INVESTIGATING PLANTING ENVIRONMENT AND SEED PHYSIOLOGICAL AGE INTERACTION ON POTATO CROP GROWTH

By

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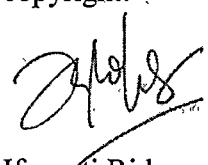

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Abstract

Seed tuber physiological age is known to influence a range of important growth processes in potato including early vigour of the plant, stem number per plant, hence tuber size distribution, time to emergence and the rate and duration of canopy cover rate of the plant. There is also an indication in published evidence to suggest that the expression of the seed tuber physiological age effects is modified by planting environment and varies with genotype. Furthermore, current process-based potato models do not capture the effect of the seed tuber physiological age and the interaction with planting environment. This reflects the lack of understanding and quantification of the effect of physiological age on potato growth. This thesis reports on physiology studies to investigate the effect of seed tuber physiological age and planting environment on stem number and component processes of pre-emergent growth and canopy development for important commercial cultivars of potato. The resultant findings are incorporated into a process-based potato model.

Investigation of a production dataset collected from commercial potato paddocks in northern Tasmania showed that tuber size distribution was correlated with stem number per plant. The investigation also showed that planting environment (i.e. location, sowing date and soil type) varied with stem number. A follow-up controlled-environment trial provided further confirmation of the interaction between seed tuber physiological age and planting environment and that the response varies with genotype.

Currently, the lack of any reliable measure of physiological seed age makes it difficult to develop response functions that can be incorporated into process-based models. With this in mind, a study was conducted to explore the possibility of using mitotic index as an indicator for tuber sprouting pattern as affected by seed tuber physiological age. Physiologically older tubers were found to have a higher mitotic index than younger tubers. However, mitotic index of the eye bud cannot be used to explain the sprouting pattern of the seed tuber having different physiological ages. Sprouting pattern was controlled by a correlative inhibition and availability of soil water.

Pre-emergent growth of sprouts after planting was characterised by an initial period of slow growth (lag phase) followed by rapid linear growth. The duration of the lag phase was strongly influenced by temperature. Linear growth of the longest sprout was significantly affected by the interaction between temperature and water potential and varied significantly between cultivars.

Physiological age of the seed tubers was found to have a significant influence on the canopy development of potato. Plants grown from physiologically older tubers were characterized by more branching on the main stem nodes and smaller individual leaf size. Leaf appearance rate was affected significantly by seed physiological age with the response varying with cultivar. In Russet Burbank, leaves generated from physiologically older seed appeared at a faster rate (39.5 °Cd per leaf or 0.025 leaves per day degree) than leaves from physiologically younger seed tubers (51.2 °Cd per leaf or 0.02 leaves per day degree). No significant difference was found between treatments for Atlantic although the first leaf in plants from older seed reached full size earlier (46.9 °Cd) than plants from younger seed tuber (75.9 °Cd). Seed tuber physiological age did not significantly affect the leaf senescence rate. However, senescence commenced earlier in plants derived from older seed tubers.

The results from the physiology studies were incorporated into a new process-based growth and development model for potato for use within the APSIM modeling framework. A conceptual model was developed for the relationship between seed physiological age, soil moisture and temperature conditions at sowing and stem number. The complete potato model (APSIM Potato) was calibrated for leaf and stem biomass, tuber yield and phenology against a dataset collected from commercial paddocks in northern Tasmania and then validated against a larger independent dataset (48 paddocks) covering a wide range of growing environments. The model was found to adequately predict tuber yield ($R^2 = 80\%$ for 48 observed vs predicted plot).

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Table of contents

List of Tables

List of Figures

List of Plates

Chapter 1 Background

As the following text will illustrate, potato is an emerging crop in Indonesia, grown primarily by smallholder farmers with low to moderate input levels (fertiliser, herbicides etc.) and producing sub-potential yields. In contrast, Tasmania is one of the largest producers of potato in Australia with production characterised by high input levels and high yields. Consequently, it is felt that there are potential synergies and future potato research and development collaboration opportunities between these two industries. The other key imperative for this study is a requirement from the funding agency (Australian Centre for International Agricultural Research, ACIAR) that the research undertaken benefit both the author's home country (Indonesia) and the donor country (Australia).

Worldwide potato production trends

Potato (*Solanum tuberosum* L.) originated in the Andes mountains of South America and has been widely cultivated all over the world. It has a very important place in the diet of people in Europe, America and Australia and it is the fourth most important food crop in the world after maize, wheat and rice. Since the 1990s, there has been an increase in demand and consumption in the developing countries of the world to the extent that by 2005 these countries were the biggest potato producers in the world (FAO 2007). The increase in production in developing countries is mostly due to an increase in harvested area. About one third of worldwide potato production occurs in China and India. However, yield recorded from these developing countries is about half of that recorded in the developed countries (FAO 2007). The increase in world population will present a number of challenges to potato production in the future. Modernisation and the demand for 'convenience food' are shifting consumption from fresh product to processed product, especially in the developing countries (FAO 2007). In order to meet this increase in demand it will be necessary to both increase yield and the area under production.

Australian potato production

Potatoes are one of the most important vegetable crops in Australia, accounting for 43% of total national vegetable production in 2005/06 (ABS 2007). The main production areas in South Australia (10,686 ha), Victoria (8,403 ha) and Tasmania (6,717 ha), cover about 75% of the national potato crop (AUSVEG 2007). National production totals over the past five years have varied in response to fluctuations in total area planted across the country (Figure 1.1) (ABS 2007).

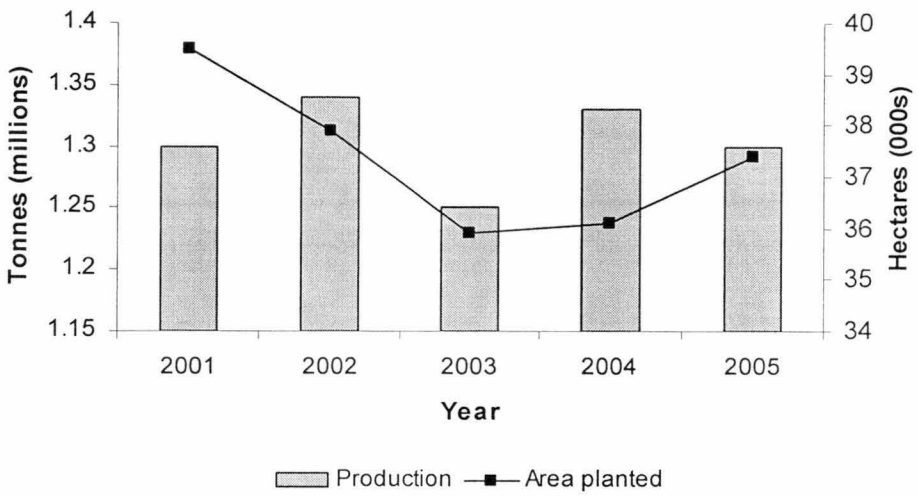


Figure 1.1. Annual production of potato and area planted in Australia from 2001 – 2005 (ABS 2007).

The main potato growing areas in Australia are in the wet temperate coastal regions of northern Tasmania, Victoria and South Australia. These areas have cool summers, annual rainfall of 800-1000 mm and relative freedom from frost (mean annual maxima of 18-20 °C, minima 7-10 °C). Management typically involves high inputs of fertilizer and irrigation and the use of a variety of herbicides and pesticides. Potato is usually grown in rotation with other vegetable, cereal, pastoral and industrial crops.

Potatoes are grown for the processing (56%), fresh (36%), and seed (8%) markets (AUSVEG 2006). Australia is becoming increasingly reliant on imported processed potato product (Figure 1.2) with the net value of imports more than doubling over the past 7 years. During 2006-07 the total imported tonnage rose by 55%, most in the form of frozen processed potato (AUSVEG 2007). The increase in imported product is due to lower production costs in other production areas, mainly Asia and New Zealand and rising costs of production are impacting the competitiveness and

profitability of the Australian potato industry (FAO 2007; AUSVEG 2006). In 2007, imports of frozen product from New Zealand increased by about 85% (AUSVEG 2007). In order for the Australian industry to maintain market share it must improve production efficiency and product quality and reduce production costs.

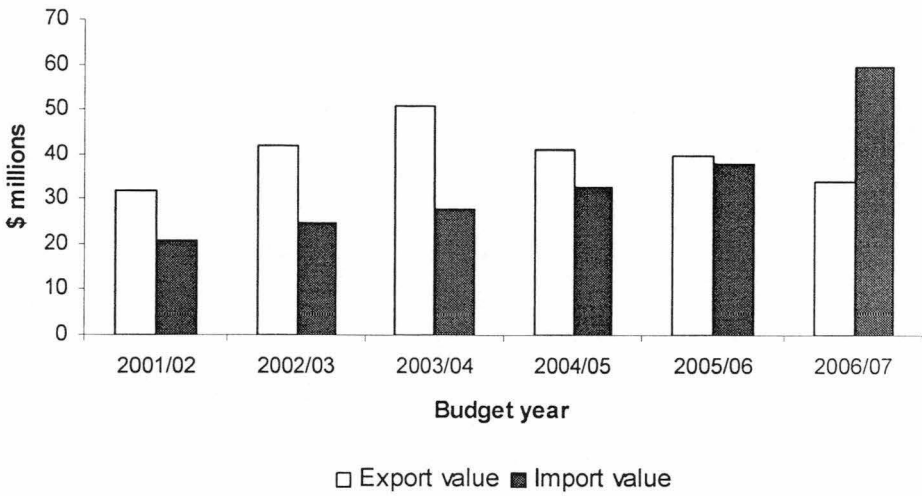


Figure 1.2. Annual values of potato exports and imports for Australia (AUSVEG 2007).

Key constraints in the potato industry include inefficient water and nutrient use, non-uniform quality and a range of disease and pest limitations (Simplot 2007). Potato production in Australia relies on supplementary irrigation to overcome rainfall deficiencies during the growing season. Improved irrigation infrastructure and scheduling that is able to deliver the right amount of water at the right time together with other water-saving agronomic practices/technologies are critical to improving water use efficiency, yield and reducing irrigation costs (Stevens *et al.* 2000). Key quality issue is uniformity of tuber size. This can be manipulated to some extent by changing the stem density and ensuring stress-free growing conditions, especially during tuber formation and growth (Struik and Wiersema 1999). Stem density is strongly influenced by seed tuber physiological status (Struik and Wiersema 1999) and affects both the number of tubers per plant and the tuber size distribution (Knowles *et al.* 2003).

The presence of pests and diseases during the growth and development of potato may lower yield and reduce the marketable tuber yield. Common scab disease is known to be the greatest economic constraint currently facing the Australian potato processing

industry (Wilson *et al.* 1999). Other pests and diseases faced by the industry include *Rhizoctonia*, eelworm/nematode, potato moth/grub, pink rot and tuber rot (Simplot 2007).

Indonesian potato production

In Indonesia, potato is the second most important vegetable crop after cabbage, and recent figures indicate that potato production in Indonesia has been growing significantly both in area and yield (Table 1.1, Biro Pusat Statistik (BPS) 2007). Between the 1980s and 1990s there was an 80% increase in production area from 30,000 ha to 50,000 ha (Gunawan 1997). The gains in both area and yield were promoted by the food diversification program implemented by the Indonesian Government which commenced in 1979 to counter the rising price of rice. In recent years however, national production has experienced a plateau (Table 1.1) in response to the restricted availability of suitable land and a range of agronomy issues related to declining soil fertility, potato disease and shortage of good quality seed (Adiyoga *et al.* 1999).

Table 1.1. Annual harvest area, production and yield of potatoes in Indonesia.

Year	Area (ha)	Production (t)	Yield (t/ha)
2001	55 971	831 140	14.8
2002	57 332	893 824	15.6
2003	65 923	1 009 979	15.3
2004	65 420	1 027 040	16.4
2005	61 557	1 009 619	16.4
2006	59 748	1 011 911	16.9

Source: BPS Statistics Indonesia 2007

Recently, rising per capita income and urbanization in Indonesia has resulted in growing demand for fast food (especially French fries) and other processed potato products such as potato flakes, potato flour and starch (Agri Source Ltd. 2004). This increasing demand, coupled with restricted local production, make Indonesia a net importer of potato products. Furthermore, farmers often fail to meet industry requirements in terms of quality, quantity and the scheduling of supply (Adiyoga *et al.* 1999). In order to meet the growing demand, potatoes are planted throughout the

year in some regions of Java and Sumatra. However, this continuous cropping pattern brings the risk of higher pest and disease incidence. To counter this constraint, other crops such as cabbage are often grown in rotation with potatoes which further lowers the capacity to satisfy market demand. Compared to Australia, potato production is less intensive with fewer fertiliser, irrigation and chemical inputs. Production is primarily rainfed with irrigation restricted to the larger producers. Potato is produced in the more elevated, cooler areas of Indonesia above approximately 1000 m above sea level. The Pangalengan district of West Java produces the highest yield of potato in Indonesia followed by North Sumatera, Central Java and South Sulawesi. The largest area of potato production is in Central Java (Batur and Dieng district).

An important consideration for the Indonesian industry is how to increase productivity in the area that is currently planted. Key constraints to increasing productivity are water and nutrient supply (W Mustafa; farmer in West Java 2005, pers. comm., 4 March; H Rapi; farmer in South Sulawesi 2005, pers. comm, 30 March). In some parts of Indonesia, such as Sulawesi, potato is usually planted at the peak of the wet season between December and January in order to ensure an adequate water supply. However, this cropping pattern also coincides with high pest incidence and increased risk of disease.

Hence, in both Indonesia and Australia, potato consumption, especially of processed product, is increasing and there is a growing reliance on imported product. The ability of local producers to meet this imbalance is being hampered by a range of production constraints/challenges related to nitrogen and water management, disease and land availability.

Role of simulation modelling

Process-based simulation models that capture the key crop growth and development responses to climate, management and soil variables have been successfully used across a range of agricultural enterprises to explore the impacts of, and to identify 'best-bet' options for a range of management variables, including water and fertiliser (Keating *et al.* 1999; Bowen *et al.* 1999; Farre *et al.* 2000). Furthermore, such models have been used to explore land suitability issues (Carberry *et al.* 1992;

Haverkort 2004). Such modelling tools can also be used to extrapolate site and season specific results to other environments; as a research tool to aid in the interpretation of experimental data and responses; as a tool for learning/training to identify knowledge gaps; and to prioritize research investment and inform government policy.

Current potato models – strengths and weaknesses

The development of potato models has progressed steadily over the past 30 years since the development of the first comprehensive potato model by Ng and Loomis (1979, 1984). Currently, there are two widely used potato models, SUBSTOR (Ritchie *et al.* 1995) and LINTUL-POTATO (Kooman and Haverkort 1995). These two models have been used across many countries and for various applications (Bowen *et al.* 1999; Mahdian and Gallichan 1997; Shae *et al.* 1999; Caldiz *et al.* 2002, Hijmans *et al.* 2003).

The suitability of these modelling platforms in exploring production and system issues in Australia and Indonesia is constrained by a number of factors including:

1. Restricted capacity to simulate the broad range of management options for potato based cropping systems in these two countries. In Australia and (to a lesser degree) Indonesia, potato is grown as part of a crop rotation and as such, is influenced by previous crops and influences following crops via residual soil effects. Consideration of these broader system interactions requires the integration of the crop models into a broader farming systems modelling framework. Such capability exists in the APSIM (Agricultural Production System Simulator) systems modelling framework developed by the Agricultural Production System Research Unit (APSRU). This framework consists of a library of individual modules that simulate the different management, biophysical and environmental components of the farming system and their associated interactions (Keating *et al.* 2003). Until recently, APSIM crop model development has focussed on grain and forage species with little consideration of vegetable crops.

2. Restricted ability to simulate certain important physiological processes relating to stem number, physiological age, tuber size distribution, pre-

emergent growth and leaf growth. A key determinant of potato crop quality is tuber size distribution, especially in crops grown for processing. Tubers that fall outside the marketable size range are rejected with resultant price and income penalties which could be detrimental to small holder farmers such as in Indonesia. While the key physiological drivers of tuber size distribution are reasonably well understood (Struik and Wiersema 1999), currently available potato models do not effectively simulate this variable. It is known that tuber size distribution is closely related to tuber number per plant which is determined by stem number per plant (Haverkort *et al.* 1990). Stem number per plant is, in turn, influenced by the physiological age of the planted seed tuber (Knowles *et al.* 2003; Struik *et al.* 2006). A reliable means of simulating tuber size distribution would represent a significant advancement in potato simulation capability and might potentially enable the exploration of options for optimising tuber size.

Pre-emergent growth is known to be influenced by planting environment especially soil temperature (Sale 1979). However, other environmental factors during planting such as moisture condition and the physiological age of the seed tubers may also alter the growth of sprouts after planting (Firman *et al.* 1992). These factors are not captured within existing potato models. Improved understanding of how these factors interact to affect pre-emergent growth may enable the development of a more reliable component model for pre-emergent growth. Similarly, the simulation of leaf growth and potato canopy architecture is simplified in current models. The models do not take into account the effects of seed tuber physiological age, genotype and nutrient status on leaf growth (Vos 1995; Firman *et al.* 1991, 1995).

3. Lack of parameterisation/validation for the specific genotypes, management and climate conditions prevailing in Indonesia and Australia. To the best of our knowledge, the leading potato models have not previously been applied in Australia and Indonesia and hence have not been parameterised/validated for the genotype, management, climate and soil conditions prevailing in these countries.

Thesis objectives

The objectives of the study reported in this thesis are as follows:

1. To conduct a broad range of physiological studies to address recognised knowledge gaps in the areas of stem number production, tuber size distribution, leaf area production and pre-emergent growth. A common thread through these studies is the effect of physiological age and its interaction with growing environment;
2. To develop process-level models that capture the key findings from the physiology studies;
3. To incorporate these process level models into a new growth and development model for potato suitable for systems analysis in Australia and Indonesia;
4. To validate the new potato model

Thesis Structure

Chapter 2 provides a background to the study and a detailed review of relevant literature. Chapter 3 investigates selected responses within a production database of the Tasmanian potato industry. Chapters 4 and 5 report on physiological investigations relating to the interaction between seed tuber physiological age and planting environment on stem number production. Chapters 6 and 7 report on studies into the effect of physiological age on pre-emergent and leaf growth. Chapter 8 describes the parameterisation and validation of the new APSIM potato model. The final chapter discusses and integrates the results from the physiology and modelling studies.

Chapter 2 Literature review

The role of simulation models in decision support and system understanding

Process-based simulation models provide a framework for capturing and integrating current understanding of crop growth and development processes and related interactions with other components of the farming system including soil, climate and management. This capacity allows the models to be used to assist in exploring a range of complex issues in agricultural production systems (Penning de Vries and van Laar 1982).

As a 'snapshot' of the current state of physiological understanding, crop models serve to identify knowledge deficiencies. Models can potentially quantify the impact of, and sensitivity to, these knowledge gaps and in doing so, help to prioritize research activity. For example, a modelling study by Farre *et al* (2000) found that a decision support tool for maize production was unable to adequately predict irrigation responses due to the inability of the parent model to predict the effect of drought on leaf senescence and canopy architecture. This formed the basis of future research investment in order to address these knowledge gaps.

Dynamic, process-based models provide a means of extrapolating site and season specific results to other environments. Field results, by their very nature, are specific to the climatic, management and soil conditions under which they are conducted. Through the use of long-term historical climate records and site-specific soil characteristics it is possible to extrapolate the results both geographically and temporally, thus increasing their value and applicability. Haverkort and van Haren (1998) describe this capacity when they used a potato crop model to examine the degree of adaptation of some potato cultivars and new genotypes to a range of contrasting growing areas and seasons around the world.

Simulation models provide a rapid, cost effective way of assessing responses to changes in management and the growing environment and, where there is sufficient confidence in model performance, identifying best-bet management options from economic, environmental or other imperatives. Field trials are both time-consuming and expensive to conduct and because of this, difficult choices need to be made in

terms of which treatments are going to be prioritized. Furthermore, as stated above, the results are specific to a given, narrow set of conditions. Modelling provides a means of rapidly screening a wider range of potential treatments with a view to short-listing the most interesting options for in-field assessment (Probert *et al.* 1997; McCown *et al.* 1996).

In addition, the modelling of trial or field results will often contribute valuable insights into the mechanisms underlying measured responses. Often the variables that are responsible for these mechanisms are either too expensive or impossible/difficult to measure in the field (Cheero-Nayamuth *et al.* 2000). As an example, Spitters and Schapendonk (1990) used a crop growth simulation as a tool to gain insights into the morpho-physiological components of drought tolerance in potato and used this knowledge to develop improved breeding strategies for the crop.

Dynamic, process-based potato models – status, strengths and shortcomings

A brief history of potato modelling

The development of potato models has been well documented in the literature over the past 30 years (reviewed by Kabat and van den Broek 1995; MacKerron 2007; Marshall 2007). Potato modelling work was started at the end of the 1970's by Hartz and Moore (1978) who developed a prediction of final yield of potato based on regression of temperature and insolation data. In 1979, an empirical potato model was developed for Australian growing conditions (Sands *et al.* 1979; Hackett *et al.* 1979a and Hackett *et al.* 1979b). The model (known as the 'pocket calculator for potato'), which was derived from a time series analysis of data from well managed experimental crops, calculates biomass accumulation and partitioning and tuber yield. The model calculates yield based on the tuber bulking rate and the timing of crop phenological events as determined by thermal time accumulation after plant emergence. However, the model does not reliably predict phenology stages, has limited management flexibility and does not take into account the effects of daylength on tuber initiation. Regel and Sands (1983) incorporated new capabilities into this model, including tuber initiation response to daylength and improved management functionality (such as plant density and cultivar effects). Estimation of tuber quality was then added into the pocket calculator by Sands and Regel (1989).

The first dynamic model to capture physiological plant organ processes and their relationship with the environment was developed by Ng and Loomis (1979, 1984) and was known as POTATO. This was the first potato model to capture the effect of radiation and temperature on photosynthesis. Many of the physiological concepts incorporated in POTATO were utilized in the development of later models such as LINTUL-POTATO (Kooman and Haverkort 1995) and SUBSTOR (Ritchie *et al.* 1995).

A number of other similar empirical and dynamic models were developed by Ingram and McCloud (1984), MacKerron and Waister, (1985), and Spitters and Schapendonk (1990). The next significant advancement came with the linkage of soil water and nutrient balance models for the estimation of stress limited yield. Models with this capability include SUBSTOR (Ritchie *et al.* 1995), a model by van den Broek and Kabat (1995) and the CropLogic Potato Calculator (Jamieson *et al.* 2004).

SUBSTOR and LINTUL-POTATO

Currently, the two most widely used potato models internationally are SUBSTOR (Ritchie *et al.* 1995) and LINTUL-POTATO (Kooman and Haverkort 1995). SUBSTOR (Simulate Underground Bulking STorage ORgans) is derived from the cereal model CERES (Jones and Kiniry 1986). SUBSTOR is designed as a potato decision support system to identify knowledge gaps and research priorities and serves as a tool to understand the plant-nutrient relation. SUBSTOR has been widely used in many countries across the world for a diverse range of applications including determining the optimum planting time (Bowen *et al.* 2002), optimum irrigation schedules (Shae *et al.* 1999) and optimum nitrogen fertilizer regimes (Bowen *et al.* 1999).

LINTUL-POTATO (LIght INTerception and UtiLisation for POTATO) was developed in the Netherlands and based on the studies of Kooman (1995) into temperature and daylength effects on the growth and development of eight different cultivars of potato. LINTUL-POTATO has been used widely across South America in the agro-ecological characterization of potato to identify yield determining, limiting and reducing factors (Caldiz *et al.* 2002; Kooman and Haverkort 1995) and to test the feasibility of new agricultural methods e.g. the use of new cultivars (Hijmans *et al.* 2003).

Phenology

Four important phenological stages in potato life are generally identified: planting to emergence, emergence to tuber initiation, tuber bulking and maturity. While SUBSTOR takes into account break of dormancy in determining the time to emergence, LINTUL-POTATO assumes that end of dormancy has occurred prior to planting. Another difference is that LINTUL-POTATO adds an extra phase at the end of leaf growth at which point 90% of biomass is allocated to tuber growth.

The end of the growing cycle in LINTUL-POTATO is defined by the leaf senescence rate while in SUBSTOR the end of organ growth (leaf, stem, root and tuber) depends on the availability of carbohydrate.

Pre-emergent growth

SUBSTOR takes into account the seed biomass reserve in the early stages of plant growth (Ng and Loomis 1984) and the effect of sprout length on sprout growth rate at planting (O'Brien *et al.* 1983). This enables simulation of growth from both sprouted and unsprouted seed. In LINTUL-POTATO, the pre-emergent phase is temperature dependent and characterized by a specified sprout growth rate (1 mm / degree days (°Cd) above a base temperature of 2 °C (> T_b 2 °C)), MacKerron and Waister 1985). For both models, the time to emergence is a function of sprout elongation rate and planting depth.

Leaf growth

Both LINTUL-POTATO and SUBSTOR calculate leaf area index (LAI) based on daily leaf expansion and senescence as determined by temperature and assimilate availability. In LINTUL-POTATO, in the early stages of crop growth, temperatures rather than assimilate availability determine leaf area expansion (Kooman and Haverkort 1995). At the optimum temperature for leaf growth, canopy development is driven by an optimum leaf expansion rate of 0.012 m^2 m^{-2} d^{-1} (adopted from Spitters and Schapendonk 1990). The leaf expansion rate is decreased linearly with temperature below and above the optimum temperature of 35 °C (Kooman and Haverkort 1995). When the temperature sum from emergence exceeds 450 °Cd or the leaf area index exceeds 0.75, the increase in leaf area is determined by the

availability of assimilates and is calculated as the product of leaf dry weight and specific leaf area.

In LINTUL-POTATO, leaves are attributed with classes based on the day on which they are formed and a specified longevity of 1000 °Cd which determines the senescence of leaves in each class. A class of leaf is senesced when the temperature sum integrated by the class exceeds the leaf longevity or when the leaf area above the leaf layer is such that shading is too strong. The leaf longevity is also influenced by tuber growth such that fast growing tubers reduce leaf longevity (Firman *et al.* 1995). Crop growth ceases when the leaves in the latest class have senesced.

In SUBSTOR, leaf area expansion is driven by air temperature (Ritchie *et al.* 1995). The model assumes an optimum temperature range for leaf expansion of 15 – 24 °C (Ingram and McCloud, 1984). Actual leaf expansion takes into account water and nitrogen stress factors. A parameter, specifying daily leaf senescence, represents the fraction of carbon in senesced leaves that is translocated prior to abscission. Neither LINTUL-POTATO nor SUBSTOR simulate branching.

Biomass production

Both SUBSTOR and LINTUL-POTATO use a radiation use efficiency approach to convert intercepted radiation into biomass (Spitters 1987; Spitters and Schapendonk 1990). Dry matter production in both models is calculated based on the amount of radiation intercepted by the leaf area and the efficiency of the plant in transforming the energy into dry matter. In LINTUL-POTATO, the efficiency of biomass conversion is sensitive to temperature and is reduced when temperature is below 19 °C or above 24 °C. In SUBSTOR, a modifier for biomass production, the photosynthesis efficiency factor, captures the combined effect of temperature, water stress and nitrogen stress on photosynthesis.

Biomass partitioning

Biomass partitioning involves allocation routines to the main plant parts namely root, stem, leaf and tuber. In SUBSTOR, after plant emergence, three carbon sources are maintained, the seed reserve, current photosynthesis and reserve carbohydrate (Ritchie *et al.* 1995). Immediately following emergence, growth is supported primarily by seed reserves and seed reserve availability decreases with increase in plant leaf area up to 400 cm^2 / plant (Ng and Loomis 1984). When total biomass from

photosynthesis is greater than the growth demand, excess carbon enters a soluble carbohydrate pool, up to a biomass equivalent to 10% of tops (stem + leaf) dry weight (Ng and Loomis 1984). This reserve carbohydrate pool is allowed to accumulate only when seed reserve is no longer available (plant leaf area is bigger than 400 cm^2/plant). To support plant daily growth, biomass from current photosynthesis carbohydrate pools is always used first. When additional carbon is required and the current rate of photosynthesis is unable to meet growth demand then one of the carbohydrate pools (seed reserve or reserve carbohydrate) is used. Prior to tuber initiation, biomass is allocated to leaf, stem and root and each organ is given equal priority. A shortage of carbon for growth during this stage results in a reduction in the growth of all plant components. After the commencement of tuber initiation, tubers receive first priority for biomass allocation. Tuber demand is a function of soil temperature and tuber expansion rate.

In LINTUL-POTATO, there is a gradual increase in the proportion of biomass allocated to tuber growth following tuber initiation and as the tubers grow they become an increasing sink for photosynthate (Kooman and Haverkort 1995). This increase continues until all daily biomass production is partitioned to the tuber (coincides with the end of leaf growth).

Tuber production

The time to tuber initiation and the length of tuber bulking are simulated differently in the two models. In both models the time to tuber initiation is temperature and daylength dependant. In SUBSTOR, tuber initiation is also sensitive to the extent of water and nitrogen stress (Ingram and McCloud 1984). In LINTUL-POTATO, the duration from emergence to the start of tuber growth depends on the development rate until tuber initiation which increases with temperature increase between 10 – 21 °C. The start of tuber growth in this model is sensitive to daylength with longer daylengths delaying the commencement of tuber growth. After tuber initiation, tuber growth proceeds at a rate of 0.37 g/g/day (Ingram and McCloud 1984). The tuber growth rate is sensitive to temperature with growth rate falling when the temperature falls below 16 °C or rises above 24 °C. The duration of tuber bulking is determined by the leaf senescence rate, with tuber filling ending when the leaf in the latest leaf maturity class has senesced.

Root growth

In SUBSTOR, root growth is simulated during early growth i.e. the pre-emergent and vegetative stage. In the pre-emergent stage, the rate of root growth is equivalent to the rate of sprout growth. In the vegetative stage, roots initially receive an allocation of biomass equivalent to that received by the leaf and stem fractions (Ritchie *et al.* 1995). This allocation gradually decreases from emergence to tuber initiation, at which point root growth is halved. Root growth is not simulated in LINTUL-POTATO (Kooman and Haverkort 1995).

Stress simulation

The original version of LINTUL-POTATO did not capture soil water and nutrient stress physiology (Kooman and Haverkort 1995). More recently, van Haren *et al.* (1998) developed a water balance model for use with LINTUL-POTATO. This revised model known as LINTUL2, simulates attainable crop production i.e. crop production under water limited conditions. Water stress indices are calculated as a function of the ratio between actual and potential transpiration. This stress factor acts on total crop growth and the partitioning of biomass between the root and other plant fractions.

Two soil water deficit factors are calculated in SUBSTOR which act to reduce the rates of leaf expansion and photosynthesis, alter the allocation of assimilate to tubers, and promote phenological development (Ritchie *et al.* 1995). These stress factors are dimensionless and range between 1.0 (no stress) to 0.0 (maximum stress). Both factors are based on the ratio of maximum possible water uptake from the soil and maximum transpiration rate. Similarly, two nitrogen stress factors are calculated in SUBSTOR and act to reduce photosynthesis and leaf expansion (Ritchie *et al.* 1995). These stress factors are based on the ratio of nitrogen supply and demand.

Some limitations of existing potato models

Potato size distribution and seed physiological age effects

For commercial potato production, marketable yield is often more important than total yield. Different markets have different size requirements, for example 40 - 70 g for seed tubers (Struik and Wiersema 1999) and > 100 g for processing tubers (Knowles *et al.* 2003). The ability to model tuber size distribution would be a useful

tool for exploring the optimum management practice to maximize marketable yield across a range of environments. A dynamic model was developed by MacKerron *et al.* (2004) to predict tuber size distribution for different market outlets. The model calculates the grade distribution based on the seed rate at planting (planting density) which determines the stem number per plant and tuber number per square meter. However, this model does not take into account the physiological age of the seed tuber, which is the key determinant of stem number per plant (Knowles *et al.* 2003; Mac Kerron *et al.* 2004; Christiansen *et al.* 2006). Stem number, in turn, is a strong determinant of tuber size distribution (Struik *et al.* 1990).

Physiological age is the physiological state of the seed tuber at any given time (Reust 1986) or '*the stage of development of the tuber, which is modified progressively by increasing chronological age, depending on growth history and storage conditions*' (Struik and Wiersema 1999 p. 76). Physiological age has been reported to affect a wide range of crop attributes (Table 2.1) (see reviews by Struik and Wiersema 1999; Coleman 2000) including the stem number per plant.

The physiological age status of the seed tuber is affected by many factors both prior to harvest and during post-harvest handling and storage (Struik and Wiersema 1999). The absence of physiological age functionality from current growth and development models, despite the reported effects of this parameter is at least partially explained by the absence of accurate measures of physiological age. Knowles *et al.* (2003) propose one of the first published attempts for predicting the stem number and tuber size distribution as influenced by the physiological age of the seed tuber. This simple empirical model predicts yield for a range of tuber size classes which can be produced by a specific range of stem numbers per plant. 2-methyl-butanol content of the seed is used as a biochemical marker of the seed tuber physiological age, and is used as an input to determine the stem number per plant, which in turn defines the distribution of size of tuber yield per plant. However, as an empirical model, plant responses to other important environmental factors are not captured in the model.

Table 2.1. The effect of seed physiological age on potato growth processes (Iritani and Thornton, 1984).

Characteristic	Young seed	Old seed
Emergence	Slower	Faster
Stand	Greater	Lesser
Early vigour	Greater	Lesser
Foliage	More	Less
Stems per plant	Less	More
Tuber formation	Later	Earlier
Formation period	Longer	More uniform
Tuber number	Less	More
Tuber bulking	Longer	Shorter
Tuber sizing	Larger	Smaller
Senescence	Later	Sooner
Early harvest yield	Lower	Greater
Late harvest yield	Greater	Lower

An improved understanding of the effect of the seed tuber physiological age on stem number production, and the inclusion of this effect in potato growth models, would represent a significant advance in potato modelling capacity.

Leaf area production

The simulation of leaf area production in the current potato models such as LINTUL-POTATO and SUBSTOR is based on an overall increase in leaf area index (Kooman and Haverkort 1995; Ritchie *et al.* 1995). No allowance is made for branching. An alternative approach for simulating leaf area production in models such as APSIM (Keating *et al.* 2003) is to model leaf area production as a function of four component/concurrent processes, namely leaf appearance, branching, leaf expansion and leaf senescence. These components are critical in defining potato canopy growth and development (Fleisher and Timlin 2006).

Differences have been reported in leaf area production between plants established from seed tubers of different physiological ages (Firman *et al.* 1995). Plants from physiologically aged seed tubers tend to have more nodes on the main stem (Firman *et al.* 1991). In later work the same authors found that the phyllochron of main-stem leaves reduced with increased seed age, although this varied between cultivars (Firman *et al.* 1995). Physiological age can also indirectly affect canopy architecture by altering the stem number. Allen and Scott (2001) argue that the physiological status of the seed tuber which determines the number of stems growing from a

mother tuber in turn influences the rate of leaf cover. Therefore success in capturing the effect of the seed tuber physiological age on leaf area production will improve the accuracy of the potato models.

Ability to simulate broader system interactions

Farming system analysis requires consideration of a complex array of interactions between the soil, climate, plant, livestock and human (i.e. management) elements of the system. In most production areas, potato is typically grown in rotation with a number of other crops and hence will be influenced by carry-over effects of preceding crops and their related inputs and management. Hence, it is important that any new potato model be incorporated into a broader farming systems modelling framework that is able to capture these processes and associated interactions. Such capability exists in the APSIM framework (Keating *et al.* 2003). APSIM has been developed by the Agricultural Production System Research Unit (APSRU), a collaborative group made up from Australia's Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Queensland State Government agencies. APSIM has been used in a broad range of applications, including support for on-farm decision making, farming system design for production or resource management objectives, assessment of the value of seasonal climate forecasting, analysis of supply chain issues in agribusiness activities, development of waste management guidelines, risk assessment for government policy making and as a guide to research and education activity (Keating *et al.* 2003). Furthermore, APSIM has been tested in a wide range of conditions across Australia (Probert *et al.* 1998; Moot *et al.* 2001; Asseng *et al.* 1998) and internationally in Africa (Robertson *et al.* 2000) and the Netherlands (Asseng *et al.* 2000).

The APSIM framework consists of a library of plug in / plug out modules which represent the key biological (i.e. crops, cattle), environmental (i.e. climate, soil) and human (i.e. management) components of the farming system. System designs of interest are 'constructed' by plugging the relevant modules into the APSIM engine (Figure 2.1, Keating *et al.* 2003).

Crop modules in APSIM are available for the main grain, forage and fiber crops grown in Australia. Currently, there is no capability for simulating potato crops in APSIM. More generally, there is no functionality for dealing with physiological age;

stem number estimation, tuber formation, and the simulation of tuber size distribution. The absence of these aspects provides the basic impetus for the body of research addressed in this thesis.

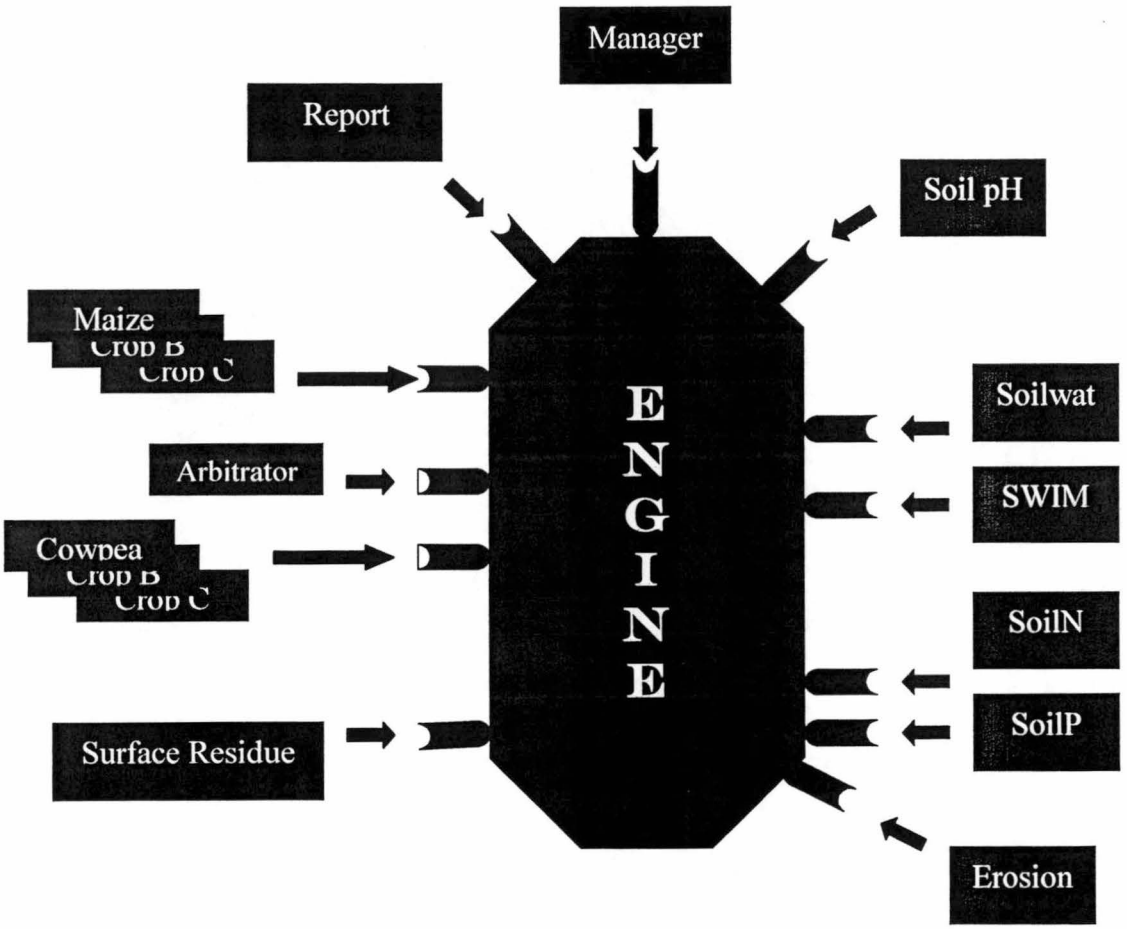


Figure 2.1. Diagrammatic representation of the APSIM simulation framework with individual crop and soil modules, module interfaces and the simulation engine (Keating *et al.*, 2003).

