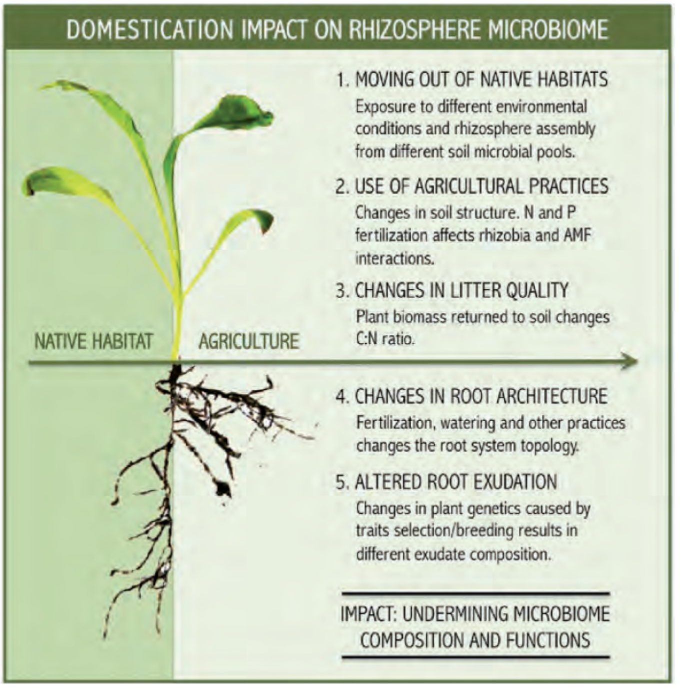

Figure 2. Changes associated to the domestication process affect plant traits and soil properties undermining rhizosphere microbiome composition and functions (Graphic © J.E.Pérez-Jaramillo, et.al. With Permission)

Irrigation is the process of watering crops by bringing in water using pipes, canals, sprinklers, or other man-made means, rather than relying on the unpredictable arrival of rainfall. Irrigation has been practiced by ancient civilisations in several regions throughout the world. Many historians hold the view that civilisation, as we understand it would probably not be possible without some form of irrigation. The success of early agriculture relied on the farmers of the area learning: how to concentrate desirable plants into a manageable area; how to prevent weeds from growing there; and how best to encourage the plants to flourish. Farmers learned to plant, weed, and water (or drain) their fields. The success of irrigation is illustrated by the fact that it is applied to 18% of cropland worldwide.

***Crop rotation**,* describes the practice where different crops are cultivated successively in a specified order on the same fields, compared with a one-crop system or to haphazardly planting crops in succession. The negative consequences of mono cropping have been widely documented. The associated buildup of soil borne pests and pathogens will result initially in yield reductions until eventually the crop will not produce an economic yield, unless there is significant input of fertilisers and pesticides. Crop rotation provides agronomic, economic and environmental benefits compared to monoculture cropping. A central tenet of crop rotation is the increase of organic matter in the soil. This has the effect of improving soil structure and protecting the soil from degradation, which will provide higher yields and greater long-term profitability. Building up the levels of soil organic matter improves water and nutrient retention, and reduces the reliance on synthetic fertiliser. By improving soil structure there is a marked improvement in drainage, coupled with reduced risks of waterlogging during floods, and a boost in the supply of soil water during droughts

Why use crop rotation?

At the **farm management** level, crop rotations are used to:

- Diversify income,
- Spread labor requirements throughout the year, and
- Spread the crop loss risk associated with weather and pests across two or more crops.

In terms of **soil management,** crop rotations are used to:

- Increase crop productivity by enhancing soil quality
- Manage weed growth and interrupt the life cycle of disease and insect pests
- Better control of adventive species
- Reduce soil erosion by wind and water
- Maintain or increase soil organic matter and improve soil structure
- Provide biologically fixed N when legumes are used in the rotation
- They help ensure that enough nutrients are available to different crops each year

Socio-economic advantages of crop rotation

A better breakdown of the workload, as crop rotation spreads out seeding and harvesting over the entire year, as well as better use of equipment and labour. Other benefits of rotation cropping systems include production costs advantages that result from increased margins, as crop rotation allows reduced use of inputs, which represent a significant expenditure item. Overall financial risks are more widely distributed over more diverse production of crops; this buffers the farmer against dramatic price fluctuations, which improves the economic security of farm.

With less reliance being placed on purchased inputs, over time, crops can maintain production goals with fewer inputs. When this is coupled with greater short and long term yields, it makes rotation a powerful tool for improving agricultural systems.

Agronomic advantages of crop rotation

Each plant has its specific characteristics and requirement in addition to its specific impact on the environment. Each crop gives rise to a specific ecosystem which could be more or less conducive to development of certain diseases, certain insect pests or certain weeds. By alternating crops, the farmer disrupts the conditions created by a given ecosystem thereby impeding the development of these diseases, weeds and pests. It is not enough to merely vary the crop succession; consideration must be given to the selection. For example, some related crops such as wheat and barley share the same enemies; it is therefore necessary to avoid having one right after the other in the rotation. Crop rotation offers better control of adventive species. Each crop family is targeted by specific diseases and adventive species; so alternating cultures makes it possible to alternate treatments and therefore to actively prevent the development of resistance.

Soil structure is improved by crop rotation because of different root profiles; the soil profile is better explored, which is reflected in improvement of the physical characteristics of the soil. This is readily understood by contemplating the differences in root architecture, where plants with fibrous roots exploit the upper layers, while plants with taproots can exploit the deeper layers.

Under crop rotation soil nutrient resources are allowed to accumulate and are better protected. Each type of plant preferentially accumulates specific nutrients and possibly returns nutrient elements for subsequent crops. Furthermore plants may leave more or less organic matter in the soil as shoot or root debris. When pulses are included in the rotation, the increase in residual nitrogen levels in the soil will benefit subsequent crops. Roots stabilise soil leading to reduced loss of soil due to runoff; this is best achieved by including permanent cover crops in the rotation to reduce erosion and runoff phenomena.

Environmental advantages of crop rotation

Crop rotation helps reduce the impact of agriculture on the quality of water and air, through a reduction in agrochemical inputs. This reduction derives from the reduced use of pesticides and reduced erosion of soil particles containing fertiliser and pesticide residues. Crop pest outbreaks require an increase in use of plant-health products, fungicides and insecticides and this is sometimes accompanied by the destruction of the natural predators of pests. A negative impact of single-crop farming therefore is a loss in terms of biodiversity and sustainability.

Crop rotation seeks the restoration of organic matter levels and biodiversity in soils and is closely related to adding plant cover to the rotation, thereby contributing organic matter. Organic matter helps bind the soil particles and minimise the risk of erosion due to water or wind.

Crop rotations therefore have many important functions:

Soil formation occurs over thousands of years as rock is broken down and colonized by plants and soil biota, leading to the formation of soil organic matter (SOM). While carbon is the primary constituent of SOM, it also contains several of the nutrients essential for plant growth such as nitrogen, phosphorus, sulphur and micronutrients. SOM is decomposed by organisms in the soil food web, which then make these nutrients available for plant root uptake. Several factors influence the rate of SOM decomposition and turnover such as the interplay between soil biota, temperature, moisture and a soil's chemical and physical composition.

This is the fraction in the soil that is most subject to human influence and is altered by having animals graze the field, by tilling the soil, by the choice of crops planted, by off-take at harvest and by the cropping rotation.

Changes due to crop rotation

- Microbial activity
- Organic matter
- Total organic carbon
- Labile carbon
- Soil inorganic carbon

Microbial activity**.** While the benefits of crop rotation have long been recognised, the basis of these benefit are poorly understood. Now, new research shows that crop rotations, irrespective of management factors, can increase the activity of soil microbes that benefit plant growth. This response is achieved through relationships between crop rotational diversity, soil structure, microbial community structure and activity, and soil organic matter chemistry. There is a considerable diversity of microbes associated with plant roots - in the order of tens of thousands of species. Microbial communities play a pivotal role in the functioning of plants by influencing their physiology and development and even to include influencing plant health. The role of this plant-associated microbial community is so crucial; it is sometimes referred to as the second genome of the plant. Different plant species, growing in the same soil can host their own unique microbial communities.

There is evidence that when pathogen or insects attack plants they can mobilise protective microorganisms to enhance microbial activity and suppress pathogens in the rhizosphere. The rhizosphere microbiome [a collection of organisms in one location] is not totally composed of species beneficial to plant growth. Plant pathogenic microorganisms also colonize the rhizosphere. They strive to break through the protective microbial shield and to overcome the plants innate defense mechanisms and introduce disease. Although the importance of the rhizosphere microbiome for plant growth has been widely recognized, we know very little about the vast majority of rhizosphere microorganisms. Crop rotation is recognised as a strategy to redirect or reshape the rhizosphere microbiome to confer advantage on microorganisms that are beneficial to plant growth and health. The objective is to promote the growth of rhizosphere antagonists to compete with pathogens and render the rhizosphere non - supportive to the pathogen

A downside of the effects of agricultural intensification is a negative impact on soil microbial diversity and function. This threat to the soil's ability to perform important ecosystem functions has implications for long-term food security, for increased greenhouse gas emission, and for a reduction in water quality. Crop rotational diversity enhances belowground communities and functions in an agro ecosystem. Soil quality is enhanced by crop rotation and even increasing rotation by one or two crops, especially if cover crops are used, will improve soil physical, chemical, and biological processes that help regulate yields and environmental quality.

***Organic matter*.** Organic matter is probably the most important component in the soil and despite that, it is also the most misunderstood. It is a reservoir of nutrients and water in the soil, where it aids in reducing compaction and surface crusting, and facilitates the increase in water infiltration into the soil. It is often both ignored and neglected, since it is assumed that organic matter is merely the plant and animal residues we incorporate into the soil e.g. leaves, manure, or plant parts. This waste product is actually organic material, not organic matter.

So what is the difference between organic material and organic matter? Organic material is anything that hitherto was alive and is now in or on the soil. Before it becomes organic matter, it must be decomposed into humus. Humus is organic material that has been converted by microorganisms to a state where is resists further decomposition. Organic material is unstable in the soil, readily undergoing changes in form and mass as it decomposes. Up to 90 percent of it disappears quickly through decomposition.

Whereas organic material is unstable organic matter is stable in the soil, because it has been decomposed to a state where it is resistant to further decomposition. It is the stable organic matter that is analyzed in a soil test. Usually, only about 5 percent of it mineralizes yearly and it takes at least 10 kg of organic material to decompose to 1 kg of organic matter. The rate of decomposition increases if temperature, oxygen, and moisture conditions become favorable for decomposition. One of the negative effects of excessive tillage is the breakdown of organic matter.

In soils that formed under grass type vegetation, organic-matter levels are generally comparatively high because organic material was supplied from both the top growth and the roots. We sometimes fail to recognise roots as a source of organic material, but a study showed that a mixed grassland vegetation had an above-ground (shoot) yield of 3.4 tonne of organic material per ha. while the root yield was about 9.6 tonne per ha. The plants were producing roots that were more than twice the weight of the shoots.

The Benefits of Organic Matter

- Nutrient Supply
  Organic matter constitutes a reservoir of nutrients that can be released to the soil. Each percent of organic matter in the soil releases 8 to 12 kg of nitrogen, 2 to 3 kg of P_2O_5, and 1 to 2 kg of sulfur per year.
- Water-Holding Capacity
  Organic matter mimics the qualities of a sponge, with the ability to absorb and hold up to 90 percent of its weight in water. Plants benefit greatly from the water-holding capacity of organic matter because it will release most of the water that it absorbs to plants. In contrast, clay holds great quantities of water, but much of it is unavailable to plants. (**Section 16**).
- Soil Structure Aggregation
  Organic matter induces soil to clump and form soil aggregates, which improves soil structure. With better soil structure, permeability (infiltration of water through the soil) improves, in turn improving the soil's ability to take up and hold water.
- Erosion Prevention
  This property of organic matter is less well understood. Data used in the universal soil loss equation indicate that increasing soil organic matter from 1 to 3 percent can reduce erosion 20 to 33 percent because of increased water infiltration and stable soil aggregate formation caused by organic matter.
  A good supply of soil organic matter is beneficial in crop or forage production.

The Soil's carbon components

Carbon is the natural building block of all living organisms and all the organic matter found in soils contains carbon. There is more living material in the soil than in living organisms above the soil surface. Soils can store, cycle and emit as gases different forms of carbon as part of the carbon cycle process. These forms may be very stable and stay in the soil for thousands of years or may be broken down in just a few hours. Soil stores more carbon than the atmosphere and plants combined. Soil carbon is the largest carbon pool in the terrestrial biosphere and includes both inorganic and organic components. Soil carbon occurs as three forms: organic, labile and inorganic carbon.

Organic carbon. Total organic carbon influences many soil characteristics including colour, nutrient holding capacity (cation and anion exchange capacity), nutrient turnover and stability, which in turn influence water relations, aeration and workability. In soils with high clay content the contribution to cation exchange from the organic fraction is generally small compared to that from clay. In sandier soils the relative contribution of the organic fraction is higher because there is less clay, even though the amount of total organic carbon present may be similar or less to that in clays.
By providing a food source for microorganisms, organic carbon can help improve soil

stability by microorganisms binding soil particles together into aggregates or 'peds'. Bacteria excretions, root exudates, fungal hyphae and plant roots can all contribute to better soil structure.

Active soil organic matter refers to a diverse mix of living and dead organic materials near the soil surface that turn over or recycle every one to two years. Active organic matter serves as a biological pool of the major plant nutrients. The balance between the decay and renewal processes in this biological pool is very complex and sensitive. The populations of microorganisms that make up the biological pool are the driving forces in soil nutrient dynamics. Together they also play a key role in building a soil structure that both retains and freely exchanges nutrients and water—a soil where plant roots thrive.

Researchers investigated the relationships among crop rotational diversity, soil structure, microbial community structure and activity, and soil organic matter chemistry. They tested five combinations of three crops -- soy, wheat, and maize -- and two cover crops -- red clover and rye. They also planted a crop of only maize, while minimizing the effects of other management practices such as variable fertilizer and pesticide inputs that interfere with the crop rotation effect. Researchers observed a 33 percent increase in soil carbon by increasing rotational diversity. As an indication of soil organic matter, the carbon content of soil is a major factor in its overall health and improves the physical properties of soil. Researchers also found that as crop diversity increased, so did total nitrogen concentrations, a sign of soil fertility.

This data is the first to support the hypothesis that increasing rotational diversity fundamentally changes microbial community structure and activity, which then has positive effects on aggregate formation and soil organic matter accrual. These findings provide further support for the use of rotational diversity as a viable management practice for promoting agro ecosystem sustainability

While it has long been recognised that legumes, like peas, provide benefits for the soil, we did not know why. Whereas agronomic studies where different crops were rotated and yields compared over the years, that type of research gave no indication as to what was happening to the soil microbes. It is known that there are up to 50,000 different species of microbes in the soil. Because they are microscopic, the only way they can be analysed is to sequence their DNA. It has only been with the advent of advanced sequencing methods in the last few years that it is now possible to actually go in and analyze the microbiome of soil.

An experiment was conducted by planting wheat in small pots in a controlled greenhouse. Before and after growing the wheat, the soil was analyzed but remained largely unchanged. But after oats and peas were planted in those pots, a new microbiome was detected. There was a five-fold increase in microbes, including fungi, nematodes, and single-celled organisms— all of which add to the health of the soil. This indicates that the microbiome of the soil immediately surrounding the roots, the so-called rhizosphere, which is absolutely critical to crop productivity and crop health, is enhanced by crop rotation.

The impact of organic matter on soil quality and functions can be summarised as follows:

Physical effects: soil aggregation, erosion, drainage, aeration, water-holding capacity, bulk density, evaporation, and permeability.

Chemical effects: cation exchange capacity; metal complexing; buffering capacity; supply and availability of N, P, S, and micronutrients; and adsorption of pesticides and other added chemicals.

Biological effects: activities of bacteria, fungi, actinomycetes, earthworms, roots, and other microorganisms.

Biological effects resulting from the activities of bacteria, fungi, actinomycetes, earthworms, roots, and other microorganisms, vary widely. Different sources of organic matter supply soils with carbon to replenish their C and nutrient pools. However, organic materials added to soils contain a wide range of C compounds that vary in their rate of decomposition. The biological breakdown of the added organic material depends on the rate of degradation of each of the carbon-containing materials. Changes in environmental factors can cause changes in the rate of decomposition of organic materials in soils, such as soil moisture status, soil aeration, soil temperature, pH, and availability of minerals.

Many different measures are used to determine the health or structure of soil:

Soil porosity is the volume of air in soil (or number of pores) and high porosity indicates good soil structure, as does high microbial biomass, and low penetration resistance.

Soil microbial biomass is the amount of tiny living organisms within a given area or amount of soil.

Soil penetration resistance is the soil's ability to withstand penetration by water or roots.

Soil aggregates are groups of soil particles held together by moist clay, organic matter (such as roots), organic compounds (from bacteria and fungi) or fungal hyphae (long, branching structure of a fungus). Some soil particles fit closely together some do not, creating different-sized spaces. These spaces, or pores, within and between soil aggregates can store air and water, microbes, nutrients and organic matter. Large aggregations of particles retain the most nutrients.

Labile carbon. Soil organic matter is composed of different pools, which vary in their turnover time or decomposition rate. The labile pool, which turns over relatively rapidly (< 5 years), results from the addition of fresh residues such as plant roots and living organisms, while resistant residues which are physically or chemically protected are slower to turn over (20-40 years). The protected humus and charcoal components make up the stable soil organic matter pool, which can take hundreds, even thousands of years to turnover.

Inert carbon is largely unavailable to microorganisms and is associated with highly weathered soils and historical burning. Although this carbon has an important role in the exchange of cations and water holding capacity, it is generally not associated with rapid microbial turnover of nutrients in agricultural soils. By contrast, the labile (bio-available) pool of carbon is primarily influenced by 'new' organic matter (originating from plants and/or animals) contributed annually and has a significant role in microbial nitrogen turnover and supply. Since labile carbon turns over relatively rapidly, it is considered a more sensitive indicator of changes in soil quality and function than the percentage of total carbon, which includes the more inert fractions.

The contribution of these labile components to the total soil organic matter pool influences the biological fertility status of the soil. A soil with 50 % of its total soil organic matter present as a labile pool, suggests a more biologically active soil with greater potential for nutrient turnover than the soil with just 5 % of its total organic matter pool 'bio-available'.

The amount of labile carbon influences both the activity and mass of microorganisms (microbial biomass) in soil. The microorganisms' capacity to release plant-available N is influenced by the quality of organic matter inputs, with net release of nitrogen from the labile soil organic matter occurring at a C: N ratio below about 22:1. High inputs of more recalcitrant residues can increase the ration of carbon to nitrogen in this labile fraction and can result in net immobilisation of nitrogen, making it unavailable for plant uptake. The C: N ratio of a residue decreases as the extent of decomposition increases and becomes more nutrient rich over time.

