THE INFLUENCE OF LIGHT INTENSITY, LIGHT QUALITY AND ROOT ZONE TEMPERATURE ON POTATO MINITUBER PRODUCTION

E. KEMPEN

Thesis presented in partial fulfilment of the requirements for the degree of Master of Agricultural Science at the University of Stellenbosch

Study Leader: R.J. van der Westhuizen

Co-Study Leader: Dr. E. Reinten

December 2007

DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in this entity or in part submitted it at any other university for a degree.

Signature:

Estelle Kempen

Date: 27/11/2007

ABSTRACT

In South Africa the production of minitubers, as starting material for seed potato production, is achieved by transplanting *in vitro* plantlets to a hydroponic growth medium in the greenhouse, but current yields for minituber production are relatively low. As commercial growers start to prefer earlier generation seed, minituber production systems need to be re-evaluated in order to maximize yields. The effect of light intensity, light quality and root zone temperature on the growth, tuberization, assimilate distribution, tuber size distribution and tuber dormancy of potato was investigated in a series of greenhouse and glasshouse experiments.

The comparison of plants grown under different light intensities indicated that shading of 20% did not have a negative impact on the potato plants' growth, net assimilation or distribution of biomass within the plant. Higher shading levels of 40% and 50% resulted in most of the biomass being partitioned to the aboveground plant parts. The total number of tubers was not affected by light intensity but the dry matter percentage of the tubers was reduced by a decrease in the light intensity. The duration of dormancy was only determined by cultivar and tuber size.

In the light quality trial, filtering some of the red light reaching the plants resulted in an increase in stem and stolon growth and a high leaf dry mass percentage, which can be associated with an increase in the photosynthetic efficiency associated with conditions favourable to tuberization. Tuber number and total tuber mass per plant also increased and a high percentage of the total biomass was allocated to the tubers. Under the blue light absorbing covers stem and stolon growth also increased but neither the tuber number nor the total tuber mass per plant was affected. The most distinctive effect the far-red filter had was a decrease in tuber number but an increase in the average fresh mass per tuber.

Finally, a glasshouse study was conducted with different root zone temperatures. Cooling of the root zone to below 15^0C resulted in plants with a reduced height, lower leaf-, stem- and stolon mass and reduced leaf areas. Final tuber number or yield was not affected, but plants were more efficient in partitioning dry matter to the tubers. The results indicated that cooling of the root medium may facilitate a decrease in stem growth without affecting tuber formation and final tuber yield.

In conclusion, it can the recommended that in order to reduce excessive foliar growth due to a large percentage of assimilates being partitioned to the haulm, minituber producers should ensure high light intensities and cool growth medium temperatures

in the greenhouse. In areas where low light intensities commonly prevail during the growing season, additional lighting with the incorporation of a red filter may for this reason help to increase minituber yields

UITTREKSEL

In Suid-Afrika word miniknolle, verkry vanaf *in vitro* plantjies wat hidroponies in die kweekhuis verbou word, as begin materiaal vir saadaartappelproduksie gebruik. Miniknol-opbrengste wat sodanig verkry word is egter relatief laag. Omdat kommersiële produsente egter in 'n toenemende mate voorkeur toon vir vroeë generasie saadaartappels, is dit nodig om die produksiestelsels van G0 miniknolle in kweekhuise te herevalueer ten einde opbrengste te verhoog.

In hierdie studie is die effek van ligintensiteit, ligkwaliteit en groeimedium temperatuur op die groei van plante, knolinisiasie, verdeling van assimilate, knolgrootte verspreiding en knoldormansie van aartappels ondersoek in 'n reeks glas/kweekhuis-eksperimente.

Deur plante te vergelyk wat gekweek is onder skadunette wat verskillende lig persentasies deurlaat, is waargeneem dat 20% beskaduing nie die loofgroei van aartappelplante, totale biomassa of verspreiding van die biomassa benadeel nie. Hoër skaduvlakke (40% en 50%), het egter veroorsaak dat die grootste gedeelte van die biomassa na die bogrondse plantdele ge-allokeer is. Die aantal knolle ge-inisieer, is nie geaffekteer deur die ligintensiteit nie, maar droëmateriaal persentasie van die knolle was laer by laer ligintensiteite. Die dormansie periode en aantal spruite wat gevorm is, was slegs afhanklik van kultivar en knolgrootte.