Factors affecting tuber number and size distribution

Both the total yield and the marketable yield are important in potato crop production, with the marketable yield being more difficult to model as it corresponds to the quality characteristics required for the specific end use. The most widely studied quality attribute is tuber size, and for the majority of crop end uses the tuber size distribution is a key determinant of marketable yield. While crop yield has been adequately simulated in the existing potato models, prediction of tuber size distribution currently is in a less satisfactory state. Size distribution within the total tuber yield is important for production of crops for major markets; processing, seed or fresh market. Tuber size distribution in the crop is important to growers as high yield is not necessarily profitable, with tubers outside of the specified marketable tuber size range being unsaleable or attracting a low price. As tuber size is a key quality attribute, much agronomic research has been done on manipulating tuber size distribution in potato crops. Specific management practices have been recommended for production of crops for different purposes in order to maximize the proportion of tubers in the target size range (Struik and Wiersema 1999; Love and Thompson-Johns 1999). Inclusion of knowledge gained from the studies identifying key factors affecting tuber number and size distribution may permit expansion of models to predict marketable yield in potato crops.

In addition to tuber size, tuber shape, appearance, absence of disease or defects, flavour and texture also contribute to quality attributes of the yield (Stark and Love 2003). For processing product, starch and sugar content are the major quality characteristics which can influence the production costs by affecting the amount of input material and the quality of the product. High starch content and low sugar levels are preferably for the processed product, and these can be achieved by harvesting the tubers at the right physiological maturity. These attributes can be influenced by the environment and cultural factors that maximize the tuber specific gravity and minimize tuber sugar content (Stark and Love 2003). Earlier destruction of haulm can result in lower starch content and higher sugar level. Likewise, in seed tuber production, quality characteristics such as the health and vigour of the seed tubers (Brown *et al.* 2003), which are commonly referred to as physiological quality characteristic (Struik and Wiersema 1999), are desirable. These characteristics can be

influenced by the seed crop growing conditions. Therefore, strategies used in manipulating tuber size also need to take into account the need to maintain good plant health throughout the tuber bulking stage, time for haulm killing and harvest related to physiological maturity.

Yield can be divided into component factors; plants per area, stems per plant, tuber numbers per stem and tuber weight. Each of these components can be examined separately to identify the factors affecting it. Plants per area and tuber numbers per stem are determined by the seed rate or planting density and the number of tubers initiated in tuber initiation process, respectively (Struik and Wiersema 1999). Stems per plant are thought to be influenced mainly by the physiological status of the seed tuber. These components in turn influence the tuber number per unit area or the total yield.

Planting density has been known to alter the proportion of tubers produced for the targeted market. Love and Thompson-Johns (1999) found that size distribution shifted from predominance of small tubers at narrow intra-row spacing to a predominance of large tubers at wide spacing, with the size of the differences being cultivar dependent. The responses were due to a decrease in number of tubers per stem with increased planting density, but increased tuber number per unit area and a corresponding decrease in the average tuber weight (Vecchio *et al.* 1991; Gregoriou 2000). The effect of planting density on the number of tubers per stem is suggested to be the consequence of changes in frequency of occurrence of lateral and branch stolon types as well as tuberization (O'Brien *et al.* 1998a). Celis-Gamboa (2002) found that increases in tuber number at low densities was due to stolon branching. Higher planting density may change the plant growth rate by increasing the competition between plants for incident radiation, thus reducing the abundance of assimilate within each plant, which is important to promote initial tuber formation (Perl *et al.* 1991) and growth of stolons and tubers.

Although planting density can be easily controlled by adjusting the planting equipment to give the specified spacing within the row, stem number per plant and tuber number per stem are less controllable. Stem density was found to increase linearly with planting density, however there was a year to year variability in this response (Bussan *et al.* 2007). This could be due to variability in stem number/plant.

Furthermore, O'Brien *et al.* (1998b) found no effect of increased planting density on the number of main stems per plant, a finding which was confirmed later by MacKerron *et al.* (2002) who stated that there was no systematic effect of changes in spacing on stem production.

Number of tubers which can be produced per stem is mainly affected by the pattern of initiation and growth of stolons and tubers on the stem (O'Brien *et al.* 1998a; Struik *et al.* 1990). These are determined by genotype and environment (Celis-Gamboa *et al.* 2003b). O'Brien *et al.* (1998a) suggest that these characteristics were found to be consistent between many cultivars, but may be altered by disease (Struik *et al.* 1990) and physiological age of the seed tubers (Firman *et al.* 1991). The number of stolons per stem is determined by number of below-ground nodes and stolon branching (Struik *et al.* 1990; Celis-Gamboa *et al.* 2003b). Under optimal conditions for tuberization, total proportion of stolons producing tubers is determined by cultivar (Struik *et al.* 1990) and inter-stem competition was not likely to reduce this proportion (Svensson 1962 cited in Struik *et al.* 1990).

Adjusting the planting density has been shown as a useful agronomic practice to manipulate the tuber size produced. The optimum spacing for the cultivar can be used to achieve the highest potential yield and early haulm killing used to ensure more of the tubers are in the small size class. However, this can result in total yield being lower than if crop had been left to fully mature. In addition, this practice can affect the yield of subsequent crop by altering the physiological quality of the tubers. Brown *et al.* (2003) found that early haulm killing (90 days after planting) resulted in seed tubers giving lower yield in the next growing season compared to later haulm killing dates.

While growers can exert a high degree of control over plant density, the management of stem number per plant and tuber number per stem is less certain. The tuber size distribution for each plant is primarily affected by tuber number per plant and total tuber yield per plant. The number of tubers per plant affects the size distribution by altering the biomass partitioning from above ground parts to the tubers. An increase in the number of tubers per plant reduces the availability of photosynthate to each individual tuber (Oparka and Davies 1985). Consequently, individual tuber size decreases with increasing tuber number per plant. Much research has been done on

the manipulation of this parameter. The major focus for management of the tuber number per plant has been through manipulation of the stem number per plant. When seed tubers are planted at the target planting density, and given that growing conditions at tuber initiation are at optimum level, stem number per plant is likely to become the major factor that determines the number of tubers per plant, and hence the tuber numbers per unit area or yield of marketable sized tubers.

The relationship between tuber number per plant and stem number per plant has been widely documented. Tuber number per given area was closely correlated to the numbers of stems per given area (Struik *et al.* 1990) and in a later study, this correlation was found in most of the cultivars (Struik *et al.* 2006). Haverkort *et al.* (1990) found some linear relationships between the numbers of sprouts and stems per seed tuber, and numbers of stolons and tubers. Increased numbers of tubers per plant were associated with plants that produced higher stem numbers and therefore more stolons per plant. Each additional stem produced by a plant may allow initiation of more tubers, resulting in higher tuber set per plant (Reust 1994 cited in Struik and Wiersema 1999).

As a consequence of increased stem number, a modification in the tuber size range is likely to occur. Work by Iritani *et al.* (1983) showed that yield of small tubers increased and larger tubers decreased with increasing stem number, with little effect on total yield (Knowles and Knowles 2006). Based on the correlation between stem number per plant and tuber number per plant, a predictive relationship between stem number and tuber size distribution has been proposed by Knowles *et al.* (2003) (Figure 2.2).

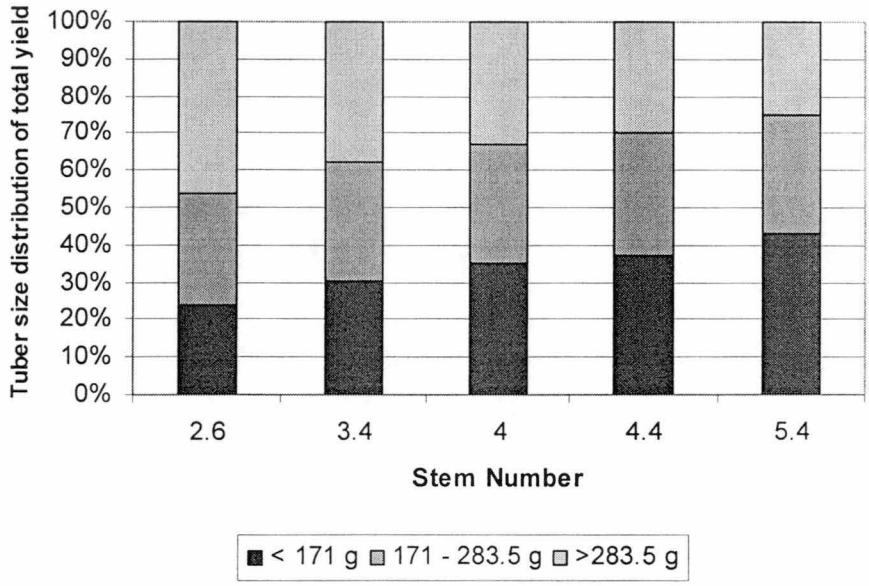


Figure 2.2. Estimation of tuber size distribution based on stem number (adopted from Knowles *et al.* 2003, the regression model on which this estimation is based was derived from two years of field data, 2001-2002).

Plants with lower stem number were likely to produce tubers in the processing size range, therefore decreasing the percentage of rejected tubers by the industry. On the other hand, plants with higher stem number were more likely to produce tubers in the size range for seed production. This signifies the importance of the stem number production in order to simulate the tuber size distribution. Therefore the first step toward the attempt is identification of factors that affects the stem production. Stem number per plant depends on several factors such as cultivars, seed tuber size and the physiological age of the seed tuber.

Physiological age of the seed tuber is the key driver to the stem number

One of the key determinants of stem number per plant is the physiological age of the seed tuber. Stem number per plant is assumed to increase with increasing physiological age of the seed. Physiologically aged seed tubers generally are characterized as producing a plant with greater stem number per plant (Olsen 2001). Physiological age of the seed tuber affects the stem number produced as a result of gradually decreasing apical dominance in the seed tuber (Knowles *et al.* 2003; Pavlista 2004; Struik and Wiersema 1999). Understanding the physiological age

effect on stem number could be a great benefit in modelling the stem number prediction which in turn can be used to simulate the quality component of the potato yield.

Physiology of sprouting

Following harvest, a seed tuber is in a dormant condition, the duration of which may be altered by genetics and the previous environmental conditions. This stage is characterized by no sprout growth even when the seed tuber is exposed to favorable conditions for sprouting. The meristematic cell activities in the bud on a dormant tuber are blocked in the G1 mitotic phase (Campbell *et al.* 1996). Following the loss of dormancy, which has been reported to coincide with decrease in sensitivity to abscisic acid (ABA) and increase in gibberellic acid concentration within tubers (Suttle 2000; Moorby and Milthorpe 1975; Claassens and Vraugdenhil 2000), mitotic activity in the bud is slowly resumed and the seed tuber starts to sprout. The resumption of cell activities signals starch breakdown (Moorby and Milthorpe 1975) and glucose-1-phosphate which derived from starch breakdown by Starch phosphorylase (STP) is converted by UDPglucose phyrophosphorylase (UGPase), Sucrose phosphate synthase (SPS) and Sucrose-phosphatase (SSP) into sucrose needed to support the growing sprout (Claassens 2002; Hajirezai *et al.* 2003).

Although dormancy breakage has been well studied, it is not clear whether the factors that affect the end of dormancy are the same as the factors that induce the sprouting. Hormonal and biochemical changes in the tuber during dormancy all point to factors that can reduce the dormant period but the factors that can induce the start of sprouting (mitotic resumption) have not been identified. Dormancy is thought to be mainly affected by genetics and the processes leading to the resumption of bud growth have no rigid environmental control (Moorby and Milthorpe 1975). Some findings of processes that occur prior to visible sprouting are an increase in invertase activities (Ross and Davies 1992), increase in reducing sugars which is accompanied by a decrease in sucrose (Dimalla and van Staden 1977), increase in gibberellic acid (GA) level (Suttle 2000) and cellular activities (Moorby and Milthorpe 1975). According to Viola (2001) resumption of cell-to-cell communication in the apical bud and in the tuber coincides with end of dormancy.

The hormonal and biochemical changes apparently lead to the start of the sprout growth processes. Hajirezai *et al.* (2003) found that mobilization of the reserves still occurred even in the absence of visible sprouting in a transgenic cultivar study. These authors argue that a metabolic signal, which may be the low level of sucrose in the tuber, may act as a trigger for starch breakdown rather than sink demand signal from the growing sprouts (Moorby and Milthorpe 1975). In addition, a decrease in sucrose level at the end of dormancy coincides with increases in the level of endogenous GA (Claassens and Vraugdenhill 2000) which is known to induce sprouting. Increase in GA does not affect the work of enzymes that regulates the starch breakdown (Clegg and Rappaport 1975 cited in Claassens and Vraugdenhill 2000).

After the break of dormancy, sprout growth follows a bud hierarchy with sprouts at the apical region of the tuber emerging first. This apical dominance process has been reviewed by Moorby and Milthorpe (1975) and Coleman (2001). Seed tubers kept in low temperature storage, which allows reserve mobilization and hormonal metabolism to take place but which will inhibit the mitotic activities on the bud meristem, leads to loss in dormancy in all buds and consequently loss in apical dominance. When the tuber is transferred from cold storage to conditions favorable for sprouting, then bigger sprouts are able to inhibit growth of smaller ones (Moorby and Milthorpe 1975).

Overview of the physiological age concept

During aging in storage, the seed tuber goes through some physiological and biochemical changes. Although the start point of aging is still being argued, the physiological and biochemical processes which may occur during aging have been well documented (Moorby and Milthorpe 1975; Coleman 2000). Aged seed tubers (from 5 months to 17 months) lose their cell membrane integrity (Knowles and Knowles 1989) and protein-synthetic capacity (Kumar and Knowles 1993a). This loss may affect the capacity of the seed tubers for mobilization and translocation of tuber reserves to developing organs, hence may affect the performance of the plant during plant establishment.

There are also changes in sprouting pattern during the aging process (Ewing and Struik 1992). Stem number of a seed piece increases with physiological age of the seed tuber until a point during aging where the number of stems decreases (Figure 2.3). After dormancy break, sprout number and vigour increase with time up to a certain level then decrease. After the break of dormancy, the presence of apical dominance causes only one sprout to grow when the tuber is considered physiologically young. Planting a seed tuber at this stage will result in a plant with only one stem at relatively low growth rate (Struik and Wiersema 1999).

Seed tubers may pass the apical dominance phase, when sprouting is inhibited by environmental conditions (e.g. low storage temperature, 2 – 4 °C), and enter the multiple sprouting stage. According to Mikitzel and Knowles (1991), the effect of apical dominance is observed to diminish with advancing age, giving a multiple sprouting stage for tubers considered as physiologically older. Planting a seed tuber at this stage will result in a plant with few stems and good vigour (Struik and Wiersema 1999). Past this point, plant vigour will decrease as a result of tuber aging and branch sprouts will be found on the seed tubers in storage (Krijthe 1962). More stems will be produced when planting in the field, but with low vigour. When tubers experience a prolonged aging, a daughter tuber can be formed on the sprout, and result in loss of vigour as a result of tuber aging.

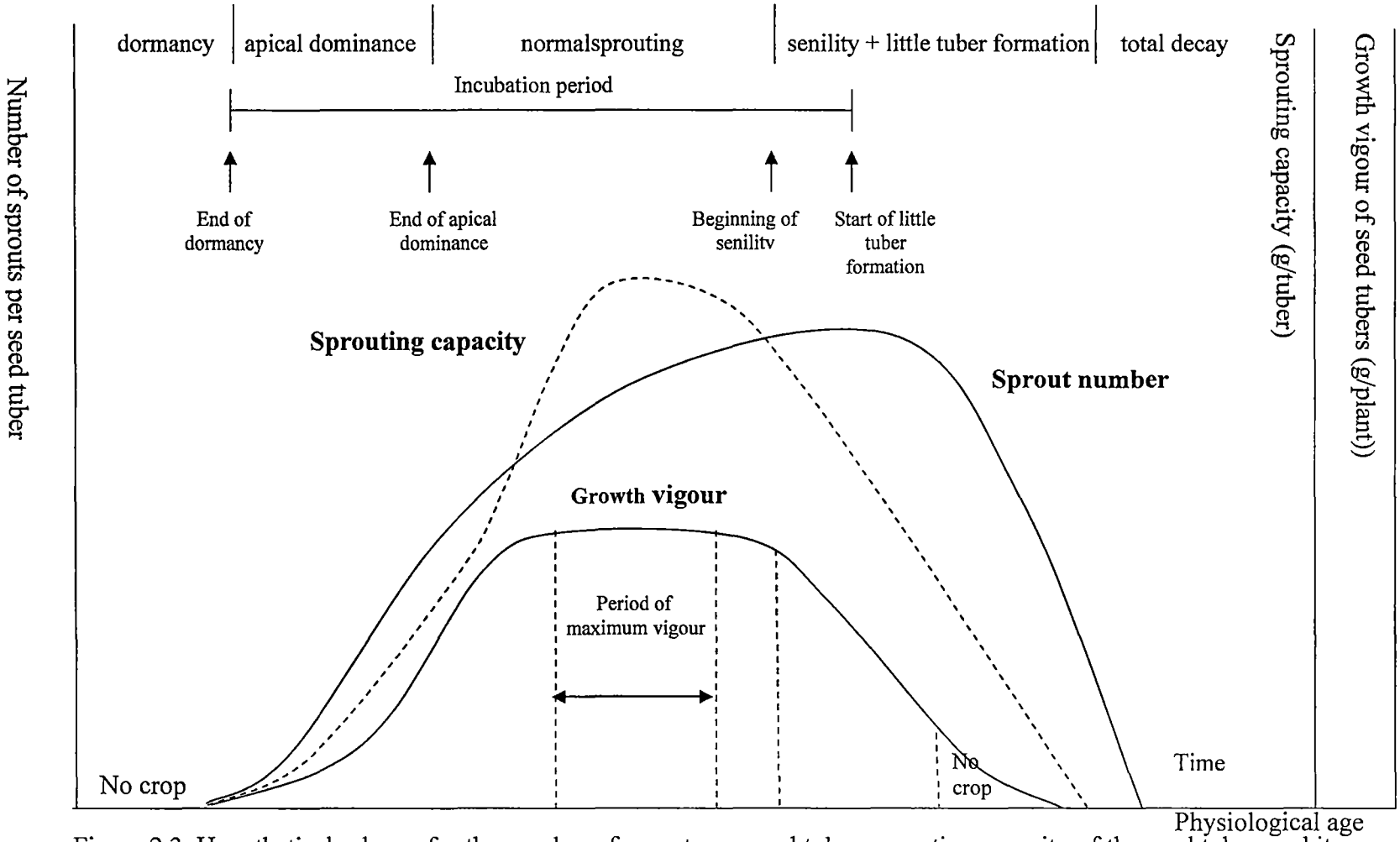


Figure 2.3. Hypothetical scheme for the number of sprouts per seed tuber, sprouting capacity of the seed tuber, and its growth vigour as function of physiological age. The units along y-axes are arbitrary (Struik and Wiersema 1999).

Stages during aging of the seed tuber have been well documented by several authors (Iritani *et al.* 1983; Pavlista 2004; Struik and Wiersema 1999). The stages include: dormancy, apical dominance, multiple sprouts and senility, and are briefly described below:

a. Dormancy

Dormancy can be defined as the physiological state where there is no cell division and in which autonomous sprout growth will not occur within a reasonable period of time (usually two weeks), even when the tuber is kept in conditions ideal for sprout growth (Moorby and Milthorpe 1975; Struik and Wiersema 1999).

b. Apically dominant

The apically dominant stage is the stage where only one apical sprout (the dominant sprout) grows from the seed tuber. This is thought to be the response of the biochemical changes in the seed tuber.

c. Multiple sprouting

When the seed is left longer in the storage, multiple sprouts may grow as the response to the loss of the apical dominance. A plant with multiple stems can result from this physiologically aged seed.

d. Senility

This stage is the latest stage of the aging event. If the seed is kept longer, daughter tubers can be formed on the seed. The seed is no longer recommended to be planted as the growth vigour is started to drop.

The physiological age of the seed tuber is mainly affected by storage conditions, especially temperature. Higher temperature during storage can influence the apical dominance status of the eyes on the seed tuber and hasten the completion of the apical dominance stage (Pavlista 2004). The degree of apical dominance can be modified by storage temperature (Hay and Hampson 1991). Thus by manipulating the storage conditions, the preferable physiological age for different stem number production may be achieved at planting.

Manipulation of the physiological age to affect the stem number

Manipulation of seed physiological age to achieve a target stem number has been the focus of many research studies (Grice 1988; Knowles and Botar 1991; Roy and Jaiswal 1997; Reust 1994 cited in Struik and Wiersema 1999; Knowles *et al.* 2003; Knowles and Knowles 2006). Seed tuber physiological age has been shown to be affected by seed crop growing conditions and seed tuber post harvest handling. Stress and disease incidence during tuber production can also contribute to the aging of the seed tuber (Struik and Wiersema 1999). In addition, management practices such as timing of haulm killing in the seed crop, also contribute to the physiological state of the seed tubers (Brown *et al.* 2003). While some management factors during tuber bulking can be controlled (e.g. maintenance of stress free conditions), some environmental factors during this stage are less controllable. Given an optimal condition during tuber bulking, physiological age of the seed tuber can be controlled by storage management.

Post harvest storage is generally considered to be the most important period that can affect the physiological aging of the seed tubers. Storage temperature and duration are the two major factors that modify the physiological aging of the seed tuber and hence can determine the sprouting pattern. This method has been used in many physiological age studies where the physiological age of the seed tubers were artificially modified by varying the storage temperature or duration (Iritani and Thornton 1984 cited in Knowles and Botar 1991; Firman *et al.* 1992, 1995; Hay and Hampson 1991). Moving the seed tuber to storage with higher temperature (15 - 20 °C) after dormancy has broken will age the seed tubers and thus can promote multiple sprouts to grow. Keeping the seed tuber in storage at low temperature will retard the aging process in the seed tubers and is more likely to produce plants with a single or few stems. Longer term cold storage is known to substantially advance the seed tuber age, thus increase the stem number per plant and the tuber set per plant without affecting the total yield (Knowles and Knowles 2006).

Plants with multiple stems, high tuber numbers and early plant maturity are highly desirable for the production of a potato seed crop. Therefore, seed tubers with multiple sprouts are preferred. In contrast, plants with lesser numbers of stems and

tubers are preferred for production of tubers in the range for processing. Thus seed tubers with two or three sprouts are preferred.

While manipulation on seed tubers age has been described in the literature, the effectiveness of the treatments commercially are not sufficient to provide a high degree of control over tuber size distribution. Many factors can affect the physiological age of the seed tuber which in turn can influence the sprouting pattern and stem number that can be produced after planting in the field. Therefore, an accurate prediction of stem number is difficult.

Deficiencies in the physiological age concept

While the concept of manipulating the stem number through seed tuber storage management has been well documented, treatments have not always resulted in production of the desirable stem number when seed tubers are planted in the field. Jenkins *et al.* (1993) found that manipulation of seed tuber physiological age by storage duration did not affect the main stem number and fewer stems were produced by seed tubers which were kept in high temperature storage conditions. Hay and Hampson (1991), using periods of storage at different temperatures to manipulate seed tuber age, found that the numbers of stems per tuber carried by a physiologically younger tuber was the same or fewer than in plants from older tubers in the field. In addition, there was a seasonal and cultivar variation found in this study. Differences in the number of stems produced by plants, from aged and non aged seed tubers, were also found between laboratory and field conditions (Hay and Hampson 1991). A linear increase in stem number with advancing seed tuber physiological age resulted in a controlled environment study by Knowles and Botar (1991) but the stem numbers produced with equivalent aging treatments was not consistent when seed tubers were planted in the field in a different season (Knowles and Botar 1992). In the second study, the number of main stems increased only slightly with advancing tuber age. This indicated that conditions at planting, or physiological state of tubers before storage, can modify the stem number produced by the seed tuber.

Cultivar differences were found in the extent of the seed physiological aging in the work by Olsen (2001). Aged Ranger Russet seed performed similarly to younger

seed in terms of stem number and tuber number per plant, while for Russet Burbank, Norkotah and Shepody the stem number and time to emergence increased with seed age. Work on physiological age of seed tubers conducted by Grice (1988) also showed that stem number per plant increased with seed tuber physiological age in cultivar Kennebec but not Russet Burbank.

Planting conditions may also play a role in determining the number of sprouts that grow into main stems. The inconsistencies in sprouting responses based on the physiological age theory result from an influence of growing conditions following planting in addition to artificially induced physiological aging by seed storage conditions. Soil temperatures during early plant growth can influence emergence and tuber set (Olsen 2001). Excess soil moisture has been reported to increase the aging process of the seed tuber, resulting in higher stem numbers (King and Stark 1997). Almekinders and Struik (1996) found that the number of stems per seed tuber increased in warm temperatures. There was also season to season variability which can influence the production of stem number. A cool, wet spring will tend to produce fewer stems per plant and take longer for seed to emerge than a warm spring season (Kleinkopf *et al.* 2003). In addition, soil moisture at planting was found to affect the maximum sprout growth rate (Firman *et al.* 1992) which may affect the number of stems by altering the apical dominance mechanism. Results from a field experiment conducted by Sale (1979) showed increased stem number could be associated with higher temperature from planting to 50% emergence for cultivar Sequoia. In this work, the seed tuber material was treated in the same storage conditions but the length of storage was different due to different planting time treatment. Based on the physiological age concept, stem number was expected to increase with later planting time as seed physiological aging occurred during storage. However, the stem number was variable across the different planting times, and there was no clear evidence in this work that the stem numbers were solely defined by the physiological age of the seed material.

These inconsistencies indicate the possibility of an interaction between seed tuber physiological age and planting environment in determining the stem number. If this is the case success in integrating this aspect will expand the capability of the existing potato model for providing a foundation for simulating the tuber size distribution.

Physiological age effect on stem number in the potato models

Seed tuber physiological age, which affects the stem number per plant, has rarely been taken into account in the existing published potato models. Few authors have tried to model the influence of physiological age of the seed tuber on crop establishment. Knowles *et al.* have attempted to model the tuber size distribution based on the stem number characteristic (Knowles and Botar 1991; Knowles *et al.* 2003; Knowles and Knowles 2006). This empirical model predicts the stem number solely based on physiological age of the seed tuber using a biological marker. A simulation model of tuber size distribution based on seed rate has been introduced by MacKerron (2005). In this model, stem number per plant is used to predict the stem number/square meter and hence the tuber number/square meter and end grade distribution. However, it is not clear how the stem number is predicted and no effect of planting environment is taken into account. Ignoring the effect of planting environment could lead to inaccuracy in the prediction of the stem number.

One of the difficulties in modelling the physiological age effect is that it is hard to quantify the physiological status of the seed tubers. Furthermore there is no indicator of the seed physiological age that is well accepted. Several authors have proposed ways to quantify the physiological age of the seed by means of simple physical, chemical or biological tests. However, there is no indicator of age that accurately represents the physiological state of the tubers which can be used in widely varying environments.

Temperature sum or accumulated day degrees is the most widely used indicator of physiological age and was first introduced by O'Brien and Allen (1978) and Wurr (1978). The accumulated degree days (> T_b 4 °C) that the seeds were exposed to after dormancy had broken indicates the physiological age of the seed tuber. The aging of the seed tuber increases with the temperature sum. Although this concept has been used widely (Jenkins *et al.* 1993; Ezekiel 1994; Roy and Jaiswal 1997; Hay and Hampson 1991), it is not always a good indicator as, for example, it is inaccurate when tubers experience a heat shock (Struik and Wiersema 1999).

Klemke and Moll (1990) suggested a measure for physiological age of the seed tuber at planting known as physiological age unit (PAU). Instead of using the linear

relation between storage temperature and seed tuber age as in the thermal accumulation, the PAU is determined based on non linear relation between the temperature and physiological aging rate of the seed tuber. Seed tuber physiological age is computed as the accumulation of daily development rates from the beginning of sprouting to planting. Consequently, under optimal condition (20 – 25 °C), one physiological age unit corresponds to the development of one day and below the optimum temperature the PAU is lesser. However, this measure seems to lack the ability to describe the effect of environmental growing conditions where seed tuber was produced.

A physiological age index (PAI) suggested by Caldiz, Fernandez and Struik (1999) may be able to be to cover the year-to-year variability of growing conditions that affect the physiological age. To calculate PAI, a determination of the end of the incubation period needs to be undertaken for different seed lots to anticipate the effects of cultivar and storage conditions. The incubation period is defined as the time elapsed from sprouting until new tuber formation on the sprouts (Claver 1953 cited in Caldiz *et al.* 2001), with samples of seed lots being exposed to standardised growing conditions (dark, 17 °C and 90-95% humidity). This method indicates that the index is not a predictive tool to mark the physiological age of the seed tuber (Struik and Wiersema 1999). In addition, Johansen (2004) found a weakness of this indicator in its lack of sensitivity in accounting for the effect of the haulm killing date. As Johansen used the varied haulm killing date for experiments in different sites to obtain similar size of the yield, PAI did not reflect the actual physiological state of the seeds.

Recently, a new indicator of physiological status of the seed tubers has been introduced by Knowles *et al.* (2003). This includes a measurement of 2-methyl-1-butanol level in the tuber to indicate the physiological condition of the seed tubers. A high correlation between the butanol level and the stem number produced for Russet Burbank was demonstrated. Little published work backing up the initial trials is available.

The accuracy of stem number prediction may also be influenced by the interaction of seed tuber physiological age and planting environment. Inconsistencies in stem number responses from specific aging treatments indicates that there could be an

interaction between the seed material and the planting environment in determining the stem number, and therefore this interaction must be considered in models incorporating stem number prediction. Prediction of stem number purely based on physiological age indicators (Knowles *et al.* 2003) is unlikely to be accurate because of the fact that planting environment may modify the effect of the age of the tuber at planting.

Effect of physiological age of seed tuber, temperature and moisture on the stem number per plant

Effects of the environmental planting conditions on stem number have not been well documented. Few studies have been conducted regarding this factor. Bohl (1995) argued that planting conditions also may affect the physiological age of the seed tuber and warm temperature during planting may negate the difference in the time to emergence between the older and younger seed. Sprouting temperature has been found to be correlated with stem production (Wurr *et al.* 2001). Despite this, understanding on how the planting conditions interact with seed physiological age in affecting the stem number is lacking. This indicates the importance of a study to investigate the relationship and to establish a method which model stem number production.

Understanding on stem number and the effect of seed tuber physiological age and planting environment can be a great advantage in increasing the capability and the flexibility of a new model. The stem number prediction based on the relationship between seed age and planting environment will add to the capacity of the new model to simulate the size distribution of the crop. Therefore the new model can be used to assist the grower to manage the crop for production for different markets. APSIM's ability to simulate the bigger frame of the farming system will be enhanced by this new knowledge to help the vegetables grower where a cropping pattern and rotation is a general practices. With the simulation model, together with the understanding of seed manipulation, the grower can decide the best management for certain production purposes.

Chapter 3 Investigation of commercial processing potato crop dataset

Introduction

Tuber quality, and in particular the percentage of tubers with quality characteristics that make them marketable, is an important yield component in the potato industry. Tuber quality is especially important in potato crops designated for processing as key tuber quality attributes, such as size and shape, affect processing factory efficiency and profitability. Therefore, an understanding of the key factors that affect the production of the marketable tuber is important, and production of tubers of uniform size and shape, able to be cut into processed product with minimum waste, has been a longstanding target of breeders and agronomists.

Stem number per plant, or more accurately stem density in the crop, is one of the factors affecting tuber size distribution. While many published studies conclude that stem number is affected mainly by the physiological age of the seed tuber (van der Zaag and van Loon 1987; Struik and Wiersema 1999), there are some indications in the literature that planting environment may also affect this parameter. Variability between seasons and sites in stem number response to tuber aging treatments (Hay and Hampson 1991; O'Brien *et al.* 1983; Jenkins *et al.* 1993) suggests that factors following ware crop planting, or prior to seed crop harvest, may have a significant effect on stem number. As these areas have not received much research attention, further evidence to support the conclusion was sought in this project through analysis of a database of commercial crop production data.

An investigation of an industrial database is a valuable tool to gain an insight into the effect of characteristics of the production system, and in this study to tentatively identify some of the key factors that may affect the stem number per plant. The Tasmanian potato industry is mainly focussed on production of processing tuber products, with the major potato production regions ranged across the North of the island state, covering a geographic range of approximately 22,800 km^2. Growing conditions, including climate

and soil type, may vary within the geographic range where potatoes are planted. All commercial processing potato crops are grown from seed supplied under a Seed Certification Scheme. Between 2003 and 2007, a large database of crop production information was generated by Tasmania's largest potato processor, Simplot Pty Ltd. The database was referred to as the Crop Management Service (CMS) scheme. The database consisted of information on management practices and yield components of crops grown under contract for Simplot across the range of Tasmanian production locations and over four growing seasons. The CMS scheme was used by the company to assist growers in benchmarking practices and outcomes against regional and state-wide figures. The database contained information on seed tuber source as well as processing crop production information and yield components, allowing investigation into factors affecting stem number. The objective of the dataset analysis undertaken in this project was to identify possible factors affecting stem number production and tuber quality to assist in defining the focus of study on key physiological factors for development of a potato production model.

Materials and methods

The Crop Management Service (CMS) dataset was kindly provided by Simplot Aust. Pty Ltd. The CMS program was conducted to provide a basis for assessment of crop management practices for participating growers within the Simplot crop contracting system across Tasmania. The dataset was in the form of a database of information collected during four seasons (2003/04, 2004/05, 2005/06 and 2006/07). Restricted availability of some of the 2006/07 data meant that only the data from three seasons of 2003/04 to 2005/06 was analysed. Data collected included information on paddock, soil, management and crop yield component. Information on soil included soil characteristics (soil group and type) and nutritional status (macro and micro elements before planting), soil moisture (monitored throughout the growing season). The database also included scouting results on pest and disease incidence. Complete crop management practices included sowing date, plant density, irrigation, pest and disease control, fertilization, harvest time, and paddock history such as cropping pattern in the previous seasons. Final harvest yield and quality data included time to emergence, stem number per plant,

yield (T/Ha), percentage of tubers in the processed size range, percentage of rejected tubers and tuber specific gravity.

A preliminary multivariate analysis of the CMS dataset was undertaken to identify possible relationships between crop factors and both stem number and marketable yield. The results of this analysis have been reported previously within a report for the Australian potato industry. This analysis helped in narrowing the focus of the univariate analysis approach by identifying key components relevant to the major parameter in this study, stem number. The multivariate analysis was conducted using SAS (Statistical Analysis Software, version 12.0; SAS Institute, Cary, North Carolina, USA) statistical package. Ware crop information categories used in the multivariate analysis were: grower (ID number), district, crop area (Ha), sowing date, soil type, row width, density, previous summer crop, summer crop 2 seasons previously, number of years since potatoes were grown in the paddock, number of years since pasture was grown in the paddock, soil structure (ranked on the scale of 1 to 10) and soil moisture during establishment (ranking 1-3) and time of 50% senescence of the crop. Seed crop information categories used in the multivariate analysis were: seed grower (ID numbers were used rather than names), district that the seed crop was grown in, planting date, soil type, previous summer crop, previous winter crop, summer crop 2 seasons previous, winter crop 2 seasons previous, number of years since potatoes were grown in the paddock, soil temperature at planting, seed temperature at planting, spacing, irrigation type, irrigation frequency (days), irrigation amount (mm), haulm killing method, date of senescence, total crop growing days, date the crop was harvested, duration of in-ground storage, and seed crop yield (T/Ha)

Further analysis was conducted focusing on some key factors identified in the multivariate analysis as affecting stem number per plant. The major factors were planting date, location, soil structure and moisture. Effect of seasons, location and soil type on stem number per plant was analysed using a univariate analysis. Only locations which had more than three data points (crops) in each season were chosen. For effect of planting date on stem number a regression analysis was performed for each season. All

statistical analysis was performed using the SPSS v. 14.0 software package (SPSS Inc. 2005).

Climate data for each location was sourced for the nearest weather stations from the SILO database (Australian Bureau of Meteorology (BOM) 2008). Climate data were daily maximum and minimum air temperature and total rainfall for each location during planting time of September, October and November for season 2003/04, 2004/05 and 2005/06. Monthly figures were generated for mean maximum and minimum air temperature and total rainfall.

Results

Several factors associated with ware crop and seed crop production were shown to have a significant correlation to the key ware crop performance characteristics of emergence time, stem number per plant, total yield and yield of processing sized tubers (Table 3.1). Seed crop factors were not linked to ware crop yield, but significant correlations were found between the timing of seed crop factors (planting date, date of senescence, date that the crop was harvested, duration of storage, date that seed was cut prior to ware crop planting) and time of ware crop emergence, and between timing of seed crop harvest and storage events and stem number per plant in the ware crop. Seed crop factors which were significantly correlated with stem number were digging date, period in the ground, days in cool store and date of cut (cutting of seed tubers to produce seed pieces for planting) before planting. The effect of these factors on the number of stems per plant was concluded to be associated to the effect of these factors on the physiological status of the seed tuber.

Ware crop factors also displayed a weaker relationship with yield than with crop emergence time and stem number per plant. Stem number per plant was affected significantly by planting date, planting density, years since pasture was planted in the paddock, soil structure and moisture. Similarly, time to 50% emergence also was affected by these factors except for moisture conditions which were not significantly

correlated with the time to emergence of the crops. In contrast, none of these factors significantly affected the yield and percentage of tubers within the processed size.

Table 3.1. Significant relationships between seed performance attributes and ware and seed crop factors. Figures are P values from the correlation matrix output of the multivariate analysis (figures less than 0.05 indicate significance at the 95% confidence interval).

Ware crop factors

	Planting date	Planting density	Years since pasture	Years since potato	Soil structure	Moisture	Date of 50% Senescence
Time to 50% emergence	<.0001	0.0002	0.0024	0.4928	0.0005	0.234	0.0432
Stems per plant	<.0001	<.0001	0.0307	0.9852	0.0016	0.003	0.0003
Yield	0.6956	0.219	0.6322	0.6343	0.1917	0.1437	0.0483
% size	0.6722	0.296	0.3251	0.814	0.8798	0.894	0.7066

Seed crop factors

	Planting date	Date of senescence	Growing days	Digging Date	In ground	Days in cool store	Date cut
Time to 50% emergence	0.0401	0.0216	0.1914	0.0257	0.8685	<.0001	<.0001
Stems per plant	0.1207	0.3738	0.8684	0.0032	0.001	0.0274	<.0001
Yield	0.4154	0.7985	0.9256	0.6858	0.2882	0.2123	0.408
% size	0.4637	0.2402	0.1552	0.4621	0.5935	0.4989	0.5026

Stem number and processed size

A significant relationship ($P<0.001$) was found across the 196 crops over three seasons between stem number per plant and the percentage of tubers of processing size. Increasing stem number decreased the percentage of tubers within the processing size range (Figure 3.1).

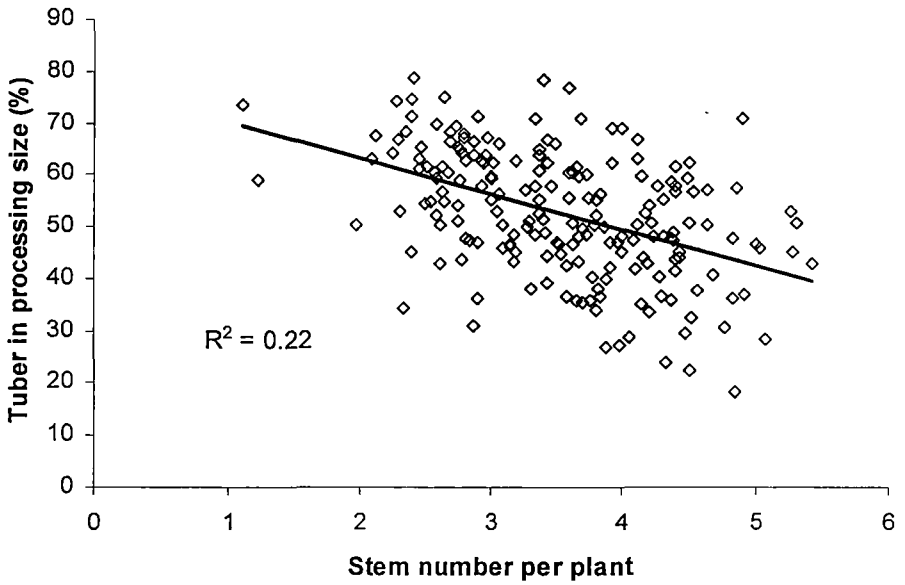


Figure 3.1. Relationship between stem number and the percentage of tubers for processing size in crops.

Stem number accounts for only a small proportion of the variation in marketable (tubers of processing size) yield as crop yield is influenced by many factors, and tuber size distribution is a function of both tuber number and yield. The significance of the relationship between stem number and tuber size distribution (measured as percentage of tuber yield in the processing size range) does however support the argument for inclusion of a measure of stem number in any potato marketable yield model.