Inorganic carbon. This carbon fraction includes lithogenic inorganic carbon, which comes from parent material, and pedogenic inorganic carbon, which is formed through the dissolution and precipitation of carbonate parent material. Soil inorganic carbon is derived from bedrock or formed when CO_2 is trapped in mineral form (e.g. as calcium carbonate). Soil inorganic carbon is far less prone to loss than soil organic carbon. Inorganic carbon is mineral-based with the most common form being calcium carbonate. Although it can dissolve, particularly under acidic conditions, soil inorganic carbon is not susceptible to biodegradation.

Crop rotation – the Protocol

Crop rotation permits farmers to maintain their fields under continuous production and assist the soil to regenerate, without the requirement for it to lie fallow. In addition crop rotation helps reduce the need for artificial fertilisers, which add to the farmers crop production costs.

At a regional level, crop rotation ensures that there is a geographic mixing of crops, which can slow the spread of pests and diseases during the growing season. Since different crops are planted and harvested at different times, this allows more land to be farmed with the same amount of machinery and labor. Planting different crops can also reduce the effects of adverse weather for the individual farmer, since adverse weather will impact differently on different crops.

Many studies have shown an increase in yield of 10-25% when crops are grown in rotation compared with monocropping; this is known as "The rotation effect". While it has been observed for several crop combinations in many regions, the basis of the effect remains elusive. Various proposals have been advanced - improved nutrition; pest, pathogen, and weed stress reduction; and improved soil structure have been found in some cases to be correlated. The effect is sometimes described as alleviating the negative effects of monocropping. Two examples to illustrate the effect: maize grain yield is about 10-15% higher in maize crops grown following soybean than in maize grown following corn. Similarly, soybean yields following maize are typically 10-15% higher than when soybean follows soybean

> ***A note of caution:*** *Crop rotation is more successful in limiting the impact of biotrophic pathogens that require living host tissue, or those pathogens with low saprophytic survival capability.*
> *However it is less successful in reducing disease caused by pathogens with a wide host range or that produce long-lived survival structures such as sclerotia or oospores.*

Crop rotation and potato soil borne pathogens

The primary objective driving crop rotation is the goal of reducing the amount of the pest population present in the soil. Some pathogens that cause diseases survive in the soil from year to year in one form or the other, usually as sclerotia, spores, or hyphae. Continuously planting the potato crop encourages a build up in the population levels of any soil borne pathogen of the crop that may be present. The populations can potentially build up so large that it becomes difficult to grow potatoes without yield losses. Changing crops in a sequence tends to decrease the population level of pests. Plants within the same taxonomic family tend to have similar pests and pathogens. By regularly changing the planting location, the pest cycles can be broken or limited. Growing a crop, that is not a host plant for that pathogen, will lead to the pathogen dying and its soil population levels lowering. Many pest populations will decline in two to three years without a suitable host. Rotating to non-host crops prevents the buildup of large populations of pathogens.
How does crop rotation influence soil borne pathogens?

- Increase the biological buffering of the soil
- Affects pathogen distribution –Vertical – Horizontal
- Affect nitrification which influences the form of nitrogen in the soil
- Breaks the host–pathogen cycle
- Reduces pathogen numbers during anaerobic decomposition of organic matter
- Stimulates microbial antagonists which directly suppress pathogen inoculum.

Soil borne disease are defined as those caused by pathogens, which persist in the soil matrix and in residues on the soil surface. Soil borne pathogens survive as:

- Soil inhabitants, organisms that able to survive in soil for a relatively long time
- Soil invaders or soil transients, those are only able to survive in soil for a relatively short time

Organisms can also survive as non-pathogenic and generally in the form of saprobes. Under certain congenial conditions these saprobes can assume a pathogenic form.
The horizontal and vertical distribution of soilborne pathogens depends on production practices, cropping history, and a variety of other factors. Along a vertical axis, the inoculum of most root pathogens lies within the top 25cm of the soil profile, the layers where host roots and tissues and other organic substrates are found. On

the horizontal plane, distribution of inoculum in a field is usually aggregated in areas where a susceptible crop has been grown.

The most familiar diseases caused by soil-borne pathogens are probably rots that affect below ground tissues (including seed tuber decay and root rots) and vascular wilts initiated through root infections. A few soilborne pathogens, however, cause foliar diseases with symptoms and damage appearing on aboveground parts of plants.

Soil-borne fungal pathogens of potatoes

The agents that cause soil-borne diseases make up a diverse group. Fungi, which are multicellular microorganisms, cause most soil-borne vegetable diseases and so are considered the most important pathogen group. Plant-pathogenic fungi fall into five main taxonomic classes based on morphological and biological characteristics:

- Plasmodiophoromycetes (*Spongospora subterranea*),
- Zygomycetes *(Synchytrium endobioticum),*
- Oomycetes *(Phytophthora, and Pythium),*
- Ascomycetes *(Alternaria),* and
- Basidiomycetes *(Rhizoctonia)*.

Many soil-borne fungi produce resistant survival structures such as melanized hyphae, chlamydospores, oospores, and sclerotia and these structures allow them to persist in soil for long periods. Due to these resting structures, rotations of three to five years may have very little effect on the population levels of certain pests in the soil. Clubroot of Crucifers (caused by *Plasmodiophora brassicae*) can persist in the soil for seven years while white rot of Alliums (caused by *Sclerotium cepivorum*) can easily survive as sclerotia in the soil for over 50 years and still infect onions and garlic
Effects of crop rotation on the incidence of soil-borne fungal pathogens and on the performance of potato have been investigated. The cropping frequency of potato influenced the incidence of stem canker caused by *Rhizoctonia solani*. The effect was confined to the potato cropping frequency, as there was no effect from the crops with which the potato was alternated in the rotation. The occurrence of black scurf was also affected by the cropping frequency of potato but less pronounced than for stem canker.

Another factor that needs to be considered is that crop rotation is not a very effective practice on pathogens that have a wide host range. Examples of these would be *Rhizoctoinia solani*, *Sclerotium rolfsii*, and *Pythium* species. These pathogens, which infect potato, have such a wide host range that it is difficult to find a suitable crop to rotate with. Crop rotations need to be selected with special care to reduce pathogens such as these.

Crop rotations had a marked effect on the incidence and severity of fungal pathogens causing wilt disease on potato crops, and consequently on crop yields. The primary cause of the disease appeared to be the “dauermycelium” form of *Verticillium albo-atrum*. The highest level of wilt occurred in continuous potatoes and in the second potato crop of a 6-year rotation, and the lowest level occurred in a 3-

year rotation. The first potato crop of a 6-year rotation had an intermediate degree of wilt.

Black dot (*C. coccodes*) occurred at a higher level than expected and at much the same level in all rotations. Stem infections by *Verticillium dahliae* depended on the cropping frequency of potato, by the crop with which the potato was alternated in the rotation and by the density and virulence of endoparasitic nematodes, especially *Meloidogyne* spp.

Root endophytic fungal communities showed a greater ability to colonise potato roots in soil samples from continuous potato sites than those from rotation sites. Moreover, the majority of endophytic root fungal community species in potato sites belonged to the potato root rot complex and storage disease (*Colletotrichum coccodes*, *Fusarium solani* and *Fusarium oxysporum*), while those in rotation sites were mainly ubiquitous or saprobic fungi.

Soil-borne bacterial pathogens of potatoes

Bacteria are single-celled organisms that have rigid cell walls but lack a membrane-bound nucleus. Soil borne bacterial pathogens cause fewer diseases than those caused by fungal pathogens. Examples of such bacteria are *Ralstonia, Erwinia, Rhizomonas*, and *Streptomyces*. Pathogens in the *Pseudomonas* and *Xanthomonas* groups usually persist in the soil for only a short time. A soil borne pathogen's ability to survive in soil depends in part on the biological group to which it belongs. Few bacterial pathogens are true, long-term soil inhabitants; most survive for limited periods as saprobes on plant debris or roots, or directly in the soil. These species' bacterial cells do not produce resilient endospores and the vegetative cells are not particularly resilient in adverse environments. Some species survive by secreting slimy material that dries to form protective layers around the cells, enabling them to withstand unfavorable conditions.

Effect of crop rotation on blemish-inducing bacteria

Infection by *Streptomyces* species induces scab-like defects on potato tubers. This adversely affects not only the marketable yield, but more importantly alters tuber skin aspect, which is increasingly important with regard to the marketing of washed tubers.

Crop rotation had no effect at all on incidence of common scab (*Streptomyces scabies*) on tubers, whereas the effect of cropping frequency of potato on netted scab was highly significant. When cultivars were grown susceptible to both scab types, netted scab suppressed common scab.

Effect of crop rotation on wilt-inducing bacteria

Erwinia carotovora. Potato plants infected with *Erwinia* display wilting symptoms. The bacterium that causes the blackleg disease of potato is one of the pathogens that are seed tuber-borne. The typical blackening and decay of the lower stem portion is the origin of the "blackleg" designation for this disease. This aerial stem rot is usually caused by *Erwinia carotovora* subsp. *Carotovora*.

The progeny tubers are also vulnerable to infection by Erwinia. There are two ways by which the blackleg bacterium may reach the progeny tubers produced on the potato plant. One important route of tuber infection is via the stolon by which the tuber is attached to the plant. An alternate route for the pathogen to attack progeny tubers is via the soil; it can survive in the soil for moderate periods and particularly following the potato crop.

The blackleg disease can cause severe economic losses to the potato crop. However, the occurrence of blackleg depends very much on the growing conditions, particularly temperature and rainfall after planting. The blackleg bacterium survives poorly in soil. Although other members of the pectolyic Erwinia survive in surface water and in the soil environment, all evidence suggests that the blackleg bacterium does not survive very well outside of association with host plant tissue. Hence, the seed tuber is the most important source of inoculum in the blackleg disease cycle. Crop rotation is not likely to play a major role in combatting infestation by *Erwinia* spp.

Ralstonia solanacearum. Another serious wilt inducing pathogen is *R. solanacearum.* But unlike Erwinia above, *R. solanacearum* can persist for an extended period in the soil – with estimates ranging from 3 to 5 to even 10 years. The bacterium can enter potato plants by way of stem injuries from insects, handling, or tools. It can also enter the plant through wounds in the roots caused by cultivating equipment, nematodes, insects, and through cracks where secondary roots emerge.

In areas where the bacterium is not yet established, the first defense strategy is to prevent its introduction and, if inadvertently introduced, then it is necessary to prevent or control subsequent movement of the pathogen in the environment. This pathogen may stay latent without showing any symptoms in the field with the consequence of high impact on tuber yield in an up-coming season. Yield losses can be high, in some instances between 50 to 100%. When fields are heavily contaminated potatoes can no longer be grown there.

Once introduced, the pathogen survives at soil depths of 1m or more, where microbial competition is low, or as slimy masses in the upper soil layers. The pathogen can survive in soil (mostly on plant debris) and in the rooting system and rhizosphere of many hosts (weeds, other host crops, potato volunteers). Survival of the pathogen in the soil is reduced by extreme cold, and the presence of antagonistic microorganisms, while volunteer host plants enable bacterial survival across seasons.

There is no agrochemical available to combat *R. solanacearum*, so phytosanitation and cultural practices are the most widely used strategies for controlling bacterial wilt in the field. Cultural methods that reduce inoculum levels in the environment include crop rotation, proper irrigation, good sanitation, soil solarisation, intercropping, delayed planting, soil amendments, positive selection, and negative selection. Phytosanitation practices include planting disease-free tuber seeds, and quarantine measures. The absolute scarcity of certified disease free tubers limits the potential use of this strategy to contain the spread of bacterial wilt.

Crop rotation to control bacterial wilt.

Crop rotation with non-host plants could be expected to reduce the *Ralstonia solanacearum* concentration in the soil. Crop rotation of 5-7 years excluding host plants – potatoes - has been recommended to control the bacteria in the soil. The biggest problems facing the control of many diseases, including bacterial wilt, is that many farmers are unable to practise crop rotation mainly due to lack of knowledge on its benefits and/or because of small farm sizes, they are forced to constantly produce potatoes on the same pieces of land or using very short rotations that are inadequate to reduce the disease. In addition, the small scale farmers have insufficient land to plant anything other than essential food crops. The quest for a successful crop rotation sycle has been researched extensively. Two approaches were investigated – firstly, planting non-solanaceous crops, or planting crops which produce root exudate which is toxic to the bacterium.

Farmers should never rotate potatoes with any other plants in the Solanaceae family such as tomatoes, bananas, egg-plants, capsicums, chillies or ground- nuts. Crop rotation of potatoes with maize led to higher potato yields than monocropping potatoes in the presence of bacterial wilt. However, it was reported that rotations of maize, cowpeas, and sweetpotatoes did not reduce the soil inoculum concentration of the bacterial wilt 'race' (R3bv2A) that colonises potato. In addition, R3bv2A may also survive by infecting plant roots of non-host crops grown in rotation. It was reported that R3bv2A could survive on sugar cane roots during rotation even though sugar cane is not a host plant.

The second approach to crop rotation, where the rotation crop produces toxic root exudate apears to offer more likelihood for success. The root exudate of Brassica crops has the potential to combat *R. solanacearum*. One hypothesis regarding the beneficial effects of brassicas is that the Brassica crops release biocidal compounds, principally isothiocyanates during the breakdown of glucosinolates in their residues, which reduce disease infection in following crops. Glucosinolates are sulfur-containing compounds present in tissues of most brassica plants. The term "biofumigation" is used to describe the allelophatic effect of soil pathogens by compounds released from Brassica tissues, and implies a greater reduction in disease inoculum than that resulting from the simple absence of a host. Thus the decaying root system is regarded as the source of the biocidal compounds. Field studies identified 2-phenylethyl-glucosinulate as the major glucosinulate present in the roots of brassica, comprising around 80% of the total glucosinolate profile.

Macerating plant tissue releases the enzyme myrosinase from the cell vacuole and it hydrolyzes the glucosinolate to release isothiocyanates. With further breakdown, a range of hydrolysis products including nitriles, sulfur, oxazolidinethione, epithionitriles, thiocyanates, thiones and various forms of isothiocyanates, which may be formed under specific conditions. The mode of action of isothiocyanates is not fully elucidated, while it may be a direct cytotoxic effect, it is thought that they may accumulate in bacteria and attack the active centre of enzymes.

Field trials investigating the effectiveness of crop rotation on bacterial wilt amelioration have produced positive responses. When a potato crop was rotated with wheat, sweet potato, maize, millet, carrots, sorghum, or Phaseolus beans the incidence of wilt was reduced by 64 to 94% while the yield of potatoes was 1- to 3-fold higher than when potatoes were grown in mono-culture.

Field trials to test the efficacy of glucosinolate hydrolysis products has demonstrated some success. A commercially available Indian mustard (*Brassica juncea*) biofumigant green manure was shown to significantly reduce bacterial wilt in a following potato crop, resulting in spectacular yield increases (from 0.3 to 22 t/ha).

Extensive studies have described the development of control methods against bacterial wilt diseases caused by *Ralstonia solanacearum*. The research has focused on control measures, such as biological, physical, chemical, cultural, and integral measures, as well as biocontrol efficacy and suppression mechanisms. The largest group of biological control agents (BCAs) have been bacteria (90%) while fungi contributed (10%). Inoculation methods for BCAs affect biocontrol efficacy, such as pouring or drenching soil, dipping of roots, and seed coatings. A number of soil bacteria and plant growth promoting rhizobacteria (PGPR) are currently being investigated for their role in the control of *R. solanacearum* in small scale experiments; however, none are currently available commercially and efficacy of the biological controls has yet to be determined on a commercial scale.

General crop rotation strategies

Rotations depending wholly on green manure legumes should be confined to the more level and fertile lands. It is desirable to include legumes (particularly deep-rooting legumes) alone or in mixtures with nonlegume sod-forming crops as a regular crop in many field rotations. In general, this should occur about once in each four-year period. Short rotations are not likely to provide the best crop balances, and long rotations on a larger number of fields may introduce complications. With a moderate number of fields, additional flexibility can be provided by split cropping on some fields. The area devoted to sod-forming, or rest, crops should be expanded at the expense of row crops on soils of increasing slopes and declining fertility. This will provide better vegetative covering to protect sloping land from excessive erosion and supply organic matter for improving soil productivity on both sloping and level lands. With lessening slope and increasing fertility, the row crops may be expanded, but this should not be done at the expense of reduction in the sod-forming crops. The differing effects of crops on soils and on each other and in reactions to insect pests, diseases, and weeds require carefully planned sequences.

The usefulness of individual field crops is affected by regional differences in climate and soil. A major crop in one region may have little or no value in another. In each region, however, there are usually row, grain, and sod, or rest, crops that can be brought together into effective cropping systems.

The 6 rotation plant families

Here below the 6 plant families through which a farmer should rotate his crop not only to improve his yield but also, probably far more important on the long run, to maintain his soil in optimal conditions.

(**The information in this section was kindly provided by Mr. Alexander Halkema, http://www.onions-potatoes.com**)

Cruciferae Formerly known as cruciferae, brassicaceae is a family of plants most commonly referred to as the mustard or the cabbage family. A large and important family, brassicaceae contains many common vegetables, such as cabbage and broccoli, as well as weeds, such as bitter cress. The mustard family consists of approximately 330 genera and 3,700 species. Brassicaceae plants can usually be easily identified by their flowers. Species generally have clusters of flowers with four petals forming a cross shape. Many species also possess glucosinolate, which gives them the odor distinctive to broccoli or cabbage

***Crops of the Cruciferae family*:**

Cabbages, Cauliflowers, Kale, Broccolis, Calabrese, Swedes, Turnips, Radishes, Land cress, Mustard.

Umbelliferae The Carrot or Parsnip Family, a distinctive group of hollow-stemmed herbaceous plants sometimes reaching great size, widely distributed throughout temperate and subtropical regions. The family takes its name from its typical inflorescence, an umbel, or flattened cluster in which the several flower stalks spring like rays from one point; many forms have "compound umbels" in which this arrangement is repeated in the branches of the clusters. Many species are ornamental; others are grown for food and medicine.

***Crops of the Umbelliferae family*:**

Carrots, Hamburg Parsley, Ordinary Parsley, Celery, Celeriac.

Solanaceae the potato family. The potatoes form the anchor at the other end of a rotation, as they need a fairly high level of nitrogen and prefer a slightly acid soil with a pH around 5.5. Usually manure is added to the plot the autumn before planting the potatoes. Potatoes, tomatoes and a host of other important fruit crops all belong to the Solanaceae plant family. But so do mandrakes, Datura and other poisonous and important medicinal plants

***Crops of the Solanaceae family*:**

Potatoes, Tomatoes, Aubergines

Alliums With over 1250 species, allium, the onion plant, is best known as one of the largest plant families in the world. Allium has recently been reclassified into its own family, Alliaceae, although it used to be in the lily family, Liliaceae. Allium is native to most countries in the northern hemisphere as well as in Africa and Brazil. The many varieties of bulbs are best known as the vegetables onions, leeks, etc. The allium bulb used most has been garlic, which is especially beneficial to heart health.