In die ligkwaliteit proef het 'n vermindering van die rooi lig wat plante bereik, sowel stingel- en stolongroei as droëmassa persentasie van die blare verhoog. Dit kan dui op 'n verbetering in die fotosintetiese effektiwiteit soos waargeneem wanneer toestande gunstig is vir knolinisiasie. Onder die rooi lig filter was die aantal knolle en knolmassa per plant ook hoër en is 'n groot gedeelte van die totale biomassa na die knolle geallokeer ge-allokeer. Plante onder die blou lig filter het ook 'n verhoging in stingel- en stolongroei getoon, maar die aantal knolle en knolmassa per plant was onveranderd. Die ver-rooi filter het 'n vermindering in die knolgetal, maar 'n toename in die gemiddelde knolmassa tot gevolg gehad.

In die glashuisstudie met verskillende groeimedium temperature het 'n verlaging in temperatuur die planthoogte verminder en 'n afname in blaar-, stingel- en stolonmassa veroorsaak. Hoewel dit laer plantblaaroppervlaktes tot gevolg gehad het, is knolgetalle nie beïnvloed nie. Dit beteken dat die verkoeling van die groeimedium die effektiewe akkumulasie van droëmateriaal in die knolle verhoog.

Ten einde oormatige loofgroei te verminder word hoë ligintensiteite en lae groeimedium temperature dus aanbeveel. In produksiegebiede waar lae ligintensiteite in die kweekhuis dus 'n probleem is, kan addisionele beligting saam met 'n rooi lig filter moontlik help om miniknol opbrengste te verhoog.

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude and appreciation to the following people and institutions:

My study leader, R.J. van der Westhuizen and my co-study leader Dr. E. Reinten for their guidance and encouragement during this study;

Professor G.A. Agenbag, Head of the Department of Agronomy, for the use of facilities and provision of funds;

Dr. B.J. Pieterse and Potatoes South Africa for providing information regarding potato seed production in South Africa and the provision of funds;

Mr. M. La Grange for managing the technical side of this study and providing assistance whenever needed;

Mr. T de Kok of Ceres Potatoes for providing information on greenhouse conditions experienced by local minituber producers and for providing plant material for use in this study;

Dr. N.J.J. Combrink for constructive suggestions during the initial stages of this study;

A special word of thanks to my husband and family for the love and support I received throughout the duration of this study.

CONTENTS

Language and style used in this thesis are in accordance with the requirements of the South African Journal of Plant and Soil. This thesis represents a compilation of manuscripts where each chapter is an individual entity and some redundancy between chapters has, therefore, been unavoidable.

CHAPTER 1

Introduction and Literature Review

INTRODUCTION

The potato (*Solanum tuberosum* L.) is the most important non-cereal crop in the world, and covers yearly worldwide about 18 million hectares (Struik & Wiersema, 1999) producing 295 million tons of potatoes yearly. In the developing world the area planted with potato is increasing, while the potato production area is declining in the developed world. According to Statistics SA (2002) 1 776 076 ton potatoes were harvested in South Africa in 2002. The potato has a high production efficiency, with the energy production (MJ/ha) of potatoes being higher than that of both wheat and rice (Struik & Wiersema, 1999) and a high use efficiency in terms of land and energy. Potential yields are highest in temperate regions, in areas where the growing season is not shortened by low temperatures during spring and autumn and the length of the growing season is not restricted by high temperatures (Struik & Wiersema, 1999). Besides climatic factors, attainable yield can also be influenced by the availability of water, nutrients, crop protectants, seed quality and the level of technology (Struik & Wiersema, 1999). The increase in area planted with potato in the developing world has been facilitated by the development of new cultivars and the founding of seed potato production schemes utilizing modern multiplication techniques (Struik & Wiersema, 1999).

Potatoes are mainly utilized as food, for the fresh market and for processing, animal feed, seed tubers and to a limited extent in industrial processes such as the production of starch.

Commercially important potato cultivars are usually clonally propagated, one of the most important disadvantages of the potato. Potatoes have a low multiplication rate compared to other crops, from four to twenty times under optimal conditions and management (Nyende, *et al.*, 2005). For this reason a large portion of crop area is devoted to the production of seed tubers and it takes a considerable time to build up sufficient amounts of commercial seed tubers (Struik & Wiersema, 1999). With every field multiplication the build-up and transfer of pathogens can increase, leading to

seed degeneration and losses in yield and therefore the reduction of the number of field generations is a key component in supplying high quality seed. Input costs of seed tubers are very high, approximately 20-30% in developed countries (Struik & Wiersema, 1999) and will not be reduced by a reduction in the number of field generations of the seed tubers, unless the yields of early generation seed potatoes, specifically the Generation 0 (G0) greenhouse grown minitubers can be increased.