Effect of location, season and planting date on stem number

Data on stem number per plant reveals that there was a significant difference in the mean stem number per plant produced between seasons in locations across Tasmania ($p<0.001$) (Table 3.2). Lowest stem number per plant occurred in season 2003/04. Mean stem number increased from 3.1 in season 2003/04 to 4.4 in season 2005/06.

Table 3.2. Stem number per plant at different production locations and growing seasons. l.s.d figures shown with extent of significance (**p<0.01).

Location	Seasons			l.s.d 0.05
	2003/04	2004/05	2005/06	
Deloraine	3.0	3.3	4.5	
East Devonport	2.8	3.6	4.3	
Forthside	2.8	3.3	4.3	
Scottsdale	3.6	3.2	4.6	
Sheffield	2.8	4.0	4.5	
Westbury	3.7	2.9	4.9	
Wynyard	3.3	3.9	4.4	
Mean	3.1	3.5	4.5	0.2**

Stem number per plant appeared to be related to the temperature at planting, with increasing stem number occurring with increasing minimum and maximum mean monthly temperatures for October and November (Table 3.3). A cooler and drier planting environment in season 2003/04 was associated with lower stem number per plant. Maximum temperature, which averaged between 12.6 and 18.7 °C, varied less than minimum temperature. Rainfall data also shows that during the three months of planting, season 2005/06 was wetter when compared to the previous seasons.

Table 3.3. Average maximum and minimum temperature and rainfall across locations in different season and month.

Season	2003/04			2004/05			2005/06		
Month-	Tmax (°C)	Tmin (°C)	Rain fall (mm)	Tmax (°C)	Tmin (°C)	Rain fall (mm)	Tmax (°C)	Tmin (°C)	Rain fall (mm)
September	12.6	3.7	131	14.5	5.6	34	14.4	6.0	136
October	14.6	4.9	31	16.4	6.6	62	16.5	8.6	167
November	18.7	8.4	17	17.4	8.0	79	18.5	9.5	126

There was no significant difference between locations in stem number ($p=0.08$). However, a trend of increase in stem number from season 2003/04 to 2005/06 was similar across locations except in the Scottsdale and Westbury regions where there was a slight decrease in stem number in the 2004/05 season. The variation in stem number between the seasons in each location followed the same trend of increasing stem number with increasing temperature and the amount of rainfall during planting months (Table 3.4). The three locations showing the lowest number of stems per plant, East Devonport, Forthside and Sheffield in 2003/04 season, were the locations that received the lowest rainfall. Similarly, decreased rainfall in Westbury in season 2004/05 was associated with the lowest stem number produced by crops in this area during this season.

Table 3.4. Average maximum and minimum temperature (T max and T min) and total rainfall in September to November at different locations and seasons across Tasmania.

Location	Season	2003/04			2004/05			2005/06		
	Month-	T max (°C)	T min (°C)	Rain fall (mm)	T max (°C)	T min (°C)	Rain fall (mm)	T max (°C)	T min (°C)	Rain fall (mm)
Deloraine	Sept.	11 9	2.8	128.4	13 9	4.5	27 8	13 7	4.6	112.8
	Oct.	14.3	4.1	22 4	16.1	5.3	55.2	16 1	7.5	146.8
	Nov.	19.2	7 6	22.0	17.8	7.5	63 0	18 7	8.7	141.2
E. Devonport	Sept.	13 2	5.0	112.2	14.3	6.7	25 8	14 1	6.4	102.7
	Oct.	14.5	6.1	18 8	16.0	7.2	54.8	16.1	9.7	135.1
	Nov.	17.7	9.6	17.4	17.4	9.9	73 4	18 3	10.6	108.5
Forthside	Sept.	12.9	4 8	117.8	14.3	6.3	32.3	14.2	6.4	113.8
	Oct.	14.6	5.8	32.4	16.0	7.4	60.2	16.1	9.3	218.6
	Nov.	18.2	9 3	21.7	17.5	9.5	86 6	18.3	10.2	160.1
Scottsdale	Sept.	12.1	3.6	151 2	14.0	5.2	35.3	13 7	5.4	146.8
	Oct.	14 5	4.7	30 2	15 8	6.2	57 3	16 0	8.2	228.5
	Nov.	18.7	8.2	16 8	17.5	8.3	108 1	18.3	9.1	159 2
Sheffield	Sept.	13 2	3.4	157.8	16.4	6 0	60.1	16 3	8.5	182.7
	Oct.	14.9	4.6	49.0	17.6	8.6	87.2	18.3	10.0	136.5
	Nov.	18.4	7.9	8.3	14.8	5.0	110 0	18.3	9.1	159.2
Westbury	Sept.	12.3	3.1	135.2	14.3	4.8	23.6	14 1	4.8	118.6
	Oct.	14.7	4.3	21.0	16.4	5.4	54.2	16 5	7.7	150.6
	Nov.	19.6	7.9	15.8	18.2	7.7	55.0	19.0	9.0	137.4
Wynyard	Sept.	12.7	3.5	115.6	14.3	5.4	33.5	14 6	5.4	104.2
	Oct.	15.0	5.0	42.2	16.6	6.2	63.4	16.4	8.0	152.9
	Nov.	19.0	8.1	14.6	18.5	8.2	56.5	18.9	9.7	89.4

The number of stems per plant increased with later planting date within each season, but the relationship varied between seasons. Regression analysis on the stem number data in each of the seasons revealed that there was a significant effect of planting date on the number of stems produced in season 2004/05 ($p<0.05$) and 2005/06 ($p<0.01$) but not in 2003/04 ($p=0.31$) (Figure 3.2). For crops planted in October and November, stem number per plant produced in the 2003/04 growing season was smaller, with a range

from 2 to 3.5 stems per plant compared to the subsequent seasons which ranged from 2 to 4 and 3 to 5 stems per plant for season 2004/05 and 2005/06, respectively.

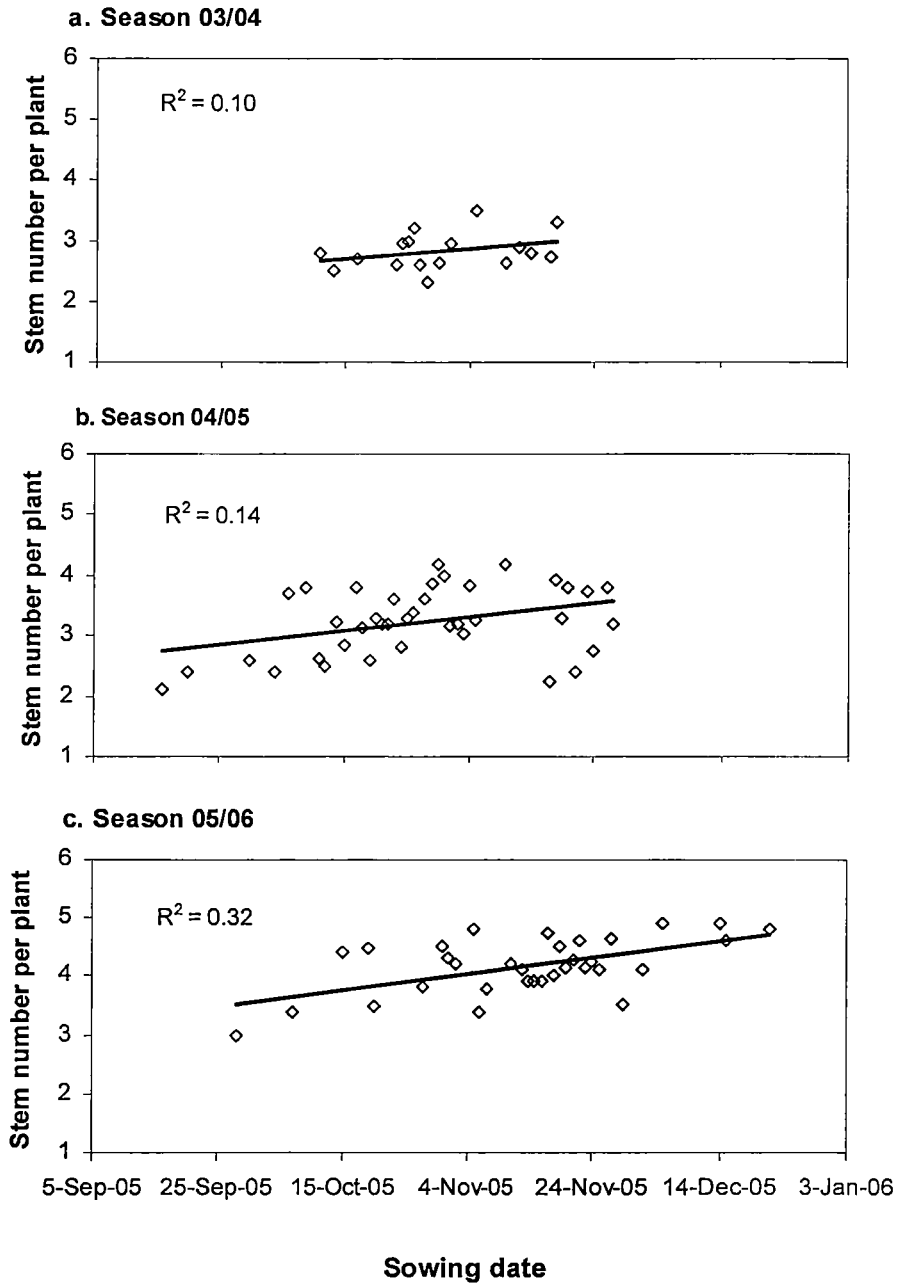


Figure 3.2.Effect of sowing date on stem number per plant in (a) 2003/04, (b) 2004/05 and (c) 2005/06 seasons.

Effect of soil type on stem number

No significant effect was found in stem number produced in different soil types within each season (p=0.826). Stem number varied between seasons with the bigger stem numbers produced in season 2005/06 compare with the other two seasons (2003/04 and 2004/05) (Figure 3.3). Seasonal effect was bigger than the soil type effect in this case with stem number per plant ranging from 4.1 to 4.8 across soil type in season 2005/06 and 3 to 3.5 in season 2003/04 and 2004/05. More stems were produced in the soil with lighter texture.

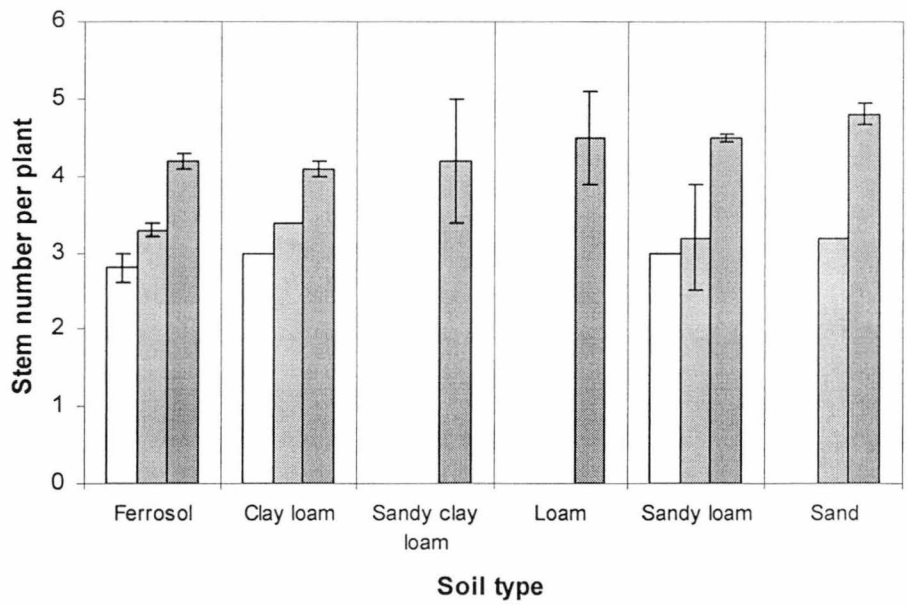


Figure 3.3. Stem number produced on different soil types in 2003/04 (□), 2004/05 (▒) and 2005/06 (▓) seasons. Bar corresponds to standard error of the mean.

Response of stem number per plant to different paddock history

Multivariate analysis revealed that there was a significant relationship between stem number per plant and paddock history (i.e. years since pasture was planted in the paddock). Table 3.5 shows the stem number changes in response to how long since pasture was planted in the paddock before the potato crop was planted on three different

soil types for each growing season. No significant effect of the paddock history ($p=0.586$) and soil type ($p=0.960$) was found on the stem number produced within season and differences were only found between seasons ($p<0.01$).

Table 3.5. Stem number per plant as affected by years since pasture was planted in the paddock. Empty spaces showed no observation on particular soil type and paddock history.

Season	Soil type	Years since pasture				
		0	1	2	4	5
2003/04	Ferrosol	2.6	3.1	3.0		
	Clay loam	2.7	3.0	3.2		
	Sandy loam	3.0	2.7	2.9		
2004/05	Ferrosol	3.4	3.0	3.4		
	Clay loam	3.1	3.6	3.3	3.3	3.2
	Sandy loam	3.2	2.7	3.4		2.4
2005/06	Ferrosol	3.9	4.0	4.6		5.1
	Clay loam	4.3	4.0			4.4
	Sandy loam	4.4	4.8			

Discussion:

Analysis of a large commercial crop database provided evidence supporting the hypothesis that stem number per plant might be affected by planting environment. Although stem number per plant varied with planting date, location and soil type, season appeared to be the major factor contributing to the variation in the stem number produced by crops in Tasmanian growing conditions. Lower stem number per plant was associated with seasons having cooler and drier conditions at planting time. Temperature and moisture are known to affect crop establishment, for example warmer planting conditions were associated with earlier time to emergence in potato (Sale 1979). However, evidence of an effect of planting conditions on stem number had not been presented prior to this study.

Although planting environment may play an important role in stem number production, the effect of seed lots used by the grower should not be ruled out in determining the number of stems produced by the seed tuber in ware crop production. Seed lot differences in performance could be associated with the physiological status of the seed tuber at planting which can be influenced by seed crop growing conditions (Wiersema and Booth 1985; Brown *et al.* 2003; Wurr *et al.* 2001), duration in cool store (Iritani and Thornton 1984; Jenkins *et al.* 1993; Knowles and Botar 1991) and pre-planting treatment e.g. seed cutting (Struik and Wiersema 1999; Struik *et al.* 2006).

Early harvest of the seed crop may result in physiologically younger seed tuber compared to late harvested crops (Brown *et al.* 2003). Soil temperature and moisture conditions prevailing during tuber fill will also effect seed physiological age. Once in store, the physiological status of the seed tuber will continually decline with flow-on effects in terms of stem number of the crop at planting. Storage temperature, humidity and the presence of wounds are all known to affect the degree of seed tuber aging (Struik and Wiersema 1999). Knowles and Knowles (2006) have reported that extended cold storage can substantially advance the seed tuber physiological age, leading to higher stem number and tuber set per plant.

Across the CMS paddocks, there will be a range of different seed lots sourced from different locations. However, given that seed tuber production typically involves optimum (non-limiting) growing conditions, and similar post-harvest handling procedures such as cool store and pre-planting treatment, the analysis of this commercial dataset indicates the importance of planting environment conditions on the seed tuber performance. Both seed tuber physiological age and planting environment will however vary between crops, so further analysis of the interaction between seed tuber physiological age and planting environment needs to be undertaken to define the combined effects of these factors on stem number per plant.

There was inconsistency in the effect of physiological age on stem number in relation to planting time. Conventional physiological age theory relates that the increase in stem number with later planting date occurs as a response to seed tuber aging in storage

(Struik & Wiersema 1999). Increase in temperature with later planting date is also associated with faster emergence (Firman *et al.* 1992; Sale 1979). However, the response did vary with season. In the 2003/04 season (compared to the 2004/05 and 2005/06 growing seasons) the results indicate that other factors may have played a significant role in determining the number of stems produced by the crop. Climatic conditions in the 2003/04 and 2004/05 seasons, such as cooler and drier conditions during the planting time (September to November) may have affected the expression of seed tuber performance as influenced by the seed tuber physiological status. Constraints in moisture availability during planting may have restricted sprout development (Firman *et al.* 1992) therefore altering the potential stem number.

Although no significant difference was shown between soil type in stem number and the seasonal effects showed a bigger effect on stem number than those produced on different soil type, there was a bigger fluctuation in stem number by crops grown in sandy soil compared to clay soil when conditions changed from cooler and drier growing season to warmer and wetter climate conditions. This was presumably due to differences in soil characteristics such as water holding capacity and thermal properties. For example, higher temperatures likely in sandy soils may lead to higher stem numbers for crops grown in these environments. Increase in soil temperature around the seed tuber has been reported to age the seed tuber and increase the stem number produced (Bohl *et al.* 1995).

Evidence revealed by the analysis on the commercial dataset of potato production in Tasmanian growing conditions has suggested an interaction between planting environment (e.g. temperature and moisture at planting) and the potential performance of the seed tuber. Taking into account interactions between factors affecting the stem density, which was shown to be related to tuber size distribution in this study and in the literature (Struik and Wiersema 1999), will be a first step toward a more accurate prediction of tuber quality. Investigation of the nature of the interactions warrants further study, and was the focus of subsequent experiments in this project.

Chapter 4 Physiological study

The literature review presented in Chapter 2 identified the key gaps in knowledge of potato tuber initiation and development required for a mechanistic model to predict tuber yield and quality. Stem number production, which is one of the key factors affecting tuber size distribution, has rarely been included in the existing potato simulation models. In order to incorporate stem number prediction in a mechanistic model, the combined effects of planting environment and seed tuber physiological age on stem number was concluded to be a key area for further study. Evidence presented in Chapter 3 reinforced the conclusion that stem number may be influenced by soil conditions at and after planting, with soil temperature and water potential suggested as components of the planting environment that may affect stem number.

Physiological age of seed tubers has been demonstrated to have a major effect on plant stem number and therefore on tuber number per plant and tuber size distribution (Struik and Wiersema 1999; Knowles and Knowles 2006). It is widely accepted that a strong relationship exists between stem number and tuber size distribution (Haverkort *et al.* 1990; Struik *et al.* 1990; Iritani *et al.* 1983), making the prediction of stem number based on seed age a potential parameter for inclusion in potato models. However, only a few models (Knowles *et al.* 2003) have taken this factor into account. The indicators of physiological age in these models are based on thermal time calculation and therefore do not take into consideration the possible effect of planting environment on stem number. In particular, the models fail to consider the effects of soil temperature and moisture levels at planting, or the possible interaction between planting environment and physiological age of the seed tubers in determining stem number.

The effect of planting environment on seed performance is not well understood, and the effects of planting conditions on stem number have not been examined. There is evidence in published field trial results supporting the hypothesis that stem number may be influenced by planting environment. For example, for seed of similar age the number of stems per plant was found to be lower when planting in autumn (2.2 stems per plant)

than in spring (3.3 stems per plant) in Tunisian growing conditions (Fahem and Haverkort 1988). This difference may have been associated with differences in temperature, with average temperatures of 27.5 °C and 10 °C during autumn and spring respectively. Higher temperatures between planting and 50% emergence were linked to increased stem number in field trials examining the effect of soil temperature on plant developmental stages in the cultivars Sebago and Sequoia (Sale 1979). Temperature at planting has also been reported to alter the physiological age of seed tubers, with higher soil temperature resulting in aging of the seed so younger seed at planting performs like older seed (Bohl 1995; Kleinkopf 2003; Firman *et al.* 1992). Similarly, according to Reust *et al.* (2001), growing conditions and soil temperature can affect the expression of vigor of old seed in the field, with low soil temperature at planting delaying emergence and decreasing the vigor of the old seed. This conclusion was also supported by Beukema and van der Zaag (1979) who proposed that a physiologically old seed tuber is susceptible to low temperature. Despite this, no data or reports of the effect of soil temperature at planting on the stem number of seed tubers from different ages have been published.

As well as temperature, moisture at planting is rarely taken into account as a factor that affects the stem number or physiological aging of the seed tuber. Soil moisture conditions at planting have been examined in many studies, but are usually associated with disease development rather than plant growth and development. Generally, recommendations state that seed tubers require sufficient moisture to support sprouts until emergence and that excess water in this stage should be avoided as it may lead to poor soil aeration which could increase disease incidence (eg. Pavlista 2003). Soil moisture also can affect the time to emergence by affecting the maximum sprout growth rate. Sprout growth rate decreases with decreasing soil water potential and this effect is greater at high temperature than at low temperature (Firman *et al.* 1992).

Water availability is known to affect many aspects of plant growth including transpiration, photosynthesis, cell enlargement and enzyme activities (Van Loon 1981). While effects of water deficit on crop establishment and yield components in potato have been extensively studied (eg. Jeffries and MacKerron 1987; Stalham and Allen

2004; Karafyllidis *et al.* 1996; Mackerron *et al.* 1988), little is known on the effect of this factor on sprouting. Letnes (1958) suggested that a considerable amount of water at planting was necessary to allow seed tubers to sprout. Water stress after planting has been suggested as a factor that may restrict stem number (Beukema and van der Zaag 1979; Letnes 1958; Van Loon 1981) however data demonstrating this effect have not been presented. Several studies have documented reduction in stem number following drought treatment (Heuer and Nadler 1995; Jeffries and MacKerron 1987; MacKerron and Jeffries 1986), but in these studies water stress treatments were imposed after plants have emerged and therefore the responses were not related to moisture conditions during planting. A decrease in stem number from 5.0 to 4.7 stems per plant was observed when soil water potential was decreased from -7 kPa to -70 kPa at the 50% emergence stage (MacKerron and Jeffries 1986). Withholding irrigation after crop emergence has also been shown to reduce stem number from 139,000/ha to 128,000/ha, with differences between cultivars in drought response also demonstrated (Jeffries and MacKerron 1987).

According to King and Stark (1997) excessive soil water at planting also affects the soil temperature, which can result in a decrease in sprout growth and delayed emergence from physiologically older tubers. This study, along with others suggesting an effect of planting environment on stem number and emergence rate, was qualitative rather than quantitative in terms of describing the effect of planting environment on stem number. Quantitative studies are required before planting environment factors can be incorporated into potato growth models to confirm that soil temperature and moisture can significantly affect stem number, and to assess the interaction between tuber physiological age and planting environment in determining stem number.

A series of experiments was undertaken in this project to examine the effects of temperature and moisture in the planting environment on stem number as a forerunner in establishing a parameter to incorporate in a potato crop model. Experiments were conducted under controlled environment conditions to cover the range of temperature and moisture conditions likely to be encountered at planting. Two key cultivars of Australian and Indonesian potato production, Russet Burbank and Atlantic, respectively were investigated for the crop model to able to be parameterised under both countries

conditions. Initial experiments focused on development of an assay system to demonstrate the effects of temperature and water potential on sprouting. Subsequent experiments examined the interaction between planting environment (temperature and water potential) and seed tuber physiological age on sprout number and vigour. Manipulation of tuber age by selection of different seed lots and storage at different temperatures was used to study the interaction between seed physiological age and planting environment on sprouting.

4.1. Effect of temperature and water potential on sprout vigour

Introduction

In many field crops, temperature and moisture conditions at sowing have been shown to affect crop establishment, and an interaction between temperature and moisture effects has also frequently been documented. Sowing time effects on crop emergence rate and stand establishment have been linked to the seasonal variation in soil water content and temperature (Jinks *et al.* 2006). Without moisture stress, rate of emergence of sorghum and sun flower increased with soil temperature, but establishment peaked between average maximum soil temperatures at seed level of 24-32 °C (Ferraris 1992). Root growth and development of sweet potato cuttings increased with increased in temperature from 20 to 24 °C and soil moisture at 80% of field capacity (Belehu *et al.* 2004). Moisture deficit decreased water usage and consequently shoot dry matter production in faba bean and resulted in poor stand establishment (Khan *et al.* 2007).

While study of temperature effects on crop establishment of potato has been reported, intensive studies of soil water potential effects on plant performance, and of interactions between temperature and moisture effects, are rare. Of those studies, the majority have focused on defining the impact of timing and rates of irrigation/rainfall on yield (Jefferies 1989) and not specifically the soil water potential thresholds affecting different growth and development parameters. Firman *et al.* (1992) found that the rate of sprout growth was lower in dry soil than in near field capacity conditions. Difficulties in maintaining constant water potentials at different temperature in volumes of growing media sufficient to contain potato tubers may have contributed to this paucity of data.

Maintaining soil water potential at a specific level is difficult to achieve in field or pot experiments. One technique to maintain water potential in a tight range is by the use of vermiculite material for growth media. The advantage of using vermiculite is that the material is capable of holding water within a wide range of water potentials, and this material is stable at high temperature (Suvorov and Skurikhin 2001). Whalley *et al.*

(1999) showed that changes in water potential during an onion seedling growth trial were relatively small when using the vermiculite as growth media.

A preliminary study which included a range of temperature and soil water potential treatments was conducted to assess the applicability of a vermiculite based sprouting assay system for investigating the effect of planting environment on the performance of seed tubers. The trial examined sprouting over a range of different temperature and moisture conditions. Temperature ranged above and below the reported optimal sprouting temperature of 20-25 °C (Klemke and Moll 1990; Krijthe 1962; Struik 2007), and water potential was within the recommended soil moisture potential range of -0.02 to -0.06 MPa for potatoes (van Loon 1981). Soil water potential at the point of field capacity and permanent wilting point are -0.02 MPa to -0.03 MPa and -1.0 to -1.5 MPa, respectively (Curwen 1993; Vos and Haverkort 2007). The study tested the hypothesis that temperature and soil water potential at planting affect the sprouting characteristics of the seed tuber. The trial also provided validation of the methodology used in further trials.

Materials and methods

Plant material

Seed tubers of the cultivar Russet Burbank, size grade 40-60 g, were used in the trial. After a curing period of 10 days at room temperature following harvest, the seed tubers were kept in a 4 °C cold store for 395 days until the start of experiment. To avoid disease, tubers were dipped in fungicide (Rovral at 1 g/L) and dried before planting.

Growth media and water potential

The growth medium used in the trials was vermiculite (Grade 2, Australian vermiculite and Perlite Co-P/L). In this experiment, three water potential treatments were utilized. A field capacity treatment (-0.01 MPa) was set up by saturating vermiculite and leaving it over night to drain based on the method developed by Whalley *et al* (2001). The remaining water potential treatments were established using the relationship between

water potential and water content developed by Whalley *et al.* (2001). The authors found that despite significant reductions water content of the vermiculite over the course of the experiment, the changes in water potential were relatively small. 0.15 g and 1.27 g water per g dry vermiculite were equilibrated to establish the -0.6 MPa and -0.02 MPa water potential treatments, respectively.

Each treatment was left overnight to equilibrate. After equilibration, the vermiculite for each water potential preparation was placed in plastic containers. The container was sealed with a lid to prevent water loss from the container and therefore to control the water potential throughout the trial. Assessment of changes in water potential in the containers over a five day period was undertaken using gypsum blocks. This method confirmed that water potential could be maintained at target levels (data not shown).

Experimental design and statistical analysis

The preliminary experiment was conducted from 19 March to 6 April 2003 and involved exposing seed tubers sourced from one seed lot to three water potentials (-0.6 MPa, -0.02 MPa and -0.01 MPa) at each of five different temperatures (10, 15, 20, 25 and 30 °C). The experiment was carried out using a Terratec thermogradient table at the School of Agricultural Science, University of Tasmania. The temperature treatments were set up on the thermogradient table by setting the temperature to 0 °C at one end of the table and 30 °C at the other end of the table. The thermogradient table was set up a week before the experiment was started in order to reach equilibrium. Temperature treatments were established by measuring the temperature at different positions on the table and setting up partitions using polystyrene material around sections of the table where the desired temperatures existed.

Containers filled with vermiculite at the target water potentials were placed at each of the partitioned zones on the thermogradient table. Four seed tubers were planted in each container at a 10 cm depth and covered by the growth medium. Containers were then sealed to prevent water loss. Using a pseudo replication design with temperature as the block, the moisture treatments were randomized within each temperature treatment with

two replicate containers for each water potential treatment at each temperature. The design therefore provided a total of 8 tubers for each temperature and water potential combination, and a total of 30 treatment combinations overall.

After 19 days, sprout and tuber weights were recorded. Sprouting capacity was calculated as gram fresh weight (FW) sprouts per gram FW tuber. An analysis of variance and least significant difference (LSD) procedure using SPSS for windows version 14.0 was performed to determine the response of the tuber seeds to temperature and moisture.

Results

Validation of methodology

The appearance and growth rate of sprouts emerging from seed tubers held in the vermiculite medium was not distinguishable from those of field or pot sown tubers. An incubation period of between 2 and 3 weeks was found to be sufficient to identify differences in sprout growth between temperature and water potential treatments. Temperature and water potential remained stable in the medium across the range of treatments tested over the duration of the trial.

Use of fungicide before planting was not effective in preventing the incident of fungus attack, especially in the high temperature and water potential treatments. Eighty percent of seed tubers in the highest temperature treatment (30 °C) were diseased, meaning the results could not be included in the analysis. No disease problems were encountered at lower temperatures, and it was concluded that the sprouting assay methodology could be used to an upper temperature limit of 25 °C.

Effect of temperature and moisture on sprouting capacity

Temperature and moisture significantly affected sprout growth rate, assessed as the sprouting capacity of the tubers (FW sprouts per FW tubers). Sprouting capacity of seed tubers increased with increasing temperature and water potential (Table 4.1.1). The increase in sprouting capacity with increasing temperature was statistically significant, with a five fold increase between the 10 °C and 25 °C treatments. An approximate doubling in sprouting capacity between the highest and lowest water potential treatments was noted, with significantly higher sprouting capacity in the higher water potential treatments (-0.01 MPa and –0.02 MPa) compared to the lowest water potential treatment (-0.6 MPa).

Table 4.1.1. Sprouting capacity of seed tubers at different temperatures and water potentials. Tubers were exposed to temperature and water potential treatments in sealed containers filled with vermiculite for 19 days before assessment. Data are means of 8 replicate tubers.

Treatments	Sprouting capacity (g FW sprouts/g FW tuber)
Temperature (°C)	
10	0.010 a
15	0.028 b
20	0.044 c
25	0.056 d
Moisture (MPa)	
-0.6	0.024 a
-0.02	0.039 b
-0.01	0.041 b

Values followed by same letter for each treatment are not significantly different (p=0.05) l.s.d.= 0.004.

Interaction between temperature and moisture on sprouting capacity

There was a significant interaction between temperature and moisture treatments on the sprouting capacity ($p<0.05$). The differences between water potential treatments were greater at higher temperature, with differences between sprouting capacity of tubers exposed to dry and wet conditions particularly evident at temperatures of 20 and 25 °C (Figure 4.1.1).

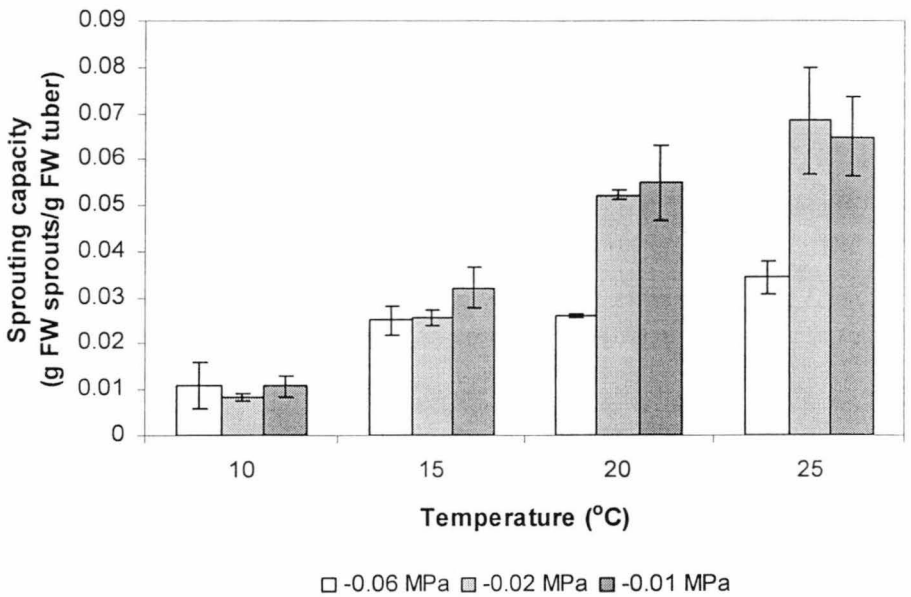


Figure 4.1.1. Interaction between temperature and water potential on sprouting capacity. Tubers were exposed to temperature and water potential treatments in sealed containers filled with vermiculite for 19 days before assessment. Data are means of 8 replicate tubers. Error bar corresponds to standard error of the mean.

It was also noted that higher water potential promoted more root development (not measured) at the base of sprouts (Plate 4.1.1). Sprout length was less variable between water potential treatments, but ranged from approximately 0.5 - 2 cm at 10 °C to 5 - 7 cm at 25 °C. Lots of variability in sprout length was observed on individual tubers. Sprout weight was associated with the weight of individual tuber (Figure 4.1.2). There was tendency that sprouts weight increased with tuber weight. This trend is less obvious at lower temperature but is evident at higher temperature (20 - 25 °C).

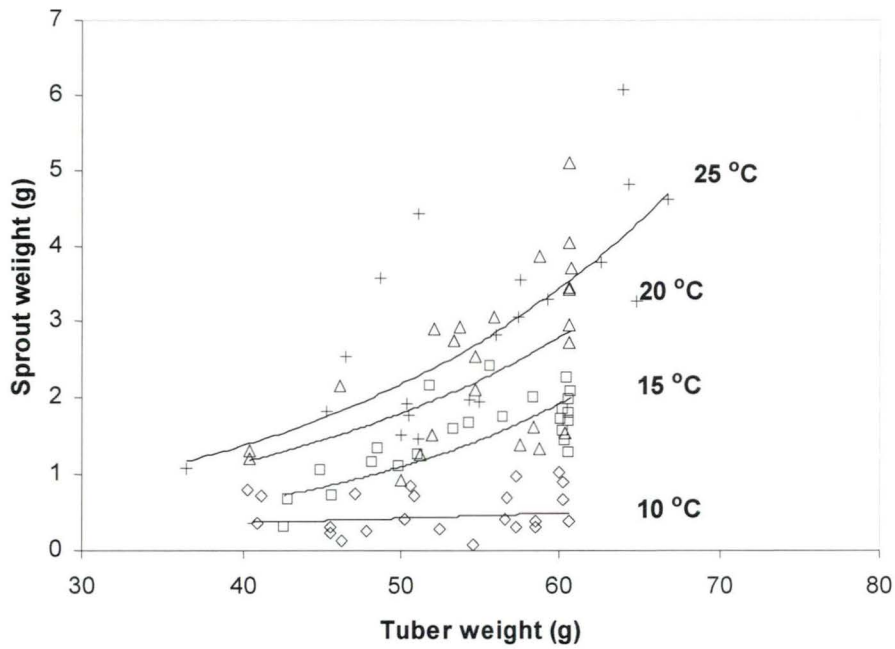


Figure 4.1.2. Relationship between sprout weight and tuber weight for tubers exposed to different temperatures of 10 °C (◇), 15 °C (□), 20 °C (△) and 25 °C (+) for 19 days in sealed container. Data comprises of all of the water potential treatments.

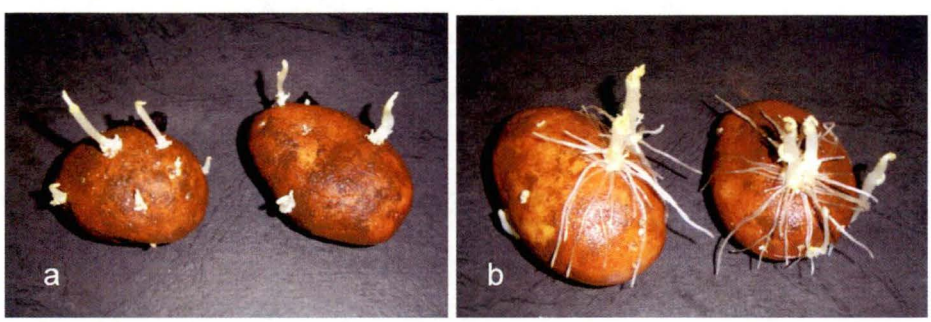


Plate 4.1.1. Sprout growth at 10 °C (a) - 0.6 MPa (b) - 0.02 MPa

Discussion

The use of vermiculite as a medium for imposing temperature and water potential treatments on potato tubers was shown to be effective. Disease problems restrict the application of the method at the highest temperature imposed in the trial. Use of 1-2 tubers per container can be recommended to reduce the risk of contamination between tubers. The results in this preliminary trial also emphasized the importance of using similar sized tubers to reduce variability within treatments. In addition to variability in sprout vigor, it was observed that bigger seed tubers tended to have more sprouts than small tubers.

The methodology was successfully used to demonstrate that temperature and water potential interact to affect sprout growth. While both temperature and water potential have been shown previously to influence sprouting (Struik 2007; Letnes 1958; Goodwin 1963 cited in Moorby and Milthorpe 1975; Firman *et al.* 1992; Krijthe 1962), this experiment demonstrated the interaction between the two factors, with differences induced by varying water potential only occurring at temperatures above 15 °C. Temperatures of 20-25 °C have previously been reported to be optimal for sprouting (Klemke and Moll 1990; Krijthe 1962), and the findings of this experiment indicate that when temperature is optimum for sprout growth prevailing moisture conditions can affect the vigour of the sprouts.

Lack of available water will influence the water uptake by the seed tuber (Svensson 1977) which is needed for physiological processes in the plant and as a medium for biochemical reactions (Taiz and Zeiger 2006) such as the transportation of soluble sugar into the growing bud. The rate of these reactions is higher at higher temperatures, so the effect of reduced water uptake associated with low media water potential would be expected to be greater at higher temperatures. Cell expansion mechanisms may also be affected by the availability of the moisture, resulting in larger sprouts at higher water potential. Soil moisture also is proposed to be important for root formation (Beukema and van der Zaag (1979), a conclusion that was supported by the observations of root development in the different water potential in the experiment. The presence of larger

roots at the base of the sprouts would be expected to increase water uptake by tubers, contributing to the differences in sprout size and vigor between water potential treatments noted at higher temperatures. Though not considered in this study, the other potential confounding factor is the changes in carbon dioxide concentration in the sealed container and the associated effect on plant growth, especially water use and radiation use efficiency.

In conclusion, the vermiculite media based methodology for investigating sprouting in tubers under a range of temperature and water potential treatments was demonstrated to be viable, and the results provided evidence that both temperature and water potential in the planting environment affect the performance of the seed tubers. This evidence of a planting environment effect on sprouting, combined with evidence from the literature (Chapter 2) and commercial crop data (Chapter 3) on possible planting environment effects on stem number, justifies further examination of temperature and water potential effects on sprout number. As seed tuber physiological age has also been demonstrated to influence stem number, further experiments should assess the interaction between physiological status of the seed and the planting environment in modifying the sprouting characteristics of the seed tuber.

4.2. Effect of temperature and water potential on sprouting of tubers of different physiological ages

Introduction

Extensive evidence exists in the literature for the role of seed physiological age as the key driver of stem number and seed tuber performance (Struik and Wiersema 1999; Knowles *et al.* 2003; Grice 1988; Knowles and Botar 1991; Roy and Jaiswal 1997; Reust 1994 cited in Struik and Wiersema 1999; Knowles and Knowles 2006). The concept of seed tuber physiological age is that the sprouting pattern of the tubers progresses through different stages associated with the physiological status of the tuber. These stages include dormancy, which is related to very young physiological age, apical dominance, few sprouts, multiple sprouts and lastly senility or little tuber stage, which is considered as very old physiological age (Struik and Wiersema 1999). Many seed tuber management practices are aimed at controlling tuber physiological age at planting to deliver a desired stem number.

While duration and temperature of storage have been shown to have the most significant impact on seed tuber physiological age (Iritani and Thornton 1984; Jenkins *et al.* 1993; Knowles and Botar 1991), other factors such as seed crop production practices and environment (Wiersema and Booth 1985; Brown *et al.* 2003; Wurr *et al.* 2001), seed tuber size (Bohl *et al.* 1995) and damage to tubers either through impacts, pathogens or cutting of seed tubers prior to planting (Struik and Wiersema 1999; Struik *et al.* 2006) affect the rate of aging of seed tubers. Despite many reports of factors affecting the rate of tuber physiological aging, precise control of stem number through management of tuber physiological age remains an elusive goal for potato growers.