***Crops of the Alliums family*:**

Onions, Garlic, Shallots, Leeks

Cucurbitaceae or cucurbit family (also commonly referred to as the cucumber, gourd, melon, or pumpkin family) is a medium-sized plant family, primarily found in the warmer regions of the world. It is a major family for economically important species, particularly those with edible fruits. Some of these represent some of the earliest cultivated plants in both the Old and New Worlds. Some have medicinal and other uses.

***Crops of the Cucurbitaceae family*:**

Cucumbers, Marrows, Courgettes, Pumpkins.

Leguminosae, the bean family of legumes. Beans and Peas are legumes, that is, they are members of the Leguminosae plant family. These plants are able to make use of atmospheric nitrogen as a food. They can therefore grow in soils that lack the nitrogenous salts, which most plants need. Anything with ***bean*** in the name, runner, French, broad, field and peas which are one of the oldest food crops grown by man. These share a wonderful ability to **fix nitrogen** from the air and so provide at least a good proportion of their fertiliser requirements.

***Crops of the Leguminosae family*:**

Black Beans, Black-eyed peas, Broad Beans, Butter Beans, Calico Beans, Cannellini Beans, String Beans, Haricot, Italian Beans,

Kidney Beans, Lentils, Lima Beans, Mung Beans, Navy Beans, Pinto Beans, Soy Beans, including black soy-beans, Split Peas, White Beans.

Planning a crop rotation

A successful crop rotation must fulfill several criteria: it must provide food for the family or provide a financial reward, sufficient to purchase the required amount of food. It must appeal to the farmer and be compatible with their agronomic and economic expectations. The chosen crops must be compatible with the location and with the farmers cropping expertise.

The following should be kept in mind when planning such a cycle:

Environment

It is essential that the soil is suitable for the planned crop. Take into account soil depth, texture and salinity. Study the climate over the various seasons when deciding which crop can be grown successfully at different times of the year.

Economy

Investigate the costs of producing various vegetable crops, as well as the income expected at various planting and harvesting times. Remember that prices are higher than normal at certain times of the year.

Diseases and pests

The same group of pests and diseases often attacks crops belonging to the same family, such as cabbage, cauliflower and broccoli, or tomato, potato and eggplant. For this reason, don't include related crops in successive plantings or even in the same three-year rotation programme.

Weeds

Choice of canopy height is an important factor to ensure success. For example a low-growing crop, such as carrots, lettuce or onions, will easily be overgrown by weed, so these should follow crops in which weeds were well controlled.

Root depth

As a general concept, crop rotation systems should be planned around the use of deep-rooting legumes. If too little use is made of them, productivity will decline; if too much land is devoted to them, wastes may occur and other useful crops will be displaced.

Rotating deep- and shallow-rooted crops constitutes an efficient use of soil water. Crops with shallow roots seem best adapted to follow a deep-rooted crop because water recharge is likely to occur only near the surface, and a shallow-rooted crop will not expend energy in search of moisture that is not there. Medium- or deep-rooted crops appear better adapted to follow shallow-rooted crops, as they take advantage of any moisture left at depth that was not used by the previous shallow-rooted crop.

Nutritional requirements

Crops with high nitrogen requirements such as cabbage should follow a leguminous crop such as green beans and peas, which fix atmospheric nitrogen. Applying too much organic manure can damage certain crops, such as carrots and beetroot. Plant these crops later, after applying organic manure to crops such as tomatoes that respond well to organic fertilisers.

Crops requiring large quantities of nutrients, such as cabbage, should follow crops with lesser needs, such as pumpkin, or less efficient feeders such as potatoes. This will allow them to make use of residual nutrients that remain in the soil after the crop has been harvested.

Crop rotation to control other pest problems

Weeds are often defined as plants growing in the wrong place. This definition is somewhat unrealistic, as barley plants growing in a potato crop would be considered weeds!

What makes these plants so undesirable? What sort of problems can weeds cause? Weeds require the same nutrients that crop plants use, often in very similar proportions. They also compete for resources such as water, sunshine and space that might be utilised by crops. This means that when weed and crop requirements are similar, there will be greater competition for those resources. Weeds are most damaging to crop yields if they have some advantage over the crop. Four factors are especially important: density, timing, size and chemistry (where weed roots secrete substances toxic to plant roots – allelopathy).

Weeds cause many problems, but especially they reduce crop yield. Of the total loss of agricultural produce each year from various pests, weeds account for 45%, insects 30%, diseases 20% and other pests 5%

Weeds cause greater crop losses if they occur in large numbers, if they commence growth before the crop emerges and get a 'head start' on the crop, if they are especially vigorous, or if they produce allelopathic substances

Effect of crop rotation on weed growth

A literature survey examined the effect of crop rotation on weed growth. The results indicate that crop rotation significantly reduced weed population density and biomass production. Crop rotation induced a reduction in emerged weed densities in test crops that were lower in 21 cases, higher in 1 case, and equivalent in 5 cases in comparison to monoculture systems.

When seed density was reported, seed density under crop rotation was lower in 9 cases and equivalent in 3 cases when compared to monocultures of the component crops.

This raises the question, how does crop rotation influence weed establishment? It is proposed that the use of crop sequences that create varying patterns of resource competition, allelopathic interference, soil disturbance, and mechanical damage disrupt the environment in which the weeds prospered hitherto and now the unstable and frequently inhospitable environment prevents the proliferation of a particular weed species.

Researchers emphasise that significant advances in the design and improvement of weed-suppressive crop rotation systems are most likely to occur if some important areas of research are addressed.

They propose that first there must be continued attention to the study of weed population dynamics and crop-weed interference in crop rotation systems. We need to increase our understanding of the effects of diversification of cropping systems on weed seed longevity, weed seedling emergence, weed seed production and dormancy, agents of weed mortality, differential resource consumption by crops and weeds, and allelopathic interactions.

Second, a study is required where there is a systematic manipulation of individual components of rotation, so as to isolate and improve those elements (e.g., interrow cultivation, choice of crop genotype) or combinations of elements that may be especially important for weed control. Such a study would be complex and time consuming; this may explain why it has not been attempted.

Crop rotation and sustainable agriculture

Sustainable agriculture is defined as the ability of a farm to produce food indefinitely, without causing severe or irreversible damage to ecosystem health. Long-term sustainability must deal with two key issues: **biophysical** (the long-term effects of various practices on soil properties and processes essential to sustain crop productivity) and **socio-economic** (the long-term ability of farmers to obtain inputs, manage resources such as labor and care for their family).

The physical aspects of sustainability are partly understood. Practices that can cause long-term damage to soil include excessive tillage (leading to erosion) and irrigation without adequate drainage (leading to accumulation of salt in the soil).

Sustainable agriculture integrates three main goals:

- Environmental stewardship,
- Farm profitability, and
- Prosperous farming communities.

These goals have been defined by a variety of disciplines and may be looked at from the vantage point of the farmer or the consumer.

Although air and sunlight are available everywhere on Earth, crops also depend on soil nutrients and the availability of water. When farmers grow and harvest crops, they remove some of these nutrients from the soil. Without replenishment, the land would suffer from nutrient depletion and be unusable for further farming. Sustainable agriculture depends on replenishing the soil while minimizing the use of non-renewable resources.

In some areas, sufficient rainfall is available for crop growth, but many other areas require irrigation. For irrigation systems to be sustainable they must be managed properly (to avoid salt accumulation) and not use more water from their source than is naturally replenished, otherwise the water source becomes, in effect, a non-renewable resource.

Sustainability is enhanced through the employment of multiple cropping systems using crop rotations and/or intercropping, since these practices may improve pest control and increase nutrient- and water-use efficiency. Practices such as crop rotation, reduced tillage, cover crops, fallow periods, manuring and balanced fertilizer application can help maintain and restore soil fertility. Intensive agriculture relies on breeding new disease resistant cultivars and the application of agrochemicals. But the need to breed for new disease resistance and to discover new pesticides can be reduced by crop rotation and the use of spatial or temporal crop diversity.

A mention for agroforestry! A rotation in which trees are included in a cropping system. Agroforestry may improve nutrient availability and efficiency of use and may reduce erosion, provide firewood and store carbon. When trees and shrubs are planted in buffer strips surrounding cultivated fields they decrease soil erosion and can take up nutrients that otherwise would be lost if they enter surface or ground waters.

In practice, there is no single approach to sustainable agriculture, as the precise goals and methods must be adapted to suit each region and even to each individual case. Of course there may be some techniques of farming that are inherently in conflict with the concept of sustainability, but there is often widespread misunderstanding of the impacts of other practices, and when they is explained fully and all the factors are accounted for, they meet the test of sustainability.

Crop rotation and soil erosion

There are many definitions of erosion. In agriculture it is defined as the mechanical process by which soil (especially top soil) is moved from the farmers field to a steam, then onto a river and finally a lake. Erosion brings huge loss of productivity to the farmer and huge pollution to the water system. The topsoil can be regarded as the life support system of the planet and when we consider that it takes 30 years to replace 25mm of material with the normal quality of topsoil, it is easy to understand why it must be protected

Crop rotation can significantly reduce the amount of soil lost from erosion by water. In areas that are highly susceptible to erosion, farm management practices such as zero and reduced tillage can be supplemented with specific crop rotation methods to reduce raindrop impact, sediment detachment sediment transport and surface runoff and soil loss. Protection against soil loss is maximized with rotation methods that leave the greatest mass of crop stubble (plant residue left after harvest) on top of the soil. Stubble cover in contact with the soil minimizes erosion from water by reducing overland flow velocity, stream power, and thus the ability of the water to detach and transport sediment.

Erosion can be severe on steep slopes where windbreaks have been cleared, or where vegetative cover is absent during the rainy season. Cover crops or reduced tillage can reduce leaching, volatilization and erosional losses of nutrients and increase nutrient-use efficiency.

Soil fertility is the basis of a productive soil. The topsoil stores the majority of organic matter, also approximately 50 percent of plant-available phosphorus (P), and potassium (K). When topsoil is lost to erosion, this contributes to a loss of the inherent soil fertility levels of N, P, K, and thus to a decline in potential crop yield. By preventing soil erosion the inherent soil fertility is preserved and this minimises fertiliser and management inputs

Climate will modify the response of erosion to crop rotation. If a region has a relatively consistent climate conditions, where annual rainfall and temperature levels are assumed, then a rigid crop rotation can produce sufficient plant growth and soil cover But in regions where climate conditions are less predictable, and unexpected periods of rain and drought may occur, a more flexible approach for soil cover by crop rotation must be adopted.

In this latter case an "opportunity cropping system" promotes adequate soil cover under these erratic climate conditions. In an opportunity cropping system, crops are grown when soil water is adequate and there is a reliable sowing window. This form of cropping system is likely to produce better soil cover than a rigid crop rotation because crops are only sown under optimal conditions, whereas rigid systems are sown in the best conditions available.

Crop rotations also affect the timing and length of when a field is subject to fallow. This is very important because depending on the climate in a particular region, a field could be at it's most vulnerable to erosion when it is under fallow. Efficient fallow management is an essential part of reducing erosion in a crop rotation system. Zero tillage is a fundamental management practice that promotes crop stubble retention under longer unplanned fallows when crops cannot be planted. A management practices that succeeds in retaining suitable soil cover in areas under fallow will ultimately reduce soil loss. When leaves of cover crops intercept rainfall, some is stored in the canopy with the remainder evaporating or reaching the soil surface either directly, or indirectly through stem flow or leaf drainage. The root system provides a pathway to infiltrate the soil and minimise the risk of surface flooding and consequent overland flow.

Planting different species in rotation will increase soil organic matter, improve soil structure, and improve the chemical and biological soil environment for crops. By increasing soil organic matter, water infiltration and retention improves, providing increased drought tolerance and decreased erosion. Soil aggregation, which also helps to reduce erosion, allows greater nutrient retention and utilization, decreasing the need for added nutrients. Soil microorganisms further improve nutrient availability and decrease pathogen and pest activity through competition. In addition, plants produce root exudates and other chemicals, which manipulate their soil environment as well as their weed environment. Thus rotation allows increased yields from nutrient availability but also alleviation of allelopathy and competitive weed environments.

A crop rotation, which rotates shallow rooting with deep rooting crops, improves water infiltration. When water can move rapidly down to the lower layers of the soil profile, it reduces the risk of surface flooding, leading to topsoil erosion.

Summary

- Crop rotation, the successive cultivation of different crops in a specified order on the same fields, in contrast to a one-crop system or to haphazard crop successions.
- Crop rotations are used to diversify income, spread labor requirements throughout the year and spread the crop loss risk associated with weather and pests across two or more crops.
- Crop rotations increase crop productivity by enhancing soil quality.
- Crop rotation provides agronomic, socioeconomic and environmental benefits.
- Crop rotation is regarded as a first defense against the buildup of soil borne pathogens
- A well-planned crop rotation can reduce the loss of topsoil by reducing the rate of soil erosion.

Remembering again: *The soil is the farmer´s greatest asset, but failure to rotate crops will contaminate and deplete it, maybe even destroys it.*

References.

Pérez-Jaramillo, J.E., Mendes, R. and Raaijmakers, J.E. (2016). Impact of plant domestication on rhizosphere microbiome assembly and functions. *Plant Mol Biol.* **90:** 635–644.

Sources accessed in the preparation of this section.

Berendsen RL, Pieterse CM, and Bakker PA. (2012). The rhizosphere microbiome and plant health. *Trends Plant Sci*. **17:** 478-86.

Liebman, M. and Dyck, E. (1993). Crop Rotation and Intercropping Strategies for Weed Management. *Ecological Applications.* **3:** 92-122.

Muthoni, J., Shimelis, H. and Melis, R. (2012). Management of Bacterial Wilt [Ralstonia solanacearum, Yabuuchi et al., 1995] of Potatoes: Opportunity for Host Resistance in Kenya. Journal of Agricultural Science; 4: 64-78.

Ola, A., Dodd, I.C. and Quinton, J.N. (2015). Can we manipulate root system architecture to control soil erosion? *Soil*, **1:** 603–612.

Scholte, K. (1992). Effect of crop rotation on the incidence of soil-borne fungal diseases of potato. *Netherlands Journal of Plant Pathology* **98:** 93.

Yuliar, Y., Nion, Y.A. and Toyota, K. (2015). Recent Trends in Control Methods for Bacterial Wilt Diseases Caused by Ralstonia solanacearum. Microbes Environ. **30:** 1–11

Section 19.

Potato Storage

Introduction

Potatoes in storage are living material and they must remain alive (respiring) throughout the storage period, hence they interact with the surrounding environment. The potato tuber can only be expected to survive and retain its quality in a storage environment that is not widely different from that in which it was grown—cool temperatures, high relative humidity and the absence of light. It is important to remember also that the potato may spend the same amount of time in the store as it spent in the soil during growth.

The typical tuber contains 80% water and 20% dry matter (comprising starch, minerals, vitamins sugars and proteins). These constituents represent a nutritious substrate for microbial growth. So until the tuber is consumed, processed or planted, the storage regime must reflect the reality of its chemical makeup. Storage efficiency of ware tubers is therefore defined using two qualifiers. The first, is to store the potatoes as long as possible while preventing them shrinkage or rotting. Second, in the case of ware potato, to prevent them from sprouting.

> ***A word of caution*** *– potatoes never improve in storage. Potato quality coming out of storage can be no better than the quality of the potatoes placed into storage. Even successful storage can only slow down the rate at which tubers deteriorate, but properly managed storage can help maintain quality and minimize deterioration of good quality potatoes.*

Background

The objective of the storage environment is to maintain the external and internal quality of potato tubers. When potatoes respire (or breathe), their stored carbohydrates are gradually converted into carbon dioxide, water and heat; this represents a loss of weight. The rate of evolution of these volatile by-products is controlled largely by the temperature of the potatoes, and the accumulation of moisture and CO_2 within the store must be controlled.

While the physical aspects of storage conditions; temperature, humidity and carbon dioxide levels are all important factors in successful potato storage; however, temperature is the dominant factor. The tuber is a plant organ, which continues to change biochemically, even after harvesting. Storage conditions therefore influence the tuber composition. To ensure that the tubers meet the requirements of the market, the processing industry and consumers or for the seed tuber to retain all its properties and its vitality, it is essential to control the storage process. This calls for the correct storage conditions, chiefly in terms of the tuber temperature also the moisture and composition of the ambient air inside the building.

The time that elapses between the potato harvest and the time when the potatoes are used means that they will spend a period in store that varies in length from a few weeks to perhaps 10 months. Production and harvesting practices exert a significant influence on the suitability of a crop for long term storage.

The main objectives of correct potato storage are to preserve all their properties (taste, technological properties and health) and to limit weight loss, while at the same time preventing the development of diseases and physiological problems.

Since the quality criteria are specific and different for each market, this will alter the priority requirements. This will call for a different approach to such topics as the storage method, storage management and even the type of storage structure and equipment.

As market requirements become stricter, so storage becomes increasingly specific and technical. Storage of agricultural products is the vital link between farmer and consumer. To farmers, storage provides a mechanism to add value and reduce risk. For the consumer, storage extends the utilization season also provides more choice and increased satisfaction.

Ware potato storage technology.

Potato storage technology involves: the processes of drying, curing and storing potatoes. Inside a potato storage facility the potatoes can pass through 5 main processes:

- The drying process.
- The curing process.
- The cooling-down process.
- The storing process.
- The warming-up process

The drying process

The objective of the drying process of potatoes is to remove all superficial moisture, while keeping the potato humid. The word "drying" is really a misnomer, because, in fact, the objective is not to 'dry' them, but to remove the excess moisture from the tuber and the soil that arrived into the store with the potatoes. The drying is a delicate process and done preferably at a temperature of about 25 °C and a Relative Humidity of about 85%. In some extreme situations humidifiers are used during the drying of potatoes to prevent tuber shrinkage. It can be stated that the potatoes are *"dry"* when there isn't any noticeable moisture, but the tuber is not *"humid"*, rather feels *"cool"* to touch.

The curing process

The curing of potatoes is a process where the potatoes are kept for a prolonged period at a high temperature and high humidity. Under these circumstances the potatoes are given an opportunity to auto-heal the small skin lesions, incurred during harvesting, transport and storing. This healing is done to improve the tubers storability. Potatoes need tight temperature control and high humidity during early storage to promote proper wound-healing and excellent suberization.

Separating vines from the tubers and bruising while digging initiate numerous physical and chemical changes in the tubers that are invisible at storage time. Healthy potatoes are impervious to bacteria and fungi but they can penetrate tubers damaged by bruising, scuffage and skin slippage. This means that the first requirement after potatoes are placed in storage is to accelerate skin healing, or suberization. A temperature of 13° to 18°C, combined with a relative humidity of approximately 90 percent, promote rapid healing of bruised areas. When these conditions are maintained for 10 to 20 days immediately following storage it promotes rapid suberization (**Section 13, Fig. 1**). In temperate regions, closing the potato storage area is an easy way to achieve the conditions needed for suberization. But unless large quantities of potatoes are available and releasing heat, associated with respiration, the target temperature 13° to 18°C may not be reached; artificial sources of heat may be required.