GROWTH AND DEVELOPMENTAL STAGES

Sprout development and plant establishment

Sprout development from tubers will only commence once dormancy has been broken. There is significant unevenness in sprout emergence depending on whether the meristem is apical or lateral on the tuber, with the apical buds spouting first and displaying an apical dominance over the lateral buds (Burton, 1989). Initially the rate of sprouting is relatively slow, but as the tuber gets older the rate of sprouting will increase (Burton, 1989). This is referred to as the sprouting capacity and is often used as an indicator of potato seed quality (Pieterse & Nel, 1999; Struik & Wiersema, 1999). The duration of dormancy is cultivar dependent and affected by environmental conditions during crop growth and tuber storage (Pieterse & Nel, 1999; Struik & Wiersema, 1999).

The potato is an annual, herbaceous, dicotyledonous plant consisting of a collection of stems, each acting independently, competing for resources such as light, water and nutrients (Struik & Wiersema, 1999). The number of leaf primordia formed on each stem is determined by storage conditions of the seed and conditions after planting (Struik & Wiersema, 1999). After forming an inflorescence, axillary buds on the main stem will develop into secondary stems, from which third level branches will develop. The number of levels that are produced per stem is cultivar dependent and can be influenced by environmental conditions, type and age of planting material and cultivation (Struik & Wiersema, 1999).

For optimal tuber formation and high yields a productive canopy is required. If crop growth rate is assumed to be proportional to the rate of photosynthesis and thus net assimilation, then maximum radiation interception is needed for as much of the growing season as possible. A delay in crop establishment and a slow canopy

development can result in a delayed maturity and reduced yields, especially in short growing seasons (Nyende *et al.*, 2005). A positive correlation between leaf area and tuber number has been shown (Kahn, Ewing & Senesac, 1983). The growth and development and determinacy of shoots differ widely between cultivars, ranging from cultivars that are essentially determinate and rely mainly on the leaf surface of the main shoot, to cultivars that are indeterminate and forming abundant branches and larger leaf areas (O'Brien, Allen & Firman, 1998). No relationship could be found between plant size at tuber initiation and final yield either within or between cultivars (O'Brien *et al.*, 1998).

The root system develops fast during the early growth of the crop and is fully developed by mid season (Burton, 1989). The fibrous root system is shallow with the majority of the roots in the surface 0.3m, although rooting depths of up to 1.2 m or more have been reported under favourable soil conditions (Durant *et al.*, 1973). During plant establishment accumulated dry matter is divided between the stems and leaves (Kooman *et al.*, 1996b). Sprout development and plant establishment can last between 30 to 70 days, depending on environmental conditions and cultivar.

Tuber initiation

Tubers normally develop from the underground branches of stems, namely the stolons, although every axillary bud on a potato stem has the potential to develop a tuber (Ewing & Wareing, 1978). There is a set and distinct pattern of distribution of stolons and tubers and tuber size along the stem axes, with most stolons and tubers and the largest tubers forming at basal nodes (O'Brien *et al.*, 1998).

Tuber initials will form at the sub-apical region of the stolon through cell division and elongation (Xu, *et al.*, 1998). An increase in the accumulation of soluble carbon compounds in the stolon tips have been observed even before any visible swelling of the stolon tip is visible (Oparka & Davies, 1985). As the stolon tip develop the accumulation of starch and patatin, a storage protein, increases (Geigenberger, Geiger & Stitt, 1998; Hendriks, Vreugdenhil & Stiekema, 1991).

O'Brien *et al.* (1998) suggests that the onset of tuber initiation can be predicted fairly accurately on the basis of chronological time from emergence. Normally tubers are induced and initiated after the formation of functional leaves and is thought to be complete within two to six weeks after plant emergence (Sale, 1976), although

O'Brien *et al.* (1998) found that initiation was normally complete within one week. The timing of completion of tuber initiation will be determined by the growth rate of the plant. In most cultivars the end of tuber initiation usually coincides with the formation of flowers (Burton, 1989; O'Brien *et al.*, 1998)

It is generally believed that the source-sink relationship is important in tuber formation and that the initiation of tubers results in the reduction of shoot- and root growth (Ewing & Struik, 1992). Early tuber initiation would thus result in small plants with smaller leaf surfaces and lower final tuber yield, while late tuber initiation leads to larger plants with larger leaf surfaces and higher final yields (Bremner & Radley, 1966). However, more recent trials suggest that tuber initiation does not affect leaf and root growth and that leaves and roots are produced at a constant rate from emergence until after tuber initiation (O' Brien *et al.*, 1998).

Aerial tubers on orthotropic stolons, aerial tubers on main stems and swellings above the attachment of side branches is not uncommon under circumstances where the tuberization signal cannot be translocated to or expressed in the stolon tips (Ewing & Struik, 1992).