The temperature and moisture conditions of the soil at planting may influence stem number. While planting environment has received little attention in the literature as a factor affecting seed tuber physiological age (Bohl 1995; Kleinkopf 2003; Pavlista 2003), the impact of temperature and water potential in the planting environment suggests either a direct involvement in the aging reactions or an interaction between planting environment and tuber physiological age in determining the sprouting pattern of the

tuber after planting (Reust *et al.* 2001). Temperature, especially during storage, has been found to have an effect on physiological aging of the seed tuber (O'Brien *et al.* 1978; 1983). Data presented in the previous section of this chapter revealed that temperature and moisture conditions in the planting environment affect sprout vigour, and suggested that there was an interaction between the two environment factors in their effect on the growth of sprouts originating from the seed tuber. Previous studies incorporating temperature and moisture treatments at planting have focused on crop establishment attributes such as sprout growth and time to emergence (Sale 1979; Firman *et al.* 1992). No studies have specifically investigated the possible interaction of planting environment and seed tuber physiological age on sprout number or stem number.

The research documented in this section investigates the interaction between planting environment and seed tuber physiological age on the sprouting of the seed tubers. A series of trials were conducted under controlled environment conditions using a thermogradient table and growth chambers to control temperature, and the vermiculite media based system documented in the previous section to control water potential. It was hypothesised that temperature and moisture at planting may affect the sprout number and vigour by altering the expression of the seed tuber physiological age effect.

Materials and methods

Five experiments were conducted to test the hypothesis that there is an interaction between planting environment and seed tuber physiological age in determining sprout number and sprouting capacity. The experiments focused on temperature and water potential as the main variables in potato crop planting environment.

Growth media and moisture treatment

The growth medium used in the trials was vermiculite (Grade 2, Australian vermiculite and Perlite Co-P/L). Water potential treatments of -0.6, -0.4 and -0.02 MPa were utilized. The relationship between soil water content and water potential in the preliminary experiment (Whalley *et al.*2001) was calibrated using a psychrometer (SC 10 thermocouple psychrometer Decagon Device, Pullman, Washington) and the following calibration for water potential,Ψ, was obtained:

$$\Psi = 0.0971\theta^{-1.1223} \quad (4.1)$$

where θ is the gravimetric water content.

Based on the calibration, the moisture treatments in all experiments were established by equilibrating 0.19 g, 0.36 g and 3.36 g water/g dry vermiculite for the driest (-0.6 MPa), medium (-0.4 MPa) and wettest (-0.02 MPa) moisture content, respectively. After a 24 hour equilibration period, the vermiculite for each water potential preparation was placed in plastic containers and sealed with a lid to prevent water loss from the container in order to maintain constant water potential throughout the trial.

The effect of fluctuating water potential after planting was examined in two of the trials. This treatment was achieved by moving tubers between two water potential conditions every four days. In both trials utilising the fluctuating water potential treatment, tubers in constant water potential treatments were also removed and then placed back into the same water potential to ensure any differences between fluctuating and constant water potential treatments were not attributable to the movement of tubers.

Plant material

Two cultivars of potato plant *Solanum tuberosum* L., Russet Burbank and Atlantic, were used (Plate 4.2.1). Seed tubers were sourced either from research trial plots or from a commercial seed grower and the date of harvest of the crop was recorded in order to calculate physiological age after storage using a thermal time model (Table 4.2.1). Seed tubers were hand graded to size differences ranging between 10-20 g in all experiments.

Experiment 1 used three different seed lots obtained from a seed potato research trial. The seed crop was planted on 25 November 2004 and individual seed lots were produced by varying haulm removal time to sections of the crop. Haulm removal of the seed crop for each seed lot was done at 120, 90 and 110 days after planting (DAP) for seed lots 1, 2 and 3, respectively. The seed tubers were harvested 10 days after haulm removal. For each seed lot, seed tubers were kept in 4 °C storage after a curing period of 14 days at room temperature until the start of the experiment.

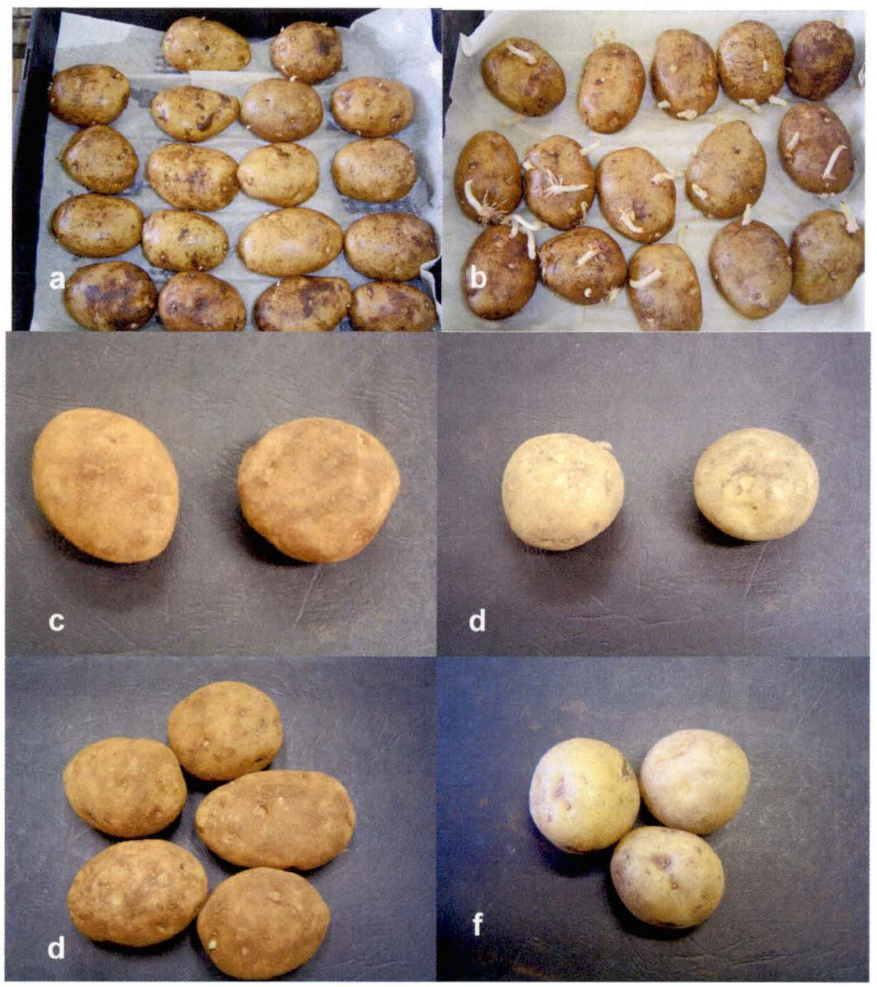


Plate 4.2.1. Plant material used in Experiments 2 and 3 for non-aged (a) and aged seed (b), seed tuber used in Experiment 4 and 5 for non aged of Russet Burbank (c) and Atlantic (d) and aged tubers of Russet Burbank (d) and Atlantic (f).

Table 4.2.1. History of the seed tubers used in the experiments.

Experiment	Seed lot/ Cultivars	Harvest date	Trial start
Experiment 1	R. Burbank		
	Seed lot 1	13/04/2004	8/03/2005
	Seed lot 2	03/03/2004	
	Seed lot 3	01/04/2004	
Experiment 2/ Experiment 3	R. Burbank	02/04/2005	13/12/2005
Experiment 4	R. Burbank	01/05/2006	8/11/2006
	Atlantic	25/03/2006	
Experiment 5	R. Burbank	01/05/2006	21/10/2006
	Atlantic	25/03/2006	

To reduce the risk of disease, tubers were dipped in fungicide (Rovral 1 g/L) and dried before planting. Seed tubers were handled with care to avoid the risk of sprouts being knocked off during handling and planting.

Aging treatment

A range of seed tuber physiological ages were achieved by exposing tubers to 15 °C storage for varying durations. The duration of 15 °C storage varied between 1.5 weeks and 2 months across all experiments (Table 4.2.2). Seed tubers for the younger seed physiological age were kept at 4 °C. Both storage treatments (4 °C and 15 °C) were set up in the dark conditions and relative humidity of 80-90%. After aging in the 15 °C storage, seed tubers were carefully placed back into the 4 °C room until the start of the trial.

Seed age, expressed as degree days or thermal time, is calculated by using equation below:

Degree days= $[(T_{max}+T_{min})/2]$ – base temperature (4.2)

Base temperature of 2 °C was used (Firman *et al.* 1992)

The sum of thermal time for each seed age treatment is shown in Table 4.2.2.

Table 4.2.2. Themal time accumulation for the seed age treatment.

Experiment/ Cultivar	Seed Status	Days in Storage				Sum of Thermal Time > T_b 2 °C (°Cd)
		Curing 15 °C	Holding 4 °C	Aging 15 °C	Holding 4 °C	
Experiment 2 / 3						
R. Burbank	Non-aged	7	204	0	23	545
	Aged	7	204	10	13	655
Experiment 4						
R. Burbank	Non-aged	14	23	0	143	514
	Aged	14	23	62	75	1184
Atlantic	Non-aged	7	68	0	143	513
	Aged	7	68	28	109	809
Experiment 5						
R. Burbank	Non-aged	14	23	0	155	538
	Aged	14	23	62	93	1220
Atlantic	Non-aged	7	68	0	155	537
	Aged	7	68	28	127	845

Equipment and facilities

Two experiments (Experiment 1 and Experiment 2) were carried out on a thermogradient table located at the School of Agricultural Science University of Tasmania. The thermogradient table was set up based on the method developed in the preliminary experiment (section 4.1). The remaining trials were conducted in growth chambers set at constant temperatures. Space available in the growth chambers was greater than in each of the defined temperature zones on the thermogradient table, allowing greater replication within treatments. In all experiments, tubers were kept in darkness for the duration of the experimental period.

Experimental designs and treatments

Experiment 1

Seed tubers of size grade 45-65 g, sourced from three different seed lots, were exposed to four temperature (10, 15, 20 and 25 °C) and three water potential (-0.6, -0.4 and -0.02 MPa) treatments. Two tubers were planted in each container at a depth of 10 cm and covered by the growth media. Containers were then re-sealed to prevent water loss. A randomized block design was employed on the thermogradient table with temperature as the block. Moisture and seed lots treatments were randomized within each temperature treatment. Two containers, each containing 2 tubers, were used for each treatment combination.

Experiment 2

Seed tubers of two physiological ages (non aged and aged) size grade 40-60 g, were exposed to three temperature (10, 15 and 20 °C) and two water potential (-0.02 and -0.06 MPa) treatments. Aging of the seed material was achieved by exposing tubers to 15 °C storage for 10 days. In this trial one seed tuber was planted in each container. A randomized block design was used with 6 replicates for each treatment combination.

Experiment 3

Tubers of two different physiological ages were exposed to three water potential treatments; wet (-0.02 MPa), dry (-0.6 MPa) and fluctuating (alternating between two water potentials every four days). Seed materials used in this trial were from the same lot used in Experiment 2 and the experiments started at the same time. All tubers were held in a single growth cabinet set at 20 °C. Seed physiological age and moisture treatments were arranged in a completely randomized design with 8 replicates per treatment combination.

Experiment 4

Tubers of two cultivars (Russet Burbank and Atlantic) and two different seed ages were exposed to two water potentials (-0.6 MPa and -0.02 MPa) in a growth chamber set at 20 °C. Seed materials were from the same seed lot as in the Experiment 5. Seed tubers were hand graded to 45-55 g and 35-45 g for R. Burbank and Atlantic, respectively. This trial commenced earlier than the Experiment 5, therefore seed tuber accumulated thermal time differed between the trials (Table 4.2.2). A completely randomized design was employed in the trial using 25 replicates per treatment.

Experiment 5

Seed tubers, size grade 40-60 g, of two cultivars (cv. Russet Burbank and Atlantic) and two physiological ages were exposed to three different temperature and soil water potential conditions. An additional treatment where water potential fluctuated between -0.02 and -0.06 MPa was also imposed. Seed tubers were moved into 15 °C storage for 62 and 28 days for Russet Burbank and Atlantic, respectively to produce the aged seed treatment while tubers were kept at 4 °C for the entire storage duration for the non-aged seed treatment. The shorter duration of exposure to 15 °C for aging of seed material for cultivar Atlantic was utilised as longer exposure would have resulted in excessive sprout growth prior to commencement of the experiment. All aged seed tubers were moved back into the 4 °C storage following exposure to the required duration of 15 °C storage.

The experiment was carried out in three growth chambers set at 10, 15 and 20 °C, with seed age and water potential treatments randomly arranged within each cabinet. A total of 25 replicates per treatment combination were used.

Observations and statistical analysis

The experimental duration was three weeks for all trials except the Experiment 3 trial which ran for 2 weeks. At the completion of each trial, sprout numbers were counted and both sprout and tuber weight recorded. Sprouting capacity was calculated from the weights, and expressed as g fresh weight (FW) sprouts per g FW tuber. Using SPSS v. 14.0 (SPSS Inc. 2005) data were analysed to investigate the response of tubers to the treatments.

Results

Interaction between temperature and water potential on sprouting of tubers from different seed lots

Temperature and water potential had a significant impact on sprout number (Figure 4.2.1) of the seed tubers. No significant difference was found between seed lots for sprout number or for sprouting capacity. This prevented examination of possible interactions between tuber physiological age and temperature/water potential. Sprout number per tuber was very high in all seed lots, indicating that the tubers were physiologically old. Sprout number increased from a mean of 9 at 10 °C to 13 at 25 °C. The effect of temperature was greatest when water potential was lowest, with stem numbers from tubers at 10 °C approximately half that of tubers held at 25 °C in the –0.6 MPa treatment. The effect of water potential on sprout number was less than that of temperature, and was more pronounced at lower temperature than higher temperature.

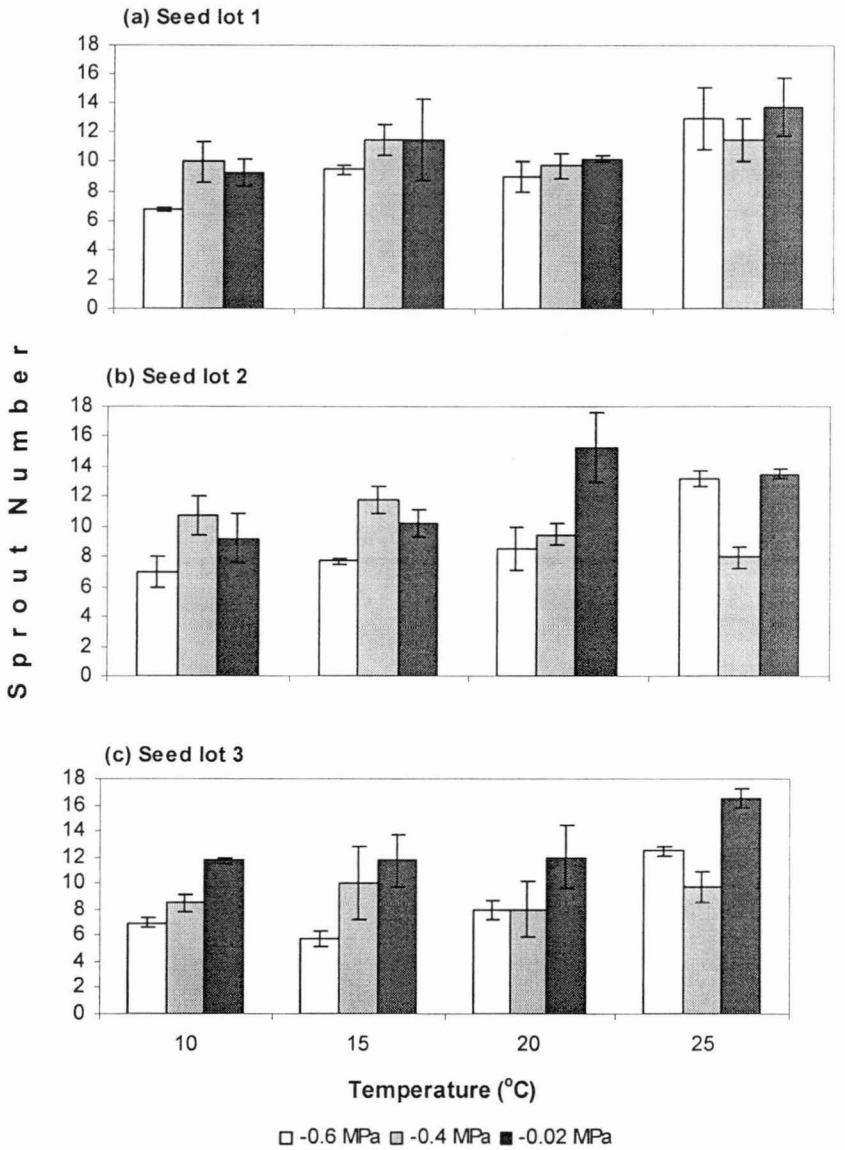


Figure 4.2.1. Sprout number of different seed lots at different temperature and water potential treatments. Tubers are exposed to temperature and water potential treatments in sealed containers for 21 days before assessment. Data are means of 4 replicate tubers. Bar corresponds to standard error of the mean.

Sprouting capacity was found to increase in response to the increase of water potential in the growth media, with the largest response again found at the highest temperature. Temperature and water potential interacted significantly ($p<0.01$) in affecting the sprouting capacity, reflecting the higher effect of moisture conditions at higher temperature (Figure 4.2.2). In contrast to the sprout number response, no significant

difference in sprouting capacity was observed between the –0.6 and –0.4 MPa water potential treatments in all temperature treatments.

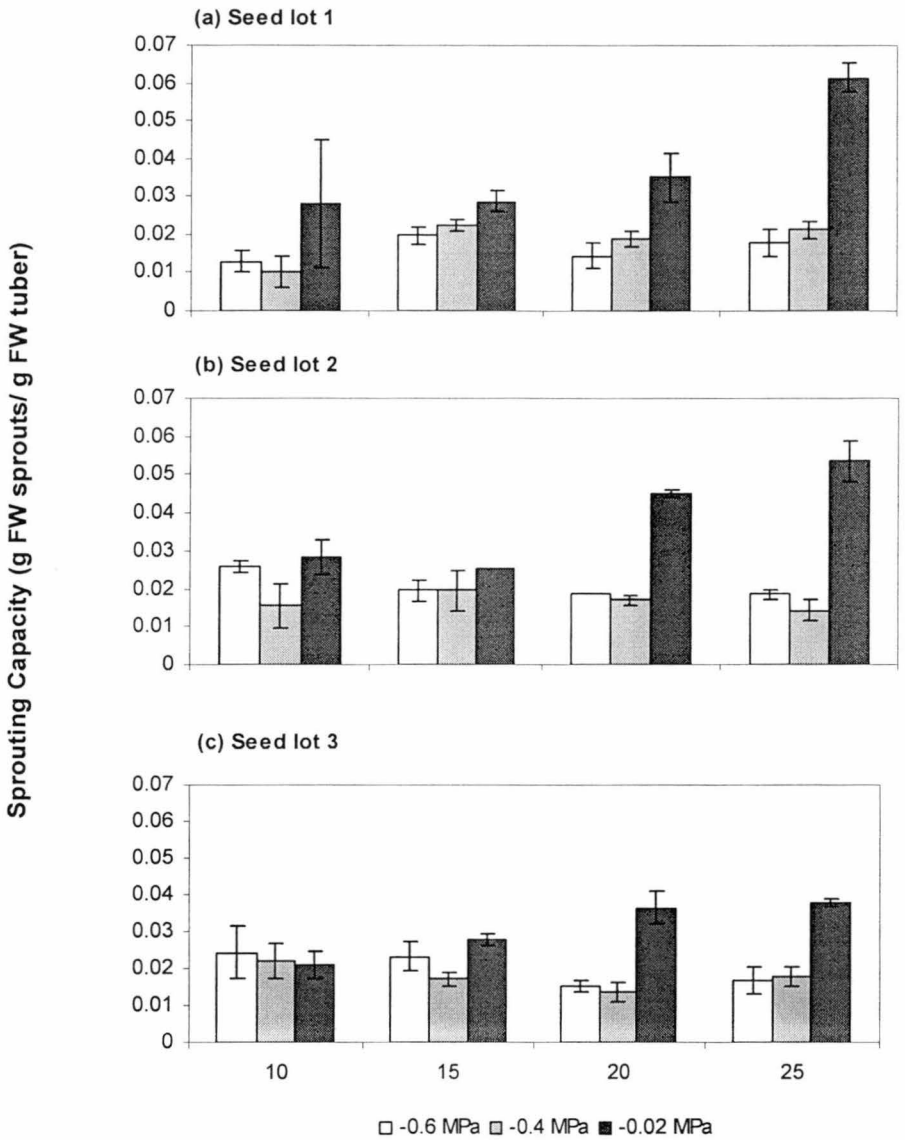


Figure 4.2.2. Sprouting capacity of sprouts of tubers from different seed lots at different temperature and moisture. Tubers are exposed to temperature and water potential treatments in sealed containers for 21 days before assessment. Data are means of 4 replicate tubers. Bar corresponds to standard error of the mean.

Effect of temperature and water potential on sprout number

As several temperature and water potential treatments were common across experiments, the results from each of the experiments undertaken in this section of the project are grouped to display overall trends in the effects of temperature and water potential on sprout number. The number of sprouts produced by the seed tubers in the study is summarised in Table 4.2.3. Large differences in sprout number per tuber were recorded between experiments, indicating variations in tuber physiological age. A trend was noted between the experiments, with sprout number increasing with increasing temperature and water potential. However the magnitude of this increase varied between the experiments.

There was a highly significant effect of temperature ($p<0.001$) on sprout number in Experiment 1 and Experiment 5 but not in Experiment 2. Sprout number per tuber increased from a mean of 3.5 at 10 °C to 4.9 at 20 °C in Experiment 5. In contrast, mean sprout number in trial Experiment 2 was in a narrow range between 5 and 5.4 in the three temperature treatments. The biggest increase in sprout number was observed in Experiment 1. An increase of approximately 30% in sprout number was noticed between the 10 °C and 25 °C treatment. The difference in sprout number between 10 °C and 20 °C treatments was however less, and was consistent with the results from the other experiments. The differences in the response between all experiments could be due to differences in seed tuber age. While calculation of physiological age based on thermal time (above a base temperature of 2 °C) during storage suggested that the tubers used in Experiment 5 were physiologically older, the tubers used in Experiment 2 were held for a much greater duration at 4 °C. This storage contributed little to tuber aging according to the thermal time model using a 2 °C base temperature, but the sprouting response of the tubers suggested that they had aged more than those used in Experiment 5.

Table 4.2.3. Sprout number of tubers as affected by temperature in three experiments. Data are means across all non temperature treatments. Values in italic are standard error of the means, N=18, 24 and 300 for Experiment 1, 2 and 5 respectively.

Experiment	Temperature (°C)			
	10	15	20	25
Experiment 1	8.9 ± *0.53*	9.9 ± *0.81*	10 ± *0.74*	12.4 ± *0.82*
Experiment 2	5.3 ± *0.24*	5.0 ± *0.35*	5.4 ± *0.34*	-
Experiment 5	3.5 ± *0.07*	3.8 ± *0.09*	4.9 ± *0.11*	-

Variation in sprout numbers between experiments was also noted in the water potential treatments, but a consistent trend of increasing sprout number with increased water potential was noted (Table 4.2.4). The biggest effect of water potential was observed in Experiment 1 where an increase of about 4 sprouts was recorded between -0.6 to -0.02 MPa treatments. The difference in sprout number between -0.6 MPa and -0.02 MPa water potential treatments ranged from 0.3 in Experiment 2 to 1.2 sprout increase in Experiment 4. As with the temperature response, the response to water potential was small in Experiment 2, while in all other experiments an increase in water potential from -0.6 to -0.02 MPa resulted in at least one additional sprout.

Table 4.2.4. Sprout number of tubers cv R. Burbank at 20 °C as affected by moisture. Data are means across all non moisture treatments. Values in italic are standard error of the means, N=24, 36, 16, 50 and 150 for Experiment 1, 2, 3, 4 and 5 respectively.

Experiment	Water potential (MPa)	
	-0.6	-0.02
Experiment 1	8.5 ± *0.11*	12.5 ± *0.13*
Experiment 2	5.1 ± *0.27*	5.4 ± *0.24*
Experiment 3	5.3 ± *0.35*	6.4 ± *0.52*
Experiment 4	5.0 ± *0.17*	6.2 ± *0.28*
Experiment 5	5.6 ± *0.14*	6.1 ± *0.16*

Statistical analysis on the sprout number parameter in each experiment revealed that there was significant interaction between temperature and moisture in Experiment 5 ($p<0.05$) but not in Experiment 1 and 2 (Table 4.2.5).

Table 4.2.5. Interaction between temperature and moisture on sprout number of tuber cv R. Burbank in three experiments. Data are means across all non temperature and moisture treatments. Values in italic are standard error of the means, N= 6, 12 and 50 for Experiment 1, 2 and 5 respectively. l.s.d (0.05) for Experiment 5 = 0.57.

Experiment	Water potential (MPa)	Temperature (°C)		
		10	15	20
Experiment 1	-0.02	10 ± *0.22*	11.2 ± *0.20*	12.5 ± *0.25*
	-0.6	6.9 ± *0.18*	7.7 ± *0.25*	8.5 ± *0.23*
Experiment 2	-0.02	5.3 ± *0.40*	5.3 ± *0.54*	5.4 ± *0.48*
	-0.6	5.3 ± *0.28*	4.7 ± *0.45*	5.3 ± *0.50*
Experiment 5	-0.02	4.1 ± *0.11*	4.4 ± *0.11*	5.6 ± *0.11*
	-0.6	3.3 ± *0.11*	4.7 ± *0.11*	6.1 ± *0.11*

Interaction between temperature, water potential and seed tuber physiological status on sprout number

A significant interaction between temperature, water potential and seed tuber physiological status was observed in the Experiment 2 trial. However no significant interaction was found in Experiment 5 trial. In the first experiment, sprout numbers were not different between the moisture treatment and seed age except at 15 °C in dry condition and when the conditions is wet at the highest temperature (Table 4.2.6).

Table 4.2.6. Interactions between moisture, seed age and temperature on sprout number in Experiment 2. Tubers are exposed to different temperature and water potential treatments in sealed containers for 21 days. Data are means of 6 replicate tubers.

Seed physiological Age	Water Potential (MPa)	Temperature (°C)		
		10	15	20
Non-aged	-0.6	5.5 bc	5.7 bc	5.0 abc
	-0.02	5.5 bc	5.5 bc	6.5 c
Aged	-0.6	5.2 abc	3.7 a	5.7 bc
	-0.02	5.2 abc	5.2 abc	4.3 ab

Values follow by same letter are not significantly different (p=0.05) l.s.d =1.7.

Table 4.2.6 above shows that seed age became the major factor in the determination of sprout number. Younger seeds appeared to be more sensitive to the change of temperature when moisture was available. At high water potential (-0.02 MPa) and when water was fluctuated the gradient of increase in sprout number of the younger seed between temperature treatments was greater compared to the older seed.

Table 4.2.7. Sprout number of aged and non-aged tubers at different water potential and temperature treatments in Experiment 5. Tubers are exposed to different temperature and water potential treatments in sealed containers for 21 days. Data are means of 25 replicate tubers. Values in italic are standard error of the means.

Soil Water Potential (MPa)	Soil Water Potential (MPa)	Temperature (°C)		
		10	15	20
Non-aged	-0.6	3.7 ± *0.21*	3.9 ± *0.20*	4.9 ± *0.27*
	Fluctuated	3.6 ± *0.17*	3.7 ± *0.20*	5.1 ± *0.26*
	-0.02	3.4 ± *0.19*	3.8 ± *0.27*	5.1 ± *0.29*
Aged	-0.6	3.4 ± *0.19*	3.7 ± *0.21*	4.5 ± *0.26*
	Fluctuated	3.8 ± *0.18*	3.5 ± *0.24*	4.9 ± *0.24*
	-0.02	3.3 ± *0.18*	4.1 ± *0.24*	4.9 ± *0.24*

No significant interaction was found between temperature and seed tuber physiological age or status. Nevertheless, a trend of increase in sprout number with temperature was observed to be consistent in physiologically younger tubers although the gradient of the increase varied between the trials (Table 4.2.8).

Table 4.2.8. Sprout number of cv R. Burbank of two seed physiological ages at different temperature. Data are means across all non temperature and seed tuber physiological age treatments. Values in italic are standard error of the means, N=12 and 75 for Experiment 2 and 5, respectively.

Experiment	Temperature (°C)	Seed physiological age	
		Non-aged	Aged
Experiment 2	10	5.5 ± *0.41*	5.2 ± *0.24*
	15	5.6 ± *0.54*	4.4 ± *0.40*
	20	5.7 ± *0.48*	5.0 ± *0.48*
Experiment 5	10	3.9 ± *0.16*	3.8 ± *0.17*
	15	4.6 ± *0.18*	4.4 ± *0.20*
	20	6.2 ± *0.18*	5.4 ± *0.20*

Interaction between water potential and seed tuber physiological status on sprout number

No significant interaction between water potential and seed age was found on the number of sprouts produced by the seed tubers, and this was consistent in all experiments. Increasing water potential resulted in increased sprout number, except in Experiment 5 where sprout number of physiologically older seed tubers decreased with increasing water potential (Table 4.2.9). Physiologically younger seed tubers showed a bigger gradient in sprout number as a response to increasing water potential from -0.6 to -0.02 MPa. An addition of at least one sprout was observed in the non-aged tubers when water potential was increased to -0.02 MPa.

Table 4.2.9. Sprout number of cv R. Burbank at 20 °C as affected by different water potential and seed status in five experiments. Data are means across all non water potential and seed tuber status treatments.

Experiment	Seed age	Water potential (MPa)	
		-0.6	-0.02
Experiment 1	Lot 1	9	10.3
	Lot 2	8.5	15.3
	Lot 3	8	12
Experiment 2	Non-aged	5.0	6.5
	Aged	5.7	4.3
Experiment 3	Non-aged	5.5	7
	Aged	5.0	5.8
Experiment 4	Non-aged	5.1	6.6
	Aged	4.9	5.8
Experiment 5	Non-aged	4.9	5.1
	Aged	4.5	4.9

Aged tubers were characterised with lesser sprouts than the non-aged tubers. The trend was consistent over the experiments. The aging treatment seemed to promote sprout growth on few buds prior to planting. In the case of non-aged seeds, no large dominant sprouts were present before planting as seed tubers were kept in low storage temperature which restricted sprout growth.

Effect of temperature and water potential on sprout vigour

The effects of temperature and water potential on sprouting capacity were not consistent over the experiments. However, similar trends were noted with an increase in sprouting capacity with increasing temperature and water potential in two out of three experiments (Table 4.2.10). The size of the response also varied between trials. A five fold increase was observed in Experiment 5 when temperature was increased from 10 °C to 20 °C while only a small increase in sprouting capacity from 0.021 to 0.024 g FW sprouts per g FW tuber was observed in Experiment 1 as shown in Table 4.2.10. A low value of

sprout vigour at 10 °C in Experiment 5 was associated with low number of sprouts and difference in seed tuber materials.

A significant interaction ($p<0.001$) between temperature and moisture in affecting sprout vigour was observed in two out of three experiments (Table 4.2.10). However no consistent trend was observed between the response to temperature and water potential. Variability between the results of all experiments was high with sprout vigour ranged between 0.004 to 0.031 g FW sprouts per g FW tuber at 10 °C and 0.016 to 0.039 g FW sprouts per g FW tubers at 20 °C.

Table 4.2.10. Interaction between temperature and moisture treatments on sprout vigour (g FW sprouts/g FW tuber) of cv R. Burbank in three experiments. Data are means across all seed tuber age treatments. Values in italic are standard error of the means, N=6, 12 and 50 for Experiment 1, 2 and 5, respectively.

Experiment	Water potential (MPa)	Temperature (°C)		
		10	15	20
Experiment 1	-0.02	0.026 ± *0.005*	0.027 ± *0.001*	0.039 ± *0.003*
	-0.6	0.021 ± *0.003*	0.021 ± *0.002*	0.016 ± *0.001*
	Mean	**0.021 ± *0.002***	**0.023 ± *0.001***	**0.024 ± *0.003***
Experiment 2	-0.02	0.031 ± *0.005*	0.033 ± *0.004*	0.030 ± *0.003*
	-0.6	0.025 ± *0.004*	0.019 ± *0.002*	0.022 ± *0.004*
	Mean	**0.028 ± *0.003***	**0.026 ± *0.003***	**0.026 ± *0.003***
Experiment 5	-0.02	0.004 ± *0.0005*	0.019 ± *0.001*	0.025 ± *0.0007*
	-0.6	0.004 ± *0.0004*	0.018 ± *0.0008*	0.023 ± *0.0009*
	Mean	**0.004 ± *0.0002***	**0.018 ± *0.0005***	**0.023 ± *0.0007***

Water potential treatments induced variable responses over the trials. Significant water potential treatment effects on sprouting capacity were recorded in three out of five experiments (Table 4.2.11). The differences in sprouting capacity were significant in

Experiment 1, Experiment 2 and Experiment 4 but not significant in Experiment 5 and Experiment 3. Sprout vigour was observed to be higher when water potential increased from -0.6 to -0.02 MPa.

Table 4.2.11. Sprouting capacity (g FW sprouts/g FW tuber) of seed tubers of cv R. Burbank at 20 °C at different water potentials. Data are means across all non water potential treatments. Values in italic are standard error of the means, N=6, 36, 16, 100 and 50 for Experiment 1, 2, 3, 4 and 5, respectively.

Experiment	Water potential (MPa)	
	-0.6	-0.02
Experiment 1	0.016 ± *0.001*	0.039 ± *0.003*
Experiment 2	0.022 ± *0.002*	0.030 ± *0.002*
Experiment 3	0.021 ± *0.003*	0.025 ± *0.003*
Experiment 4	0.022 ± *0.001*	0.032 ± *0.001*
Experiment 5	0.023 ± *0.001*	0.025 ± *0.001*

Interaction between temperature, water potential and seed tuber physiological status on sprout vigour

The f-test result on sprouting capacity showed that there was no significant interaction between temperature, moisture and seed age either in experiments 2 or 5 (Appendix B5 and B10 for experiment 2 and 5, respectively) (Table 4.2.12).

Table 4.2.12. Interaction between moisture, seed tuber physiological status and temperature on sprouting capacity (g FW sprouts/g FW tuber) of tubers in two experiments.

Experiment	Seed physiological age	Soil Water Potential (MPa)	Temperature (°C)		
			10	15	20
Experiment 2	Non-aged	-0.6	0.015	0.012	0.017
		-0.02	0.035	0.020	0.021
	Aged	-0.6	0.018	0.026	0.028
		-0.02	0.043	0.046	0.038
Experiment 5	Non-aged	-0.6	0.004	0.017	0.025
		-0.02	0.004	0.018	0.024
		Fluctuated	0.005	0.018	0.020
	Aged	-0.6	0.008	0.019	0.026
		-0.02	0.011	0.022	0.027
		Fluctuated	0.010	0.022	0.023

Interaction between water potential and seed tuber physiological status on sprout vigour

Although there was no significant interaction found between moisture and seed tuber physiological status, aged seed tubers appeared as having a higher sprouting capacity than the non aged tubers. The difference between sprout vigour of the seed tubers was slightly higher when water potential was low and this was consistent over trials except in Experiment 2 (Table 4.2.13). Physiologically younger tubers (non-aged tuber) were found to be more sensitive to changes in water potential (Figure 4.2.3).

Table 4.2.13. Sprouting capacity (g FW sprouts/g FW tuber) of seed tuber cv R. Burbank at 20 °C as affected by different water potential and seed status.

Experiment	Seed physiological age	Water potential (MPa)		
		-0.6	-0.02	Fluctuated
Experiment 2	Non-aged	0.017	0.021	-
	Aged	0.028	0.038	-
Experiment 3	Non-aged	0.009	0.017	0.010
	Aged	0.033	0.032	0.035
Experiment 4	Non-aged	0.021	0.027	-
	Aged	0.028	0.028	-
Experiment 5	Non-aged	0.022	0.025	0.022
	Aged	0.024	0.026	0.022

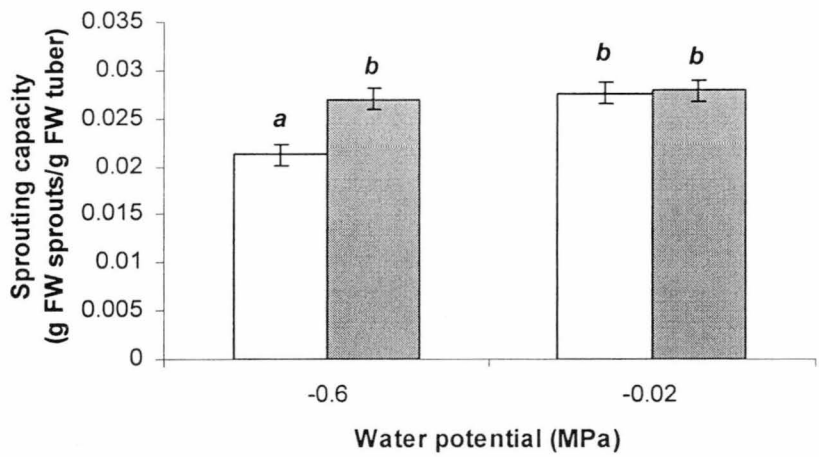


Figure 4.2.3. Sprouting capacity (g FW sprouts/g FW tuber) of aged (▩) and non-aged (□) tubers at different water potentials in Experiment 4. Data are means across all non water potential treatments. Error bar corresponds to standard error of the mean (N= 50). *Bars with same letter are not significantly different (p=0.05).*

Cultivar differences in sprout number and vigour

Response of cultivar to temperature and seed tuber physiological status on sprout number and vigour

Russet Burbank was shown in this study to be more sensitive to temperature changes than Atlantic in terms of sprout number and sprouting capacity (Figures 4.2.4 and 4.2.5). This difference was more evident in non-aged seed tubers (Table 4.2.14). This sensitivity can be shown further by the significant interaction ($p<0.01$) between temperature and cultivar on the sprouting capacity.

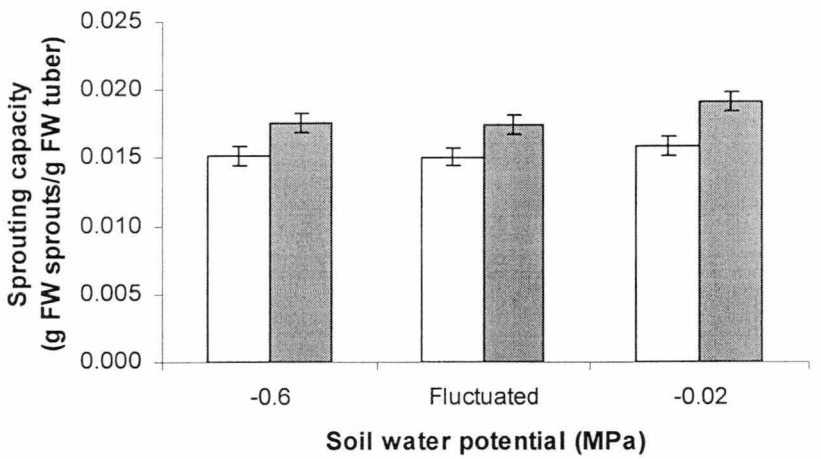


Figure 4.2.4 Sprout number of seed tubers cv R. Burbank (□) and Atlantic (▩) at different temperatures. Data are means across all non temperature and cultivars treatments. Bar corresponds to standard error of the mean (N=150).

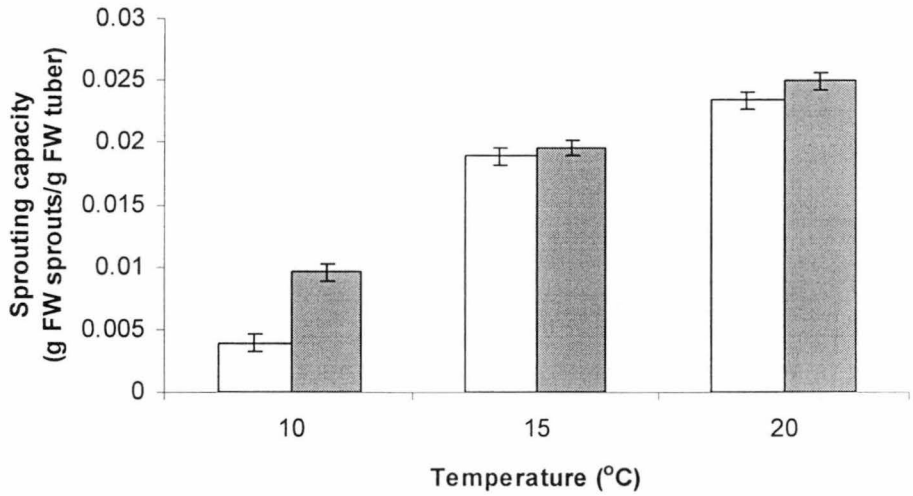


Figure 4.2.5. Sprouting capacity (g FW sprouts/g FW tuber) of seed tubers cv R. Burbank (□) and Atlantic (▩) at different temperatures. Data are means across all non temperature and cultivar treatments. Bar corresponds to standard error of the mean (N=150).