During the first 10 days of storage, air circulation within the storage area is more important than air exchange to the outside. This is necessary to maintain the high relative humidity needed for suberization. Avoid condensation and dripping in the storage area because it provides an environment for rapid growth of microorganisms if it accumulates on the tubers. If storage temperatures cannot be raised above 13 °C then the curing period should be maintained for three weeks because healing is much slower at lower temperatures.

Temperatures above 24°C promotes the growth of bacteria and fungi more than wound healing. Under this situation, tuber diseases such as ring rot, black leg, fusarium rot, scab and soft rot will require more diligent storage management. Rotting potatoes will affect other potatoes.

Note: *If there is the slightest possibility of a Phytophthora infestans (Potato Late Blight) infection, the curing process must be discarded and the tubers should be brought as soon as possible to their required storage temperature.*

The cooling-down process.

Cooling the potatoes to the required storage temperature is the next step after the curing period has been completed. Lowering the temperatures should be acomplised over a period of several weeks or even longer if the only other alternative is bringing in very cold air. Introducing very cold air to the potato store increases the risk of condensation forming and and then dropping on the potatoes. To avoid condensation, it is crucial to reduce the temperature by not more than 0.5° to 1 °C per day.

Cooling should be done in such a way that the potatoes lose as little weight as possible, which explains why it should be done gradually. The air used for cooling should have a sufficient cooling capacity but the temperature of the cooling air should not be more than 2 °C cooler than the potatoes. During this whole process the air used should be sufficiently humid, around 85% Relative Humidity. Cooling can be accomplished for smaller storage areas by allowing air to enter the storage area during nights and cool days and closing vents during warm outside temperature periods.

> ***Very important:*** *Under no circumstances should the temperature increase during this process. As the potato is being cooled down, the chemical messaging system is conditioning the tuber for continued dormancy. But if suddenly the temperature increases, the tuber sprouting mechanism is triggered, because the potato messaging system interprets the rise in temperature a signal that dormancy should end and that the tuber should prepare for regrowth.*

The storing process.

Potatoes stored at temperatures between 3° and 4°C will remain dormant the longest. Maintaining appropriate temperature and humidity can reduce shrinkage due to moisture loss.

Storage temperature should ideally be maintained within 0.5° to 1°C of the recommended limits. After several months in storage, potatoes have converted a considerable amount of starch to sugar, which acts as a protective agent if temperatures drop to 0°C. Aside from this defence mechanism, under normal circumstances, conversion of starch to sugar in potatoes would introduce an undesirable sweet flavor in the cooked product. However, storing potatoes at room temperature in darkness overcomes this problem, reducing the sugar content and returning the potato to its original flavor.

Temperatures below 7°C will cause sugar levels to increase and darken the color of fried potatoes (low temperature sweetening). Warming potatoes for a week prior to frying can lighten the color of tubers which had been stored at 2° to 4 °C.

Keep stored potatoes away from light to prevent greening of exposed tubers. Greening may impart a bitter flavor to cooked potatoes. To avoid excess illumination, low-wattage, shielded lights should be used in the storage area and used only for short periods of time.

The final destination of the potato determines its storage temperature.

The warming up process

This step involves increasing the temperature of the potatoes after storage.

After storage, the potatoes should be warmed up for two reasons:

- To give the Reducing Sugars, formed during the time the potatoes were below °8C, the time to respire off, so as to avoid the Maillard reaction induced darkening of cooked product.
- Those potatoes that go to the fresh market should be raised in temperature to avoid condensation in the market place.

This process of increasing the temperature of the potatoes at the end of the storage period mirrors the process of decreasing the temperature and therefore the temperature should be raised slowly and with the same degree of care.

Ware potatoes sprouting during storage.

Most potato cultivars stored below 4 °C will not sprout.

The higher the storage temperature, the more sprouting may become a serious problem.

Various commercial products in the form of gases and powders exist that can be of great help avoiding the sprouting of the tubers. (See below for further details)

Factors determining successful storage

As potatoes respire, or 'breathe'! the respiration process results in the oxidation of the starch (a polymer of glucose) contained in the cells of the tuber, which converts it into water, carbon dioxide and heat energy. During this transformation of the starch the dry matter of the tuber is reduced. The respiration process can be approximately represented by the oxidation of glucose:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy}$$

The foregoing equation illustrates the significant loss of weight through water loss. When weight loss was partitioned between vapour loss and respiration loss, it was observed that respiration loss accounted for between 10 and 50% of the moisture loss from stored tubers

The rate at which the respiration by-products are given off is controlled largely by the temperature of the potatoes, and the accumulation of the CO_2, moisture and heat within the storage must be controlled.

Insulation

The role of insulation in a potato store is to prevent the ingress or escape of heat. Insulation is a key factor for a potato store, much more so than it is for general -purpose buildings. The extent to how well a potato store performs is largely a function of the quality of the insulation. In a modern well-insulated potato store, the crops can spend as long in the store as they do in the ground. A well-insulated store allows potatoes to be stored free from condensation under changeable weather conditions. A store having an inadequate level of insulation or inadeqate air circulation may experience excess moisture buildup. This can result in water dripping on the pile which must be avoided at all costs in order to minimize the danger of rot.

In a well-insulated store, maintaining temperatures above freezing point is seldom a problem due to the quantity of respiration heat produced in a large store. However, any heat that leaks into a store has to be removed by expending energy, either in the form of ventilation or refrigeration. Good insulation minimises the heat gains from warm weather conditions, and if installed correctly also helps to overcome air leakage into the store; another factor, which increases energy costs, incurred when removing it.

Keeping harvested potatoes in a refrigerated store permits holding them in prime condition, ready for sale, at the times when customers require them, allowing the grower to get the best price. Unless the store is well insulated the cost of running refrigeration equipment becomes prohibitively expensive. This is particularly the case when ambient temperatures start to rise. Insulating the store can reduce running costs.

With a growing customer demand for all-year-round, quality potatoes, growers need to store for longer. To provide optimum storage conditions for potatoes, certain essential design and equipment characteristics must be present. These include sufficiently strong foundation and lateral wall support to hold the weight of the pile; adequate insulation and moisture barrier; an air circulation system capable of providing a uniform supply of air to the entire storage; equipment for supplying moisture to the circulation air.

Temperature

Temperature is regarded as the single most important factor in the keeping quality of stored potatoes. It influences respiration, sprouting, water loss, relative humidity, chemical composition and the development of storage diseases. Respiration consumes oxygen and releases carbon dioxide, volatile gases, water and heat. For the majority of varieties, temperatures below 3 °C and above 15 °C cause dramatic increases in respiration and are not recommended. Length of dormancy during storage is determined by variety, temperature and the physiological age of the tubers, all of which vary from year to year. At temperatures below 4.0 °C most potato varieties will remain dormant during a normal storage season (up to 8 months). At temperatures above 4.0 °C the dormant period decreases as the temperature increases. When table potatoes and especially potatoes for processing are stored at temperatures above 4.0 °C for more than a few months, a sprout inhibitor will be required. Maintaining uniform temperatures is critical as fluctuations shorten dormancy.

The most important biochemical process affected by temperature is the accumulation of sugars, which influences the cooking and processing quality of potatoes. At temperatures below 7.2 °C, reducing sugars accumulate leading to dark chips and French fries when the potatoes are processed. At temperatures below 3.0 °C the accumulation of sugars is so great that flavor and boiling and baking quality are affected (low temperature sweetening).

The appropriate storage temperature depends on the potato market

- Seed potatoes are stored at low temperatures, around 3 – 4 ˚C, to minimize decay and to control the physiological age of the tubers.
- Fresh market or table potatoes are kept at around 4 - 5 ˚C to minimize weight loss and maintain a fresh, good-looking tuber.

- Chips require potatoes stored at 6 – 9 ˚C,
- French fry and crisping potatoes need to be stored at higher temperatures; 7 – 9 ˚C, to minimize the level of reducing sugars. Reducing sugars accumulate below and above 9 °C, and the changes induced by higher temperatures are irreversible.
- Potatoes for the manufacture of starch should be stored 4 °C

Temperature has an important relationship with relative humidity (RH). Warm air holds more moisture than cold air. Thus, even small changes in temperature can cause dramatic changes in relative humidity. For the same reason water loss from the tubers is greater at higher temperatures. Air at 10.0 °C and 90% RH will cause more "shrink" than air at 4.0 °C and 90% RH. To avoid fluctuations in RH, which stress the tubers and can lead to condensation problems, it is essential to maintain a uniform temperature in the store, irrespective of changes in the ambient temperature.

Ventilation

Potato storage facilities require air movement through the pile of potatoes to remove field heat immediately after harvest and to remove the products of respiration during the storage period. Potatoes should be stored in well-ventilated, cool, dark, and humid place. If it pays to store potatoes for several months, it will pay to ventilate so as to maintain top quality. In general, a ventilation system should force air up through the pile of potatoes. The air must be maintained at the proper temperature and relative humidity. A practical method of forcing air through a pile of potatoes is to introduce the air into a system of delivery ducts installed under the pile.
The role of ventilation therefore is to:

- Control potato temperature,
- Supply and/or control humidity,
- Remove surface moisture (condensation),
- Suppresses the growth of fungal and bacterial pathogens then
- Provide oxygen and remove CO_2.

Air Requirements: Here below the recommended storage temperatures and relative storage humidity for potatoes according their final destination

- Potatoes for Chips … 7° to 10 °C, Relative Humidity 90%.
- Potatoes for French Fries … 5° to 6 °C, Relative Humidity 90%.
- Table (fresh) Potatoes … 4° to 7 °C, Relative Humidity 90%.
- Seed Potatoes … 4° to 5 °C, Relative Humidity 90%.
- Potatoes for Potato Starch … 4° to 5 °C, Relative Humidity 90%.

The amount of air required will vary with the storage period, the climate, and the variety of potatoes. The maximum amount of air is required for the wound healing and curing period. This is immediately after the potatoes are placed in storage. It is necessary to remove the field heat as rapidly as possible to reduce the possibility of creating a favorable climate for the growth of decay and disease organisms. A minimum of 150 m^3 air t^{-1} potatoes.$hour^{-1}$ is required during this period. Depending the location of the store, there may be relatively few hours per night when the outside air is cool enough to bring into the storage during potato harvesting. However, all cool night air should be utilized, and air should be circulated frequently during the day to prevent hot spots from forming within the pile of potatoes.

Air movement includes both through-the-pile ventilation and over-the-pile ventilation (= recirculation). Through-the-pile ventilation is necessary to dry and cool the potatoes, supply fresh air, and remove carbon dioxide, volatiles also excess heat and moisture from the storage. Recirculation aids in maintaining uniform temperature conditions throughout the storage and sweeps moisture from the walls and ceiling.

It would be helpful at this time if refrigerated air could be supplied to the storage in order that the potatoes could be cooled faster. After the potatoes have been cooled to storage temperature, and after the outside air temperatures are somewhat lower than during harvest, a smaller amount of air will maintain storage temperature. This reduced rate will tend to reduce shrinkage from dehydration.

The major factor affecting the storage environment is tuber respiration. Respiration is sometimes considered the opposite of photosynthesis. Energy stored in sugars is now released for use in maintenance of the tuber. Respiration changes over time, with tuber temperature and with variety. In general, any type of stress causes respiration to increase. Stresses to watch for: lack of fresh air (O_2, CO_2), handling, temperature fluctuations, exhaust gases (CO, C_2H_4) and even with season.

Relative humidity

Relative humidity is defined as: *the ratio of the actual amount of moisture in the air to the maximum amount of moisture the air could hold at that temperature*. Relative humidity (RH) is expressed as a percentage. Relative humidity is a means of expressing the amount of moisture in a given volume of air in relation to its maximum moisture-carrying capability. So if 1m^3 of air at 4°C is at 50% RH, it contains 50% or 3.2g of the maximum 6.4g/m^3 moisture that air can hold.

Correct humidity is essential to maintain proper tuber weight and tuber quality. When potatoes are stored at relative humidity below 90%, there is a significant increase in weight loss. Maintaining high relative humidity (90-95%) preserves the quality and firmness of the tuber. Weight loss or shrinkage can reduce returns by diminishing the quantity and quality of saleable potatoes. Many components of the storage environment impact shrinkage, but the most critical is the RH. Shrinkage loss in storage is directly proportional to the length of the storage season and inversely proportional to the relative humidity conditions maintained within that storage. The current recommendation is to maintain 95 percent RH or above for minimizing early storage tuber losses due to dehydration.

Stored potatoes loose weight by two processes; giving up water to the surrounding air (transpiration) and also through the process of respiration. Tubers loose far less weight due to respiration than transpirational water loss. Transpirational water loss cannot be prevented, only slowed by maintaining as high an RH as possible

After the potatoes are cooled to the holding temperature, high ventilation rates can cause drying of the potatoes and increase shrinkage losses. The relative humidity (RH) of the air is very important and should be 95% to 98% to keep shrinkage losses low. Shrinkage losses are two times higher at 90% RH than at 95% RH. If potatoes are stored for 6 months at 90% RH versus 95%, the shrinkage difference would likely be 3%. The percentage RH should be appropriate for the required task. High humidity is essential to maintain proper seed weight and tuber quality. Weight loss significantly increases at relative humidity below 90%. Maintaining high relative humidity (90-95%) preserves the quality and firmness of the potato. But again a note of caution; excess humidity prevents drying of "leakers", allows free water to accumulate on tubers and stimulates microorganisms.

Possible store management decisions: *(**Please note:** this is a general guideline and does not constitute advice.)*

- If there is no rot - 92 % at 10 °C
- If some rot (< 5 %) - 80 - 85 %
- If the rot is >5%, try to unload the store ASAP!

(Helpful Hint! There are many electronic instruments that will accurately measure the RH of the potato store. A simple low cost technique is to exhale your breath in the store. If your breath is visible in a light, at any temperature—even though there is no wetness on the potatoes or store surfaces—the RH of the air is between about 95 and 99 percent. That is the desired value – but of course the actual value should be measured regularly)

Dew point

Condensed water is referred to as dew, when it forms on a solid surface. Dew Point is defined as: *the temperature at which the water vapor in a volume of air at a constant pressure will condense into liquid water, at the same rate at which it evaporates*. Put simply! If air is cooled and gaseous water vapor begins to condense to the liquid phase, the temperature at which condensation occurs is deemed as the dew point temperature. Dew Point is associated with relative humidity. A high relative humidity indicates that the dew point is close to the current air temperature. At 100% relative humidity the dew point is equal to the current temperature.

Implications for potato storage management: If air with a dew point higher than the tuber temperature is delivered to a pile, condensation will form on the surface of the tubers. If air with a dew point lower than the tuber temperature is delivered to the pile, drying conditions exist. If this latter condition persists for an extended period, weight loss and shrinkage will occur.

Condensation

Condensation: *describes the process whereby water vapour, present in the air as a gas, is altered to liquid water*. Condensation normally occurs when warm, moisture-laden air comes into contact with cold surfaces, but condensation always occurs when a temperature difference exists between the air and a surface, i.e. warm air on cold door, ceiling or walls; cold air on warm potatoes; cold air meeting warm, moist air. Warm air can carry more moisture vapour than cool air. For example, at 20°C, air can carry 17.5g/m^3 but at 4°C, it can only hold a maximum of 6.4g/m^3. Condensation water, or free water on potatoes represents a serious problem since it will encourage the development of soft rots.

Condensation may occur if there are temperature differentials with the tuber clamp. Condensation on the crop can occur in a number of situations, but will only do so directly if the air surrounding the potatoes is warmer than the potatoes, and the potatoes' surface temperature is below the dew-point temperature of the air. As a general rule, a temperature difference of 4°C or more between the warm air and the cooler crop will cause condensation. But in some situations (eg at cold temperatures) this difference might only need to be as little as 1°C for condensation to occur. However, cool air coming into contact with warmer potatoes is not a condensation risk

Carbon dioxide

Respiration consumes oxygen and releases carbon dioxide, volatile gases, water and heat. The rate of respiration is minimal at 7.2 °C and increases above and below that temperature. For most varieties, temperatures below 3 °C and above 15 °C cause dramatic increases in respiration and are not recommended

A highly sealed store is likely to have an elevated level of CO_2 unless the air is freshened daily. Air movement includes both through-the-pile ventilation and over-the-pile ventilation (= recirculation). Through-the-pile ventilation is necessary to dry and cool the potatoes, supply fresh air, and remove carbon dioxide, volatiles and excess heat and moisture from the storage

High levels of CO_2 can accumulate in the store –they are often in the region of 0.3-0.5% (3000-5000 parts per million), which is about 10 times the 0.04% level normally found in open air. At these high concentrations, CO_2 can cause dark fry colours. Respiration rate increases following "fogging" (For fogging - See section on sprout suppressants below) to inhibit sprout growth and the consequent levels of CO_2 can rise considerably.

Tuber greening

Potato tubers, like haulm, turn green when exposed to light. Exposure of potato tubers to light - either in the field (Fig. 1), in storage, on the store shelf, or at home, will induce the formation of a green pigmentation on the surface of the potato. This is called "greening" and indicates the formation of chlorophyll. This green coloration cannot be reversed. The pigment is completely safe and is found in all plants, lettuce, spinach etc. It is primarily found in leaves and is responsible for a plant's ability to make food, through the process of photosynthesis. Greening of 5% of a lot of tubers is regarded as 'damaging' and the lot will be graded down. Therefore, green potatoes should be graded out before reaching the retail market.

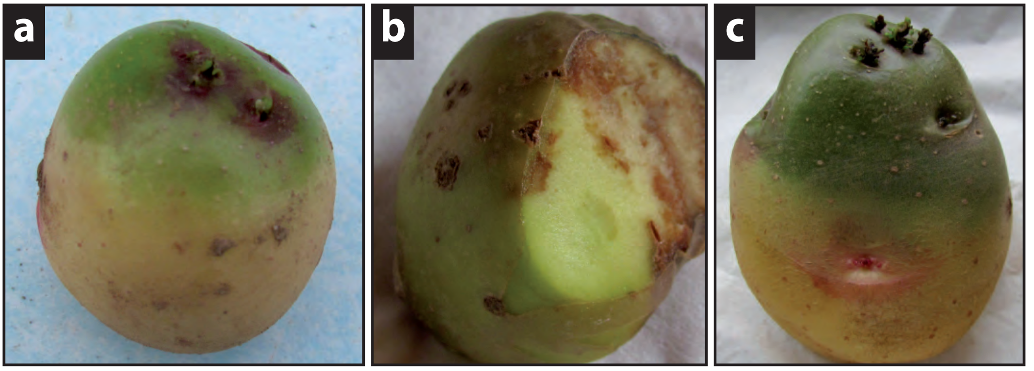

Figure 1
Tuber greening due to inadequate soil cover (a). Partly exposed tubers can become infected with late blight (*Phytophthora infestans*) (b). Partly exposed tubers can commence sprouting while still attached to the stolon (c). (Photos © Author)

Greening is strongly affected by three factors: light quality, duration, and intensity. Chlorophyll is green because it reflects green light while absorbing red-yellow and blue light. Chlorophyll formation is most efficient under red-yellow light. Under green light, there is practically no potato greening and there is little under blue or ultra-violet lights. "Daylight" fluorescent lights are quite capable of inducing greening, more so than incandescent light.