At 10 and 15 °C, non-aged and aged tuber did not show much difference in sprout number in both cultivars (Table 4.2.15). It is only when temperature increased to 20 °C that the non-aged and aged seeds of cultivar Russet Burbank showed difference while Atlantic remained the same. This indicates that temperature seems to affect Russet Burbank more than Atlantic in terms of sprout number. Despite this, differences between seed age in terms of sprout vigour were more evident for cultivar Atlantic than Russet Burbank at all temperatures.

Table 4.2.14. Sprout number and sprouting capacity (g FW sprouts/g FW tuber) of non-aged and aged seed tubers of cv R. Burbank and Atlantic at different temperatures in Experiment 5. Values in italic are standard error of the means.

Cultivar	Seed age	Temperature (°C)		
		10	15	20
Sprout number				
R. Burbank	Non-aged	3.8 ± *0.2*	4.6 ± *0.2*	6.2 ± *0.2*
	Aged	3.8 ± *0.2*	4.4 ± *0.2*	5.4 ± *0.2*
Atlantic	Non-aged	3.3 ± *0.1*	3.0 ± *0.2*	3.9 ± *0.2*
	Aged	3.2 ± *0.1*	3.1 ± *0.1*	4.1 ± *0.2*
Sprouting capacity (g FW sprouts/g FW tuber)				
R. Burbank	Non-aged	0.004 *a*	0.0019 *d*	0.023 *e*
	Aged	0.004 *a*	0.0019 *d*	0.024 *e*
Atlantic	Non-aged	0.004 *a*	0.017 *cd*	0.023 *e*
	Aged	0.015 *bc*	0.023 *e*	0.027 *f*

Values followed by same letter are not significantly different (p=0.05).

Response of cultivars to water potential and seed status on sprout number and early vigour

No significance difference was found between the responses of the two cultivars to water potential and seed physiological age treatments in sprout number and sprouting capacity (Table 4.2.15). Water potential increases resulted in increased sprout number and sprout vigour of the seed tubers for both cultivars.

Table 4.2.15. Sprout number and sprouting capacity of seed tuber of two cultivars at 20 °C as affected by different water potentials and seed status. Data are means of 25 replicate tubers.

Experiment	Cultivar	Seed age	Water potential (MPa)		
			-0.6	-0.02	Fluctuated
Sprout number					
Experiment 4	R. Burbank	Non-aged	5.1	6.6	-
		Aged	4.9	5.8	-
	Atlantic	Non-aged	5.1	5.2	-
		Aged	4.2	4.9	-
Experiment 5	R. Burbank	Non-aged	6.1	6.3	6.1
		Aged	5.1	5.9	5.3
	Atlantic	Non-aged	3.7	3.9	4.2
		Aged	3.8	4.0	4.5
Sprouting capacity (g FW sprouts/g FW tuber)					
Experiment 4	R. Burbank	Non-aged	0.019	0.032	-
		Aged	0.025	0.032	-
	Atlantic	Non-aged	0.023	0.023	-
		Aged	0.029	0.024	-
Experiment 5	R. Burbank	Non-aged	0.022	0.025	0.022
		Aged	0.024	0.026	0.022
	Atlantic	Non-aged	0.028	0.022	0.019
		Aged	0.027	0.029	0.024

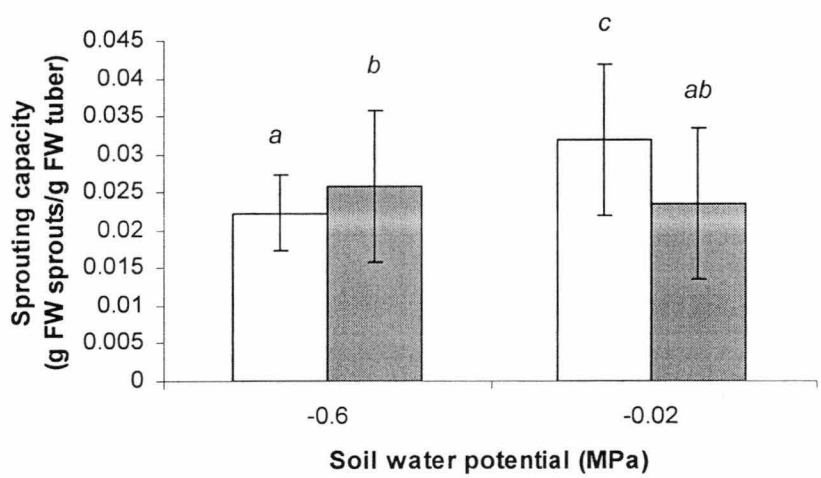


Figure 4.2.6. Sprouting capacity (g FW sprouts/g FW tuber) of tubers cv R. Burbank (□) and Atlantic (▩) at different water potential in Experiment 4. Data are means across seed tuber physiological status treatments. Error bar corresponds to standard deviation (N=50). *Bars with same letter are not significantly different (p=0.05).*

Russet Burbank was shown to be more sensitive to changes in water potential than Atlantic in sprouting capacity (Figure 4.2.6) in trial Experiment 4.

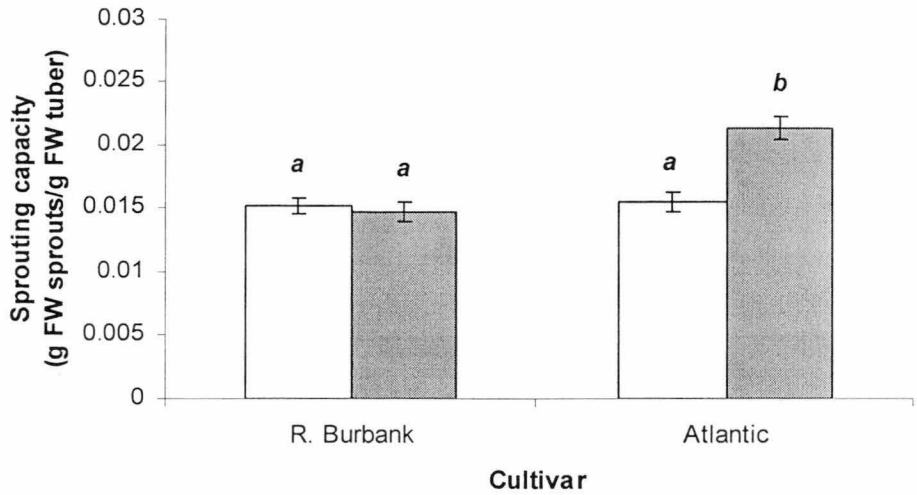


Figure 4.2.7 Sprouting capacity (g FW sprouts/g FW tuber) of aged (▒) and non aged (□) tubers cv R. Burbank and Atlantic in Experiment 5. Data are means across seed tuber physiological status treatments. Error bar corresponds to standard error of the mean (N=225). *Bars with same letter are not significantly different (p=0.05).*

A strong interaction was found between cultivar and seed age on sprouting capacity in Experiment 5 ($p<0.001$) (Figure 4.2.7). Sprouts of Russet Burbank tubers were found to be smaller in size than in Atlantic despite having more sprouts on the tuber. Differences in sprouting capacity between seed ages in Russet Burbank cultivar were not as evident as in Atlantic.

Discussion

This study has shown that planting environment (temperature and water potential at planting) can significantly affect both sprout number and sprout vigour. Increased sprout number and sprouting capacity with increasing temperature and water potential was recorded across the 5 experiments, and this trend was also consistent with the results of the preliminary experiment reported in section 4.1. The magnitude of the responses

varied between trials, indicating that variation in responses to planting environment were related to differences in the physiological age or status of the seed tubers.

The sprout number response to temperature was greater in non-aged tubers than in tubers that were exposed to a period of higher temperature during storage. Sprouting capacity, which has been used as an indicator of seed aging (Krijthe 1962), was generally higher in the aged seed tubers than the untreated tubers. However, in sprouting pattern, the untreated seed tubers displayed a multiple sprouts pattern, a pattern characteristic of more advanced physiological age. Interpretation of these results is complicated by the effect of the aging treatment on sprout development prior to imposition of the temperature treatments. The aging treatment tended to induce some sprout growth prior to planting, meaning that sprout weight at the conclusion of the trials was a combination of growth prior to and during the experiment. Visually, sprout growth during the experiments greatly exceeded that prior to the imposition of temperature treatments, suggesting that the anomaly between sprout number and sprout vigour in terms of describing physiological age was a valid observation, but measurements were not made to confirm this conclusion. Advanced sprout growth on eye buds, which has been attributed to the stages of seed tuber physiological aging, may also suppress the growth of other sprouts and thus influence sprout number. According to Moorby and Milthorpe (1975), exposing seed tubers to high temperature storage lead to few sprouts becoming dominant, an observation that was consistent with the results of this study.

Variations in water potential in the growth media were also shown to alter the sprouting pattern of the seed tubers. Lower water potentials decreased the sprout number, which is in agreement with Letnes (1958) who found that the sprouting may be restricted when planting seed tubers in dry soil. However, the response was found to be variable between experiments between tubers of different physiological status. Larger reductions in sprout number were observed in physiologically younger seed tubers. This finding is evidence that soil moisture conditions at planting may interact with the physiological status of the seed tubers to alter the seed performance. This might be related to differences in characteristics of cells in the physiologically older tuber which affect the ability of the tissue to adjust its internal water potential to maintain growth in low water potential

conditions. Water potential of the growth media influences the availability of water to be taken by the seed tuber to support the sprout growth, and seed tuber status may determine the uptake process (Svensson 1977).

Despite the effect of water potential on sprout number, the effect of water potential of the growth media on sprout vigour was not consistent between experiments. Nevertheless, sprouting capacity tended to decrease in lower water potential treatments. Low water potential in the media may be expected to influence sprout growth through a reduction in cell expansion, therefore resulting in smaller sprouts. This is comparable with the response of other plants to water deficit where cell expansion is the most sensitive to water deficit (Fitter and Hay 1989). Other authors have documented a decrease in potato stem fresh weight due to drought treatment (Heuer and Nadler 1995).

Russet Burbank was found to be more sensitive to the changes in temperature than Atlantic in terms of sprout number. Russet Burbank was also found to be more sensitive to changes in water potential in relation to sprout number and sprouting capacity. Previous studies have documented cultivar differences in response to drought. Cultivar Atlantic was found to maintain lower stem water potential compared to cultivars Norchip and Monona in response to low water potential conditions (Coffey *et al.* 1997). Differences in water relations between cultivars could therefore contribute to variation in response to changing water potential during crop establishment.

The evidence presented in this section supports the conclusion that besides factors that are already known to affect the stem number, such as seed size (eye number), storage duration and conditions, temperature and moisture conditions at planting can affect sprout number from seed tubers. These factors appear to interact to alter the expression of the physiological status of the seed tubers in determining seed performance. This study also leads to the conclusion that, in order to quantify the stem number production, seed tuber physiological age is not the only factor that defines the stem number per plant but temperature and moisture at planting also need to be considered.

The results of this study then may lead to an explanation for the inconsistency in physiological age studies and on the difference between studies in the lab and in the field.

Study in the lab was almost always carried out in controlled temperature using the optimum temperature for sprouting (15 to 20 °C) while conditions in the field such as soil temperature and water potential is hard to control and may vary or fluctuate. Planting environment then may interact with the physiological status of the seed tubers and alter the potential of seed tuber performance. Beside that it is hard to come up with a generalisation of the response of seed tubers to physiological aging. Nevertheless, new ideas have been initiated by this study which provides an indication of the possible interaction between planting environment and seed tuber age. Further study is needed to undertake to include a broader range of seed tuber physiological status as it is important to acknowledge that seed tuber materials used in this trial could be in a very narrow physiological status and the thermal time concept as an indicator of seed aging is not sufficiently accurate. The thermal time concept has been modified recently by Struik *et al.* (2006) who suggest that the temperature sum after the end of dormancy is more crucial for the process of aging of the seed tuber. Despite this, there has not been a unifying indicator for the physiological age of the seed tuber. Study then needs to be conducted to investigate a method to quantify the seed tuber status which in turn may influence the sprouting pattern of the seed tubers.

Chapter 5 Investigation of water potential effect on sprouting and mitotic index as an indicator of the sprouting pattern of tubers of different physiological ages

Introduction

The physiological aging process of the seed tuber is triggered by factors inside the tubers through biochemical and physiological changes (Kumar and Knowles 1996; Hajirezai *et al.* 2003; Claassens and Vreugdenhil 2000). The changes in seed tubers during storage are associated with physiological processes such as hormonal metabolism, carbon metabolism and membrane integrity, with some of these processes contributing to loss of apical dominance in tubers during storage. An understanding of these different pathways in the tubers may lead to identification of a biochemical indicator for seed tuber aging (reviewed in Coleman 2000). However, to date there has been little success in finding an indicator as many changes in biochemical pathways are specific to certain conditions and therefore a unifying marker that works in all conditions and circumstances has proved difficult to identify.

While studies have focused on identifying an indicator of physiological age within the tuber, less attention has been given to changes occurring within the sprouts on the tuber. At the end of dormancy, the initiation of sprout growth may be regulated by changes associated with the aging process, but may also be influenced by processes occurring within the sprouts. In addition, as changes in the number of sprouts emerging from a tuber are characteristic of physiological aging, changes in cellular activity within the sprouts may be an early indicator of physiological aging. According to Caldiz *et al.* (2001), the influence of physiological age of the seed tuber is modified by additional effects of conditions and treatments on the behaviour of the sprouts after dormancy breaking. Other authors suggest that when sprouting starts in storage, both mother tuber and sprout age affect the sprouting pattern of the tuber (van Ittersum 1992; Krijthe 1962). After planting, temperature and water potential of the planting media also affect the sprouting pattern of tubers, and it is possible that this effect is through processes

occurring in the sprouts rather than, or in addition to, processes in the mother tuber. While tubers are in storage, sprout growth is generally restricted by low temperature and water availability, so the major processes involved in aging are likely to be in the mother tuber. Following planting, however, the sprouts become the major sites for cell growth and development processes. As external conditions may influence the rate and timing of growth and development processes, investigation of the effects of temperature and water potential on sprout development processes may explain the effect of planting environment on stem number.

Sensitivity towards storage environmental conditions, especially temperature, during different stages of physiological development of the seed tuber may vary before and after dormancy break due to changes in metabolic processes taking place (Struik *et al.* 2006). While these authors may have considered growth and development of the sprouts in the eyes of the tuber after sprouting to be part of aging, it is potentially a different set of processes than those within the tuber (hormones, membrane properties and carbon metabolism). However, evidence for separate processes is rare.

Mitotic index is one way to measure the growth and development of cells in plant tissue. Mitotic index is the percentage of cells within an area of tissue that are dividing at any given time. During dormancy in potato tubers, where no sprout growth occurs even when the seed tuber is exposed to favourable conditions for sprouting, the sprout meristem within the eye bud was found to have its meristematic cell activity blocked at the G1 phase, an intervening phase in cell cycle before DNA synthesis phase takes place (Hopkins and Huner 2004 *p.* 343), resulting in a low mitotic index (Campbell *et al.* 1996). This index gradually increased following the loss of seed tuber dormancy. The mitotic index could be used for describing the growing capacity of each eye on the tuber. Increase in mitotic index in the lateral buds was found to coincide apex removal in pea (*Pisum sativum* L.) seedlings (Nagao and Rubinstein 1976). This indicates that release from apical dominance in this instance could be marked by the occurrence of cell divisions in the buds. Only a few studies related to mitotic index in potato during tuber formation (Duncan and Ewing 1984) and bud dormancy (Faivre-Rampant *et al.* 2004) have been published. Low temperature storage will allow reserve mobilization and

hormonal changes to take place (Hajirezai *et al.* 2003) but may restrict or inhibit the mitotic activities on the bud meristem (Campbell *et al.* 1996).

Experiments were undertaken to investigate the relationship between mitotic activity of the eye buds of seed tubers and physiological age of the seed tubers, and changes in sprouting pattern induced by temperature and water potential treatments. The experiment was designed to test hypotheses that there are differences in growing capacity of the eye buds of potato tubers at different positions on the tuber and there is a correlation between the growing capacities of the sprouts and the net growth and sprout number. It is proposed that differences in mitotic activity between eye buds may influence the sprouting pattern.

Materials and methods

Experimental design and treatments

The trial contained eight treatments; two cultivars (Russet Burbank and Atlantic) and two different seed ages. Seed tubers were aged by exposing tubers to 15 °C storage for 2 months while seed tubers for the younger seed physiological age treatment were kept at 4 °C. Both storage treatments (4 °C and 15 °C) were set up in dark conditions and a relative humidity of 80-90%. After aging in the 15 °C storage, seed tubers were carefully placed back into the 4 °C room until the start of the trial. Each age and cultivar combination was grown in two moisture conditions (-0.6 and -0.02 MPa for dry and wet treatment, respectively) in a single growth cabinet set at 20 °C. Vermiculite (Grade 2, Australian vermiculite and Perlite Co-P/L) was used as the growth medium and water potential for each moisture treatment was established as in previous experiments using Equation 1 in section 4.2, *p.* 64 in Chapter 4. Three eye bud positions were marked (Plate 5.1) and initial length of each sprout was measured using a dissecting microscope fitted with an eyepiece micrometer. Prior to commencing the treatment, an initial sample was taken to establish mitotic activity of sprouts at the completion of the storage period.

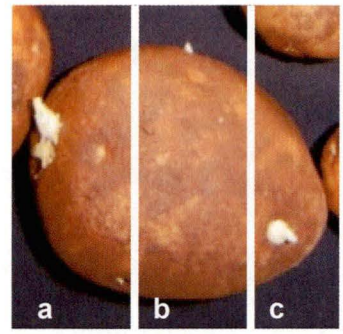


Plate 5.1. Determination of the sections on the seed tuber
(a) apical end (b) median (c) basal end

Tubers were either left intact or the selected eyes were isolated using a cork borer to obtain a core sample. Each intact tuber was planted in a single plastic container (0.75 L round container) at 10 cm depth and the core samples (three for each tuber) were planted approximately five cm apart. A completely randomized design was employed with 25 replicates, resulting in a total of 400 samples. After three weeks, assessment of sprouting at each position was undertaken and the length of sprouts was recorded. Percentage of eyes sprouting (% sprouting) and net growth of each sprout was calculated. Percentage sprouting for each position was recorded as the proportion of eye buds where sprout growth was recorded from all replicates. Data then was analysed with SPSS v.14.0 (SPSS Inc. 2005) software package.

Mitotic index assessment

For each seed tuber, eye buds from three different positions were marked (Plate 5.1). Shoot apical meristem of each bud was excised and prepared based on the squash method described below. Prior to excision, sprout length and diameter then were measured for each of the buds. The sprout tip was dissected from the remaining tuber and sprout tissue (Plate 5.2.a) and the apical dome (Plate 5.2.b) was then dissected using a dissection microscope.

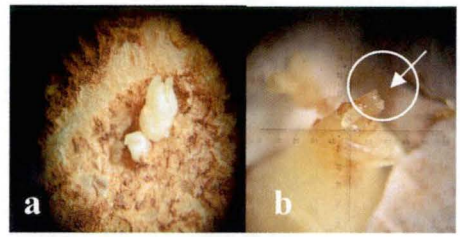


Plate 5.2. Picture of a. an eye with buds; b. sprout apical meristem with apical dome shown between the leaf primordia

The sample was carefully transferred on to a glass slide using a small scalpel. A drop of the staining solution, 1% aceto-orcein, was added and the glass slide was warmed with an alcohol lamp. A cover slip was placed over the meristematic tissue and the apex tissue was gently squashed with the cover slide. These processes were repeated twice to make sure the cells were separated and evenly spread.

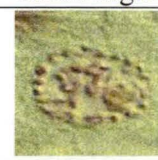
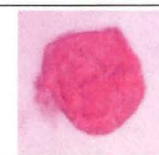
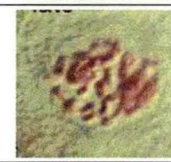
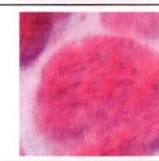
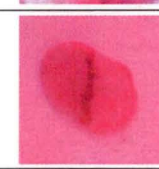
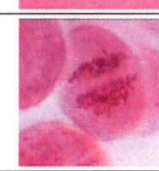
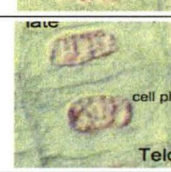
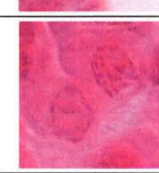
Using a Carl Zeiss Microscope with Nomarski phase (a Differential Interference Contrast method), mitotic activity of shoot apical meristem cells of eyes at different position on the seed tubers was qualitatively determined.

Technical information for the microscope:

- Filter 473600 (polarising filter)
- DIC condenser 465279
- Type 3 Interference-contrast slide: Inco slide, 474433

Mitotic index was determined by counting the number of cells in the four mitotic stages (Prophase, Metaphase, Anaphase and Telophase) in 5 different fields of view for each sample. Mitotic stages are described briefly in figures in Table 5.1. Before entering the mitotic stage, the cell is in Interphase, which is indicated by a nucleus with firm shape and no chromosome condensation.

Table 5.1. Mitotic stage in the cell cycle of green algae (Koning 1994) and potato (this chapter).

Cell Cycle Stages	Green algae	Potato
Prophase		
Prometaphase		
Metaphase		
Anaphase		
Telophase		

Results

Mitotic index assessment

There was no significant difference in mitotic index of sprout apices between eye bud positions ($p=0.246$) and seed tuber status ($p=0.808$) for cultivar Russet Burbank. Similarly, this was also observed for cultivar Atlantic ($p=0.745$ and $p=0.791$ for eye bud position and seed age, respectively) (Table 5.2). Mitotic index of the sprouts were found to be within a range of 40 to 60%.

Table 5.2 Mitotic index of eye buds at three different position of seed tuber in different physiological ages. Values in italic are standard errors of the means (N=10).

Cultivar	Seed tuber physiological status	Mitotic index (%) at bud position		
		Apical	Median	Basal
R. Burbank	Non Aged	43.5 ± *6.8*	50.6 ± *9.2*	50.8 ± *6.0*
	Aged	41.2 ± *7.8*	57.2 ± *6.0*	50.4 ± *5.5*
Atlantic	Non Aged	44.1 ± *9.6*	50.3 ± *4.0*	40.3 ± *6.2*
	Aged	50 ± *3.9*	45 ± *7.0*	44.4 ± *7.2*

While the differences were not statistically significant, there was a trend towards sprouts on physiologically older tubers having higher mitotic index than on younger tubers. No consistent trend in mitotic index was shown within the bud position for both cultivars. Although differences between eye bud positions were not significant, mitotic index of sprout apex at median and basal were higher than apical sprouts in cultivar Russet Burbank for both young and old seed tubers. This trend was not observed in Atlantic where highest mitotic index was found in sprouts at the median position in younger tuber while physiologically older tubers showed highest mitotic activity in the apical sprout.

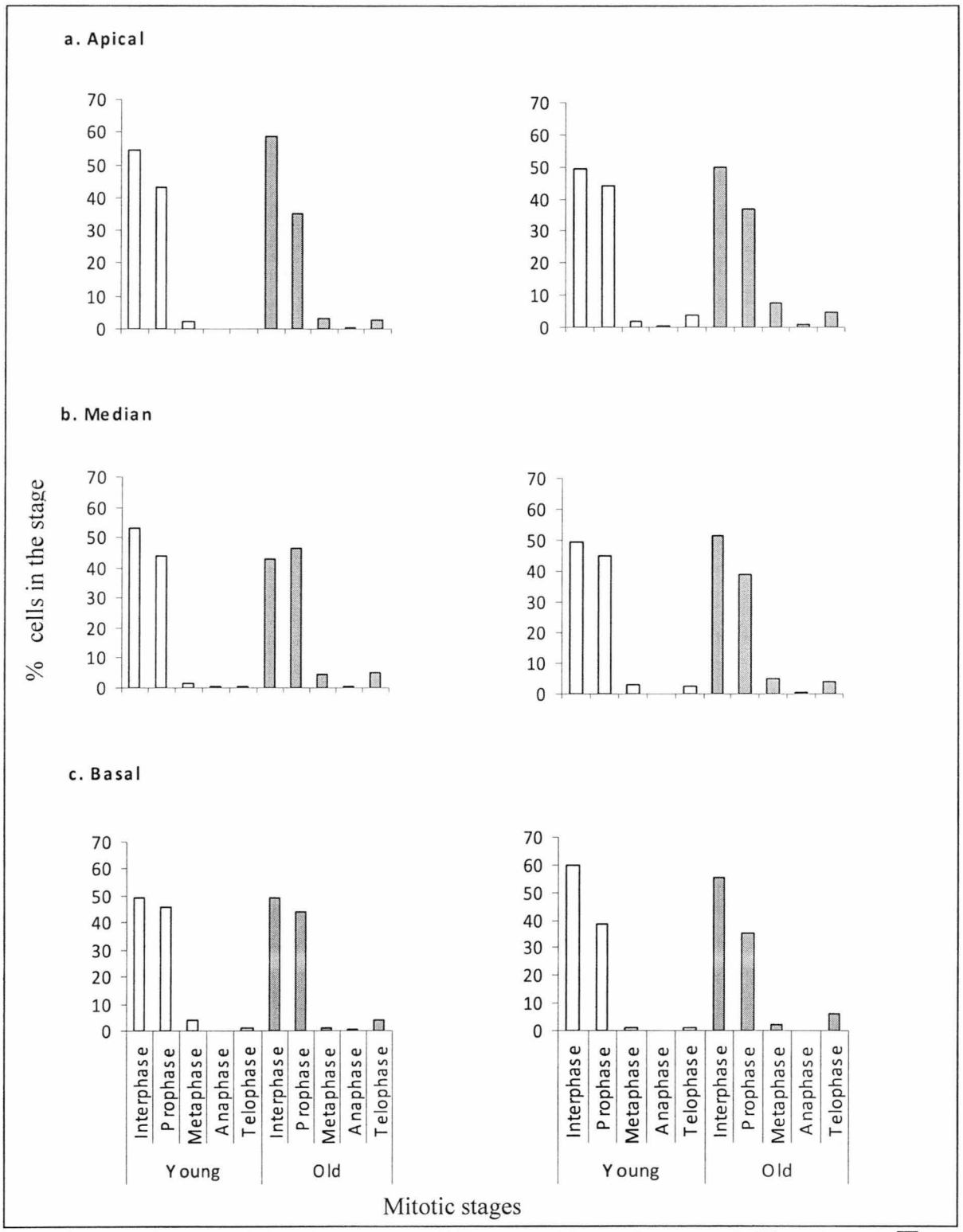


Figure 5.1. Cells activity of sprouts on different positions of non-aged (□) and aged (▩) tubers of cv R. Burbank (left) and Atlantic (right).

Mitotic assessment also shows that more cells at the later stages of mitosis were found in the sprouts of physiologically older seed tubers in both cultivars (Figure 5.1. and Table 5.3) however no significant differences between bud positions were found. More cells in the metaphase stage were found in aged tubers of cultivar Atlantic than non aged tuber but not in cultivar Russet Burbank.

Table 5.3. Proportion of cells in different mitotic stages in sprout apical meristem of eye buds at different positions and seed tuber status of cultivar Russet Burbank and Atlantic. l.s.d. figures shown with extent of significance (*p<0.05, **p<0.01, ***p<0.001, n.s not significant).

Cultivar	Mitotic Stage	% of cells in the mitotic stage		l.s.d
		Non Aged	Aged	
R. Burbank	Interphase	52.4	50.4	n.s.
	Prophase	44.2	42	n.s.
	Metaphase	2.6	3.3	n.s.
	Anaphase	0.2	0.5	n.s.
	Telophase	0.7	4.0	0.6**
Atlantic	Interphase	55.1	52.3	n.s.
	Prophase	40.9	37.1	n.s.
	Metaphase	1.9	5.1	1.0*
	Anaphase	0.1	0.5	n.s.
	Telophase	2.0	5.1	1.1*

Correlations between mitotic activity and sprout growth

Mitotic index was not significantly correlated to either percentage sprouting (p=0.701) or net growth (p=0.747) of the eye bud at different positions (Appendix C7) across all moisture treatments. Mitotic index differences between aged and non aged seed tubers did not explain the sprouting of the eye bud at different positions (Figure 5.2).

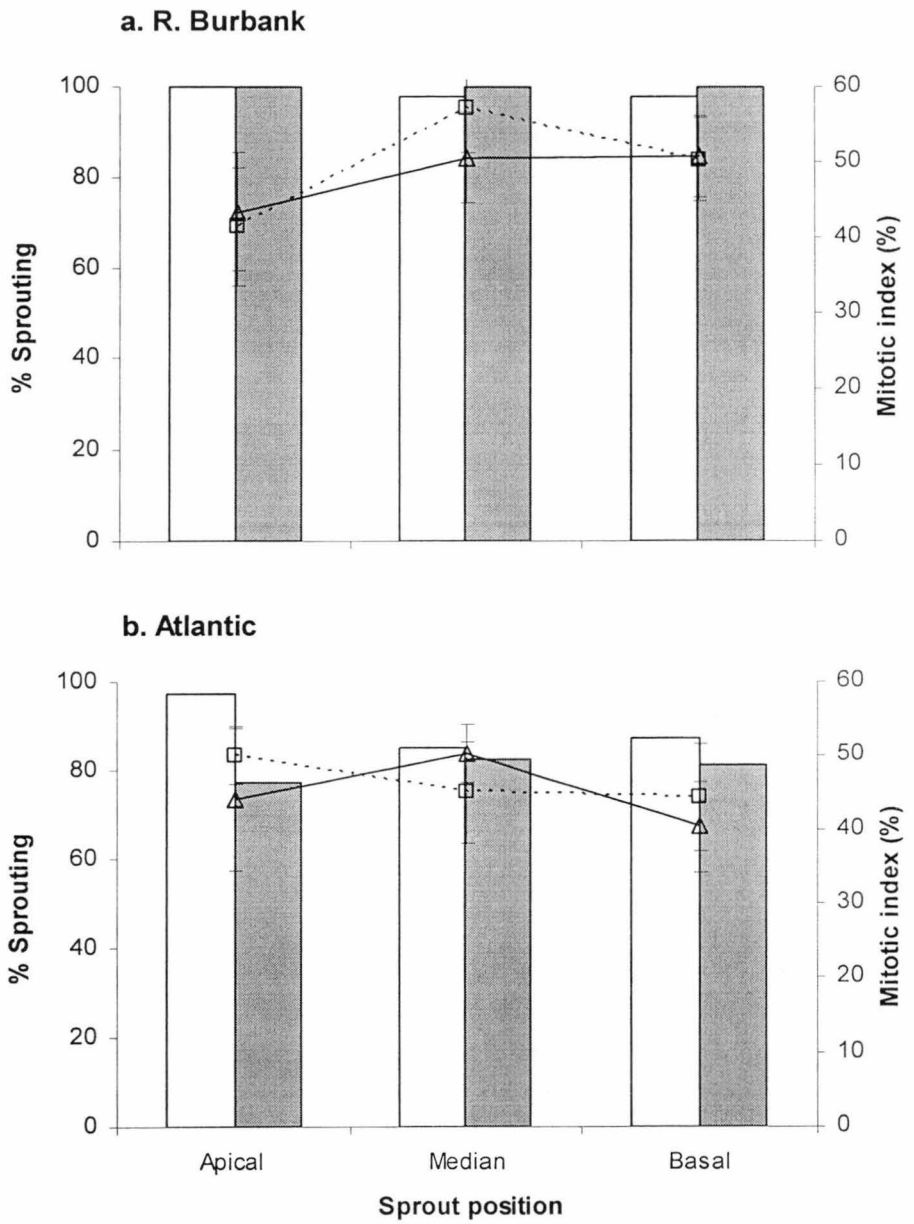


Figure 5.2 Mitotic index (symbols and lines) and % sprouting (bars) of sprouts of isolated eye bud at different position on seed tuber of non-aged tuber (__△__, □) and aged tuber (----□----, ▩) of cv R. Burbank (a) and Atlantic (b). Bar corresponds to standard error of the mean (N=10).

Mitotic index did not explain differences between the eye bud positions on seed tubers having the same physiological status. Although no significant difference was found in

the net growth between the isolated buds at different positions in both cultivars, lower net growth in median position sprouts was recorded in cultivar Atlantic. Data showed that mitotic index of sprouts at this position tended to be higher than at the basal or apical positions. However sprout growth of the eye buds within the same seed tuber physiological status did not follow the trend of mitotic index. This indicated that other mechanisms within the seed tuber may regulate the difference in mitotic index between the eyes while seed tuber aging processes affect the growth rate of sprouts after planting.

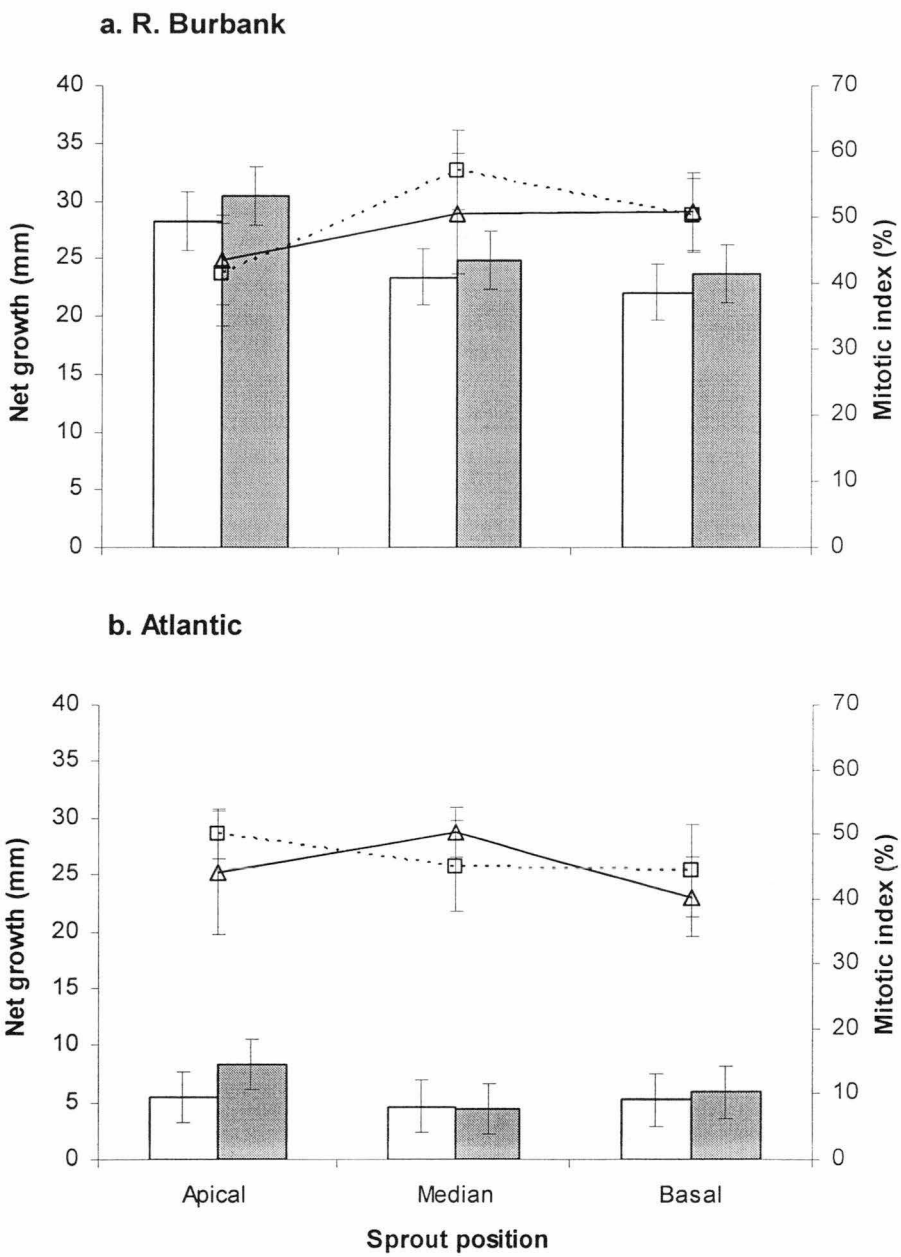


Figure 5.3. Mitotic index (symbols and lines) and net growth (bars) of sprouts of the isolated eye bud at different position on seed tuber of two cultivar (a) Russet Burbank and (b) Atlantic of non-aged tuber (___Δ___, □) and aged tuber (----□----, ▩). Bar corresponds to standard error of the mean (N=10 and N= 50 for mitotic index and net growth, respectively).

Interaction between eye buds on % sprouting and net growth

The effect of apical dominance on sprouting was evident when sprouting of intact tubers was compared to sprouting in cores taken from equivalent tubers (Figure 5.4). There was a significant apical dominance effect ($p<0.01$) when the buds were left intact on the mother tuber in cultivar Atlantic but not in Russet Burbank ($p=0.133$) across all moisture treatments.

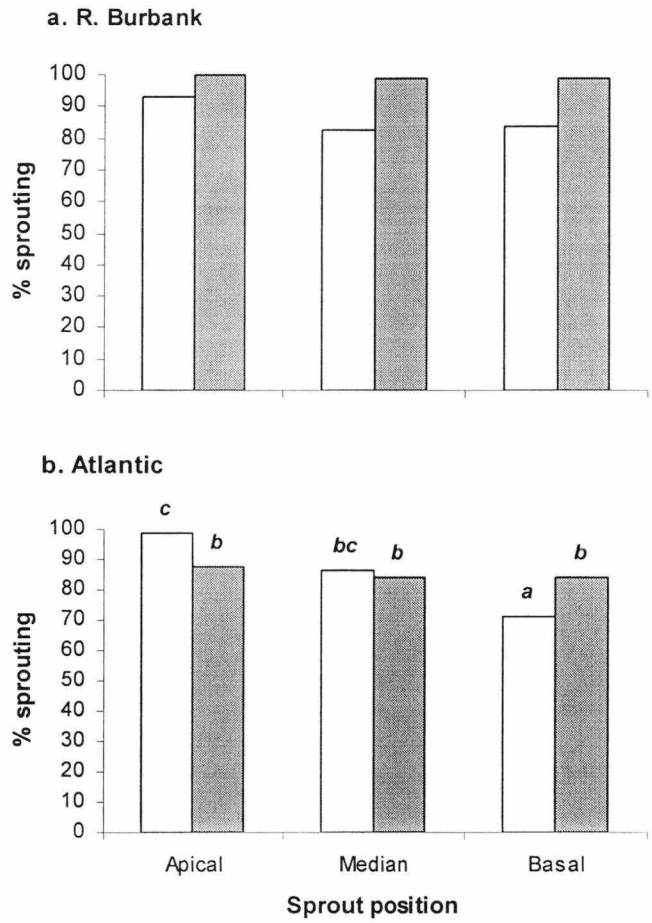


Figure 5.4. % sprouting of sprouts at different position for (a) Russet Burbank and (b) Atlantic in intact tuber (□) and core samples (▩). *Bars with same letter are not significantly different (p=0.05).*

There were no significant differences between seed tuber physiological age in the % sprouting found between eye buds at different positions both in intact or isolated buds. This response was consistent both in cultivar Russet Burbank ($p=0.267$) and Atlantic ($p=0.875$) (Figure 5.5). For cultivar Russet Burbank, sprouting potential increased to 10

and 15% in median and basal sprouts, respectively in physiologically older (aged) tubers when the eye bud was isolated from the dominance of the apical sprouts. This trend also was observed in physiologically younger seed tuber but only for sprouts at the basal end of the tuber. For cultivar Atlantic, apical dominance was observed both in physiologically older tubers and younger ones when the eye buds were intact in the mother tuber. Isolating the eye buds from the apical sprouts did not increase the percentage of sprouting of eye buds at median and basal position.

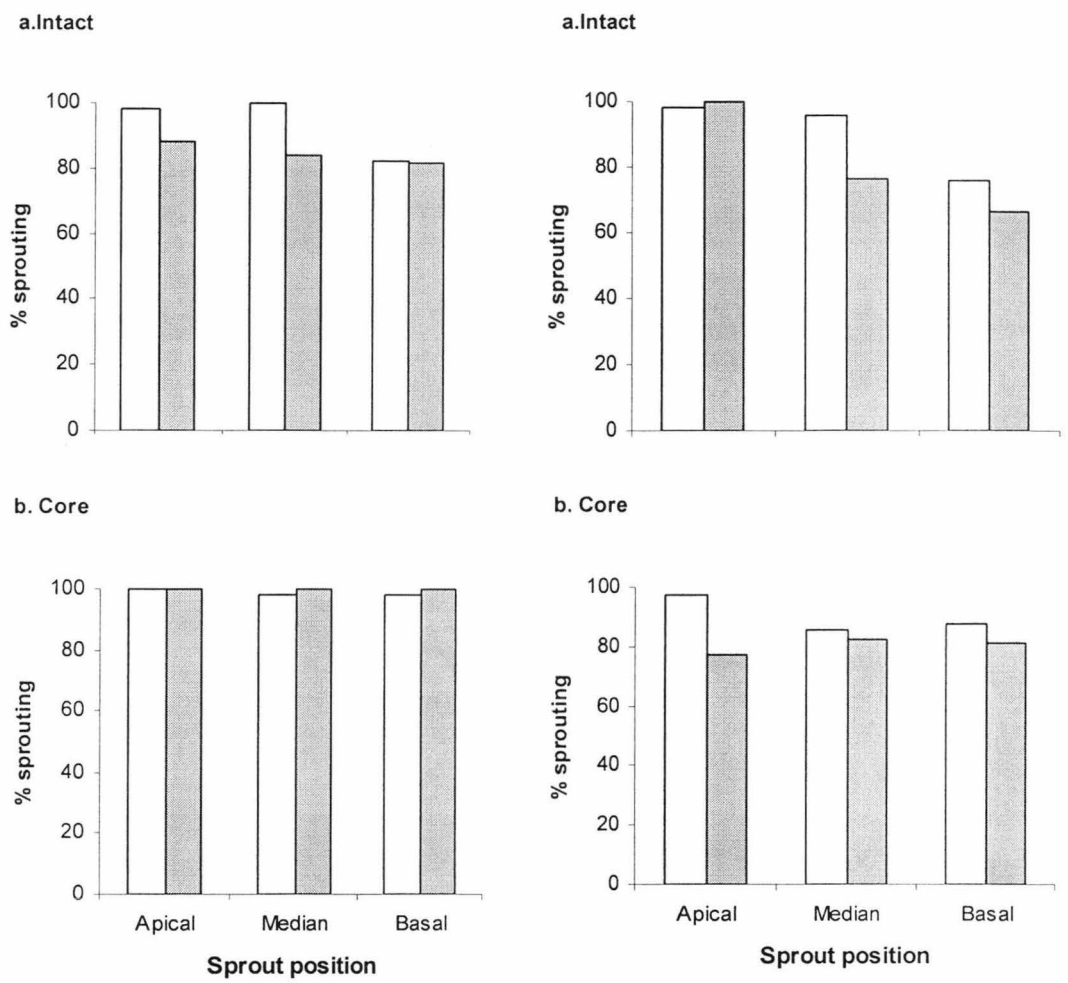


Figure 5.5. % sprouting of sprouts at different position in non-aged seed tubers (□) and aged tubers (▩) physiologically young and old tubers in (a) intact and (b) core samples of cultivar Russet Burbank (left hand side) and Atlantic (right hand side).

For cultivar Atlantic, apical sprouts were found to have significantly higher net growth compared to median and basal sprouts when the eye buds were intact ($p<0.001$) (Figure 5.6). This difference was smaller when eye buds were isolated, although there was always higher sprout growth in apical sprouts either in intact or core samples. Apical dominance was stronger in cultivar Atlantic compared to Russet Burbank. The suppression followed a hierarchy based on bud position, with basal buds the most suppressed. Although isolation in Atlantic eliminated the dominance of the apical sprouts, it also resulted in sprouts with lower net growth compare with intact bud. Isolation did not reduce the growth of sprouts in Russet Burbank.

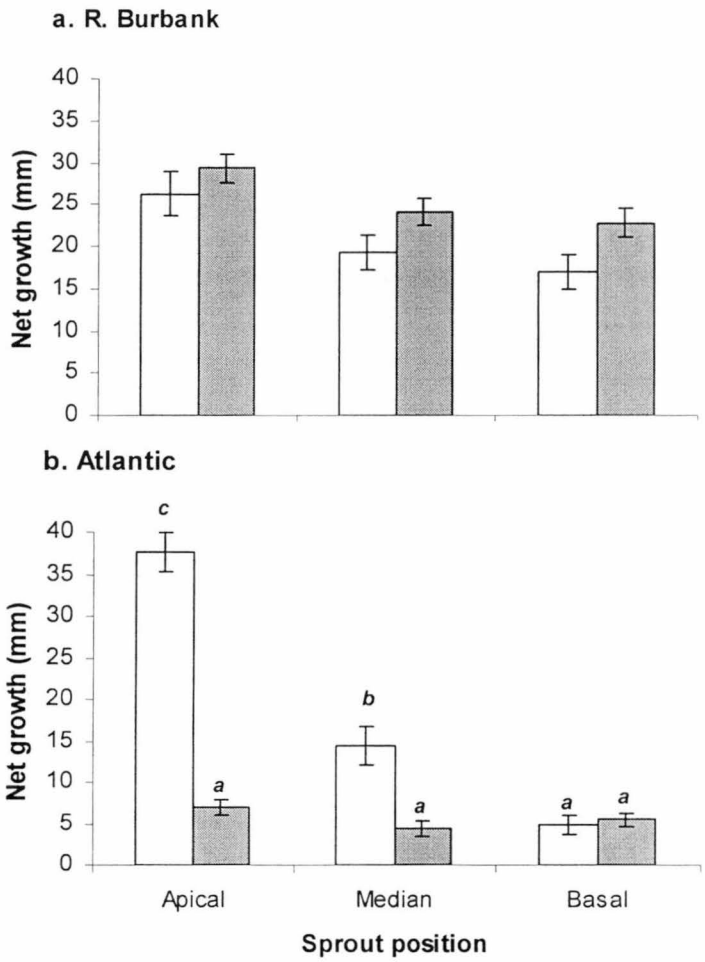


Figure 5.6. Net growth of isolated (▩) and intact (□) sprout at different bud position. Bar corresponds to standard error of the mean (N=100). *Bars with same letters are not significantly different (p=0.05).*

Nevertheless, no significant differences were found between seed tuber physiological ages in sprout growth in this study for both cultivars (Table 5.4).

Table 5.4. Net growth of sprout at different bud positions on seed tubers different in physiological ages. Data are means across tuber types. Values in italic are standard error of the means (N=100).

Cultivar	Seed tuber physiological status	Net growth (mm) at:		
		Apical	Median	Basal
R. Burbank	Non-aged	25.4 ± *2.0*	21.9 ± *2 0*	20.1 ± *1.9*
	Aged	30.2 ± *2.5*	21.6 ± *1.8*	19.7 ± *1.9*
Atlantic	Non-aged	21.5 ± *2.5*	12.0 ± *2.2*	5.0 ± *1.0*
	Aged	23.1 ± *2.4*	6.9 ± *1.5*	5.5 ± *0.9*

The growth of sprouts at the median and basal end of the seed tuber were more suppressed in cultivar Atlantic than in Russet Burbank when older and younger seed tubers were compared. Cultivar Atlantic showed longer apical position sprouts at planting compared to Russet Burbank (Table 5.5). It is interesting to note that while mean sprout length was higher in the apical than median and basal positions for Atlantic, the mitotic indices of the apical meristem were not significantly different (Table 5.2). This indicates that mitosis/cell division has already commenced during storage.

Table 5.5. Initial sprout length of sprout at different eye bud position of two cultivars. Data are means of 100 replicate tubers. Values in italic are standard error of the means.

Seed tuber physiological age	Bud position	Initial sprout length (mm)	
		R. Burbank	Atlantic
Young	Apical	1.0 ± *0.05*	1.2 ± *0.05*
	Median	1.2 ± *0.05*	0.9 ± *0.05*
	Basal	0.9 ± *0.04*	0.9 ± *0.04*
Old	Apical	1.3 ± *0.1*	1.8 ± *0.09*
	Median	1.3 ± *0.06*	0.9 ± *0.05*
	Basal	0.9 ± *0.05*	0.9 ± *0.06*

Effect of moisture and seed tuber physiological age on growth of sprouts at different positions

The sprouting potential and net growth of the sprouts on the seed tuber was influenced significantly by moisture and whether the eye bud was isolated or left intact on the tuber for both cultivars ($P<0.001$). There was no significant effect of seed tuber physiological age ($p=0.843$) on net growth, but sprout position showed significant effects on this parameter ($p<0.001$). Only a small effect of seed tuber age was found in the sprouting percentage parameter ($p=0.021$) for cultivar Atlantic but there was no effect on seed tuber age in Russet Burbank.

Sprouting potential and net growth of the sprouts increased with water potential (Table 5.6 and 5.7). Increase in sprout numbers could be related to the increase in sprouting potential of sprouts in the median and basal section.

Table 5.6. Percentage of sprouting and net growth of buds at different positions on aged and non aged seed tuber of cv R. Burbank. l.s.d. (0.05) = 2.8 and 2.0 for % sprouting and net growth, respectively.

Seed Physiological Status	Water Potential (MPa)	Intact			Core		
		Apical	Median	Basal	Apical	Median	Basal
%Sprouting							
Non-aged	-0.6	96	72	80	100	96	96
	-0.02	100	92	92	100	100	100
Aged	-0.6	84	76	68	100	100	100
	-0.02	92	92	95	100	100	100
Net growth (mm)							
Non-aged	-0.6	18.6	14.5	12.0	14.8	8.2	7.8
	-0.02	26.5	26.2	24.4	41.7	38.7	36.3
Aged	-0.6	28.3	17.6	11.0	18.8	12.2	8.1
	-0.02	31.7	19.3	20.7	42.0	37.5	39.1

Table 5.7. Percentage of sprouting and net growth of buds at different positions on aged and non aged seed tuber of cultivar Atlantic. l.s.d. (0.05) = 4.9 and 1.8 for % sprouting and net growth, respectively.

Seed Physiological Status	Water Potential (MPa)	Intact			Core		
		Apical	Median	Basal	Apical	Median	Basal
%Sprouting							
Non-aged	-0.6	100	96	76	95	75	75
	-0.02	96	96	76	100	96	100
Aged	-0.6	100	65	62	59	65	67
	-0.02	100	88	71	96	100	96
Net growth (mm)							
Non-aged	-0.6	42.8	26.0	1.5	2.1	0.9	1.6
	-0.02	32.3	12.7	8.2	8.8	8.3	8.8
Aged	-0.6	41.9	6.1	5.2	2	1	1.6
	-0.02	33.7	12.7	4.8	14.7	7.8	10.3

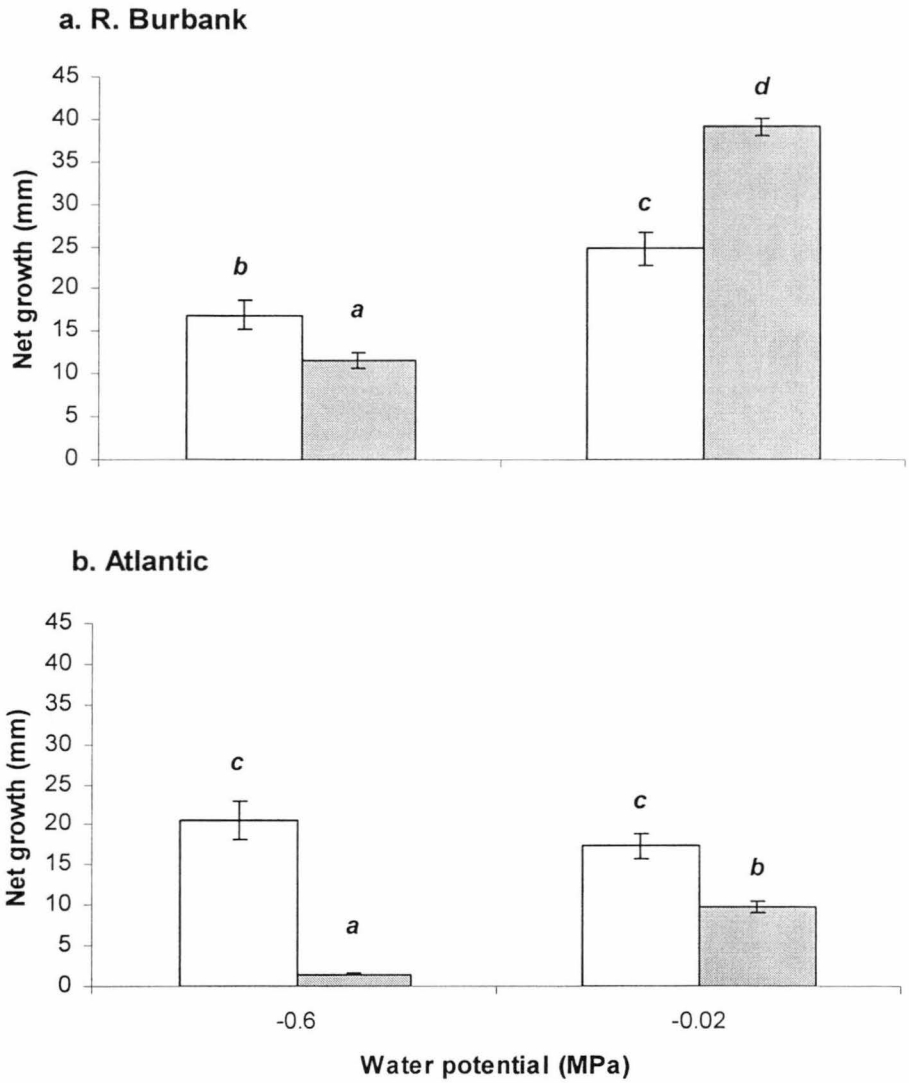


Figure 5.7. Net growth of sprouts of intact (□) and isolated (▩) of cv (a) R. Burbank and (b) Atlantic at different water potential. Each data point is average across seed tuber physiological status and sprout positions. Bar corresponds to standard error of the mean (N=150). *Bars with same letters are not significantly different (p=0.05).*

Sprout net growth decreased with water potential, and the effect was particularly evident in core samples compared to when the eye buds were intact on the mother tuber (Figure 5.7) in both cultivars. In intact tubers, sprout growth was maintained presumably by seed tuber adjustment to water deficit. When moisture is not limiting growth, net growth was higher in core samples than intact tuber as there was no competition between eye

buds. Growth in Russet Burbank was affected to a greater extent by change in water potential than Atlantic.

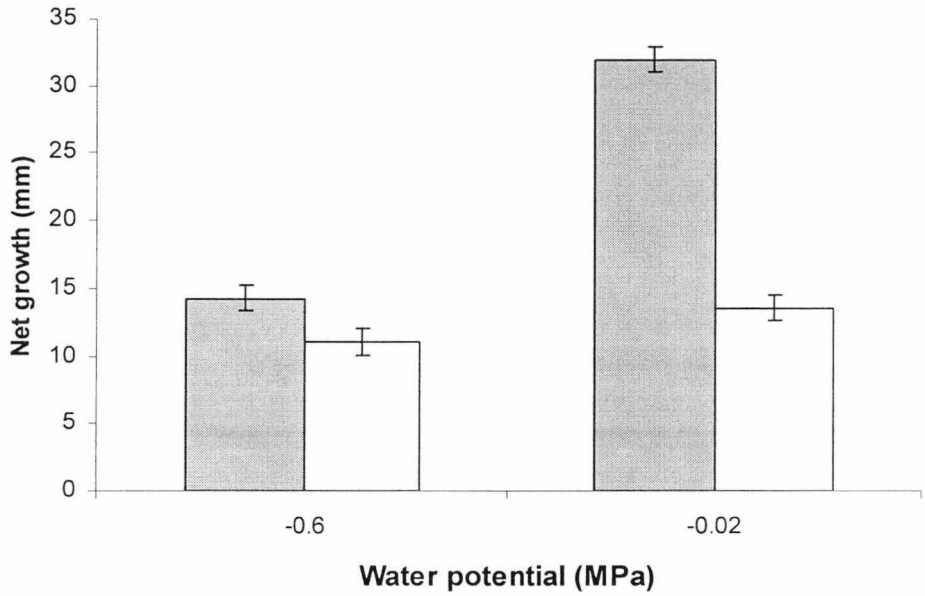


Figure 5.8. Sprout growth of cv R. Burbank (▩) and Atlantic (□) at different water potential. Data are means of all non cultivar and water potential treatments. Bar corresponds to standard error of the mean (N=300).

Discussion:

The mitotic index of sprouts were found to be within a range of 40 to 60%, which was similar to previously published values of non-dormant, actively growing sprout apices of potato (Campbell *et al.* 1996). The mitotic index of sprouts prior to planting was not correlated with sprout development after planting. There was no significant difference in mitotic index between sprouts at apical, mid tuber and basal positions, but significant differences were recorded in the percentage of sprouts that elongated and in the growth rate of the sprouts. The rate of cell division in the sprout meristem at planting was therefore not an indicator of growth potential of the sprout. The presence of sprouting during storage could account for the elevated mitotic level at planting as cell division and expansion are needed for sprouting. This may explain the non significant differences

in mitotic index and warrants further assessment of mitotic activity of buds during storage and sprouting.

The small range of the mitotic index values between physiologically young and old seed tubers may indicate a narrow range of physiological aging of the seed tubers used, and this conclusion was supported by the sprout growth measurements between the seed tuber age treatments. Comparison of sprout growth rates between intact tubers and isolated cores containing a single sprout demonstrated that an apical dominance response was present in both young and old tubers of both cultivars. Although mitotic index at planting was similar between eye buds on the seed tuber, sprouting growth of the bud at median and basal positions was reduced by this correlative interaction between the buds. The sprouting pattern associated with apical dominance was consistent with published observations (Goodwin 1966; Hay and Hampson 1991), with a greater reduction in sprouting potential the further the distance of the bud from the apical complex.

The degree of apical dominance was found to vary between cultivars and with seed tuber physiological age, which is in agreement with Phillips (1975) who suggested that physiological conditions of individual plants influence the degree of disadvantage experienced by the lateral buds. Aging of seed tubers in higher temperature storage increased this inhibition mechanism, presumably by promoting a few sprouts to grow bigger and thus suppressing other buds. In both cultivars, the proportion of cells in telophase stage was significantly higher in sprouts of aged seed tubers, which may indicate that aging seed tubers in higher temperature storage increases the cellular activities in the eye bud (Moorby and Milthorpe 1975). Isolation of eye buds from the apical dominance increased the chance of sprouting by eliminating the competition with other eyes in utilising the resources for growth (Coleman 2000).

When the correlative inhibition of growth by the apical sprout was eliminated by isolating eye buds into core samples, each eye was given a chance to grow. The growth of the isolated sprouts reflected the physiological state of the sprout after storage. The proportion of cells in the later mitotic stages appeared to be associated with the net growth of the sprouts at different positions on the tuber. Advanced mitotic activities

found in physiologically older seed tubers, especially in apical sprouts, as a result of sprouting during storage, resulted in higher net growth in the sprouts of older tubers compared to younger. Mitotic activities also showed differences between cultivars in the proportion of cells actively divided in the median and basal eye buds which may explain the difference of apical dominance between these cultivars. The higher the storage temperature, the higher the rate of physiological ageing of seed tubers (Wurr 1978), and cultivar differences have also been found in sensitivity to ageing (van Ittersum *et al.* 1990). Cultivar differences also have been shown in section 4.2 of Chapter 4. Cultivar Atlantic, which showed strong apical dominance especially in the physiologically older seed tubers, had a lower number of sprouts than Russet Burbank in this study.

In addition to the apical dominance effect, soil moisture and resource availability, i.e. carbohydrates in isolated cores, was also found to have a significant impact on the percentage of sprouting and net growth of sprout on eye bud at different positions. Reduction in sprout growth and the number of sprouts on all buds were observed in both cultivars and whether buds were in a correlative inhibition or separated from the dominance of the apical sprout (Faivre-Rampant *et al.* 2004; Claassens 2002; Dimalla and Staden 1977). This was also also evident in Experiment 5 in term of sprout number and sprouting capacity. This supports the key findings of Chapter 4 where sprout number and sprouting capacity were reduced when conditions was dry. This indicates that sprouting pattern may be regulated by the existence of apical dominance and soil water availability (Letnes 1958) and prediction of stem number production needs to take into account seed tuber physiological status and planting environment.

The physiological studies described in Chapter 4 and the current chapter provide evidence of the interaction between seed tuber physiological status and planting environment in affecting stem number production. These findings expand the current understanding on the key factors that may affect the number of stems and hence stem density which in turn can partly determine the production of marketable tubers. Incorporation of this knowledge in a crop model will be the next stage of the project to allow this physiological understanding to be utilised by the industry as a decision support system. In addition, the modelling work also needs to include the effect of seed

tuber physiological age on other crop growth processes such as pre-emergent growth and leaf area production.

Chapter 6 Effect of planting environment and seed tuber physiological age on the pre-emergent growth of potato

Introduction

The incorporation of planting environment parameters in a mechanistic model requires knowledge of the effects of the key environment components, temperature and water potential, both on stem number and stem growth rate. Data on stem number effects has been presented in the previous two chapters. This chapter focuses on the effect of planting environment and seed tuber physiological age on the pre-emergent growth of potato.

Pre-emergent growth can be broken down into three distinct phases, namely: (i) dormancy (ii) a lag period prior to the commencement of; (iii) linear elongation of the sprouts and roots. Considering each of these in turn:

(i) Dormancy

Dormancy can be defined as the physiological state where there is no cell division and in which autonomous sprout growth will not occur even when the tuber is kept in conditions ideal for sprout growth (Moorby and Milthorpe 1975; Reust 1984; Struik and Wiersema 1999). Dormancy commences at tuber initiation and reaches its peak at harvest time and then gradually begins to break down during storage (Struik and Wiersema 1999). The length of dormancy is affected by several factors including genotype, conditions during seed growth and most importantly, the duration and temperature of subsequent storage conditions (Krijthe 1962). The duration of dormancy varies with genotype from 1 – 15 weeks after harvest of the seed crop (Moorby and Milthorpe 1975; Wiersema 1985; Struik and Wiersema 1999). Dormancy is said to be broken when at least one of the eyes is showing visible sprout growth (Classens and Vreugdenhil 2000). Another definition for dormancy is when 80% of uniform size tubers show sprout development of at least 3 mm at 20 °C and relative humidity of 90% (Wiersema 1985). Seed tubers are typically planted after dormancy breakage.

(ii) Lag and linear phases of sprout elongation

Following the end of dormancy, sprout growth follows a sigmoidal path, commencing with a lag phase followed by a period of linear growth prior to emergence (Firman *et al.* 1992). The duration of these phases is affected by soil temperature and moisture and the physiological age of the seed tuber (Vos 1995; Fulton and Fulton 2001; Struik and Wiersema 1999; Firman *et al.* 1992).

Temperature is known to be the key driver of these phases (Krijthe 1962). Cardinal temperatures for sprouting range from 0-3 °C for base temperature (Firman *et al.* 1992; Struik and Wiersema 1999; Sale 1979; MacKerron 1985), 15-20 °C for optimum temperature (Wiersema 1985; Sale 1979; Wang 1982; Struik and Wiersema 1999) and 30-35 °C for maximum temperature (Wang 1982; Midmore 1984). Firman *et al.* (1992) report that a pre-warming treatment before planting can affect the lag phase duration of sprout growth. High temperatures increase cell activity up to a threshold maximum temperature, beyond which cell growth is impaired.

When soil moisture content is adequate, the time between planting and emergence depends on sprout length at planting and soil temperature (Sale 1979). While seed pieces at the recommended size of 50 to 70 g have sufficient moisture to support sprout growth up to emergence, low soil moisture content during planting has been reported to reduce the maximum rate of sprout growth (Firman *et al.* 1992). Conversely, excess soil water in this stage can encourage the growth of pathogenic organisms (Pavlista 2003).

Physiologically older tubers have shorter lag and linear phases than younger tubers (Klemke and Moll 1990; Kawakami 1952; Hartman and van Loon 1987; Struik and Wiersema 1999; Bohl *et al.* 2003; Firman *et al.* 1992). Firman *et al.* (1992) propose that the lag phase typically ends with a sprout length of ~10mm, after which linear elongation occurs. Based on this definition these authors estimated the duration of the lag phase to be ~60 °C d (T_b 1 °C) while the duration for young tubers may be longer.

Vos (1995) reports that sprout elongation rate increases with physiological age up to a certain threshold age, beyond which it declines. According to Bohl *et al.* (1995), warm temperatures during planting may negate the difference in time to emergence

between older and younger seed. King and Stark (1997) also argued that wet soil conditions can increase stress for the seed piece and increase the physiological age of the seed tuber. Despite this, no data have been presented on the interaction between planting environment, e.g. temperature and moisture, and seed tuber physiological age on the pre-emergent growth of potato.

Attempts to quantify the response of pre-emergent growth to physiological age have been unsuccessful to date (Firman *et al.* 1992; Klemke and Moll 1990; Knowles and Botar 1991). This is due in part to the absence of any reliable means of quantifying the physiological age of the seed. Furthermore, previous studies have not quantified (Bohl *et al.* 1995; King and Stark 1997) the effect of planting environment, specifically soil temperature and moisture, on the physiological age of the seed and the resultant effects on pre-emergent growth. In addition, the effect of temperature on the physiological aging of the seed tuber is known to be highly cultivar specific (Struik *et al.* 2006). Little is known about the physiological age impacts on pre-emergent growth of the main potato cultivars used in Australia and Indonesia.

Modelling pre-emergence of potato

In SUBSTOR (Ritchie *et al.* 1995), the period from planting to emergence is divided into three phases: pre-planting, germination and emergence. Three options are available to the user for modelling of pre-emergent growth. The simplest relies on a user-defined input for emergence date. The other two options estimate time to emergence based on whether the seed is unsprouted or sprouted. The calculations employ a relative temperature factor which ranges between 2 °C and 33 °C (Ingram and McLoud 1984) to determine daily sprout elongation. For unsprouted seed, germination occurs after 7.35 days and subsequent elongation occurs at a specified daily elongation rate of 28.4 mm/day under optimum soil temperature conditions (i.e. 15 to 22 °C). The elongation rate drops if soil temperatures fall below or above this temperature range. When planting sprouted seed, a sprout-length dependent elongation rate (based on O'Brien *et al.* 1983) determines the rate of sprout growth. For both unsprouted and sprouted seed, emergence occurs when the cumulative sprout length exceeds the sowing depth.

The pre-emergence component of the LINTUL model assumes that seed dormancy and germination have occurred prior to planting and calculates the date of emergence using planting depth, initial sprout length and the sprout growth rate reported by MacKerron and Waister (1985): 1 mm / °Cd > T_b 2 °C (Kooman and Haverkort 1995).

Based on results from a controlled environment chamber and previous work by Sands (1989) on the pre-emergence growth responses to temperature, Firman *et al.* (1992) developed a model to predict emergence of potato that takes into account both the lag and linear phases and the effects of soil moisture on pre-emergent growth. Firman *et al.* (1992) calculated a maximum sprout growth rate of 17.7 ±1.4 mm/day in 'wet' soil compared with 12.1 ± 1.3 mm/day in 'dry' soil. The model is as follows:

$$T_{EM} = [(L = Lo + a + b^s)/(T-1)] + D/[Ro(1-(T-T_b)^2/(T_a-T_b)^2) \quad (6.1)$$

Where:

T_{EM} = time to emergence
L = lag period (day degree > 1 ° C)
Lo = the lag period for well sprouted seed (60 °C d > 1°C)
s = sprout length at planting (mm)
a and b = constants (276 and 0.625 ± 0.0445, respectively)
T = Soil temperature
D = Planting depth
Ro= maximum sprout growth rate (17.7 mm/day on wet soil and 12.1 mm/day on dry soil)
Ta = base temperature
Tb = optimum temperature

None of the aforementioned models take into account the effects of seed physiological age on pre-emergent growth, nor the genotype-specific effect of planting environment (via its effect on physiological age). Hence the objective of this trial is to:

a) investigate the effect of temperature, seed age and soil moisture on the pre-emergent growth processes for two commercial potato cultivars (Russet Burbank and Atlantic), and;

b) to develop and parameterise a new pre-emergent growth model for potato.

Materials and methods

Experimental design and treatments

This study was carried out in conjunction with Experiment 5 (Chapter 4). Three temperatures (10, 15 and 20 °C) and three water potentials (wet (-0.02 MPa), dry (-0.6 MPa) and fluctuated between wet and dry) were applied to two lots of cv Russett Burbank and Atlantic seed tubers with physiological ages, 'young' and 'old'. The approaches used to establish the target water potentials and aging treatments are described in the materials and methods for Experiment 5 (Chapter 4, *p.* 64-68). A completely randomized block design was employed with temperature as the block strata. All possible combinations of seed tuber physiological age, cultivar and moisture treatments were randomized in each temperature level with 25 replicates of each.

Observations and statistical analysis

The length of the longest sprouts of 3 tubers for each treatment combination were measured prior to planting and at 9, 13, 17 and 21 days after planting. Sprout length was measured with a dissecting microscope fitted with an eyepiece micrometer and ruler. The method for estimating the time of lag phase completion and the rate of linear sprout elongation was based on that reported by Firman *et al.* (1992). The end of the lag phase was taken as the time at which rapid linear sprout growth commenced. The linear growth rate was taken from the slope of the linear regression line fitted to the sprout growth plot beyond a sprout length of 10 mm. F-test analysis was made to identify factors affecting lag phase duration and linear growth rate. Statistical analysis was undertaken using the SPSS v. 14.0 software package (SPSS Inc. 2005).

Results

Growth of the longest sprout was characterised by an initial period of slow growth up to a sprout length of ~10mm, followed by a period of more rapid linear elongation (Figure 6.1).

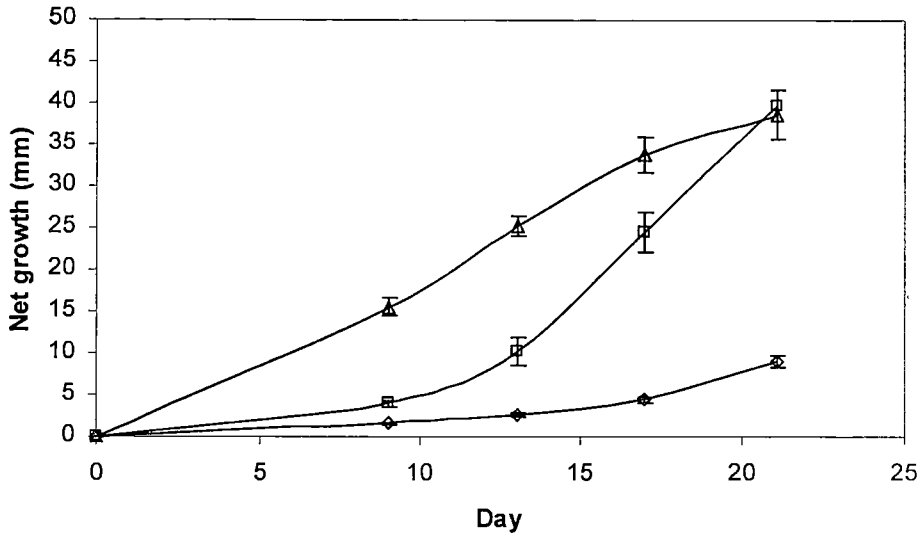


Figure 6.1. Response of sprout growth to temperatures of 10 ° C (◇), 15 °C (□) and 20 °C (△). Each data point is an average across all non temperature treatments and replicates. Bar corresponds to the standard error of the mean (N= 36).

Lag phase duration

Significant interactions ($p<0.05$) were found between cultivar, temperature, soil moisture and the duration of the lag phase (Table 6.1). A decrease in water potential at 10 °C from -0.02 MPa to -0.6 MPa extended the lag phase for cv Atlantic from 20 days to 23 days. Significant interactions also occurred between cultivar, seed age and soil moisture ($p<0.05$). For cultivar Atlantic, increasing the water potential from -0.6 to -0.02 MPa shortened the lag phase of younger tuber but lengthened the lag phase duration for older tuber. There were no significant differences in lag phase duration across the Russet Burbank moisture treatments.

Despite those interactions, there were highly significant main effects of temperature and cultivar ($p<0.001$). Lag phase duration consistently declined with increasing temperature across all treatment combinations from 20 - 21 days at 10 °C to 3 - 5 days at 20 °C (Figure 6.2). Lag phase duration for Russet Burbank (5 - 21 days or 90 - 168 °Cd > T_b 2 °C) was typically longer than for Atlantic (3-20 days or 54-160 °Cd >T_b 2 °C).

Table 6.1. Lag phase duration of sprout growth for different temperature (T_1= 10 °C, T_2=15 °C, T_3=20 °C), cultivar (CV_1 = Russet Burbank, CV_2= Atlantic), seed age (PA_1= young, PA_2= old, and water potential (M_1= -0.6 MPa, M_2= fluctuated between -0.6 MPa and -0.02 MPa, M_3= -0.02 MPa) combinations. l.s.d. figures shown with extent of significance (*p<0.05, **p<0.01, ***p<0.001, n.s.=not significant).

	M_1						**Ave M_1**	**M_2**						**Ave M_2**	**M_3**						**Ave M_3**
	CV_1			**CV_2**				**CV_1**			**CV_2**				**CV_1**			**CV_2**			
	PA_1	**PA_2**	**Ave**	**PA_1**	**PA_2**	**Ave**		**PA_1**	**PA_2**	**Ave**	**PA_1**	**PA_2**	**Ave**		**PA_1**	**PA_2**	**Ave**	**PA_1**	**PA_2**	**Ave**	
T_1	20.0	20.4	**20.2**	23.3	22.1	**22.7**	**21.5**	22.9	19.8	**21.4**	20.4	18.1	**19.3**	**20.3**	21.1	24.0	**22.5**	19.4	21.7	**20.6**	**21.5**
T_2	9.7	11.8	**10.8**	9.2	7.8	**8.5**	**9.7**	12.2	10.1	**11.2**	9.4	10.4	**9.9**	**10.5**	10.2	11.5	**10.9**	7.7	10.4	**9.0**	**10.0**
T_3	5.6	5.6	**5.6**	3.3	1.4	**2.3**	**4.0**	4.7	3.7	**4.2**	2.8	4.2	**3.5**	**3.9**	5.6	3.3	**4.4**	1.7	4.5	**3.1**	**3.8**
Ave	**11.8**	**12.6**	**12.2**	**11.9**	**10.4**	**11.2**	**11.7**	**13.3**	**11.2**	**12.2**	**10.9**	**10.9**	**10.9**	**11.6**	**12.3**	**12.9**	**12.6**	**9.6**	**12.2**	**10.9**	**11.7**

Main effect:		**Interactions:**	
Temperature (T)	***0.54******	CV*T	n.s
Cultivar (CV)	***0.37*** ***	CV*PA	n.s
Seed tuber physiological age (PA)	n.s	T*PA	n.s
Moisture (M)	n.s	CV*T*PA	n.s
		CV*M	n.s
		T*M	n.s
		CV*T*M	*2.2**
		PA*M	*1.28**
		CV*PA*M	*1.8**
		T*PA*M	n.s
		CV*T*PA*M	n.s

Table 6.2. Linear growth rate for different temperature (T_1= 10 °C, T_2=15 °C, T_3=20 °C), cultivar (CV_1 = Russet Burbank, CV_2= Atlantic), seed age (PA_1= young, PA_2= old, and water potential (M_1= -0.6 MPa, M_2= fluctuated between -0.6 MPa and -0.02 MPa, M_3= -0.02 MPa) combinations. l.s.d. figures shown with extent of significance (*p<0.05, **p<0.01, ***p<0.001, n.s.=not significant).

	M_1						Ave M_1	M_2						Ave M_2	M_3						Ave M_3
	CV_1			CV_2				CV_1			CV_2				CV_1			CV_2			
	PA_1	PA_2	Ave	PA_1	PA_2	Ave		PA_1	PA_2	Ave	PA_1	PA_2	Ave		PA_1	PA_2	Ave	PA_1	PA_2	Ave	
T_1	1.3	1.2	**1.3**	0.9	1.1	**1**	**1.2**	0.4	1.5	**0.9**	1.3	2.6	**2**	**1.5**	1.2	0.7	**1**	1.6	0.9	**1.3**	**1.2**
T_2	3.4	4.5	**4**	4.5	4.3	**4.4**	**4.2**	4.1	4.2	**4.1**	3.6	4.3	**4**	**4.1**	5.2	3.7	**4.5**	4	4.3	**4.1**	**4.3**
T_3	4.3	4.7	**4.5**	1.5	2.4	**2**	**3.3**	2	3.5	**2.8**	3.1	4.6	**3.9**	**3.4**	2.4	2.1	**2.3**	4.4	4.7	**4.5**	**3.4**
Ave	**3**	**3.4**	**3.3**	**2.3**	**2.6**	**2.5**	**2.9**	**2.2**	**3.1**	**2.6**	**2.7**	**3.8**	**3.3**	**3.0**	**2.9**	**2.2**	**2.6**	**3.3**	**3.3**	**3.3**	**3.0**

Main effect:	
Temperature (T)	***0.34******
Cultivar (CV)	n.s
Seed tuber physiological age (PA)	n.s
Moisture (M)	n.s

Interactions:	
CV*T	n.s
CV*PA	n.s
T*PA	n.s
CV*T*PA	n.s
CV*M	n.s
T*M	n.s
CV*T*M	***1.47****
PA*M	n.s
CV*PA*M	n.s
T*PA*M	n.s
CV*T*PA*M	n.s

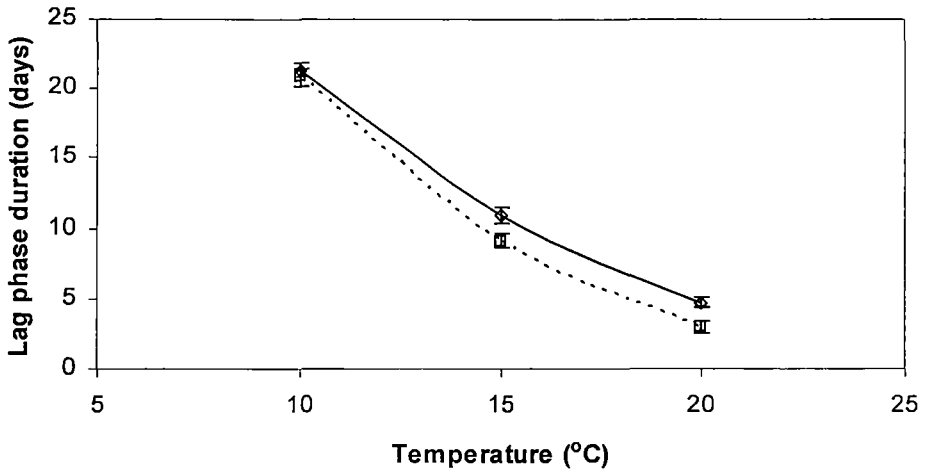


Figure 6.2. Response of lag phase duration of sprout growth to temperature for cultivar Russet Burbank (◇, ____) and cultivar Atlantic (□, --------). Each point represents an average across all non temperature treatments and replications. Bar corresponds to the standard error of the mean (N= 18).

Linear sprout elongation

There was a weak interaction between cultivar, temperature and moisture ($p<0.05$) and the rate of linear elongation (Table 6.2). In the case of Russet Burbank, linear elongation rate decreased with increasing water potential at 20 °C only. In contrast, for Atlantic, elongation rate increased from 2 mm/day to 4.5 mm/day with increase in water potential from -0.6 MPa to -0.02 MPa at 20 °C. There was no significant difference between moisture treatments at 10 and 15 °C (Figure. 6.3).