As a rule, fluorescent light above 3 Wm^{-2} exposure at room temperature, 20 °C, for three to five days will start the greening process. Light intensity may be as low as 5 $W.m^{-2}$ and light durations as short as 12 hours and yet may cause greening of some potato varieties.

A further factor is temperature during light exposure. This is important because greening is an enzymatic response and enzyme activity is increased with increasing temperature. There is no greening when temperature is less than 4.4 °C, refrigeration temperature, and is most rapid at 20 °C, room temperature. The difference in greening at 10 versus 20 °C is how long it takes to fully green.

The speed at which greening occurs is dependent upon the exposure of the tuber to light. The green color is provided by chlorophyll, which is harmless, however, it is an indication that increased level of a glycoalkaloid compound called 'solanine' may be present. There are two facets to the question of green potatoes. One is the market appearance of potatoes and the other is health concern relating to eating a green potato. These are two separate though related issues. Marketing appearance problems are associated directly with greenness, which is due to chlorophyll biosynthesis. Health concerns are due to a parallel biosynthesis of glycoalkaloids, mainly solanine. Solanine biosynthesis occurs parallel but independent of chlorophyll biosynthesis; it is not directly related to it, each process can occur without the other.

When the potato turns green, solanine often increases to potentially dangerous levels. Increased solanine levels are responsible for the bitter taste in potatoes when they are cooked. Unlike chlorophyll, light is not needed for solanine formation but is substantially promoted by light. The formation of solanine in potato is localized to the skin, usually no deeper than 3 mm. In processed potatoes such as chips and fries, there is little hazard since peels are removed.

Light contains ultra-violet radiation as well as visible rays. Ultra-violet and visible light in the blue-violet region promotes the formation of glycoalkaloids, steroid-like compounds, and, for potatoes, most notably solanine in tubers. When tubers are exposed, the solanine content in the peel may increase as much as ten times.

Sprout suppressants

Effective sprout control is a primary indicator of successful potato storage. In the 'pre-pack' market in particular, an absence of sprouts is an important visual indicator of quality. Furthermore, potatoes destined for processing as chips or French fries cannot be stored at temperatures sufficiently low to suppress sprout growth bacause of the association between low temperature storage and dark fry colours due to the Maillard reaction. An alternative approach to sprout control is called for and chemical suppressants fulfill this role.

*(**Note:** The following section describing sprout suppressants is provided for information purposes only. It does not constitute a recommendation for their use. Suitably trained personnel should only apply these products)*

Some examples of sprout suppressants are:

Chlorpropham (or CIPC) is isopropyl-N-(3-chlorophenyl) carbamate, and is widely used as a sprout suppressing agrochemical applied to stored potatoes. Its mode of action is to inhibit cell division, which then prevents sprout development. Effective sprout suppression is a fundamental component of maintaining the quality of stored potatoes. CIPC is particularly important for potato storage in the processing sector, where its use - on a global basis - is almost universal. CIPC has been in use for over fifty years and was being used even before refrigeration/temperature controlled storage was an option to growers. Typically applied to stores by trained and dedicated "fogging contractors", using specialist equipment. CIPC maintains potato tubers in a state of high quality for up to a year.

Maleic hydrazide (1,2-dihydro-3,6-pyridazinedione) known as MH is a herbicide with plant growth regulator activity. When applied to the foliage of a mature healthy potato plant the MH is absorbed and stops cell division but not cell expansion. By interfering with cell division, the MH controls the sprouting that would otherwise occur during long-term storage of the potato crop. No significant differences in yield or specific gravity of tubers due to MH-40 spray treatments were found.

Increasing concentrations of MH-40 spray resulted in a reduction in sprout development and loss of tuber weight in stored potatoes. Application three weeks before harvest was more effective in reducing losses in storage than application two weeks before harvest. A greater loss in tuber weight and more sprouting occurred at 20 °C. than at 7.2°–12.8° C. Applications of MH-40 caused no change in chipping or cooking quality of tubers.

Ethylene is also a sprout suppressant agent. Ethylene has been used in potato stores on a commercial scale since its use was introduced in 2003. It is a simple, unsaturated hydrocarbon (formula C_2H_4), which is a gas at room temperature.

Ethylene is found widely in plant tissue where it functions as a plant growth regulator. It has the capacity to readily diffuse through plant tissues, and is associated with a wide range of plant responses. When maintained at an appropriate concentration in the store headspace, ethylene acts as a sprout suppressant, and potatoes treated with it are widely regarded as 'residue-free'. Plant responses to ethylene are usually mediated through ethylene receptors present in all higher plants.

Naturally occurring sprout inhibiting compounds

When potatoes sprout during storage, due to escape from tuber dormancy, there is an associated weight loss and tuber softening. Sprout-preventing chemicals, such as chlorpropham (CIPC), can negatively impact the environment and human health, however naturally occurring alternatives exist

The history of using plant derived essential oil components in the inhibition of sprouting goes back for many centuries. For generations, the growers of South America have buried their potatoes in pits covered with soil and the leaves of Muña plants. Muña plants belong to the genera *Minthostachys* and *Satureja*, members of the mint family (Lamiaceae). The Muña plants contain rich amounts of essential oils that are comprised of over 98% monoterpenes. Oil from Muña plants was shown to be more effective than CIPC in reducing sprouting, fresh weight loss, and tuber rot over a period of 225 days. Certain volatile monoterpenes obtained from various plants have been shown to be potent growth inhibitors of plants. Studies have suggested that volatile monoterpenes, such as 1,8-cineole, carvone and pulegone, could be used for application as volatile sprout suppressants for potatoes. Most of these compounds have low toxicities to humans and are widely used in flavorings, medicines and perfumes.

The sprout inhibiting properties of the monoterpene carvone has been studied extensively. Its sprout inhibiting properties have been confirmed as well as a lack of toxicological risk from use. Carvone forms two mirror image forms or enantiomers: R-(–)-carvone smells like spearmint leaves. Its mirror image, S-(+)-carvone, smells like caraway seeds.

The monoterpene carvone ((S)-(+)-carvone) was tested in small-scale experiments. The vapour of this compound fully inhibited bud growth of tubers stored at 23°C without affecting bud viability throughout 6 months of treatment. The most effective range of carvone vapour concentrations was between 0.34 and 1.06 $\mu mol\ mol^{-1}$. Furthermore, carvone showed antifungal activity against various fungal diseases in both in-vitro and in-situ experiments. Activity was obtained against the potato storage diseases *Fusarium sulphureum*, *Phoma exigua* var. *foveata* and *Helminthosporium solani*.

When potato tubers were exposed to thermal fogging with mint essential oil *(Mentha spicata* L.), it inhibited sprouting in eight potato cultivars during large-volume 6-month storage: the tubers remained firm with 38% lower weight loss after

140 days of storage. The sprout-inhibitory action may be nullified: when treated tubers were washed with water, they resumed sprouting within days, showing reduced apical dominance. The application of mint essential oil caused local necrosis of the bud meristem, but a few weeks later, axillary bud growth was induced in the same sprouting eye.

Post harvest losses

Since potatoes are sold by weight, shrinkage due to weight loss will directly affect profit, where it can represent as much as a 15 % reduction or more. Millions of tonnes of potato are needlessly lost each year in storage. Storage losses in Europe are down from 10-15% to 6% in 25 years after significant investment in research and development. Postharvest losses of the potato crop in the USA exceeded 1.7million tonne, or approximately eight percent of the total crop. Postharvest losses can be due to a variety of factors including:

- Fungal and bacterial diseases
- Bruising
- In-storage shrink

The amount of shrinkage that could be expected from potatoes stored at 7.2 ^{0}C and RH values ranging 80 to 98% is illustrated in Fig. 2. If weight loss is compared over 6 months of storage at various RH levels, potatoes stored at 90% RH could loose 9% in weight or nearly twice as much as those stored at 95% RH

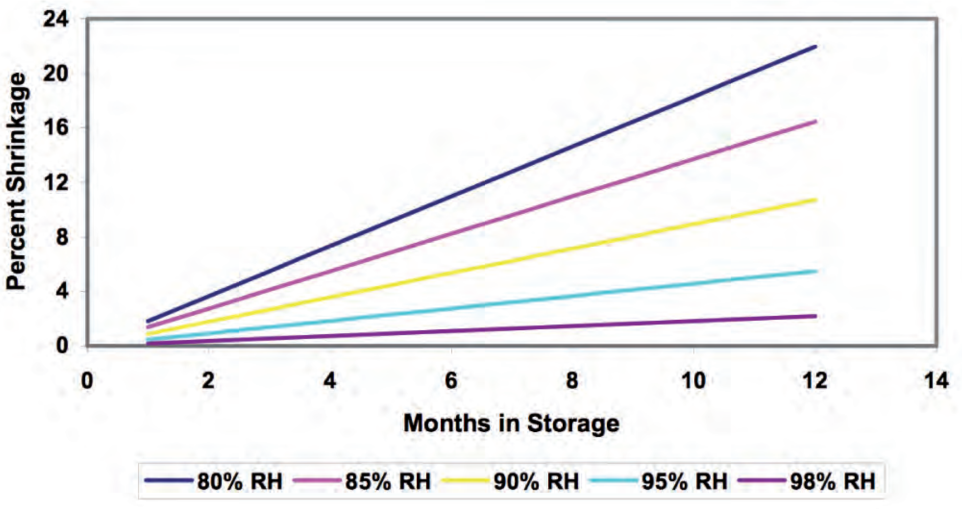

Figure 2

Effect of store relative humidity on weight loss in storage (Temperature 7.2 ^{0}C)
(Diagram © Prof. R. Brook, MSU, Extension, With Permission)

Storage Disease Management

Potatoes can incur significant losses from storage diseases. Storage pathogens find their way into the tuber at harvest from wounds or bruises and from contaminated storage facilities. Early curative treatment right after harvest/before storage and intermittent applications during storage can help in reducing the incidence and severity of storage losses. Temperature and free water are the primary prerequisites facilitating pathogen activity in stored potatoes. Microbial activity is much higher at 10 °C than 3-4 °C

Many post-harvest disease problems are associated with field locations where water saturation or excessive soil moisture occurs. These areas need to be identified before harvest so that the resulting tubers can be stored only if the storage facility is capable of handling problem lots. Storage diseases are difficult to control when tuber infection approaches 1 to 3 percent unless the storage facility is equipped to supply high volumes of air. Soft rot, water rots, dry rot, and tuber blights are the most common disease problems in long-term storages.

Bacterial Pathogens

Soft rot, caused by the bacteria *Erwinia carotovora*, (Now reclassified as Pectobacterium spp.) is the most serious of all storage diseases. This organism will spread rapidly from tuber to tuber if the conditions are appropriate. In addition, they can infect other sites where fungal diseases, such as dry rot, are present. Storage management includes high airflow to those infected areas to prevent the spread. Researchers have found little evidence that growers can control bacterial soft rot by applying disinfectants or bactericides to the circulation air that moves through the potato pile.

Fungal Pathogens

Dry rot, caused by *Fusarium sambucinum*, can be a serious storage disease of potatoes. However, proper handling and harvest conditions usually accomplish control of this pathogen. *Fusarium sambucinum* can only infect tubers through wounds in the tuber skin, which occur mainly during harvest or handling.

Wet spots in the pile at the beginning of storage are usually associated with pythium leak (*Pythium ultimum*). Pythium leak is not related to wet soil conditions but to harvest wounds in connection with high tuber temperatures. This disease is often more severe under dry harvest conditions because hard clods cause more tuber damage.

Another water rot that may come into the storage from field locations with saturated soil conditions is *Phytophthora erythroseptica* or pink rot. It may spread in storage if a secondary bacterial infection occurs. Control measures include constant fan operation to dry out the infected tubers before they can become a problem.

Silver scurf, caused by the fungus *Helminthosporium solani,* is a troublesome condition that causes silvery blotches on the surface of the tuber. It assumes particular importance when potatoes are produced for the washed pre-pack market. This disease can also spread in storage if conditions are right for spore germination. Although tubers are usually downgraded because of surface blemishes, the disease organism does not cause storage rot or decay of the infected tubers. Control conditions in storage include lower relative humidity and storage temperatures to limit surface growth of the fungus. However, reducing the humidity and decreasing the storage temperatures may limit marketing strategies.

Late blight (*Phytophthora infestans*) and early blight (*Alternaria solani*) are usually considered to be foliar diseases. However, both also have destructive tuber rot phases. Late blight-infected tubers will decay slowly in storage but can become infected with bacterial soft rot that will accentuate tuber decay and allow the soft rot to spread rapidly in storage. Late blight infection will not spread in storage but a potential exists for tuber infection if wet conditions occur in storage. Early blight lesions can limit the marketability of infected tubers, but this disease does not cause tissue breakdown in storage. Both early blight and late blight infected tubers are normally a result of field infection during harvest and handling. Control measures with frequent fungicide sprays during crop growth can minimize infection before harvest and, thus, limit the impact of tuber blights in storage.

Seed tuber storage

Introduction

Since the potato is vegetatively propagated the seed tubers must be stored between seasons and prepared for replanting to establish the next crop. The major difference between ware and seed storage is of course that ware potatoes are stored in darkness whereas tubers destined for replanting are stored in the light. Apart from this obvious difference all of the foregoing discussion applies equally to tubers seed tubers as well as ware tubers. Storage loss of seed tubers will be equally as severe as ware tubers unless equal care is take at harvest, post harvest handling, store filling and during storage.

Seed Store Design

When potato tubers sprout in darkness the sprouts are spindly and extension growth is rapid. These sprouts are completely undesirable, as they will inevitably break off prior to or during planting. The desired sprout length is 8-12mm with a ‘stubby’ configuration that will resist removal during handling and planting. Extension growth of sprouts is inhibited by light and this requirement dictates the major prerequisite of seed store design.

The International Potato Centre (Centro International de Papa, CIP) has researched the topic of seed store design and has developed many prototypes, appropriate to different regions, where the requisite materials for construction are most readily available. They do not produce a standard design but rather encourage the understanding of the principle of diffuse light seed storage. Farmers and Development workers who have learned the principle have used it to build stores of many different designs, suiting their own needs and the materials and existing buildings available to them. All the structures share the common criteria; permitting light to enter, while at the same time protecting the seed tubers from temperature extremes and the moisture loss from tubers that accompanies sprouting. This type of store is widely referred to as a Diffused Light Store or by the acronym - DLS.

It has long been known that light will reduce sprout elongation and influence the physiological ageing process. Farmers in tropical countries can construct a store that uses natural diffused light to control sprout growth on potatoes.

The basic requirement is a simple shed, which will protect the potatoes against rain and direct sunlight. The store size can be modified to match end use – a seed tuber co-operative would require a large store (Fig. 3 a&b), whereas an individual farmer would require a store of more modest proportions (Fig. 3 c)

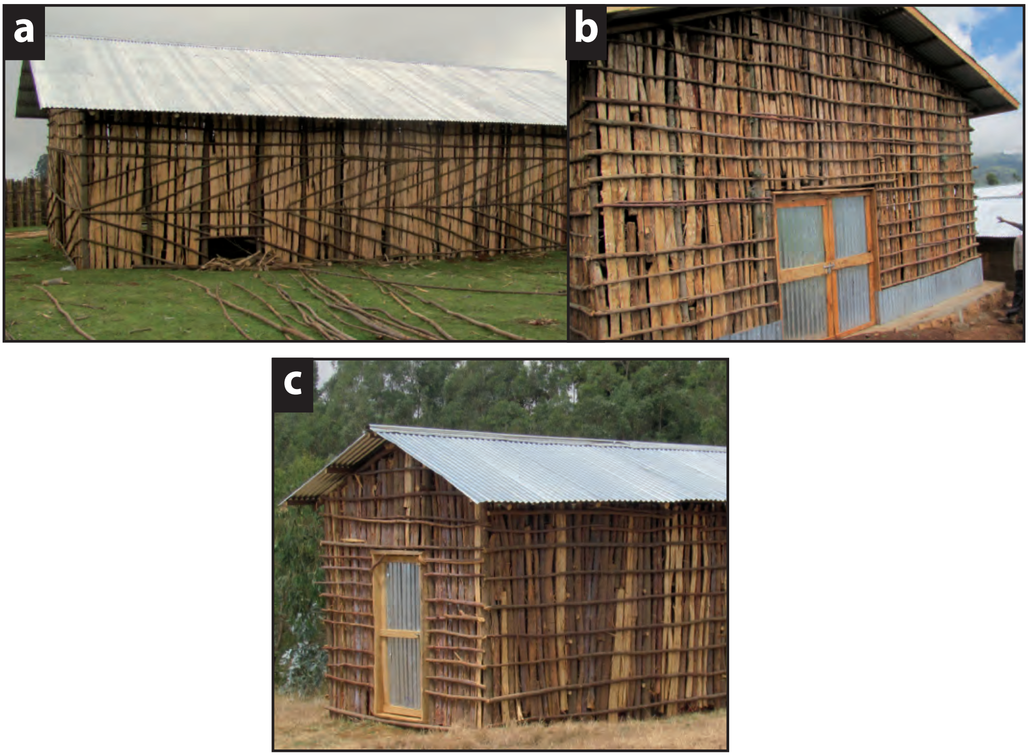

Figure 3.
Exterior view of a diffused light store. Large stores can be built to store tubers for a seed co-operative (top) or for an individual grower (below).
(Photos © Author).

Inside it is equipped with shelves on which the potatoes are spread in shallow layers (Fig. 4 a & b). When stored here for a few weeks the seed tubers will develop a green hue and produce short, sturdy and green sprouts.

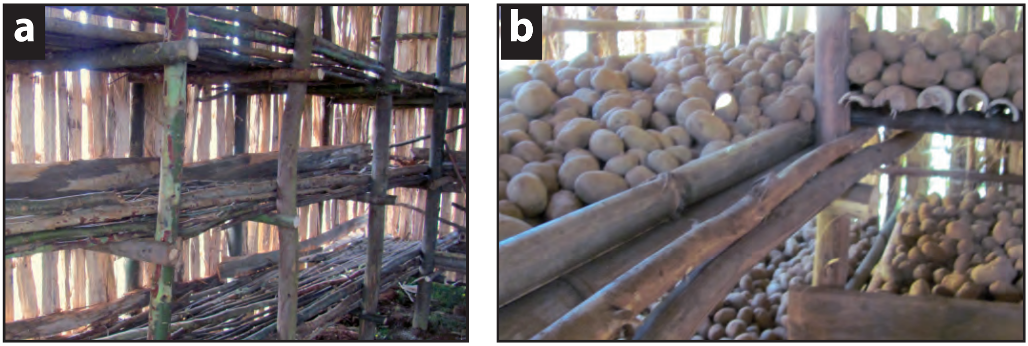

Figure 4.
Shelving arrangement in the store (a). Tubers in shallow layers on the shelves (b).
(Photos © Author)

Effect of in-store light intensity on sprout growth

The effect of light intensity on sprout growth in seed potato tubers was examined using diffuse daylight and diffuse artificial light. When the mean temperature was maintained below 20 °C, the tubers produced strong sprout growth; it was inhibited by both daylight and artificial light, at visible irradiances above 0.01 Wm^{-2}. When the temperature was suitable for substantial sprout growth in the absence of light, the percentage inhibition of sprout growth increased linearly with the logarithm of the irradiance, 50% inhibition being at 0.04 - 0.1 Wm^{-2}. The 50% inhibition point was not significantly affected by cultivar and temperature. Even at high irradiances growth inhibition was never reduced to zero, but sprout length was reduced up to 95%; short, robust green sprouts remained. Daylight increased sprout numbers, but artificial light did not. This is a particularly useful response when the seed tubers are planted to raise a seed crop. During a storage season of 180 days diffuse daylight also reduced the total weight loss from seed tubers.