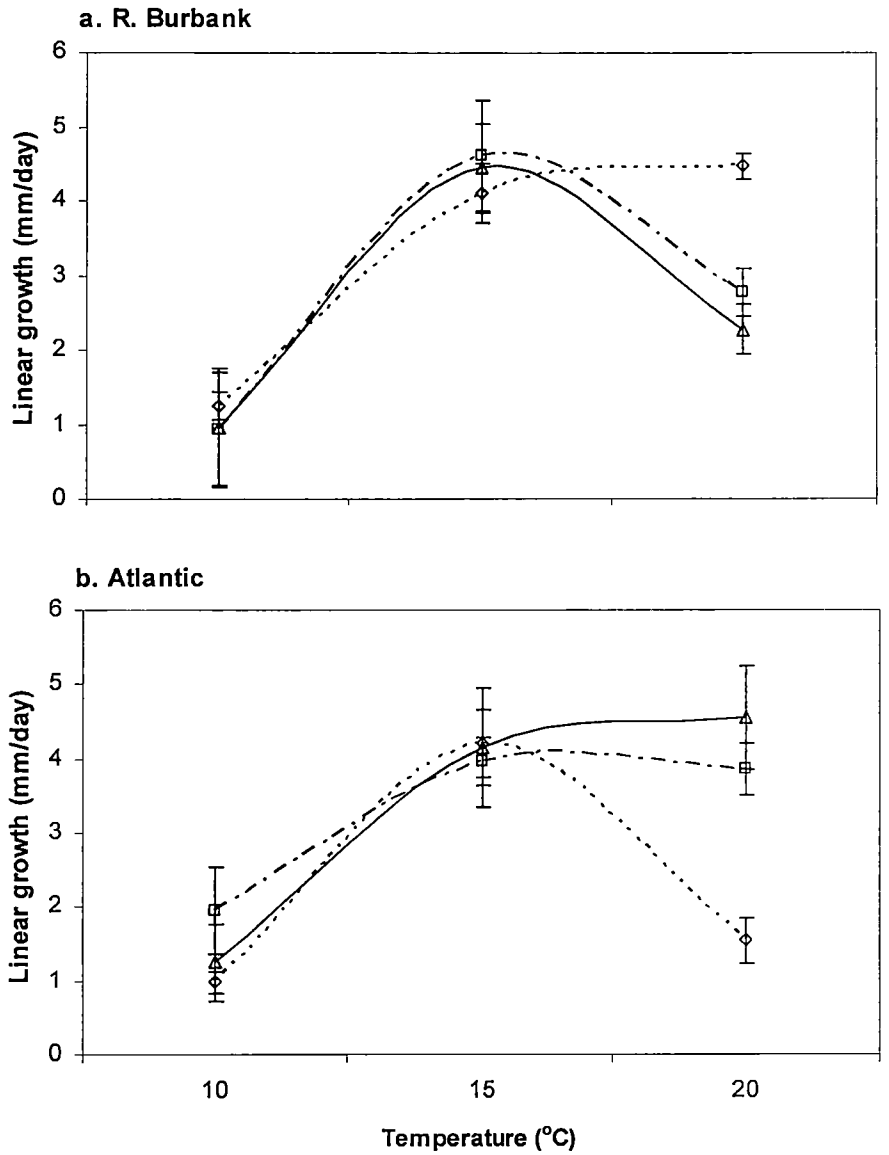


Figure 6.3. Elongation rate of the longest sprout of cultivar (a) R. Burbank and (b) Atlantic at 10, 15 and 20 °C and -0.06 MPa (◇, -----), fluctuated between -0.6 and -0.02 MPa (□, -.-.-.-.) and -0.02 MPa (△, ____). Each data point is an average of seed tuber physiological age treatments and replicates. Bar corresponds to the standard error of the mean (N= 6).

Discussion:

The results of this study show that pre-emergent growth of potato can be broken into two distinct phases; a period of slow initial growth (lag phase) followed by a period of faster linear growth. The key driver of these phases is temperature. This supports the need for a two phase pre-emergent model as adopted by Firman *et al.* (1992). The lag phase duration for cultivars Russet Burbank and Atlantic in this study (90-160 and 50-160 °Cd (> T_b 2 °C), respectively) were shorter than those reported by Firman *et al* (1992) which ranged from 160 – 230 °Cd (> T_b 1 °C) for cultivar Estima. They were however comparable to the 125 °Cd (> T_b 2 °C) duration reported by MacKerron (1984) for unsprouted seed tubers of Maris Piper. The differences are attributable to cultivar differences and/or differences in the sprout length at planting, which is reported by Firman *et al.* (1992) to be correlated with lag phase duration.

The rate of linear sprout growth was found to be highest for the 15 °C temperature treatment. This aligns with the findings of Struik and Wiersema (1999) who report an optimum temperature for sprout growth in the range of 15 – 20 °C. An increase in temperature up to the optimum level can increase the cell temperature and stimulate growth. A further rise in temperature can impair enzyme activity and reduce the growth rate (Fitter and Hay 1987). The linear growth rate measured in this study (4.5 mm/ day) was lower than that reported by Firman *et al.* 1992 for cv Estima (> 10 mm/day) but higher than that reported by Sands (1989) for cultivars Sebago and Sequoia (3 mm/day).

The interactions found between genotype, soil moisture and temperature for lag and linear phases and between genotype, seed age and soil moisture for the lag phase, indicate the complex way in which these factors interact to determine the duration of pre-emergent growth. The inconsistent nature of this response is, as a consequence, difficult to capture in a simulation model.

On this basis, the component pre-emergent growth model in APSIM Potato is comprised of separate thermal-time dependent lag and linear phases. The linear elongation rate is taken as the slope of the regression line fitted to sprout length versus time data (6.26 °Cd/mm, T_b=2 °C) from all treatments (Figure 6.4). The lag

phase duration (72 °Cd, T_b=2 °C) is taken as the x-intercept of this line of best fit. Emergence occurs when the sprout length is equivalent to the planting depth.

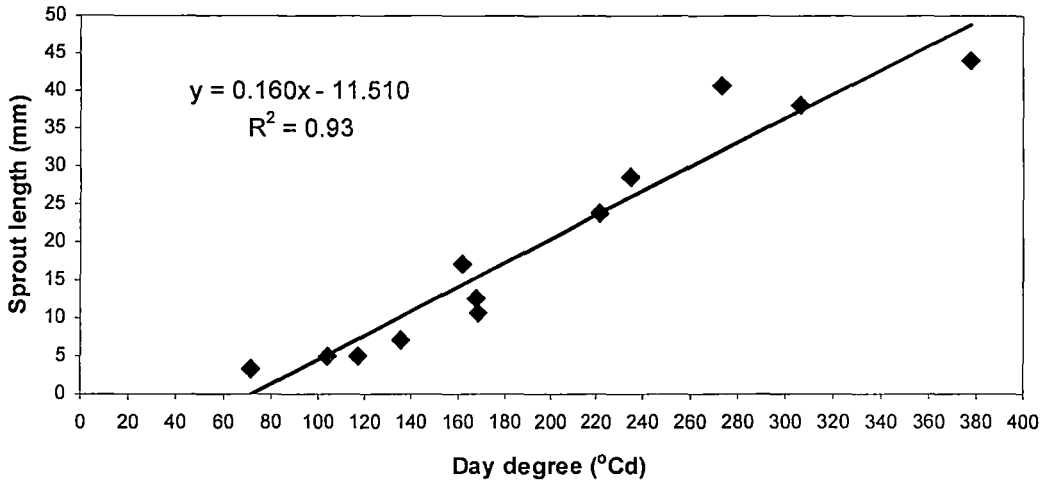


Figure 6.4. Sprout growth rate based on heat units (above base temperature of 2 °C). Each data point is an average of the replicates of all treatments expressed in thermal time.

Chapter 7 Effect of seed tuber physiological age on leaf area production of potato cultivars Russet Burbank and Atlantic

Introduction

Potato canopy architecture

The architecture of the potato plant is described by Vos (1995). The main stem (MS) is the stem that grows from the tuber (Figure 7.1). From the main stem, branching consists of basal lateral branches (BLB) and apical lateral branches (ALB) (usually called sympodial branches). The basal lateral branches can occur either above (AGBLB) or below (BGBLB) ground (usually called secondary stems) while apical lateral branches occur above ground only on the top part of the branch, each terminating in inflorescences.

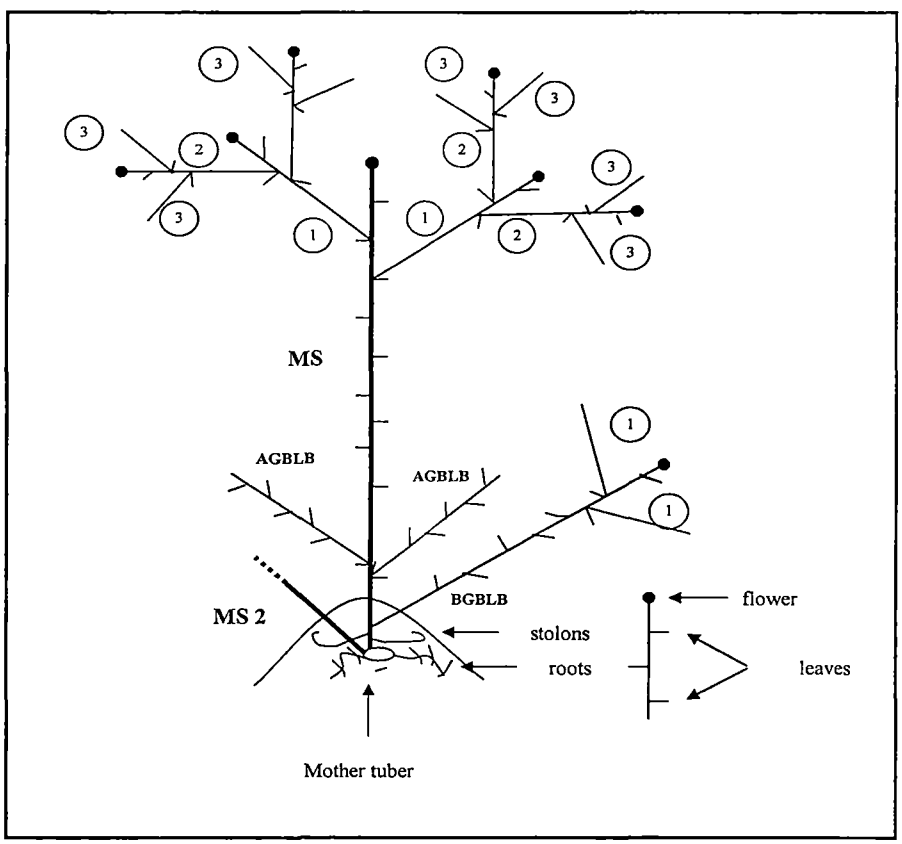


Figure 7.1. Schematic representation of morphological component of potato plant. MS: Main stem, MS2: main stem grows from seed tuber; AGBLB: Above Ground Basal Lateral Branch; BGBLB: Below Ground Basal Lateral Branch; ALB: Apical Lateral Branches; BLB: Basal Lateral Branches. Numbers in circle shows the order of the branches. The figure is adopted from Vos 1995.

Potato cultivars are distinguished into two types, determinate and indeterminate (Struik 2007). Determinate type cultivars tend to be short and initiation of leaves ceases with the appearance of flowers and do not produce any successive order of branches. In indeterminate cultivars, initiation of new leaves does not cease with the appearance of the first flower on the main stem. Branches can emerge from any leaf axil on the main stem and can produce the next order of branches (Vos 1995).

Leaf area growth

Leaf area growth in potato is a function of stem number per plant, leaf appearance and leaf number per stem (including branches), individual leaf area and leaf senescence.

Stem number

Seed size and seed tuber physiological age are recognised as the key drivers of stem number per plant (Struik and Wiersema 1999). Seed size determines the number of eyes with larger seeds producing more sprouts. Seed age influences the proportion of eyes that produce sprouts and the proportion of sprouts that produce stems (Knowles and Botar 1991). Older seed tends to generate more stems per plant compared to young seed.

Leaf appearance and leaf number

The leaf appearance rate is strongly correlated with air temperature (Borah and Milthorpe, 1962; Firman *et al.* 1995; Vos and Biemond 1992; Kirk and Marshall, 1992) with the reported base temperature for leaf production ranging from 0- 9 °C (Firman *et al.* 1995; Biemond and Vos 1992; Kirk and Marshall 1992; and Vos 1995; Rahman *et al.* 2000; Midmore 1984); the maximum temperature from 31 – 36 °C (Rahman *et al.* 2000; Midmore 1984); and the optimum temperature is 24 °C (Rahman *et al.* 2000; Benoit *et al.* 1983; Sale 1979). The reported leaf appearance rate for potato varies from 31.5 – 41.2 °C d per leaf (T_b 0 °C) (Vos and Biemond 1992; Kirk and Marshall 1992; Jeffries 1989).

The total number of nodes on the main stem both below and above ground varies with cultivar and seed physiological age, but typically ranges between 17 and 27

(Bald 1946; Taylor 1953; Krijthe 1962). Firman *et al.* (1991) found that there was an increase in the number of nodes with increasing physiological age of the seed. This is attributed to a higher sprout development rate, which results in longer sprouts at planting and earlier canopy development (Struik and Wiersema 1999).

Leaf area expansion

According to Vos (1995), leaf size can be analysed in terms of the rate of expansion and the duration of expansion. The leaf area expansion rate is affected by genotype, temperature, moisture, nitrogen and available leaf assimilate (Firman *et al.* 1995; van Delden and Haverkort 2000; Bhagsari *et al.* 2004). The rate of leaf expansion increases with temperatures up to an optimum temperature of 20 - 25 °C and decreases thereafter (Benoit *et al.* 1983; Khurana and McLaren 1982; Struik and Wiersema 1999). The minimum temperature for leaf expansion is reported to be ~7 °C (Moorby and Milthorpe 1975). Final leaf size and the maximum leaf area index vary with genotype (Bhagsari *et al.* 2004; Firman *et al.* 1995; Jeffries and MacKerron 1987).

Among all factors affecting leaf growth, soil moisture is the most important. Drought significantly reduces the final size or area of potato leaves (Jeffries 1993; Heuer and Nadler 1995) by decreasing the leaf expansion rate (Munns 1993; Jeffries 1993). This response varies between genotype (Jeffries and MacKerron 1987). In an irrigation trial conducted by Heuer and Nadler (1995), leaf area was reduced by 76% when irrigation was withheld during the vegetative stage.

Kirk and Marshall (1992) report that the thermal time duration for the expansion phase of leaves on the main stem is relatively constant at about 150 - 200 °Cd (> T_b 0 °C) up to leaf position 10. At higher leaf positions, the thermal time duration was similar or greater. The same authors report that final leaf size increases with leaf position up to a maximum area and then decreased at higher leaf positions.

Despite a higher node and leaf number on the main stem, physiologically older seed may have a lower maximum leaf area (Struik and Wiersema 1999). Kirk and Marshall (1992) report more stems and smaller fully expanded leaf area associated with older seed. It is assumed that this is due to competition between main stem

leaves for growth substrate. In addition, the leaf expansion rate decreases with seed age (Knowles and Botar 1991).

Leaf senescence

The rate of leaf senescence in potato is reported to be 100 to 136 °Cd per leaf (> T_b 0 °C) (Vos and Biemond 1992). The rate increases with temperature (Ingram and McCloud 1984). A fully expanded leaf is estimated to have a lifespan of 460 °Cd at 20 °C. According to Vos and Biemond (1992) the lifespan of leaves is influenced by leaf position in a similar manner to the dependency of full-grown leaf area on leaf number. Leaves with the largest full-grown area have the longest life span, i.e. middle leaves on the main stem. Longer photoperiods are known to delay senescence (Demagante and van der Zaag 1988).

Plants from physiologically older seed tubers are known to senesce and mature earlier (Struik and Wiersema 1999; Asiedu *et al.* 2003) however no reference could be found for an estimate of leaf senescence rate for plant grown from seed tuber of different physiological age.

Modelling leaf growth

The two reviewed models (SUBSTOR and LINTUL) estimate the leaf area index based on leaf expansion rate. In LINTUL, after emergence, an initial leaf area index of 0.0155 is specified, after which leaf area increases at a relative rate of 0.012 m^2/m^2/day (adapted from Spitters and Schapendonk 1990, Kooman and Haverkort 1995). Leaves are divided into classes based on the time at which they appear. Each class differs in terms of time of senescence which is due when the class exceed a specified leaf longevity of 1000 °Cd. Longevity is reduced under shading conditions and tuber growth such that fast growing tubers reduce leaf longevity (Kooman and Haverkort 1995).

Similarly, in SUBSTOR, daily potential leaf expansion is calculated by taking into account the plant leaf area (cm^2/plant) and a temperature-dependent relative leaf growth rate adopted from Ingram and McCloud (1984). The rate is 0.5 kg/kg/day over the temperature range of 15 to 24 °C (Ritchie *et al.* 1995) and is lower when the temperature falls above and below this optimum range. The daily potential leaf expansion is reduced by water and nitrogen stress. Daily potential biomass

partitioned to leaves is equal to the potential leaf expansion divided by the specific leaf area. For both LINTUL and SUBSTOR, leaf area index (LAI) is calculated by multiplying the net biomass translocated to leaf by the specific leaf area.

Neither LINTUL nor SUBSTOR capture the effects of genotype and seed physiological age on leaf growth and canopy architecture. The objectives of the trial reported in this chapter are to explore and quantify the effect of physiological age on leaf growth for the two cultivars Russet Burbank and Atlantic and to develop and parameterise a new process-based potato leaf growth model for incorporation into the APSIM modelling framework. This is a plant-based approach that simulates leaf area as a function of plant density, stem number per plant, branch number per stem, node or leaf number per stem and branch, leaf area per node and leaf senescence, and relates these component processes to management, genotype and seed physiological age.

Materials and methods

Experimental design and treatments

The trial was established in a glasshouse at the University of Tasmania Horticultural Research Centre (42°50'S, 147°21'E) and conducted from 27 November 2006 until 26 March 2007. The experiment consisted of two treatment factors, namely cultivar (i.e. Atlantic and Russet Burbank) and seed tuber physiological age (i.e. young and old). Seed materials were obtained from commercial seed growers and were the same seed lot that was used in Experiment 3 (Chapter 4). Seed tubers were hand graded to a range between 50-60 g. The physiologically older seed tubers were created by following the aging treatment described in Chapter 4. The trial was set up as a complete randomized block design in a glasshouse with four replicates.

Management

The plants were grown in bag pots under non-limiting nitrogen and water conditions. One seed tuber was planted in each pot to a depth of 15 cm. Each bag was 35 L in volume and filled with potting mix comprised of composted pine bark and coarse sand (4:1 ratio) containing 3 kg/m^3 Osmocote Plus (a slow release fertiliser with N:P:K:Mg ratio of 16:3.5:10:1.2 plus trace elements of S, B, Fe, Mn, Mo, Zn and Cu), 4 kg/m3 dolomite, 0.75 kg/m3 FeSO4 and 0.75 kg/m3 Wettasol Granules). A

topdress application of Osmocote Plus was made at 40 days after sowing at a rate of 50 g/bag. Each pot was irrigated to field capacity with drip irrigators (application rate of 24 litres per hour) at a frequency of once each day up until emergence and twice a day thereafter. Surplus water was allowed to freely drain from holes in the base of the bags. Pests and diseases were controlled using both chemical pesticides and biological control methods. The plants were sprayed with Neemtech (300 ml/10 Litres) and Crown 2 ml/10 litres) at 30 days after sowing to control white flies (*Trialeurodes vaporarioum*). After that the white flies were controlled with *Encarsia Formosa,* applied at 60, 70 and 95 days after sowing.

Observations and sampling procedure

Node (leaf) appearance was recorded by monitoring the occurrence of new nodes on the main stem. The number of nodes on the main stem and braches were counted throughout the experiment every two days and each new leaf was numbered on the lamina with a permanent felt pen until the occurrence of the first flower. The rate of node appearance on the main stem to the first flower was calculated as the slope of the linear regression fitted to the plot of leaf number versus thermal time (above a base temperature of 2 °C). The time of full leaf expansion was determined by monitoring (non-destructively) the length and width of each leaf (terminal leaflet only). When there was no change in these dimensions, the leaf was said to be fully expanded.

Leaves were considered to have senesced when 50% of the leaf turned yellow. The leaf was then detached from the plant and the time noted. Detached leaves were then brought back to the laboratory for determination of individual leaf area using the leaf scanner (EPSON Expression 10000 XL). Glasshouse temperature was monitored using a tiny tag data logger to enable thermal time calculation.

Statistical analysis

Analysis of variance procedures were performed using SPSS software (v. 14.0, SPSS Inc. 2005) to determine the significance of measured plant responses to treatments. The responses tested were leaf area and leaf number on main stem nodes and branches. Further analysis of leaf appearance and senescence rates was performed using SAS (v. 9, SAS Institute, Cary, North Carolina, USA) in order to fit linear

regression lines and to analyse the significant difference of regression parameter values e.g. slopes of each treatment.

Results

Stem number per pot/plant

Stem number per plant was significantly affected by cultivar only ($p<0.05$). Cultivar Russet Burbank had an average of 4.5 main stems (average across all treatments and replicates) per plant compared to 2.7 main stems for cultivar Atlantic. There was no significant differences ($p=0.31$) in stem number between older and younger seed tubers although older seed appeared to have higher stem number. Observation on the day of emergence also revealed that older seed had more leaves at emergence than younger seed for cultivar Russet Burbank but not for Atlantic.

Leaf appearance

The appearance rate of fully expanded leaves on the main stem increased linearly with thermal time (Figure 7.2). There was no seed age effect on leaf appearance rate ($p = 0.988$) in the case of cultivar. Atlantic with leaves appearing at a similar rate of ~57 °Cd for both young and older tubers. In contrast, leaf appearance rates for cultivar Russet Burbank did vary significantly with seed age ($p<0.001$). That is, older seed tubers had a faster leaf appearance rate of 39.5 °C d per leaf (0.025 leaves per day degree) compared with 51.2 °C d per leaf (0.02 leaf per day degree) for younger seed. The total number of nodes on the main stem until the first flower ranged from 13 to 16 nodes and 14 to 15 nodes for cultivar Atlantic and Russet Burbank, respectively.

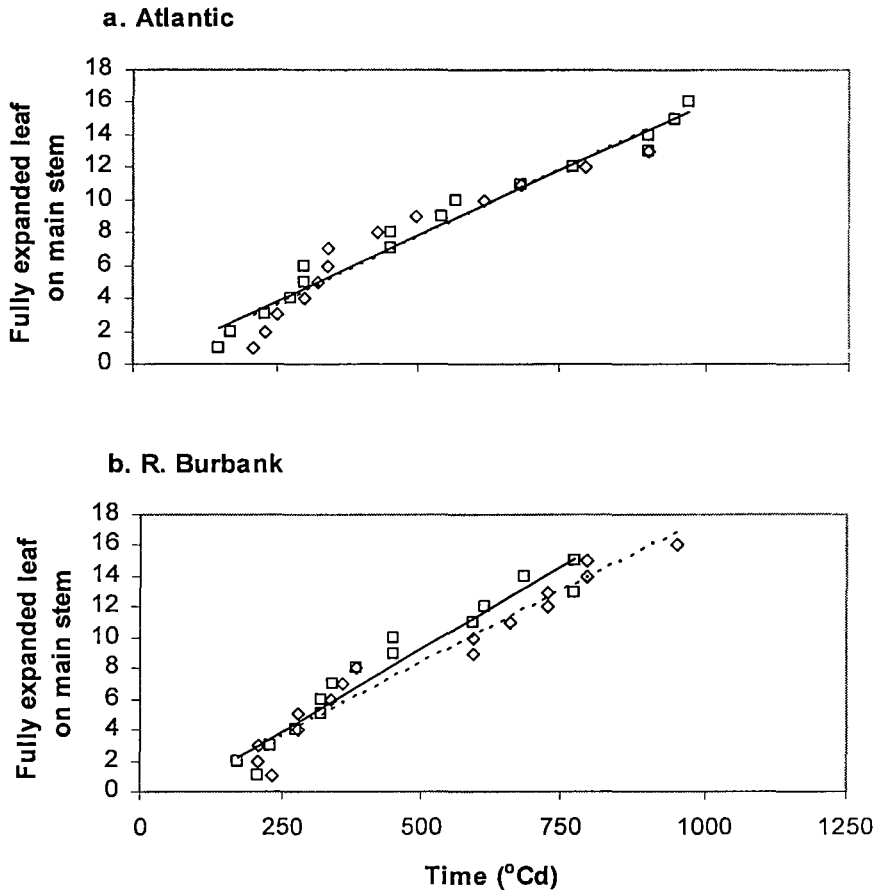


Figure 7.2. The appearance of fully expanded leaves of cultivar Atlantic (a) and R. Burbank (b) of plants from young seed (◇,------) and old seed (□, ____).

Leaf senescence

Leaves on the main stem were observed to senesce linearly with time (Figure 7.3). There was no significant effect of seed age and cultivar on the rate of senescence of the leaves on the main stem nodes. A single regression line fitted across all measured responses of cultivar and seed age treatments resulted in a rate of leaf senescence of 102 °Cd per leaf (0.01 leaves per day degree). While the differences were not significant, physiologically older seed tubers tended to senesce earlier (488.7 °Cd) than younger tubers (610.4 °Cd).

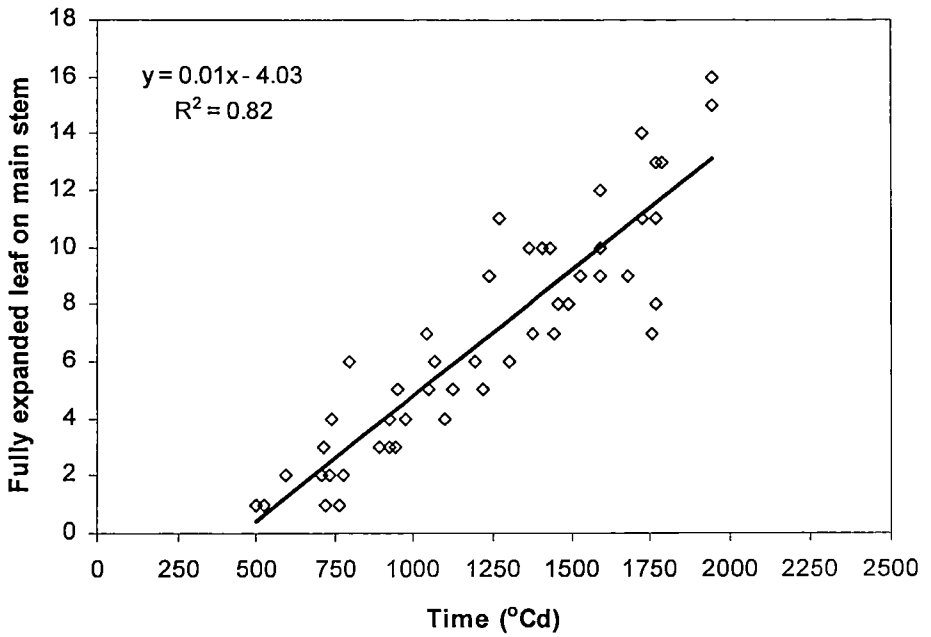


Figure 7.3. Senescence of leaves on the main stem nodes across all measured responses of cultivar and seed tuber physiological age treatments. Each data point is an average of 4 replicates.

Individual leaf area per main stem node

The leaf area of successive leaves on the main stem node initially increased up to about node 7 or 8, and then plateaued until about node 11 before decreasing at higher node numbers (Figure 7.4). In the case of cultivar Atlantic, seed age did not significantly affect fully-expanded leaf size. However, in the case of Russet Burbank, leaves of plants established from young seed were larger than those associated with older seed ($p<0.01$).

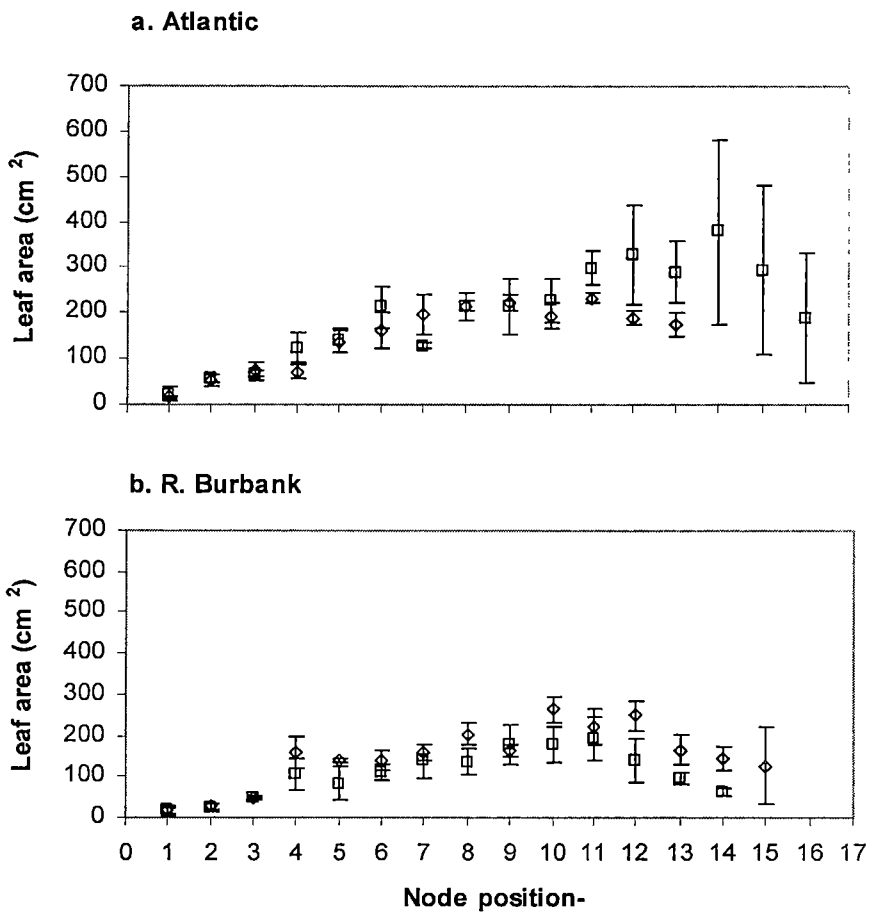


Figure 7.4. Individual leaf size of leaf on main stem node for Atlantic (a) and R. Burbank (b) for young seed (◇) and old seed (□). Each data point is an average of 4 replicates.

Branching

Canopy architecture was found to vary between the two cultivars and seed ages in this study due to differences in leaf area profile, stem number per plant and the location of branches on the main stem and associated leaf area. Figure 7.5 shows the total fully expanded leaf area for each main stem node, comprised of the sum of the main stem leaf and branch leaf area (arising from that node). Across the cultivars and seed age treatments, branching varied according to node position on the main stem. More leaves due to branches were found on basal and apical region of the plant than on the nodes in the middle region ($p<0.01$).

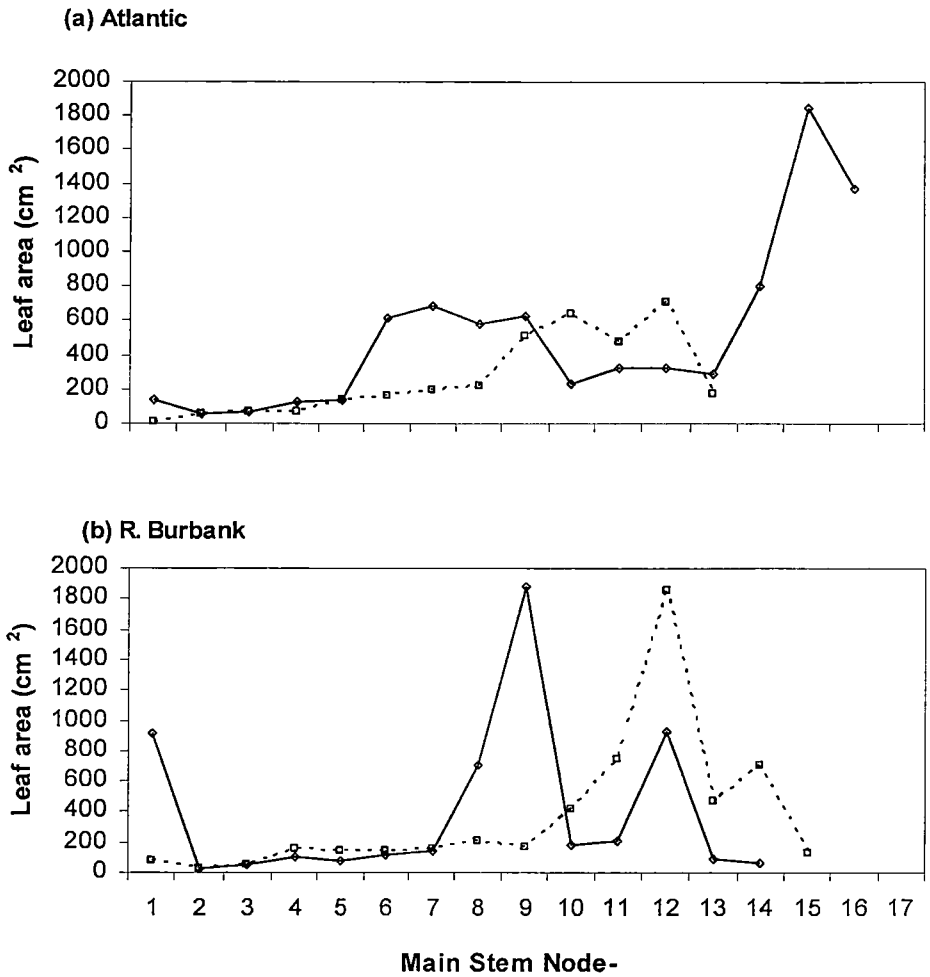


Figure 7.5. Total leaf area (main stem + branch leaves) of cultivar Atlantic (a) and R. Burbank (b) established from physiologically younger seed tuber (-----□-----) and older seed tuber (__◇__). Each data point is an average of 4 replicates.

Discussion:

This study has shown that seed age and genotype have a significant influence on many of the component processes of leaf growth. Russet Burbank had significantly more main stem nodes per plant compared to Atlantic. While not significant, older seed tended to have a higher number of main stems per plant. The response of leaf appearance to seed age was cultivar specific with older seed of Russet Burbank having faster leaf appearance compared with younger seed. As a consequence, leaf on plants grown from older Russet Burbank seed, senesced earlier than leaf derived from younger seed, although the difference was not significant. The response of leaf

senescence to seed age was also cultivar specific with younger Russet Burbank having larger leaf area profiles than Atlantic. Genotype and seed age differences were found for the location and extent of branching on the main stem. These results are in line with previous findings by Knowles and Botar (1991) and Firman *et al.* (1995) that plants from older tubers are more likely to have earlier emergence and a higher leaf number and development rate at an early growth stage. Similarly, Struik and Wiersema (1999) and Asiedu *et al.* (2003), report that plants from older seed have smaller maximum leaf area and earlier senescence. Cultivar differences have previously been reported by Firman *et al.* (1995). In their work, a decrease in the phyllocron with advancing seed age was found with cultivars Home Guard and Estima but not with other cultivars that were evaluated. These authors argue that the existence of nodes in older seed tubers before planting can lead to a faster rate of leaf appearance. While no observations were made of the initial node number at planting; in the case of Russet Burbank, older seed had more leaves at emergence than younger seed

The simulation of leaf growth in APSIM Potato involves dividing the leaf canopy into strata aligned with each main stem. The total leaf area for each cohort is comprised of the sum of the main stem leaf area plus the areas of the nearest (vertically) branch leaves. Cohorts appear at the same rate as the appearance of main stem leaves, expand for a specified period, then enter a lag phase once they have fully expanded before senescing. Each cohort has maximum potential leaf area. With this cohort approach it is possible to adjust each parameter value to represent different genotypes and seed ages. The leaf growth model is explained in more detail in the modelling chapter (Chapter 8).

Chapter 8 APSIM-Potato: Model description, calibration and validation

Model description

The review of the two main process-based potato models in Chapter 2 identified a number of shortfalls in the prediction of stem number, pre-emergent growth and leaf growth. The experimental work described in Chapters 3, 4, 5 and 6 explored these knowledge gaps in order to develop a better understanding of the underlying processes and to develop functions for incorporation into a new potato model within the APSIM framework. In this chapter, the structure and functionality of APSIM-Potato is examined and the performance of the model against an independent dataset assessed.

The key parameters and constants used to specify the processes of APSIM-Potato are listed in Table 8.1 and described in the following text.

Table 8.1. Key parameters and constants for APSIM-Potato.

Parameter	Units	Value
Pre-emergent growth		
Sowing to emergence	°Cd	288 – 335 (Chapter 6)
Lag phase of sprout elongation	°Cd	72 (Chapter 6)
Rate of linear sprout elongation	°Cd/mm	6.26 (Chapter 6)
Post emergent-phenology		
Basic vegetative period	°Cd	251 – 296 (Ritchie *et al.* 1995, Chapter 8)
Tuber initiation to end of tuber bulking	°Cd	1400 – 1500 (O' Brien 1998; Chapter 8)
Tuber bulking to maturity	°Cd	466 – 489 (Chapter 8)
Cardinal temperatures		
Base temperature	°C	2 (Spitters and Schapendonk 1990)
Optimum temperature	°C	20 (Ritchie *et al.* 1995)
Maximum temperature	°C	35 (Ritchie *et al.* 1995)
Biomass production		
Node production rate	°Cd/node	55 (Chapter 7)
Node senescence rate	°Cd/node	102 (Chapter 7)
Leaf growth period	°Cd	(Chapter 7)
Cohort 1		150
Cohort 4		250
Cohort 9		400
Cohort 13		500
Cohort 17		500
Leaf lag period	°Cd	(Chapter 7)
Cohort 1		150
Cohort 4		250
Cohort 9		250
Cohort 13		250
Cohort 17		250
Leaf senescence period	°Cd	(Chapter 7)
Cohort 1		150
Cohort 4		150
Cohort 9		150
Cohort 13		150
Cohort 17		150
Leaf area potential	mm^2/cohort	(Chapter 7)
Cohort 1		20,000
Cohort 4		70,000
Cohort 9		70,000
Cohort 13		150,000
Cohort 17		150,000

Radiation use efficiency	g/MJ PAR	1.6 / 2.5 (Allen and Scott 2000; Kooman and Haverkort 1995)
Extinction coefficient		0.55 (Allen and Scott 1980)
Biomass partitioning		(Kooman *et al.* 1996)
Vegetative period		
Leaf fraction		0.5
Tuber fraction		0
Root		0.2
Tuber initiation period		
Leaf fraction		0.5
Tuber fraction		0.1
Root		0.2
Tuber bulking period (90 % biomass to tuber)		
Leaf fraction		0.0
Tuber fraction		0.90 (Kooman *et al.* 1996)
Root		0.1

Phenology

APSIM-Potato partitions the growth of the potato crop into six stages as defined in Table 8.2. Progression through each stage is driven by the accumulation of thermal time. Daily thermal time accumulation is calculated from crop-specific cardinal temperatures (base, optimum and maximum temperatures) and average daily air temperatures. The potato model uses base, optimum and maximum temperatures of 2, 20 and 35 °C, respectively (Firman *et al.* 1992; MacKerron and Waister 1985; Struik and Wiersema 1999; Ritchie *et al.* 1995). The base temperature of 2 °C is used in the model for all events.

Table 8.2. Phenology stages in APSIM-Potato.

Stage	Description
Planting	From planting to germination
Emergence	From germination to emergence
Tuber initiation	From emergence to tuber initiation
Start tuber fill	From tuber initiation to start of tuber fill
End tuber fill	From the start to end of tuber fill
Maturity	From the end of tuber fill to final harvest

Planting to germination

Germination is independent of the soil moisture status and is assumed to occur on the day of planting of the crop (i.e. pre-sprouted seed, past dormancy).

Germination to emergence

Pre-emergent growth is broken down into two sub-phases; a lag phase of fixed thermal time duration followed by a period of linear sprout elongation ending in emergence of the seedling. Parameter values for lag phase duration and linear sprout elongation rate were derived from the experiment described in Chapter 6, 72 °Cd and 6.26 °Cd per mm, respectively.

Emergence to tuber initiation

The time of tuber initiation is simulated in the same manner as floral initiation in other APSIM crop modules. According to Ritchie *et al.* (1995) tuber initiation in potato is photoperiod sensitive with initiation delayed by daylengths in excess of a cultivar-specific maximum optimum photoperiod. At shorter daylengths, the thermal

time duration to tuber initiation is fixed and photoperiod insensitive. In the absence of parameters for the cultivars in question, the photoperiod sensitivity has been disabled, with the duration from emergence to tuber initiation set to 275 °Cd (from Ritchie *et al.* 1995).

Tuber bulking

The duration of the stages from tuber initiation to the start of tuber fill and from the start of tuber fill to the end of tuber fill are defined by fixed thermal time targets of 100 °Cd and 1400 °Cd (O'Brien *et al.* 1998a). The time of end of tuber fill typically corresponds with crop senescence.

Maturity

It is normal field practice following haulm death to keep the crop in the ground for another 2 weeks to ensure skin set and to avoid tuber greening. Maturity (and harvest time) in the model is set to 400 °Cd after the end of tuber fill.

Flowering is not simulated in APSIM-Potato as it does not have any significant bearing on growth or development (Kabat *et al.* 1995). The phenology parameters are the only variety-specific parameters in APSIM-Potato. All others are species specific.