Tuber Dormancy

Potato tubers are normally propagated vegetatively. To counter what is often an unfavourable climate at the end of their growth period, they enter a dormant phase. The onset of dormancy is considered to be the point of the physiological maturity of the tubers. The dormancy period is associated with reduced endogenous metabolic activity during which the tuber shows no intrinsic or bud growth, although it retains the potential for future growth. Dormancy is varietal characteristic. It is also affected by other factors, temperature is the most important but others, including moisture, oxygen and CO_2 content of the storage atmosphere, the extent of wounding and any disease of the tuber, real or putative, although normally of lesser importance may, occasionally, have an over-riding effect.

Dormancy duration during storage is determined by variety, temperature and the physiological age of the tubers, all of which vary from year to year. At temperatures below 4.0°C most potato varieties will remain dormant during a normal storage season (up to 8 months). Some varieties may require temperatures below 3.0 °C to completely inhibit sprouting. At temperatures above 4.0°C the dormant period decreases as the temperature increases. Maintaining uniform temperatures is critical as fluctuations shorten dormancy.

During dormancy, the endogenous metabolic rate of tubers is at its minimum and the dry matter losses are correspondingly reduced. Skin permeability in tubers exerts a significant control on the rate of respiration. If the periderm is immature due to inadequate skin set before harvest, it is permeable and thus permits greater levels of respiration than similarly harvested mature tubers. A respiration rate of about 17mL O_2/kg/h immediately after harvest has been established for immature potato tubers, compared to a rate of 5ml O_2/kg/h when physiologically mature.

Transpiration is water loss through the skin pores of the tuber and can effectively be described as evaporation. Some 97% of the water lost from the tuber during storage is lost through the skin with only 2.4% being lost through the lenticels with the CO_2. Notwithstanding the ambient conditions prevailing in the humid tropics, potatoes will continually lose water to the surrounding air on account of the tubers high moisture content. Several factors affect this loss of water, which can be significant in several ways. The greater the velocity of air moving over the tubers, the faster is water lost though transpiration. However, this air movement (or ventilation) through the tubers is essential to remove the heat and CO_2 produced by the respiration of the sprouting tubers. It is important to keep the rate of air movement as low as practical to prevent excessive loss of moisture. Hence the dichotomy for the seed store – allow sufficient light to enter to retard sprout elongation but restrict air movement to restrict excessive moisture loss from the tubers.

Tuber Sprouting

Dormant tubers can be stored satisfactorily with minimum loss of weight. When dormancy is broken and sprouting begins, there is a rapid increase in the rate of dry

Figure 5 a.
Sprouting commences – the appearance of small white buds (Photo © Author).

matter loss. This occurs, as the formation of sprouts requires energy, which is drawn from the tubers' carbohydrate reserves. There is a parallel increase in water loss and if this becomes excessive, the tubers dry out.

Sprouting is a physiological stage that marks the termination of dormancy. It is considered the major visible milestone in one system of determining tuber physiological age. The formation of short whited buds represents the earliest observable stage of sprouting (Fig. 5a). It is often termed "pipping" or "peeping"

Central to the success of sprouting is the type of sprout that will be formed. At low light intensity, such as in a dark building or at the bottom of a deep pile of tubers the shelves of a DLS, elongated spindly sprouts will form (Fig. 5 b). These sprouts are weakly attached to the tuber and are unlikely to survive the handling during store unloading and during planting operations. The tuber reserves invested in the production of these sprouts will be wasted if they are broken off. By contrast, the sprouts in Fig. 5c have all the desirable characteristics. They are short, the bases are thickened, which will help them resist being 'rubbed off' during handling, in addition, shoot and root primordia have begun to emerge.

The pattern of sprout growth is influenced by the physiological age of the tuber but the basis is genetic. Several factors affect the physiological age of the tuber: growing conditions, storage conditions, and length of the storage period.

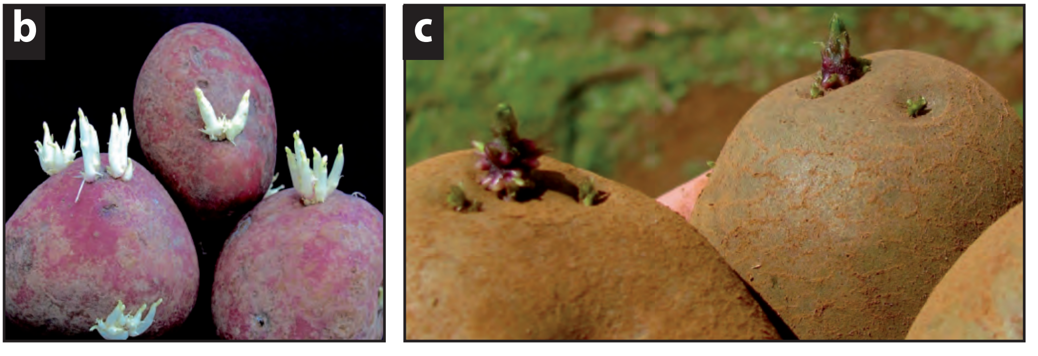

Figure 5.
Excessively long fragile sprouts (b) compared with desirable sturdy sprouts (c).
(Photos © Author)

Storage steps for seed tubers

Store loading

This step can have a significant impact on the quality of the seed emerging at the end of the sprouting period. Tubers should be size graded before being placed on the shelves. This step will reduce the handling at planting time and reduce the risk of sprouts being broken off. Having the seed tubers size graded will facilitate the planting operation since the inter-tuber distance can be easily adjusted to take account of the different tuber sizes.

Gentle handling during store loading is called for to reduce bruising and it's associated moisture loss. Stack height is another factor needing attention; deep stacking on the shelves or low light intensity, due to excessively wide shelving (Fig. 6) will result in undesirable long sprouts.

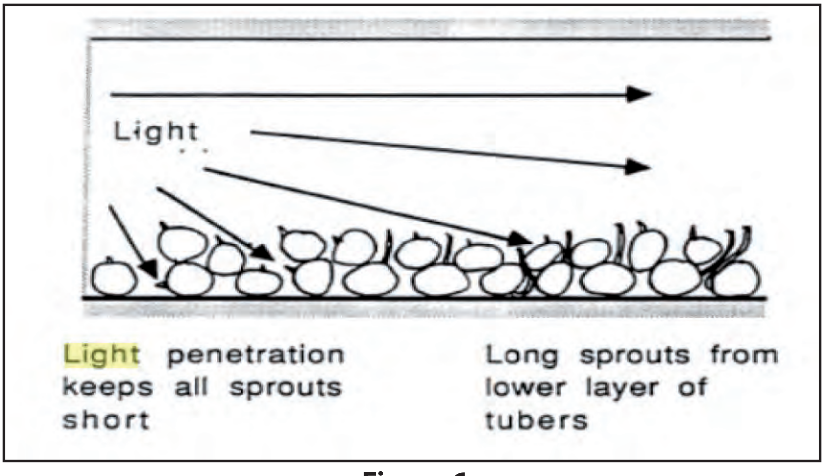

Figure 6.
Effect of light intensity on sprout length of tubers in store
(Diagram © CIP. With permission.)

Store monitoring

Sprout growth in seed tubers is associated with elevated rate of respiration and the concomitant moisture loss.

The variation in weight loss observed among cultivars has been attributed to either their periderm characteristics and/or their sprouting behavior. Un-sprouted tubers loose most moisture through their periderm, with a smaller proportion being lost through the lenticels. Periderm thickness and the number of lenticels per unit of surface area will influence moisture loss. Sprouted tubers loose more weight than un-sprouted; elevated respiration rate and high permeability of the sprout wall explain this response. This helps to explain why a significant correlation has been established between weight loss and both the length of the longest sprout and number of sprouts per tuber.

The store operator should be conscious of moisture loss from sprouting tubers and reducing wind speed over the tubers during the night can reduce this. Because the barrier is only in place during the hours of darkness, a wide choice of material can be employed for this task.

Control of insect pests of stored potato

The potato tuber moth (*Phthorimaea operculella*) is considered the principal insect pest of stored potatoes. Pest surveys in East Africa carried out by CIP in 1987 showed that the potato tuber moth caused the majority of damage problem. The moth was also observed to cause extensive damage in stored potatoes on seed farms in several African countries. The larval stage causes the most severe damage (Fig. 7). It is about 1 cm in length, has a dark brown (or black) head and a body, which may be white, yellow, pink or green. They tunnel extensively into the tuber flesh causing the infected tubers to rot, mainly because of a secondary infection of pathogens

Figure 7.
Tuber moth tunnel (Photo © Author)

Female potato aphids can live out part of their lifecycle on the sprouts of potatoes in store. Following emergence, they commence feeding on perennial weeds, with a preference for plants in the family Chenopodiaceae. Later they migrate to potato and other crops. Potato aphids can also attack potato sprouts in stores and infect the tubers with the persistent virus, Potato Leaf Roll Virus. Seed borne infection generally results in small, stunted, badly impaired plants, which have reduced, yield both in tuber numbers and in tuber size. Applying an insecticide can prevent infestation by this virus.

Aphids, feeding on sprouts in the seed store can spread the non-persistent virus, PVY. Aphicide will not prevent the spread of this non-persistent virus due to the short feeding time. The problem is best addressed by using aphid proof netting to exclude the aphids.

Summary

- Potatoes in storage are living material and they must continue respiring throughout the storage period, hence they interact with the surrounding environment.
- The main objectives of correct potato storage are to preserve all their properties (taste, technological properties and health) and to limit weight loss, while at the same time preventing the development of diseases and physiological problems.
- Physical storage conditions, temperature, humidity and carbon dioxide levels are all important factors in successful potato storage; however, temperature is the dominant factor.
- The final destination of the potato determines its storage temperature and humidity.
- Ingesting improperly stored potato tubers can result in exposure to high levels of the glycoalkaloid, solanine.
- Storage conditions for seed potato tubers should minimise weight loss and promote the growth of sprouts that will resist removal during planting.

Sources accessed in the preparation of this section.

Calverley, D.J. B. (Edt.) (1998). Storage and Processing of Roots and Tubers in the Tropics. Publ, FAO, Rome http://www.fao.org/docrep/x5415e/x5415e00.htm#Contents

Cunnington, A. and Pringle, R. (2012). Store managers guide. Publ. Potato Council, Sutton Bridge Crop Storage Research. 55pp.

Jarvis, M. C. (1981). Diffuse-daylight Seed Potato Stores: Light and Sprout Growth. Publ. CIP, Peru. 36pp.

Kleindopf, G.E., Oberg, N. A., Olsen, N.L. (2003). Sprout Inhibition in Storage: Current Status, New Chemistries and Natural Compounds. *Am. Journal of Potato Res.* **80:** 317-327.

McGee, E., Booth, R. H., Jarvis, M.C. and Duncan, H. J. (1988). The inhibition of potato sprout growth by light. II. Effects of temperature and light intensity. Ann. App. Biol. **113:** 137-147.

Timm, H., Bishop, J.C. and Hoyle, B.J. (1959). Investigations with maleic hydrazide on potatoes I. Effect of time of application and concentration upon potato performance. *Am. Potato Journal* **36:** 115.

Tuyen, T. (2016). Control of Potato Storage Conditions for the Management of Post-harvest Losses due to Diseases. Publ. Canadian Horticultural Council. http://www.academia.edu/15407256/

Section 20.

Seed Potato Production

Introduction

The potato crop is the worlds' most widely grown crop, produced by vegetative propagation. Potato is an herbaceous dicotyledonous plant that is propagated vegetatively through tubers. Vegetative propagation or asexual propagation is the method of reproducing plants by which the new individual arises from a vegetative part of the parent (root, stem, leaf, etc.), and possesses exactly the same characteristics of the parent plant. The potato tuber is a swollen apical part of an enlarged fleshy underground stem and bears a number of nodes or eyes. Each eye carries one or more buds. New plants are produced from the buds on the eyes. Potato plants produced asexually from portions of the, stem, of adult individuals are genetically identical to the parent.

Vegetative propagation can allow a genetically superior plant to produce unlimited copies of itself without variation, with the new plant being always genetically identical to the parent. Genotypes of many crop plants including fruit trees, ornamental plants, grapes and strawberry are also maintained by vegetative propagation.

Vegetative propagation, like many processes, has its advantages and disadvantages. It is beneficial for plants that are well suited for their environment and when the environment is stable. These conditions prevail widely where commercial potato crops are grown.

Remember that asexual reproduction results in genetically identical plants, so these plants must be well adapted to their environment in order to survive. Because asexual reproduction doesn't allow for evolution and adaptations to occur as frequently as sexual reproduction, vegetative propagation confers no benefit on plants that live in changing environments. In unstable environments, plants that are identical to each other may all die out at once, for example, destruction of a potato crop as a consequence of severe *Phytophthora infestans* infestation. When plants are genetically different, which is a consequence of sexual reproduction, some plants may survive in an unstable environment.

The potato (Solanum tuberosum) is an autotetraploid with four sets of homologous chromosomes (n=12). The species contains a high level of genetic variation and hybrids will retain their heterozygous nature due to vegetative propagation. Conventional breeding programmes depend on the production of variation through sexual hybridisation and the subsequent selection of the best recombinant clones for further evaluation and vegetative propagation.

One of the largest constraints to potato productivity worldwide is the inefficiency of the seed propagation system. Access to affordable high quality seed tubers is considered to be the major constraint to potato production in Sub-Saharan Africa, where seed tubers can represent 30-50% of the variable costs of potato production

Advantages and disadvantages of vegetative propagation

Advantages

- The plants are genetically identical and therefore advantageous traits and genetic improvement are fixed.
- The newly generated population is uniform
- Only one parent is required which eliminates the need for special mechanisms such as pollination, etc.
- Plants are able to tide over unfavourable conditions. This is because of the presence of organs of asexual reproduction like the tubers can be stored and protected from otherwise destructive environmental conditions.
- Vegetative propagation is especially beneficial to the farmer; the crop can carry out part of its growing cycle in the store before being transferred to the field.
- The modern technique of tissue culture can be used to grow virus-free plants.

Disadvantages

- Crops grown in this way are usually homogeneous, they are vulnerable to disease
- Systemic diseases are passed between generations
- They are more prone to diseases that are specific to the species. This can result in the destruction of an entire crop.

Seed Certification.

Vegetative propagation causes certain problems of disease incidence in potatoes that are non-existent or of lesser importance in plants reproduced from seed. The high water content of the potato seed tuber (approx. 80%) compared with true seed, leaves it vulnerable to acquiring infection or facilitates the carry over of field-acquired infection from the previous season.

The fundamental objective underlying potato seed certification is to produce a crop of seed tubers, identical for variety to the parent crop and free from seed borne disease and pests so that the commercial crop will not be compromised either for yield or quality.

Potato Seed Certification is a systematic approach for the maintenance of varietal purity, identity and phytosanitary status of seed crops through standards administered by an official certifying agency. Seed certification is a program of documentation, planned production, record keeping, unbiased inspections, and rigid standards to insure the production of high quality seed that is genetically pure. Seed certification is based on the premise that proper identification of varieties is essential to everyone who handles seed—the geneticist, the breeder, the commercial conditioner-distributor, and the farmer.

The certification process must be supported by legislation designed to encourage the production of top-quality seed potato tubers through adherence to rigorous testing and inspection requirements, and through research to improve seed potato quality and testing. Trained inspectors inspect seed fields to make sure they meet the high standards required for Certified seed. Harvested seed lots must pass rigid quality standards. Certified seed, labeled with a distinctive tag, provides a standard for seed quality for ware farmers. Certified seed is then recognized in national and international legislation as seed meeting high standards for genetic purity and quality. It is a fully traceable, guaranteed seed product with superior quality to alternatives and is part of a worldwide quality assurance system. It provides an insurance/risk management tool against sub-standard crop establishment, thus protecting the other investments necessary to produce a profitable potato crop.

The basic purpose of seed certification is to maintain and make available to the ware grower high quality seeds of superior varieties, grown and distributed under restricted conditions as to ensure genetic identity. Through the certification process, the limited quantity of improved seed and propagating material released by plant breeders as new varieties is increased to quantities adequate to meet the needs of the potato industry. The certification staff monitors the field seed multiplication process, removes diseased plants and verifies that the production has met the criteria necessary to protect the genetic identity of these new varieties.

Ensuring varietal purity is of primary driver in seed certification. Other factors such as freedom from diseases are important in providing seed tubers, which the farmer can plant with reasonable assurance of obtaining a good stand of healthy plants of the desired variety without introducing undesirable plants or infecting their fields with soil borne disease.

Plant breeders continue to produce superior potato varieties and seed certification programmes permit the rapid increase of these new varieties and discontinuance of older ones. This encourages the production of ample supplies of high quality seed of superior varieties grown and distributed under the most careful conditions to assure genetic identity and purity

A brief history of seed certification

Seed certification owes it origins to the work of Dr Otto Appel in Germany in 1914 where he sought to control Potato Leaf Roll Virus. A similar programme was established in Scotland in 1914 to control wart disease caused by the organism *Synchytrium endobioticum*. The success of these certification programmes led to the concept being adopted in several countries across many continents. Today, certification provides the basis permitting the widespread movement and trading of seed potatoes both nationally and internationally.

Potato seed certification is the most extensive and long-lived effort in vegetative crop certification and has provided the basis for many more crop certification programmes.

Concepts underlying a typical seed potato certification scheme

Seed certification programs permit the rapid increase and dispersal of new varieties and discontinuance of older ones. Such schemes have been established in countries around the world and are structured to meet legislative, organisational and biological requirements. It might be expected therefore that, while they differ in detail, they share some common characteristics.

The Administrative Organisation

An autonomous organisation, free from outside influence is required to ensure that the scheme functions effectively to formulate realistic crop standards for disease tolerance limits and enforce uniform certification standards in all regions within the country. A legal basis is essential to coordinate and administer the programme, carry out field and store inspections, tagging, labeling and enforce export regulations. There is a financial cost related to seed certification and fees must be agreed and collected as appropriate.

Organisational requirements.

Success is predicated on recruiting and training administrators and technical staff who will organise the work schedules, visit the fields to carry out the evaluations and eliminate the crops that do not meet the requirements set out in the protocol. Field inspection staff must possess the integrity to reject crops, which do not meet the certification standards, regardless of pressure from family, friends wealthy growers or local politicians. The major decisions to grant or withhold certification will be made during this field inspection stage. Only highly trained and experienced staff will possess the skills to successfully identify crop diseases, volunteer plants and varietal off types, based on foliage symptoms. These symptoms will be highly influenced by the environment and the growing conditions in addition to the normal constraints associated with the vagaries of the prevailing weather on inspection day.

Biological requirements

A well-organised seed certification programme will ensure a supply of pure seed with defined quality aspects. Seed certification is built around the primary concepts:

- Superior variety
- Genetic purity
- High seed quality standards
- Disease level tolerances. These will range from zero to agreed maxima.
- Soil testing to establish freedom from infection with soil borne disease and pests.

The concept of limited generations underpins potato seed certification. Breeder's seed is used for the production of foundation seed. Foundation seed produces registered seed, which in turn, produces certified seed. Each generation increase is inspected. Varietal purity is determined by using distinct morphological characteristics of the variety, other varieties are rogued from the production field; the seed is monitored from the field to storage, then onward through the conditioning facility, sampling and labeling. Seed, meeting or exceeding quality standards (tuber size specifications, varietal purity, freedom from disease) is tagged with the appropriate tamper proof certification tag.

Disease and pest threshold levels
The first task of a seed certification organisation is to establish the full gamut of diseases, bacterial, viroid, fungal and mycoplasma-like-organisms, which colonise the potato crop in the area under their control. In addition to pathogen attack, pests also attack the potato crop.

Pathogens can be divided into two main groups: those for which there is zero tolerance because of the severity of the risk and which are tolerated at threshold levels, again governed by the severity of the risk associated with their infection. A classic example of a pathogen, for which zero tolerance would exist, is bacterial wilt (caused by *R. solanacearum*). This is a destructive pathogen, which can survive for an undetermined period in the soil, being able to colonise a range of hosts and is known to wipe out the potato crop at high levels of infestation.

Viruses, while being destructive, have never been recorded to totally destroy a crop, so therefore tolerance values can be set to determine permissible levels of infection at different generations of the seed production cycle.

Soil testing would reveal the presence of cyst forming nematodes or the larvae of Tuber Moth (*Phthorimaea operculella*). Information on the level of soil borne infection would be used in deciding whether to permit a potato crop, destined for seed certification, to be grown on the land.

Cyst nematodes (*Globodera pallida* and G. *rostochiensis*) are serious soil pests in many potato-growing regions throughout the world. Their presence can be detected by taking soil samples and subjecting them to laboratory analysis. Infected fields can be eliminated from the seed certification programme.

Haulm killing to prevent virus infection could be scheduled by monitoring aphid buildup in the growing crop.

Seed tuber quality

In addition to addressing issues of tuber health, a seed certification scheme must also focus on tuber quality. The main topics to be considered here are seed tuber vigour and seed tuber size.

Seed tuber vigour
Seed tuber growth vigour is a function of its physiological age. Vigour can be defined as the potential to produce a well-developed plants in a short space of time. The

relation between the chronological age of the seed and growth vigour relies on several factors, especially storage temperature and cultivar. Physiological age also affects the growth of the tubers, but the response is modified by environmental conditions.
The specialist seed grower seeks to manipulate the number of main stems per hill, as this parameter has the largest influence on tuber size distribution in the offspring crop. A list, comparing the response of various plant metrics of physiological aged and young seed, is presented in Table 1.

Table 1. Characteristics of young compared with old seed

Young Seed	Old Seed
Slow emergence	Rapid emergence
Few main stems per hill	More stems per hill
Low tuberisation period	Uniform tuber set
Low Tuber set	Higher tuber set
Long bulking period	Shorter tuber bulking period
Larger tubers at harvest	Smaller tubers at harvest

Seed tuber size

Seed tuber size will exert its influence on offspring tuber number and consequent tuber size distribution through variation in the number of main stems produced by seed tubers of varying sizes. It is normal practice to plant the mixture of seed tubers graded 35-55mm. With increasing demand to manipulate the size distribution of the offspring crop, many growers now split the seed grade into tubers graded 35-45mm and then 45-55mm. This provides an opportunity to fine tune seed tuber inter planting distance and consequently, the related main stems number.

A standard requirement of potato seed certification schemes is regulation of the upper and lower permitted size limits. The smallest acceptable tubers are generally 30-35mm while 55mm is widely used as the largest acceptable size. Growers wishing to sell potatoes into this market must seek to maximise yield in this size grade. An obvious approach therefore is to attempt to maximise tuber number. Another approach is to manipulate mean tuber size

The size of the seed tubers planted induces significant differences in the number of tubers harvested. Plants established from large seed produce a high number of smaller sized tubers, whereas those established from small sized seed produce fewer, but large tubers. While there is widespread adoption of the 35-55mm size as the ideal value for seed, these values are somewhat arbitrary – yet at sizes above and below these sizes, tubers for seed production becomes non-optimal in terms of maximum obtainable yields. Using seed tubers much larger than 55mm would be difficult to justify in economic terms. Tubers smaller that 30mm may lack the reserves to produce additional stems if the initially formed shoots are damaged by hail or frost.

Plant population density has also been shown to significantly influence tuber number at harvest. Crops established at high mainstem density produce a larger number of tubers than crops established at densities of decreasing order, where the number of tubers will decline, but average tuber size will increase. The highest tuber yields are achieved at medium population density level, followed by plants established at low-density level. Plant population density (as main stems) also affects tuber number, with the highest numbers also achieved by medium to low density. This was due to the availability of adequate space for root and tuber expansion and less competition for light, water and nutrients.

Improving seed tuber quality - positive and negative selection

The potato crop is vegetatively propagated, and this feature has greatly assisted its dispersion to new areas and facilitates its seasonal propagation. A significant problem associated with vegetative propagation however, is seed quality deterioration – widely referred to as 'seed degeneration'. This phrase describes the infection of seed tubers with virus and bacterial pathogens, as a consequence of successive cycles of vegetative propagation,

In the ideal world, certified seed tubers would be available, at prices the grower could afford. In Sub-Saharan Africa, certified seed tubers are not widely available even when growers can afford then. But then, when available, they represent 30-50% of the total cost in potato production. Smallholder farmers in SSA can rarely afford the high price of certified seed and are forced to rely on farm-saved seed. When seed tubers are selected from the harvested bulk of tubers, the primary selection criterion is simply seed size. The phytosanitary status of such seed is often compromised and therefore results in reduced yield, reduced profitability and introduces food and income insecurity.

Positive selection

To address the problems associated with self-supply, neighbour supply or local market purchase of seed potatoes, CIP have pioneered techniques designed to improve the health status of home saved seed tubers. One such example is referred to as "**positive selection**". Positive selection is a simple technique that involves identification, marking and monitoring healthy-looking potato plants during field growth, until they are harvested, the produce stored separately and **the tubers subsequently planted as seed**. It is important to harvest the selected parent plants before harvesting the bulk of the crop for consumption or sale. The simplicity of the technique belies its effectiveness. Researchers have recorded an average yield increase of up to 35% when the progeny of positively selected seed tubers was compared with a crop established using a selection from the harvested bulk of tubers.

Positive selection and bacterial wilt

The major route of introduction of bacterial wilt is through infected seed tubers, but of course it can also survive in the soil. The infected seed tubers may not display the classical symptoms of infection, but when planted, the wilting symptoms appear. Infected plants can be readily identified in a growing crop and when only isolated

plants are present, these must be carefully removed, ash or lime added to the hole and the infected plant material burned.
Positive selection only has a useful role in combatting bacterial wilt when the infection in the field is at a very low level. When infection levels exceed 2%, positive selection becomes more difficult since a plant should never be selected if it is growing close to an infected plant. This means that in fields where the level of infection is high, the possibility of finding 'clean' tubers diminishes.

Positive selection and virus infection
Virus spread starts with infection of the foliage and from here the virus moves to the tubers. All tubers on an infected plant will carry the virus. Unlike bacterial wilt above, virus infection is sometimes more difficult to diagnose in the field. Another comparison with bacterial wilt is that virus infection does not kill the plant but will severely impact on tuber yield. This reduction can range from mild at 5-10% to severe, at 80-90%. Virus transmission is discussed in **Section 11** and aphids are the major source of transmission. Several factors affect the visibility of symptoms in the canopy, from infection type, prevailing weather on the inspection day to crop growth stage. For example, plants showing symptoms of infection with Potato Leaf roll virus are readily visible and such plants can be "rogued out". Viruses that merely induce slight colour changes in infected leaves, are more difficult to detect, unless experienced observers are available. The optimum time of assessment coincides with peak canopy development, i.e. just before the first flowers appear. It is easier to observe symptoms under light cloudy conditions rather than under bright sunlight

Negative selection

Negative selection describes the selection and removal of plants, **which will not be used for seed**. This strategy helps maintain high quality in the seed crop. The technique is not suitable for fields with a high number of infected plants since negative selection will induce an excessive loss of yield, rendering the technique unattractive for smallholder potato farmers.

Central to the success of these selection procedures is growing the crop in an area of low disease pressure, for instance, cooler high altitude areas with low aphid populations. It is essential to state that positive or negative selection techniques are not a substitute for good agronomy practice such as crop rotation and removal of weeds that might act as secondary hosts.

Authorities must seek to make available supplies of disease free, high quality seed to 'flush out' the contaminated material and provide seed growers with clean stock, capable of providing high yield of seed tubers, which in turn will produce high yields of ware tubers for consumption or for sale

WARNING

Certified seed tubers are not guaranteed to be disease free. They are certified to have shown no more than certain low percentages of pest and disorder symptoms during the inspections required by a state's seed certification program. The allowable level of symptom expression for each pest or disorder is called a tolerance level, and these levels vary from state to state.

A zero tolerance exists for certain pests, such as bacterial wilt bacterial ring rot and root knot nematode. To meet these tolerances, seed lots must be inspected at least twice in the field during the growing season and be inspected in storage or at the time of shipment.

Seed Piece Cutting

'Normal' potato cultivars produce a generous number of tubers per plant. Due to a preference for larger size potato tubers in certain countries, markets and processing sectors, specialized potato breeding has resulted in varieties that predominantly produce larger tubers resulting in the prevalence of the need for the acceptance of cut seed. These large tubers are particularly sought after to produce baking potatoes and potatoes for the fresh chip trade. Due to the reduced number of tubers and a mean tuber size distribution weighted towards large, there will be very few tubers in the certified seed grade 35-55mm. The answer to this problem is seed cutting.

Whole versus cut seed: There are several advantages to using whole over cut seed. Uniform lots of small, whole uncut tubers ranging in size from 60 to 110 g can produce plants with:

- High vigour
- Increased stem count
- Increased tuber set
- Uniform tubers that tend to be smaller because of the heavier set
- Less disease

The advantages of cutting seed potato tubers include:

- Advancing the physiological age of the tubers
- Cost benefits for the grower- economise on seed costs
- Convenience in spreading planting workload
- Opportunity to cure under controlled storage conditions
- Provides earlier emergence
- Vigorous early growth and higher plant and stem populations
- Allows for the utilization of varieties that are short in supply, and maximize their use.

However, the performance of cut seed is related to size uniformity. This is a critical parameter to be considered, -in order to maximise harvest yields and ensure uniform planting. Multiple-cut seed pieces may not perform as well as those with only one cut surface. An ideal seed size range is between 40 to 85 grams so producers should manage seed cutting so the average seed piece is 60 g. Specialty market needs may demand different seed sizes and growers should verify these needs before cutting commences. Each seed piece must have at least one eye. Only seed lots of known physiological age should be pre-cut, since precutting ages the seed. Also, the size of a seed piece affects early plant vigour as larger seed pieces emerge faster than smaller ones.

Effect of seed tuber size on seed piece size

Oversize seed tubers result in many cut-seed pieces that are too large or too small. On average, seed pieces cut from large mother tubers (>225g) are not as productive as pieces of the same weight cut from smaller tubers (Fig. 1). Seed pieces cut from larger tubers have fewer eyes and may result in blind seed pieces (no eyes), causing a reduced stand. But the number of eyes and stems produced per seed piece increased as cut seed piece size increased. A seed size range of 45g to 65g is generally the acceptable aim, depending on the variety being cut and the desire number of eyes per seed piece required

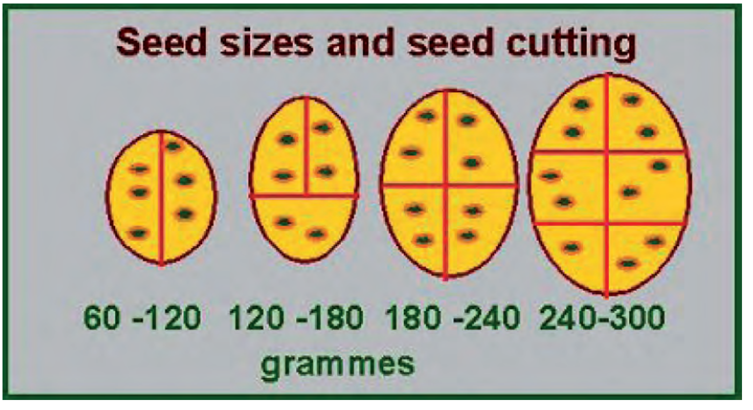

Figure 1. Relationship between seed size and seed piece size.
(Diagram © Aardappfel the Netherlands, With Permission)

Small seed pieces <45g produce weak, unproductive plants. Percent of cut seed pieces that did not produce a plant (blind) was significantly higher between cultivars, especially with smaller cut seed pieces. In one study the 28 g cut seed had 24% blind seed pieces. It is important to eliminate small size cut seed (less than 28 g) and 'slithers' as these do not produce viable plants

Large seed pieces (greater 90 g) are no more productive than ideal (43-85 g) seed pieces but cost more to plant. Clones with low eye numbers produced four times as many blind seed pieces in all size categories as clones with high eye numbers.

If hand cutting is required, the Potato Specialist must demonstrate the proper seed sizes and shapes to the seed cutters.

- No more than 10% should be less than 28g or more than 70g.
- If there are 100 seed pieces in 4.54 kg, the average size is 45g;
- If there are 91 seed pieces, the average size is 50g;
- If there are 80 seed pieces, the average size is 56g.
- Count out 100 seed pieces and weigh them —
- 4.3 kg would have an average size of 43 g,
- 4.9 kg would have an average size of 49 g, and
- 5.7 kg would have an average size of 57 g.

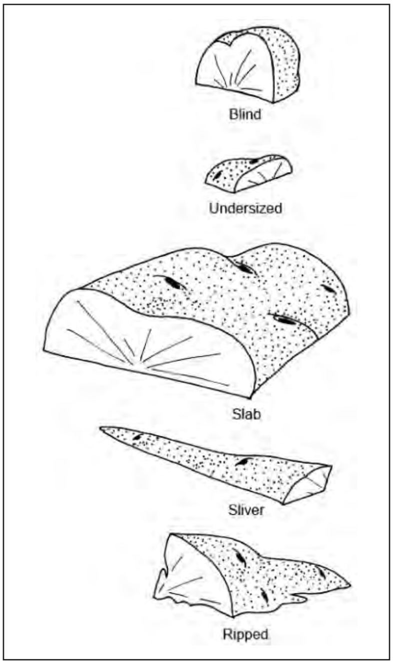

Figure 2. Diagrammatic representation of defective seed piece cutting, yielding waste pieces like slivers or blind
(Diagram, Courtesy: University of Maine Cooperative Extension. With permission)

The cutting process
Cutting seed creates easy entry routes for disease organisms; especially bacteria and cut seed tubers are more susceptible to seed piece decay under extreme circumstances such as temperatures and humidity. Susceptibility to seed piece decay may be variety dependent. Therefore each seed lots should be stored, cut and handled under sanitary conditions. All equipment, storage, tools and pallet boxes that contact the seed potatoes should be sanitized using an approved product. (*A list of useful sterilising agents is presented below*)

Cold seed should be warmed to about 10°C a few days before cutting. Warm seed not only cuts better with less tissue tearing, but also is also more physiologically active and heals faster than cold seed. Seed pieces should have a minimum of cut surface; that is, blocky seed pieces are preferred over 'slivers' and 'slabs' (Fig. 2). Each seed piece should have one to several eyes depending on the variety. Some varieties may have few eyes near the tuber stem ends and produce a high percentage of "blind" (eyeless or budless) seed pieces unless special care is taken. Such varieties may call for larger seed pieces.

Keep the cutting knives sharp to avoid ripping of the seed piece (Figure 2).

Pathogens associated with seed piece cutting
Eliminating cutting reduces the risk of spreading tuber-borne diseases. Since there are no cut surfaces, seed decay is less likely.

Seed piece decay is reduced when seed pieces are planted under conditions that favor rapid suberization; Fusarium cannot infect cut surfaces after they are suberized. Warm the seed tubers to 10°C before cutting, and keep cutting and handling equipment disinfected. Plant when the soil temperature is at least 7°C and when soil moisture is 60 to 80% of field capacity. If possible, avoid irrigation before emergence. When planting conditions are likely to favor seed piece decay, treat cut seed pieces with wood ash or a fungicide, to prevent pathogens invading the cut surface. The fungicides Maneb, Mancozeb, Thiabendazole or Thiophanate-methyl applied immediately after cutting, have been demonstrated to prevent infection.

The percentage emergence may be lower if cut seed is used (due to seed piece decay). In general the percentage of emergence is inversely proportional to the size of the cut tuber pieces.

Another disadvantage of cutting may be the transmission of certain diseases by means of the knife: PVX, PVS, ring rot (*Corynebacterium sepedonicum*), brown rot (*R. solanacearum*), blackleg (*Erwinia carotovora var. atroseptica*).

The following measures are relevant to reduce risks:

- Do not cut seed when there is a risk transmitting of dangerous diseases (contaminated lots).
- Periodically disinfect cutting tools in a 1% solution of calcium hypochlorite.
- Do not cut physiologically old seed.
- Do not use cut seed when soil temperature is high (e.g. 25 C).
- Do not cut seed of varieties susceptible to Fusarium and which are slow in wound healing.

Note. *Cut seed pieces should not be exposed to hot sun or wind for even a short time or they will severely shrivel and may decay (keep cut seed in the shade).*

When possible, seed should be planted soon after cutting into warm (above 7°C), moist but not wet soil. For rapid growth and emergence, sprouts should be "peeping" (slightly enlarged) at planting and physiologically active in preparation for rapid growth and emergence

Wound healing following cutting

Seed pieces, either freshly cut and planted or properly healed before planting, can be just as productive and healthy as whole small seed tubers. Soil conditions at planting are frequently favourable for suberization or healing of the cut surface so that freshly cut seed pieces can be planted directly after cutting. This requires that the cutting operation and the planting operations be synchronized to avoid holding unplanted cut seed pieces in a heap for an extended length of time.

It is safe to cut seed tubers some time ahead of planting if storage conditions promote healing of the cut surfaces.