Leaf area production

The simulation of leaf area production involves integrating the component processes of leaf appearance, leaf expansion, branching and leaf senescence as described in Chapter 6. Leaf cohorts comprised of main stem and branch leaves that are at similar stages of development, appear at a rate of 55 °Cd/cohort (from Chapter 7). These cohorts then expand for a specified period, enter a lag phase once they have fully expanded before senescence commences. Each of these leaf growth stages has a cohort-specific thermal time duration as specified in Table 8.1. The potential leaf area of each cohort is also specified in Table 8.1 (from Chapter 7). The thermal time duration and potential leaf area of each cohort were derived from the observation data in Chapter 7. Two leaf area indices (LAI) are calculated each day by the model: 1) today's potential LAI is based on the above parameters and; 2) an actual LAI that takes into account the discounting effect of water and nitrogen stresses.

Biomass accumulation

Potential dry matter production (DM, g/day) is based on the amount of photosynthetically active radiation intercepted by the canopy (I, MJ/day) and the efficiency with which this radiation is converted into biomass (radiation use efficiency, RUE, g/MJ). That is:

$$DM = RUE \times I \quad (8.1)$$

The amount of radiation intercepted is calculated from the amount of incident PAR (I_o), the extinction coefficient (k) and leaf area index (L) according to Beer's law (Loomis and Connor 1992):

$$I = I_o \times \{1 - \exp^{(-k \times L)}\} \quad (8.2)$$

APSIM-Potato uses the same light extinction coefficient (0.55) as the SUBSTOR model (Allen and Scott 1980 cited in Ritchie *et al.* 1995).

Radiation use efficiency is a species-specific parameter. In APSIM-Potato, RUE is set to 1.6 g/MJ from emergence to tuber initiation according to Allen and Scott (2001). Thereafter it increases to 2.5 g/MJ based on the work of Kooman and Haverkort (1995). Wassink (1968, cited in Sale 1979) reported that higher radiation use efficiencies are likely to occur for a period in the middle of the potato growing season once the crop canopy has closed. Sale (1979) also demonstrated that there was an increase in RUE after tuber initiation which is related to growing demand of sink to photosynthetic assimilates.

RUE is modified with temperature according to the relationship developed by Robertson *et al.* (2002) and shown in Figure 8.1. RUE is reduced when the mean daily temperature drops below 19 °C and rises above 24 °C according to the work of Kooman and Haverkort (1995).

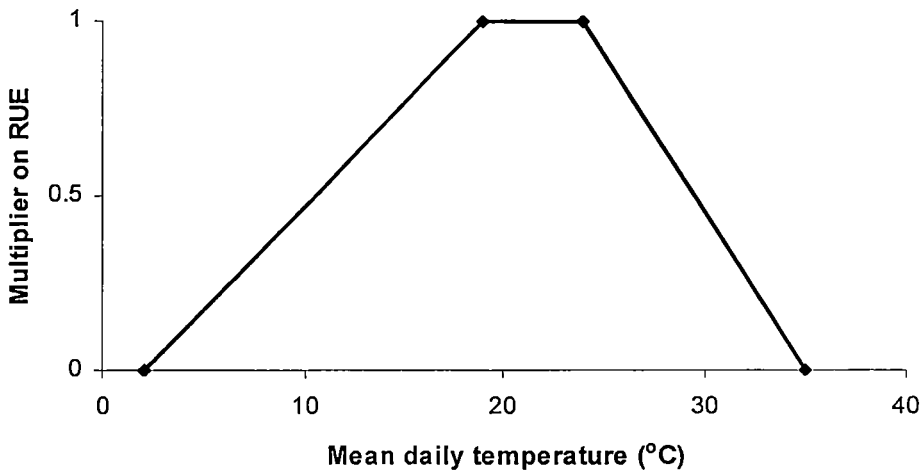


Figure 8.1. Response of RUE to temperature.

Biomass partitioning

Four biomass pools are modelled in APSIM-Potato; leaf, stem, tuber and root. Between emergence and tuber initiation, 20% of daily biomass production is allocated to roots and the residual distributed amongst the leaf (80%) and stem (20%) components. Tuber initiation changes the partitioning routine with the tuber receiving first priority for daily biomass allocation. The allocation to root remains at 20% up until the start of tuber fill while the stem allocation drops to 10% over the same period. Tuber allocation increases linearly from 10% at tuber initiation to 70% at start of tuber fill at the expense of leaf allocation which declines from 80% to 20% over the same period. Between the start of tuber fill and the end tuber fill, only 10% of the daily biomass production is allocated to root. The allocation of daily biomass production to tuber increases over this period from 70% to 90% at the expense of allocation to stem and leaf which drop to 0% at end of tuber fill.

The partitioning coefficients used in the model were based on figures from literatures (Kooman *et al.* 1996) and the sequential harvest collected in the plant monitoring activity for the calibration described in section 8.2.1 in this chapter (Table 8.3).

Table 8.3. Proportion of daily biomass production (%) partitioned to various plant part of potato crop in different phenology stages.

Plant component	Emergence	Tuber initiation	Start of tuber fill	End of tuber fill
Root	20	20	20	10
Non-root:	80	80	80	90
Leaf	80	80	20	0
Stem	20	10	10	0
Tuber	0	10	70	100

Crop water uptake

The actual rate of water extraction is the lesser of the potential extraction rate and the transpiration demand. The potential extraction rate is calculated using the approach first advocated by Monteith (1986). It is the sum of potential root water uptake from each profile layer occupied by roots. If roots are only partially through a layer available soil water is scaled to that portion that contains roots. The potential rate of extraction in a layer is calculated using a rate constant (*kl*), which defines the fraction of available water able to be extracted per day. Available water is calculated as the difference between the current water volume in each layer and the water volume at crop wilting point or the lower limit. Following Sinclair (1986) and Monteith (1986), transpiration demand is modelled as a function of the current day's crop growth rate, divided by the transpiration efficiency. Transpiration efficiency is related to the daylight averaged vapour pressure deficit (*vpd*), estimated using the method proposed by Tanner and Sinclair (1983). Whenever the transpiration demand is above the potential extraction rate, two water deficit factors (derived from the ratio of these two terms) are activated; one to reduce the rate of leaf area expansion and the other to reduce RUE.

Crop nitrogen uptake

In APSIM, nitrogen is supplied via three processes (Robertson *et al.* 2002) namely 'mass flow', active uptake and nitrogen fixation (legumes only). Potential N supply from mass flow and active uptake are a function of rooting depth, mineral N and soil water content in each soil layer. Crop N demand is determined by the amount of N

required to maintain the critical (non-stressed) N concentration in each plant part. The model specifies cardinal N concentrations (maximum, critical and minimum concentration) for each plant part (leaf, stem and tuber). Each day, N demand is calculated as the sum of the demands associated with pre-existing biomass of each part required to reach critical N content plus the N required to maintain critical N concentration in the current day biomass production. When plant N uptake by mass flow, which is the first option for the N movement into the plant system, cannot satisfy the N demand then it is supplied by active uptake. If there is insufficient N available to achieve the critical N concentrations then process-specific N stress factors derived from the N supply to N demand ratios act to reduce the rate of photosynthesis (via a reduction in RUE) and leaf expansion and to hasten the time of tuber initiation

Plant responses to soil water and nitrogen were not measured in this project so pre-existing generic parameter settings are used in APSIM-Potato. Where possible; potato-specific cardinal N concentrations have been sourced from available literature.

Seed tuber physiological age effects on stem and tuber number and tuber size

The physiology studies discussed in Chapter 4 concluded that stem number is affected by physiological age and that the response of the seed tuber to this factor is modified by temperature and moisture conditions at planting. Existing datasets are not adequate enough to develop an operational model to capture these responses. Furthermore, there is no reliable way of quantifying the physiological age of seed tubers. In spite of this, the findings from the physiology studies have been used to develop a conceptual model that captures the interaction between seed age, sowing environment and stem number. The functions that underpin this conceptual model have been incorporated into APSIM-Potato but have not been operationalised.

The conceptual model comprises two steps. The first step involves the calculation of a potential stem number (PSN) which is the maximum stem number under optimal sowing conditions. PSN is derived from an as-yet-unknown relationship with tuber seed physiological age (PA). This is shown as a linear relationship in Figure 8.2. The second step involves capturing the effect of soil moisture and temperature at sowing. The results from this project have shown that stem number increases with soil

temperature at sowing and that the extent of that increase varies with PESW (plant extractable soil water between crop lower limit and field capacity). In order to capture these responses, the conceptual model reduces the PSN via a multiplier (0 to 1) called the 'stem number index' (SNI). The slope and intercept of the sowing temperature X SNI relationship varies with PESW (Figure 8.3.).

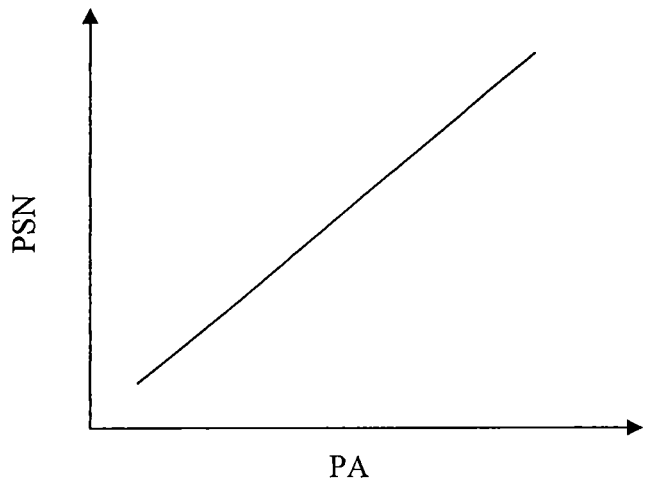


Figure 8.2. Conceptual relationship between seed tuber physiological age (PA) and potential (maximum) stem number (PSN).

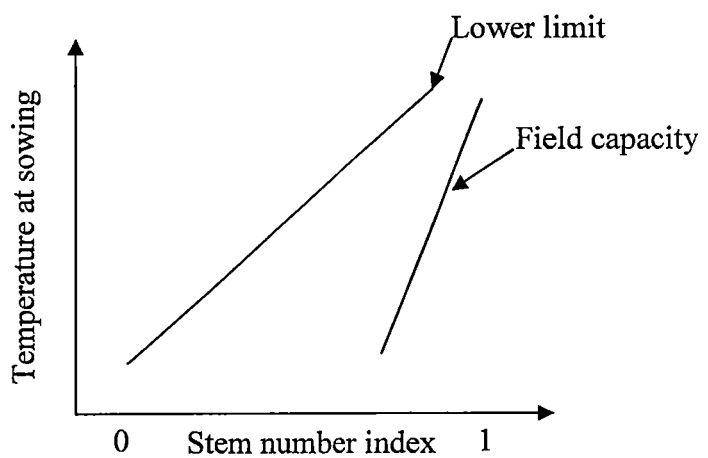


Figure 8.3. Stem number index based on temperature and moisture (plant extractable soil water) conditions at planting.

Tuber number and size

Tuber number per plant is estimated from the linear relationship between stem number and tuber number, as derived from the plant monitoring activity described in Chapter 3 (the CMS dataset, based on 160 crops) and own data from monitoring activity described in section 8.2.1 in this chapter (Figure 8.4). Average tuber size is calculated as total plant biomass production divided by tuber number per plant.

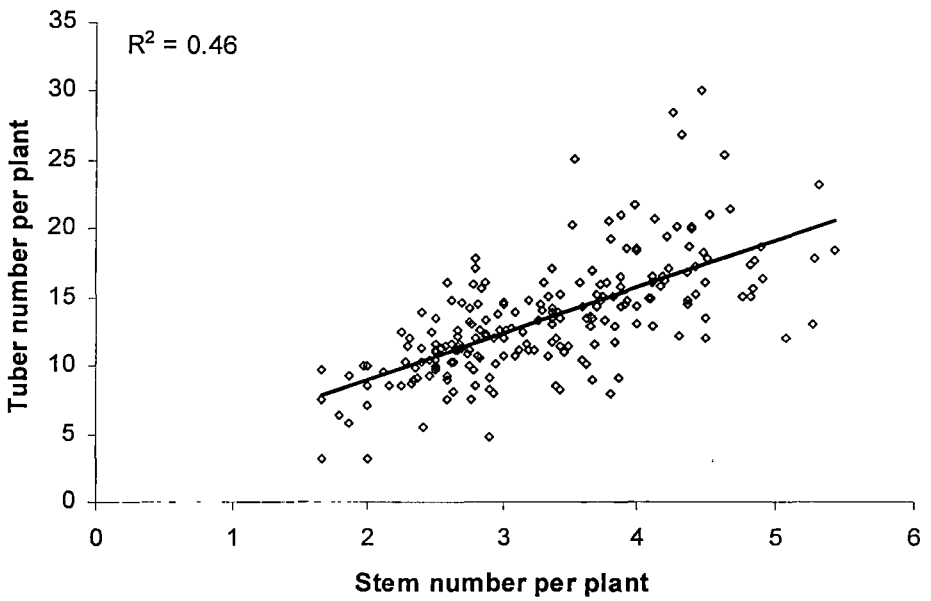


Figure 8.4. Relationship between stem number per plant and tuber number per plant. Data was compiled from plant monitoring activities that took place in the 2003/04, 2004/05 and 2005/06 growing season as described in Chapter 3. Additional data was sourced from own monitoring work in the 2006/07 growing season as described in the section 8.2.1 in this chapter.

Model calibration

When constructing a complex, process-based model such as APSIM-Potato, there are always parameters that have not been directly measured or for which there is some uncertainty in their value. These parameters are adjusted (within sensible limits) during an exercise in which the performance of the model is compared against a typically small, but reliable calibration dataset. Once there is reasonable agreement between the calibration dataset and the model, the model is then tested (without subsequent modification) against a larger independent validation dataset, typically covering a wider range of growing conditions. This section describes the calibration of APSIM-Potato.

Calibration was limited to Australian growing conditions as a complete high quality dataset for Indonesian conditions was not available during the project. A field trip was carried out in March 2005 to collect data as a part of the datasets inventory activity, either from government bureaus, farmers or from library databases however, none of the colleted information meet the requirement for calibration dataset. This was partly due to lack of electronic database availability either from industry or farmer.

Description of calibration dataset

The calibration dataset was obtained from intensive field monitoring of two commercial potato paddocks during the 2006/07 season. The paddocks have contrasting soil and climate profiles and are situated in northern Tasmania, at Epping Forest (41°50′39′′S 146°19′05′′ E) and Latrobe (41°14′ 52′′S 146°27′ 15′′ E). Both paddocks are participants in Simplot's Crop Management System (CMS) as described in Chapter 3. Full paddock management and soil details are summarised in Table 8.4.

Destructive plant samples were collected on seven separate occasions during the growing period; October 30 2006, November 23 2006, etc. At each sampling, six plants along a 2 m length of row (equivalent to 1 m^2) were taken from four randomly selected locations across the paddock. The number of main stems and tubers per plant were recorded for each sample. The total fresh weight of above-ground biomass and tubers was measured. A sub-sample was taken, weighed (fresh) and separated

into leaf and stem components. The samples were placed in a drying oven for 48 hours for determination of partitioned dry weights. Another sub-sample was used for the assessment of leaf area index. The laminas were separated from the petioles and run through a leaf scanner (EPSON Expression 10000 XL).

Four replicate sampling areas, each of 1 m^2 (6 plants) size were pegged out at the commencement of each crop for the purposes of non-destructive monitoring of emergence, tuber initiation and crop maturity. Time to emergence was considered to have occurred when the first leaf was visible at the soil surface in 50% of plants monitored. End of tuber fill was deemed to have occurred when 50% of the plants were 50% or more senesced (Kooman and Rabbinge 1996) and the time of tuber initiation was interpolated from data collected during the sequential harvests.

Table 8.4. Key details for selected calibration.

	Latrobe	Epping Forest
Soil type	Clay Loam	Sandy Loam
Nearest weather station	Latrobe	Epping Forest
Genotype	R. Burbank	R. Burbank
Row spacing (cm)	82	86
Set spacing (cm)	33	33
Planting Date	18-Oct-06	07-Nov-06
Harvest Date	19-Apr-07	16-May-07
Irrigation (mm/day)	30 / 6	50 / 5
Fertiliser:		
Pre planting	0 kg/ha N, 70 kg/ha P, 100 kg/ha K, 90 kg/ha S	0 kg/ha N, 2.4 kg/ha P, 680 kg/ha K, 2.8 kg/ha S
At planting	180 kg/ha N, 195 kg/ha P, 100 kg/ha K, 75 kg/ha S	150 kg/ha N, 130 kg/ha P, 220 kg/ha K
Top Dress	- 14-Dec-06: 50 kg/ha N - 26-Dec-06: 26 kg/ha N, 30 kg/ha P, 20 kg/ha K	- 2-Jan-07: 50 kg/ha N - 12-Jan-07: 40 kg/ha N - 22- Jan-07: 50 kg/ha N 50 kg/ha K
Yield (T/ha)	75	35.2

Daily climate data for the model runs was sourced for the nearest weather stations from the SILO database (Australian Bureau of Meteorology (BOM) 2007). Monthly figures for each growing season and for each site are summarised in Table 8.5.

Table 8.5. Monthly figures of climate data of monitored paddocks.

Paddock	Month-					
Latrobe	Oct '06	Nov '06	Dec '06	Jan '07	Feb '07	Mar '07
Monthly rainfall total (mm/month)	11	14	25	60	76	33
Average daily Tmax (°C)	16.0	18.6	20.0	22.2	23.8	21.3
Average daily Tmin (°C)	6.4	8.4	9.7	13.2	15.2	11.0
Average daily Radiation (MJ/m2)	19.7	21.7	24.3	21.6	21.0	16.8
Epping Forest	Nov '06	Dec '06	Jan '07	Feb '07	Mar '07	Apr '07
Monthly rainfall total (mm/month)	21	15	46	34	58	30
Average daily Tmax (°C)	17.0	20.0	23.1	25.2	27.0	22.5
Average daily Tmin (°C)	3.8	5.6	7.6	11.1	13.1	8.9
Average daily Radiation (MJ/m2)	20.4	22.0	24.7	22.3	20.9	16.8

Over the growing season, Epping Forest received ~15 mm less total rainfall than Latrobe. Temperatures during the growing season were generally higher in Epping Forest than at Latrobe. Radiation did not vary greatly between the two sites.

Calibration of key parameters

Phenology

The model adequately simulated all of the observed development stages (Figure 8.5). No adjustments were made to pre-calibration settings.

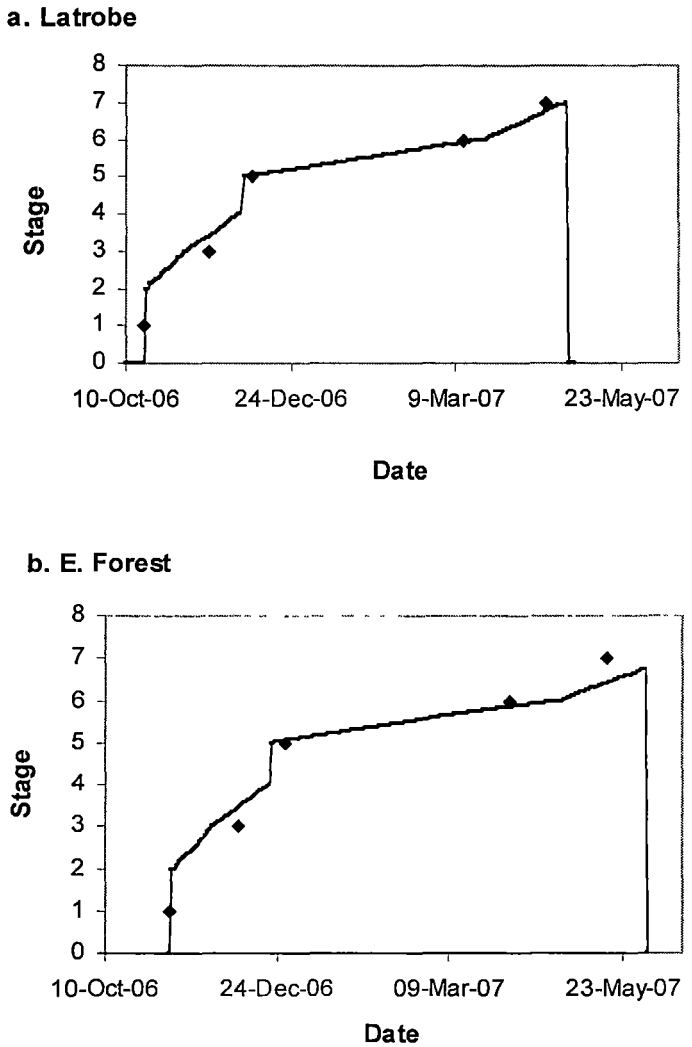


Figure 8.5. Observed (♦) and simulated (line) crop development for (a) Latrobe and (b) Epping Forest. Stages shown are 1: Sow; 3: Emergence; 5: Start tuber fill; 6: End tuber fill; 7: Maturity.

Leaf area index

Leaf area index was calibrated by adjusting the specific leaf area values and thermal time ranges for cohort leaf growth. Cohort leaf areas were not adjusted. Final calibration results for the two sites are shown in Figure 8.6.

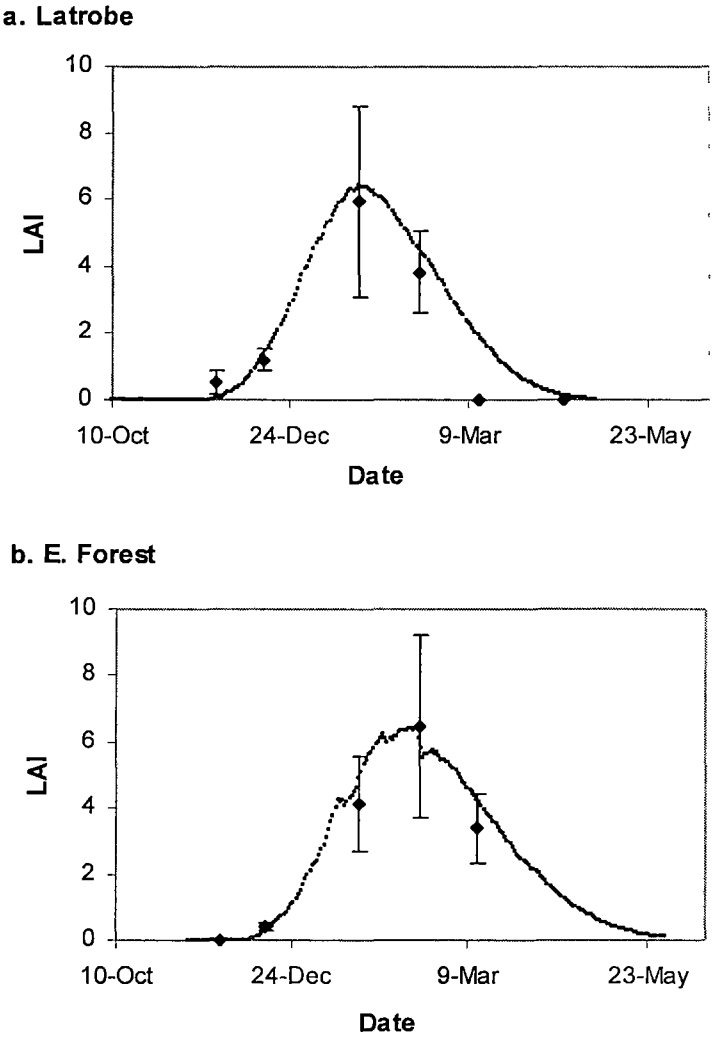


Figure 8.6. Observed (♦) and simulated (line) leaf area index (LAI) results for Latrobe (a) and Epping Forest (b). Standard error bars are shown for the observed results (N=4).

Biomass accumulation and partitioning

Calibration of the model for biomass prediction was conducted by adjusting the biomass partitioning coefficients. Prediction of leaf and tuber biomass at both locations was adequate and within the standard error bars for observed results (Figure 8.7.a and 8.7.c). The model had a slight tendency to over-predict stem biomass. Attempts to correct this were unsuccessful (Figure 8.7.b). The sharp divergence for stem biomass observed at Latrobe was due to a stem fungal infection of Rhizoctonia that occurred late in the crops life. Infection was restricted to the stem of the plant only.

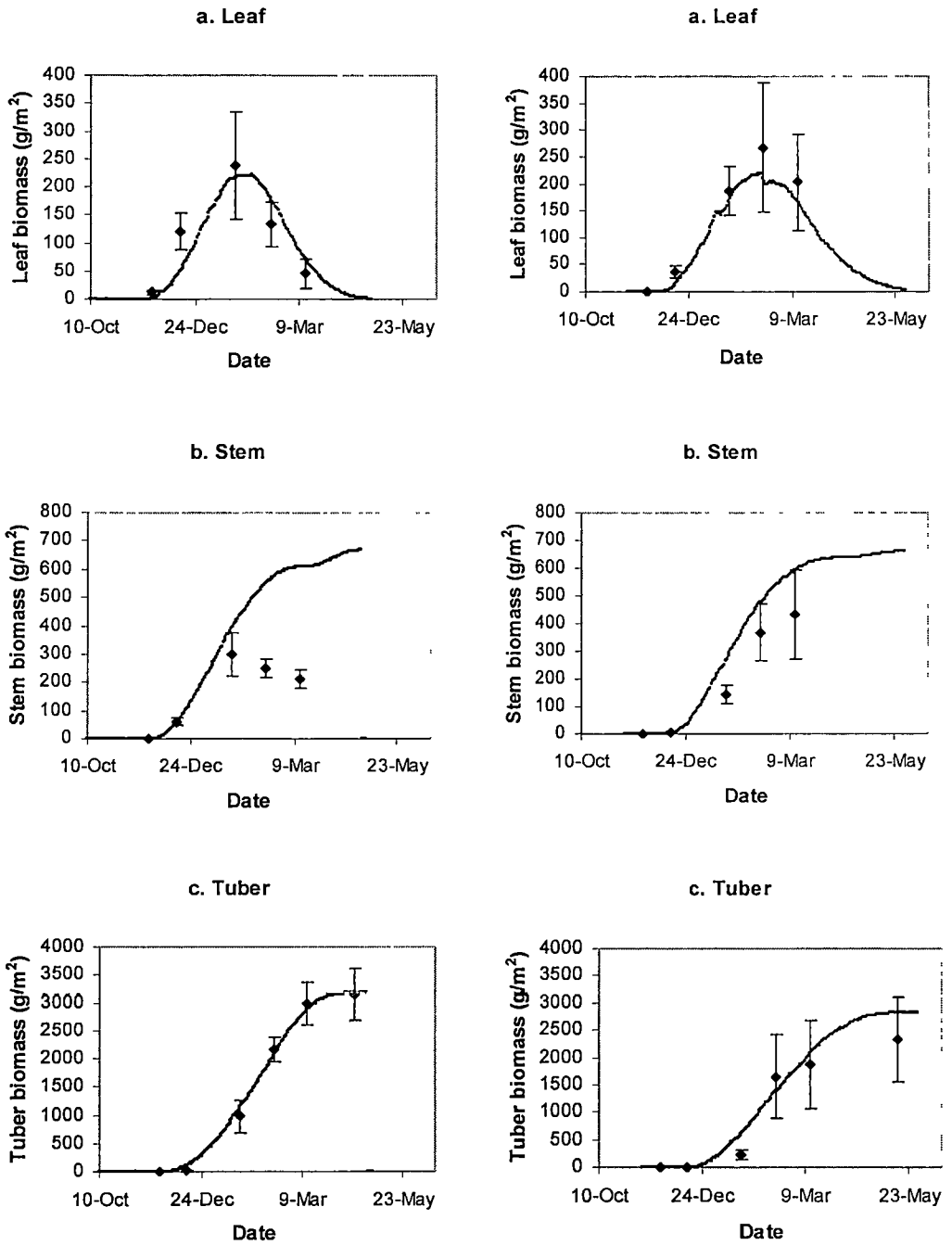


Figure 8.7. Observed (♦) and simulated (line) biomass accumulated and partitioned at Latrobe site (left hand side) and Epping Forest (right hand side). Standard error bars are shown for the observed results (N=4).

Model Validation

Description of validation dataset

A total of 48 paddocks were selected from the CMS database described in Chapter 3. Paddocks were selected to cover a range of soil, climate and management conditions and not to be limited by factors that are not captured in the model (e.g. disease, weed competition, insect infestation). Key details for these paddocks are summarised in Appendix F. Daily climate files were sourced for the nearest climate station from the SILO database (Australian Bureau of Meteorology (BOM) 2007). Representative soil characteristics were used in the simulations. Validation was restricted to tuber yield by the scope of the CMS database. Tuber DW data was generated from the specific gravity (SG) of each crop.

Validation for tuber yield

Validations of predicted versus observed tuber yield is shown in Figure 8.8. The degree of accuracy in predictions, with the model accounting for 75% of the variation in tuber yield, is comparable to other APSIM crop modules (Robertson *et al.* 2002; Carberry 1995).

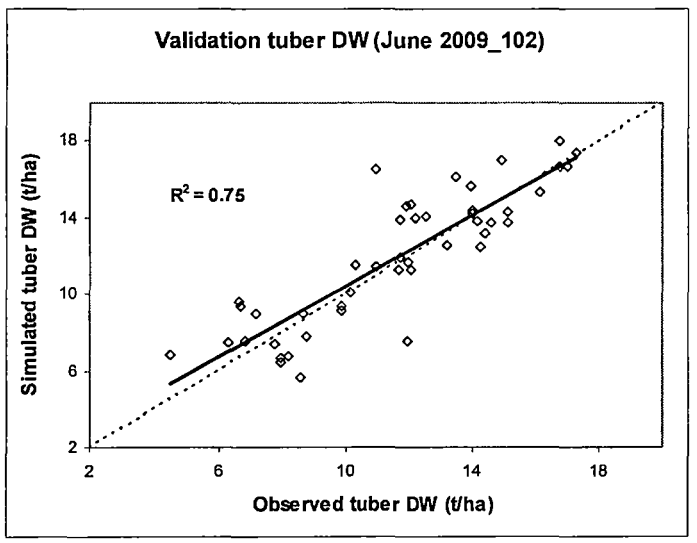


Figure 8.8. Validation plot of observed and simulated tuber yield (__) linear regression line (--) 1:1 line.

Discussion:

The new model adequately predicts tuber yield for cv Russet Burbank across a wide range of climate X management X soil combinations in Tasmania. Importantly, the validation dataset covers a wide range of growing conditions and yields (~35-85 t/ha fresh weight). Nevertheless, given that the model has been developed as a generic potato model suitable for use across a wide range of environments, further validation in other locations and for other cultivars is needed in the future. The tendency for the model to slightly over-predict in lower-yielding paddocks is not surprising as some of the factors which reduce yield in the field are not captured in the model (e.g. disease, insect damage, weed competition).

The parameterisation of the component model relating seed physiological age, growing environment and stem number requires additional and more comprehensive datasets and the development of a reliable index for estimating physiological age. Other processes requiring attention include the impact of daylength and nitrogen supply on the commencement of tuber initiation (Ewing and Struik 1992).

Chapter 9 General discussion

Computer simulation models can advantage the potato industry by providing a means to help in decision making, especially in key agronomic issues. The capacity to simulate effects of crop management practices and environmental conditions on one of the most important crop quality attributes, the yield of tubers within a size range specified by the target market, has been lacking in previously developed models. Tuber number per plant is related to stem density in a crop (Struik *et al.* 1990), and an understanding of the factors that affect stem number is therefore important for the development of a model to simulate the tuber quality. A major finding of this project was that the interaction between seed tuber physiological age, which until now has been considered the key driver of stem number, and soil water potential and temperature at planting had a significant effect on stem number. This thesis provides results from studies at tissue (tuber eye) level, tuber level and whole plant system, and presents a mechanistic model incorporating, at the conceptual level, the capacity to predict stem number as a basis for simulation of tuber size range.

Seed tuber physiological age is known to affect many processes of crop growth such as early vigour of the plant (Krijthe 1962), time to emergence (O'Brien *et al.* 1983; Firman *et al.* 1992), stem number per plant and hence tuber size distribution (Struik and Wiersema 1999), and canopy growth and duration (Knowles and Botar 1991). Despite these reported effects, the physiological age of the seed tuber has rarely been taken into account in the existing potato models. The existing potato crop models and decision support systems that do simulate tuber quality (MacKerron *et al.* 2004; Knowles *et al.* 2003) do not take into account the combined effects of seed tuber physiological age and planting environment on stem number. The current study showed that, based on evidence of an the interaction between seed tuber physiological age and planting environment affecting stem number, failure to take into account the soil temperature and moisture at planting in these models would not allow accurate prediction of stem number. Findings in this current study contribute a new consideration to the conventional

physiological age concept that not only seed tuber physiological status but its interaction with the planting environment determines the stem number.

At the whole plant level, differences in stem number per plant may alter inter- and intra-crop interactions such as shading which is known to have an effect on the senescence of the leaves. Physiologically older tubers tend to have more stems per plant and more branches on the main stems, and this may result in greater shading of the leaves on the lower nodes. Strong shading is known to reduce leaf longevity (Kooman and Haverkort 1995) therefore earlier senescence can be found in crops established from physiologically older tuber (Asiedu 2003). This indicates that stem density is not only important in determination of tuber size distribution but also crop yield, and inclusion of stem number prediction in a crop growth model or decision support system is an advancement to the current knowledge status of crop growth model.

In order to produce tubers in a target size range, a grower can manipulate the planting density by adjusting seed rate (number of seed tuber per unit area planted). A higher seed rate is usually used in seed crop production to ensure production of small sized tubers which are desired in seed tuber production. In contrast, lower seed rate is used for production of tubers for processing. Optimum seed rate is determined by the number of stems expected per seed tuber, the optimum stem density required for the target crop and expected yield (Firman and Allen, 2007). Firman *et al.* (2004, cited in Firman and Allen 2007) suggested a quantification of the number of stems based on seed tuber physiological age. However, evidence of a planting environment effect on the major seed tuber performance characteristics, sprout number and sprouting capacity, suggests a more complex method of predicting stem number is required.

Exclusion of the effect of seed tuber physiological age on stem number in the existing potato models is partly due to lack of reliable seed tuber aging indicator. Many studies have been focused on identifying an indicator of seed tuber physiological aging (Krijthe 1962; O'Brien and Allen 1978; van Ittersum *et al.* 1990; O'Brien *et al.* 1983; Caldiz 2001; Knowles *et al.* 2003) and several biochemical and physical alternative indicators

have been proposed (reviewed by Coleman 2000). However, none of these can sufficiently explain the changes of stem number with physiological aging of the seed tubers. This could be partly due to the planting environment effect. Sprout number and vigour changes with temperature and moisture therefore any indicator of seed tuber physiological age may not reflect the possibility of changes in the growth potential of eye buds when planting in the field.

Sprouting tests associated with physiological age studies are generally carried out under optimal temperature and moisture conditions (Krijthe 1962; Goodwin 1967b; Wiersema 1985), whereas field temperature and moisture conditions may fluctuate over a broad range. Interaction between seed tuber physiological age and planting environment may explain the difference between results obtained in controlled environments and in the field (Hay and Hampson 1991) and seasonal variations in stem number production (van Loon 1987; Roy and Jaiswal 1997; Johansen 2006). Variation in stem number occurs between sites, and from year to year (Chapter 3) supporting the conclusion that planting environment plays a significant role in the regulation of sprouting and stem number production.

After dormancy is broken, sprout growth increases linearly with temperature up to an optimum level of 20-25 °C (Krijthe 1962; Sale 1979; Klemke and Moll 1990), then decreases with higher temperatures. Delays in plant emergence and low vigour following early planting in temperate region have been associated with cold soil temperature (Reust *et al.* 2001) which also was shown studying the experiments reported in Chapter 6 where temperature was found to be the key driver of sprout growth for the pre-emergent phases. While the effect of temperature on sprout vigour is documented, sprout number has rarely been associated with changes in temperature.

In contrast to temperature, the effect of moisture on sprouting has not been given much attention. A number of studies where soil water potential treatments have been imposed after emergence have reported stem number (MacKerron and Jeffries 1986; Jeffries and MacKerron 1993), but have not involved imposing different moisture condition

treatments at planting. Stem number did not change significantly in these studies, however it is likely that stem number was established before the water stress treatments were imposed. The current study extends these previous findings, and demonstrates that sprouting can be affected by soil moisture conditions, with greater water deficit during planting decreasing the number of stems per plant. In addition, early plant vigour can be influenced by moisture at planting, a conclusion supported by the findings of Huer and Nadler (1995) that decreased stem fresh weight was caused by the soil water stress at early stage.

As a tuber is a modified stem, the plant-water response noted for sprouts after planting may resemble the effect of water deficit to leaf growth and expansion. Vos and Haverkort (2007) noted that permanent wilting point or lower limit (LL) was different between crops at early (young crop) and later (older crop) developmental stages. Older crop had a higher (-1.0 MPa) threshold than younger crops (-0.6 MPa), meaning that younger crop were more susceptible to water deficit. This may also be the case with seed tubers. Seed tubers that were not aged displayed a significant change in sprout number and vigour when water potential was reduced from –0.01MPa to -0.6 MPa, while physiologically older tubers were only slightly affected. This may explain the difference associated with tuber age in the magnitude of the response of the seed tubers to temperature and moisture treatments, with tubers not exposed to aging treatments more affected than physiologically older tubers.

Sprouting pattern is thought to be regulated by a correlative effect of bigger sprouts, usually at the apical region of the seed tuber, inhibiting small ones (Goodwin, 1967b; Hay and Hampson, 1991). In this study, it was found that sprout number increased with temperature, but the presence of big sprouts appeared to inhibit other sprouts which in turn may have affected the final number of stems produced. This supports the conclusion that sprout development prior to planting is important in stem number determination, as proposed by O'Brien *et al.* (1983). In addition, the planting conditions such as temperature and water availability can modify the interaction between eye buds. While sprout size at planting may be considered part of the tuber aging process, it has not been

considered as a quantifiable component of physiological age indicators but should be included in the assessment of tuber physiological status for more accurate prediction of stem number.

The capacity to predict stem number was considered a three-way function of seed tuber physiological status, temperature and moisture conditions at planting. This function was built in APSIM-Potato, the new model that also covers more comprehensive simulation of plant canopy development which is important in determining the area effective for radiation interception. The model takes into account leaf growth components, canopy architecture and stem density in determining the leaf area index. The new model is integrated in a bigger frame work which means provides a tool to simulate a broader human-plant-animal system.

Unfortunately comprehensive data for calibrating the relationship between seed tuber physiological age and planting environment in the model was not available to be generated in the project, therefore the conceptual function in the model is yet to be applicable. In addition lack of indicator for seed tuber physiological aging warrants future study. Success in the quantification of seed tuber physiological age along with calibration of the functionality will allow the model to be able to predict stem number, hence, simulate the production of tuber in marketable size required by the industry based on stem density. At current the model was validated against data only for yield and not the tuber size range due to unavailability of dataset. More calibration and validation needs to be undertaken prior the model can be used to predict tuber size distribution. Nevertheless, the availability of the potato model in the APSIM framework provides the possibility for the simulation of some key issues in the Australian and Indonesian production systems. Some agronomic application issues proposed for simulation of marketable tubers of potato are nitrogen and irrigation management. Simulation of cropping pattern in Australia and Indonesia, with potato as one rotation crop in the cropping pattern, would permit identification of the best-bet scenario of cropping pattern. Risk analysis of planting potato following a continuous crop or pasture system, through the simulation of the effect of the cropping system on the soil conditions (nutrients,

structure and availability of moisture), would be possible. The current study provides results which cover two key cultivars Russet Burbank and Atlantic used in Australian and Indonesian conditions, respectively. This will enable the key functions of crop growth to be calibrated and parameterised under Indonesian conditions, a target region in a broader program linked to this project, for the specific cultivar.

Re-evaluation of the relation between stem number and seed tuber physiological ages is recommended in order to take into account the effect of fluctuating soil temperature and moisture conditions in the field. While the current study showed evidence of the relationship between seed tuber physiological age and planting environment, a broader range of seed tuber physiological ages needs to be assessed. The study did not cover response from young seed tubers and the aging treatment (15 °C in the dark) used in this study also resulted in seed tubers with advanced sprout development prior to planting. The existence of a few big sprouts before the temperature and water potential treatments were imposed limits the interpretation of results, as noted by Haverkort *et al.* (1990b). Furthermore, sprouts may have been knocked off during handling or at planting which may have acted to break tuber apical dominance.

In addition, study of the response of seed tubers to different moisture conditions within the range assessed in this study is also recommended as only two moisture conditions were used in the current study. Results presented in this thesis were also restricted to comparing tubers in a similar size range as tuber size can influence the number of eyes, hence sprout number, and vigour. Further research utilising a range of seed tuber sizes, as well as a greater spectrum of seed tuber physiological age and planting environment treatments, is required to provide not only the data for APSIM-Potato model validation but also knowledge of the physiological basis of tuber sprouting pattern.

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