Either plant cut seed directly in moist soil and cover immediately **or** cut seed prior to planting and store a few days under conditions favourable for suberization.

Wound healing is best accomplished by:

- Holding the cut seed pieces 3 to 5 days at temperatures of 13-18 oC,
- Maintaining a relative humidity of at least 85 percent, and
- Providing good ventilation to ensure sufficiently high oxygen content in the air.

Failure to provide any of these conditions can lead to seed piece decay.
A suggested list of solutions to sterilise cutting knives and surfaces in contact with the freshly cut tubers.

- Quaternary ammonium compounds at 1.6 cups of a 10% solution/45 l water
- Trimethylammonium chloride at 30 g of a 10% solution/9 l water (400 ppm)
- Calcium or sodium hypochlorite in a 1,000 to 2,000 ppm chlorine solution; for example, 4.5 l of 5.25% calcium or sodium hypochlorite (household bleach) /45 l water
- Chloropicrin at 1 to 600 g/30 m3 of space. For storage fumigation, surfaces must be moist for effective control. Use a professional applicator for safety.
- Copper 8--Quinolinolate (Mitrol PQ 57). Use a 5% solution in a 1:99 dilution

Plant disease free seed!
Inspect seed for disease symptoms. Some disease symptoms can be treated, but the presence of others should be grounds to reject the seed.

- If more than 20 small or 10 large Rhizoctonia sclerotia are visible on one side of the seed tuber, consider using a different seed source. Seed with less than 20 small or 10 large sclerotia should be treated before use.
- Seed lots with less than one half of one percent (0.005) of tubers with Fusarium symptoms can be used if the diseased tubers are removed before cutting and seed treatments are used on the remainder of the lot.
- Tubers with five percent or more of the surface affected with silver scurf should not be used for seed. No seed treatment has been shown to be highly effective in controlling the pathogen that causes this disease.
- Seed lots with more than one percent of the tubers showing blackleg symptoms or soft-rot symptoms should not be used. The presence of pinkeye, early blight or late blight lesions on the tubers could act as inoculum for new crop infections. This seed should not be used.
- Know the source and history of a seed lot and try to avoid those that have had heavy infection with Verticillium spp.
- Seed-borne scab can contaminate a field without a history of scab and should be used only in fields with a history of scab. Seed with scab should be treated to control this disease. High levels of scab on the seed warrant rejection of the seed lot. Adjusting pH of the fields greatly aids in the control of scab.
- Generally, a "five percent rule" applies with seed lots. A seed lot with five percent or more total defects is too high to use. Seed is a large investment. Each grower should strive to use the highest quality seed obtainable.

Soil Free Propagation of Potato Seed Tuber.

Introduction

Potatoes are susceptible to a variety of diseases that reduce yields and tuber quality. This is usually because pathogens accumulate in successive generations of tubers and also in the soil, if there is frequent cropping. Repeated field multiplication of vegetatively propagated seed result in build-up of seed-borne diseases; if the cycle is not broken, there can be subsequent dissemination to new fields. Unless good quality seed is planted, attempting to grow a high yielding crop of potatoes, that meets market requirements, is futile. A pre-requisite of sustainable potato production is the supply of a constantly renewed supply of disease-free planting material – known as 'flushing out'. A major innovation for the potato industry was the widespread adoption in the 1970s of tissue culture – or micro propagation - as a means of multiplying disease-free plants that can then be used to produce healthy seed tubers for farmers.

Background

Potato is an herbaceous dicotyledonous plant that is conventionally propagated vegetatively through tubers. However, during this vegetative propagation, seed tubers can become contaminated with different diseases resulting in poor quality and reduced yields.

In tropical and subtropical areas it is difficult to produce seed tubers of potato due to lack of appropriate storage facilities and transport, as well as the presence of active virus diseases vectors. Through tissue culture, seed growers have access to an efficient method for production and rapid propagation of pathogen-free material.

Micropropagation

Micro propagation provides an alternative to conventional propagation of potatoes. *In-vitro* propagation methods, where meristem tips, nodal cuttings and micro tubers are employed, provide a reliable procedure to ensure that the genetic integrity of the multiplied clones are maintained.

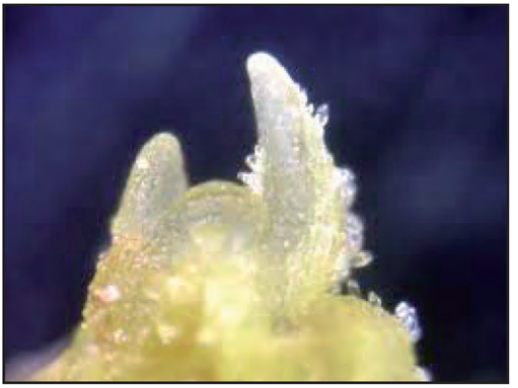

Figure 3. Potato meristem, apical dome and leaf primordia
(Photo © Taiwan Agric. Res. Inst. With permission)

The micro propagation techniques

Tissue culture

Meristem cells possess many features, which facilitate their use in regeneration: they are undifferentiated, have thin walls, are more isodiametric (they have a near equal diameter in all directions) in shape and contain more protoplasm. Meristem-tip culture is predicated on the excision of the organized apex of the shoot from a selected donor plant for subsequent *in vitro* culture. In potatoes, the normal source is sprout tip meristem. The success of this step relies on the conditions of culture being regulated to allow only for organized outgrowth of the apex directly into a shoot, without the intervention of any adventitious organs. The excised meristem tip is typically small (often <l mm in length) and is harvested by removing it, using sterile dissection, under a microscope. The explant comprises the apical dome and a limited number of the youngest leaf primordia (Fig. 3); it is important not to include any differentiated provascular or vascular tissues.

A significant advantage of utilizing such a small explant is that is presents an opportunity to exclude pathogenic organisms that may be present in other parts of the donor tissue. A further advantage is the technique facilitates genetic stability since plantlet production is from an already differentiated apical meristem and it allows avoiding propagation from adventitious meristems. Through achieving shoot development directly from the meristem, this avoids callus tissue formation and adventitious organogenesis, which ensures that genetic instability and somaclonal variation are minimized.

When the donor tissue is free from virus infection (Fig. 4) the simpler technique of shoot-tip culture will be suitable for plant propagation. Here the explant still takes the form of a dissected shoot apex, but it can be larger, which is easier to remove and contains a relatively large number of developing leaf primordia. Then the development *in vitro* can still be regulated to allow for direct outgrowth of the organized apex.

It is feasible to employ meristem culture under conditions where the donor plant is infected with viral, bacterial, or fungal pathogens, whether or not symptoms of the infection are visible. The eradication technique is predicated on the unlikelihood that

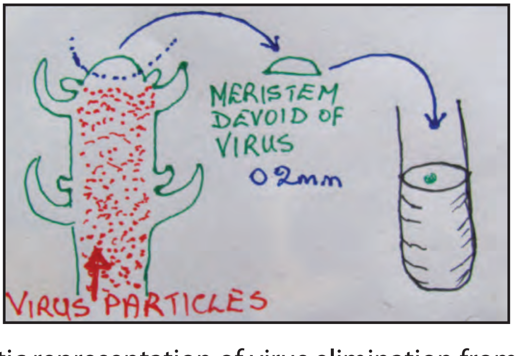

Figure 4. Diagramatic representation of virus elimination from a potato meristem, using tissue culture

the terminal region of the shoot meristem, above the zone of vascular differentiation, contains pathogenic particles. By removing a very small explant from an infected donor and then raising it *in vitro*, affords the possibility that the derived culture will be pathogen-free. When the output of these cultures, are screened and certified, they can form the basis of a guaranteed disease-free stock, which can then be used for further propagation.

When the meristem-tip technique is linked with heat therapy, this will improve the efficacy of disease elimination; also antiviral, chemotherapeutic agents may be investigated. The plantlets derived from meristem-tip culture will produce axillary buds of *in-vitro* and these may also be used as a secondary propagule. This is undertaken when the *in vitro* plantlet has developed expanded internodes, and then it may be divided into segments, each containing a small leaf and an even smaller axillary bud. By placing these nodal explants on fresh culture medium, the axillary bud will grow directly into a new plantlet and now the process can be repeated. The addition of this technique to the original meristem-tip culture technique provides a high propagation rate, and combined, the techniques constitute the basis of micro propagation.

Meristem tip culture

The method can be described briefly as follows: a thin slice of meristematic tissue is taken from the bud of a sprout and transferred onto culture medium, where it will ultimately grow to generate a new plant (Fig. 5). The exact method varys according to the treatment of sprouts that are used prior to the cultivation of meristems, like thermotherapy, chemotherapy, x-rays etc. The procedure permits options for the choice of meristematic tissue; it can be excised from sprout or shoot; it can be lateral or apical.

Figure 5. In-vitro propagation of potato meristem tip.
(Photo © Dr, C. Lee, NDSU Plant propagation. With permission)

Meristem culture, coupled with thermotherapy, has become a useful and successful tool for eliminating virus from infected plants; it has been successfully employed in potato for the development of virus free plants. Since meristem tips are largely free from viruses, this tissue is suitable for the generation of virus free plants.

The use of micro propagation techniques permits rapid multiplication of disease free material in useful quantities. In addition, this in-vitro technology can be used to conserve, store and distribute potato germplasm, whether in the form of breeding lines, new varieties or micro tubers. Tissue culture facilitates very rapid propagation. Under traditional propagation, one tuber yields approximately 8-12 seed size daughter tubers in one growing season. By contrast, employing tissue culture, it is possible to produce 100,000 identical disease free plantlets in eight months; when these are transferred to the field, they could produce up to 50 MT of potatoes.

The Virus Problem

Virus and viroid diseases are among the major significant disease in potato seed production and they can be eliminated through certification. They include: Potato leaf roll virus (PLRV), Potato virus A (PVA), Potato virus M (PVM), Potato virus S (PVS), Potato virus X (PVX), *Potato virus Y* (PVY) and *Potato spindle tuber viroid*(PSTVd).

The most common viruses affecting potato throughout the world are PVY, PVX and PLRV. The presence of viral disease is an important reason contributing to low yield of potato varieties; where infection by some viruses can induce a yield reduction of up to 75%. Research results have established that PVX may cause yield reduction of 15-30%; while PLRV and some strains of PVY frequently reduce tuber yield by 50-80%. The first objective therefore of a successful seed propagation and certification is to produce tubers free from virus infection.

Soil free culture

Two main systems of soil free culture are in common use, hydroponics and aeroponics. Hydroponics includes nutrient film technique (NFT) and deep flow technique (DFT), where the roots are bathed in varying arrangements of a circulating nutrient solution. Under aeroponics the roots are suspended in air and regularly exposed to nutrient solution as a mist of fine droplets. This provides the advantages of a soil less culture under a growth-controlled environment. Minitubers are the progeny tubers produced after *in-vitro* derived plantlets have been planted out and allow to grow to maturity. The term refers to their size, and they represent an intermediate option: they are smaller than conventionally grown seed tubers but larger than in-vitro tubers (or micro tubers) produced under aseptic conditions on artificial media.

A study to compare the productivity performance of NFT, DFT and aeroponics illustrated significant differences attributed to the diverse plant densities facilitated by the three systems; these being 6.25 (NFT), 11 (DFT) and 17 (aeroponics) plants per m^2.

Aeroponics requires the spraying or fogging the roots of the plants with a nutrient solution, at precisely timed intervals. The plants are usually housed in a box like structure (Fig. 6), with the leafy part of the plants separate from the roots. Normally the roots are fully exposed (Fig. 7) and sprayed according to a timed schedule with microbursts of atomized nutrient solution.

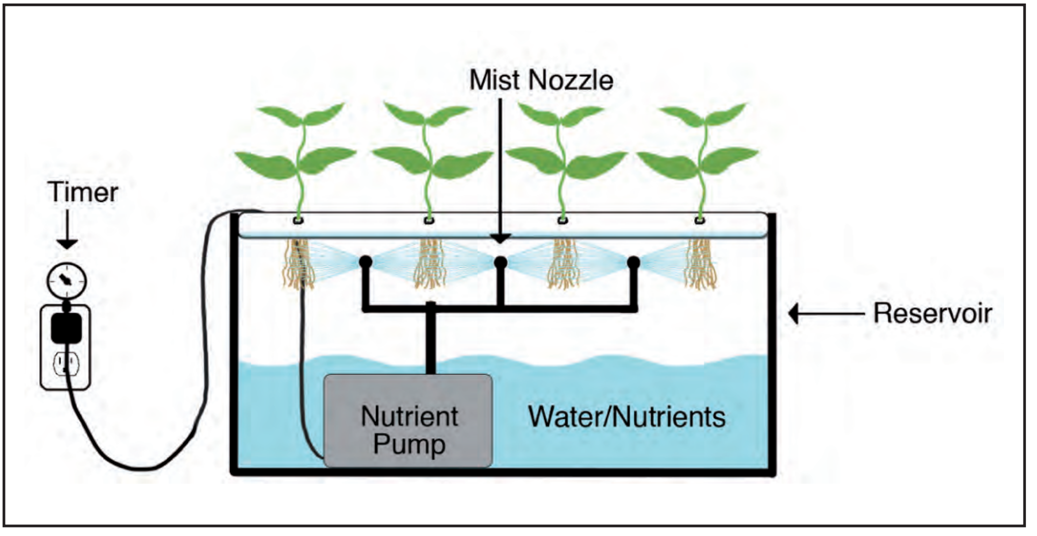

Figure 6. Diagrammatic representation of an aeroponic minituber propagation system. (Diagram © Green desert.org, With permission)

The nutrient solution fog is generated by pumping the liquid through nozzles located beneath the cover of the chamber and close to the roots, using an electrically powered pump. The choice of misting frequency and duration will be dictated by each unique set-up. Typically the aeroponic system is calibrated to mist for 5 min at 15 min intervals, but published details describe systems that mist for intervals upwards from 10 s at 20 min intervals. The draining solution is collected at the base of the structure and flows back into the reservoir tank by gravity.

The nutrient solution must be monitored throughout the cultivation process in order to ensure the proper growth and development of the plants. However, it is only feasible in practice to measure the total concentration of the salts rather than their individual concentrations. Monitoring is accomplished using an electrical conductivity meter and a pH meter. Conductivity should remain within the limits of 2-3 mS cm^{-1} while pH should be in the range 5.5-6.0. Values of nutrient pH above 6.0 may reduce the absorption of micronutrients and promote infection by *Streptomyces scabies*, which is a common potato disease. It is possible that the concentration of salts could become unbalanced during the cultivation process due to differential absorption of nutrients by the roots. In order to overcome this problem the nutrient solution in the reservoir should be replaced every 30 days

Figure 7. The tubers form on the stolons. (Photo © CIP, With permission)

Figure 8. Upper view of aeroponics system - the canopy and minitubers harvested per plant (Photo © CIP, With permission)

Advantages of this technology:

- Through the conventional system, 3-6 mini-tubers per plant are obtained while through the aeroponics technique, a yield of 80-100 tubers per plant can be obtained.
- The aeroponic tubers grow roots, hanging in complete darkness in a compartment (as illustrated above) and are nourished by a spray system. They are free from infectious disease and produce up to 20 times more seeds than conventional techniques.
- The technique needs lesser number of generations of seed potato multiplication in the field, thus lowering costs.
- The seeds can be harvested at any seed size – from 5 to 30 grams – since the fertilizing sprays that are applied to the roots allow the plant to grow without

interrupting its vegetative cycle of up to 180 days. Again, this is not possible with conventional techniques.

- This technique can lower costs by eliminating some generations of multiplication compared to the conventional method.
- The cost of growing a tuber using aeroponics is about one-quarter the cost of a conventionally grown tuber.
- This new technology offers higher yields per plant, and, in the long-term, at a significantly lower cost. Aeroponic systems require much less water and fewer fertilizers than conventional systems-
- As the seed tuber roots are suspended in air, the aeroponic system promotes excellent circulation of air, which strengthens the roots.
- Aeroponics system provides precise plant nutrient requirements for the crop, thereby reducing fertilizer requirements and minimizing the excessive fertilizer residues moving into the subterranean water table.
- Aeroponics has a number of potential attributes to make seed potato production more efficient. The technique also has very low requirement in terms of space as the mini-tubers are multiplied in greenhouses.

Note: *If this technology is to yield clean tubers, there is need to invest in manpower since aeroponics operations need knowledge, skills and dedication. Unless stringent precautions are taken, pathogens can invade and negate all the hard work.*

Producing disease free tubers – in brief

- Meristems, free from viruses and other pathogens, can be produced by holding sprouting tubers in a controlled environment at high temperature (thermotherapy) (Fig. 4).
- The disease-free shoot tips of the plants are then placed on a standard nutrient medium in glass containers in a completely sterile laboratory environment.
- The tips develop into plantlets that are then transferred to either a greenhouse or a field protected from insect pests,
- The multiplication process can be speeded up by the use of cuttings – the plantlet is subdivided into several single-node segments, each with an axillary bud, which will give rise to another plantlet
- In a green house, the plantlets grow at the same rate as normal potato plants but produce smaller tubers (called "mini-tubers").
- After harvesting, mini-tubers need to be stored at low temperature. After about 45 days – and for a period of up to seven months thereafter - they can be moved to a warmer environment to induce sprouting.
- Once planted, they go on to produce normal-size, disease-free seed tubers ready for delivery to farmers.

Summary

- Vegetative propagation is the method of reproducing plants by which the new individual arises from a vegetative part of the parent and possesses exactly the same characteristics of the parent plant.
- A potato seed certification scheme seeks to produce a crop of seed tubers, free from seed borne disease and pests so that the commercial crop will not be compromised either for yield or quality.
- The certification process must be supported by legislation and inspection requirements, to encourage the production of top-quality seed potato tubers
- Seed tuber vigour and seed tuber size have a significant impact on crop performance.
- Seed can be planted whole or after cutting – both systems have advantages and disadvantages.
- Aeroponics can rapidly produce a high yield of clean minitubers

Sources accessed in the preparation of this section.

Haapai, T. (2008). Production of disease free seed tubers. Publ. FAO http://www.fao.org/potato-2008/en/potato/seedtubers.html

Masarirambi, M.T., F.C. Mandisodza, A.B. Mashingaidze and E. Bhebhe, (2012). Influence of plant population and seed tuber size on growth and yield components of potato (*Solanum tuberosum*). Int. J. Agric. Biol., **14:** 545–549

Rosenberg, V., Tsahkna, A., Kotkas, K., Tähtjärv, T., Särekanno, M. and Liiv, K. (2010). Somaclonal variation in potato meristem culture and possibility to use this phenomenon in seed potato production and breeding. *Agronomy Research* **8:** 697–704.

Wiersema, S. (1985) Physiological development of seed tubers. Technical information Bulletin 20. International Potato Centre Peru.

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John J. Burke worked in the agronomy section of the Teagasc Crop Research Centre at Oak Park, Carlow, Ireland. He holds a M.Agr.Sc. from the University of Melbourne, Australia and a PhD from the National University of Ireland. Now retired, he is engaged in volunteering work as a Potato Agronomist with the Irish NGO, Vita.