Tuber bulking

As tuber initiation starts and through tuber bulking, the amount of dry matter being allocated to the tubers at the expense of the shoots increases (Kooman *et al.*, 1996a). Cells in the medulla increase in number and size, causing the tuber to increase in size. Cells in the tuber can increase up to 18 times their normal size due to the accumulation of starch and water (Steyn, 1999) and tuber bulking can continue up to three months depending on the cultivar and environmental conditions. Towards the end of this phase the tuber skin will start thickening (Steyn, 1999).

Cultivars seem to differ in their ability to retain initiated tubers, so that for some cultivars the final tuber number at plant maturity may be only 60% of the tubers present earlier in the season (Walworth & Carling, 2002). Tuber re-absorption is considered by some to be more important in establishing tuber size distribution than tuber initiation (Struik *et al.*, 1990). This should be kept in mind when concluding on yield when conducting trials where tubers are harvested before full maturity. Earlier studies on the tuber initiation and development of Shepody revealed that this cultivar retain most of the tubers formed early on in the season (Walworth & Carling, 2002).

Tuber maturation

During this phase photosynthesis will decrease, and the vines will eventually die back while the growth rate of the tuber also slows down. Slow maturing cultivars may therefore not be fully mature upon harvest. The skin will also thicken, protecting the tuber from infections and damage. As the tuber matures the buds become successively dormant, starting from the stolon end (Burton, 1989; Steyn, 1999). "Dormancy is the physiological state of the tuber 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" (Reust, 1986).

Although no morphological changes are visible during tuber dormancy, biochemical and physiological developments are taking place. The intensity of dormancy is also not constant over time. Dormancy is suggested to start at tuber initiation (Burton, 1987), increasing during tuber growth, intensifies after haulm removal and then start decreasing after a certain time (Struik & Wiersema, 1999).

FACTORS INFLUENCING GROWTH, TUBER INITIATION AND YIELD

A series of physiological events, triggered and modified by environmental- and genetic factors and regulated by plant hormones will lead to tuber formation (Ewing & Struik, 1992; Struik & Wiersema, 1999). Cultivars differ with respect to the number of tubers that will develop and be retained, the pattern of tuberization and the degree that environmental factors will influence tuberization and tuber growth (Ewing & Struik, 1992).

Photoperiod

Photoperiod is possibly the most important environmental factor influencing tuberization in the potato (Jackson, 1999). The potato is a short-day plant, with the length of the dark period being critical, although the critical photoperiod (i.e., the longest photoperiod that still permits tuber initiation) may differ between genotypes (Ewing & Struik, 1992). Growing plants in 12 h days, as opposed to 16 h days

generally results in earlier tuberization (Demagante & Vander Zaag, 1988). Some *tuberosum* cultivars will however tuberize under continuous light given that other environmental conditions are inductive (Ewing and Struik, 1992). More recently it has been suggested that a critical photoperiod does not necessarily exist, but that photoperiod has a more gradual effect on tuber initiation (Kooman *et al.*, 1996b).

Under long days, vegetative growth will be favoured, but tubers will eventually be formed, three-five weeks later than plants growing under short days (Chapman 1958). Plants kept under continuous light conditions soon after plant emergence can cause delayed tuber initiation, and increased stolon elongation and branching, leading to an increased number of tuber initials and a yield consisting of smaller tubers (Struik *et al.*, 1990). Short days generally favour tuberization instead of stolon growth, but shortening of the photoperiod when other factors are unfavorable for tuberization, will promote stolon production (Ewing & Struik, 1992).

Under short day (SD) conditions the photosynthetic rate per unit leaf dry weight increase, more starch accumulates in the leaves during the day and assimilate export from the leaves increases (Lorenzen & Ewing, 1992). These effects have been found to precede tuber initiation. Increasing the photoperiod from 12 to 18 hours, can also cause a decline in the net carbon assimilation rate (A_{net}) (Stuttle, Yorio, & Wheeler, 1996).

The effect of photoperiod on tuber initiation and duration of initiation is influenced by other environmental factors. The decline in A_{net} upon increasing the photoperiod is most pronounced under high light intensities (412 μmol m^{-2} s^{-1} compared to 263 μmol m^{-2} s^{-1}) (Stuttle, Yorio, & Wheeler, 1996).

O'Brien *et al.* (1998) suggests that under field conditions in temperate regions, neither the timing of onset of tuber initiation, nor the timing of completion of tuber initiation will be influenced by changes in photoperiod.

Temperature

The potato is best adapted to conditions as encountered at the centre of its origin, cool climates such as tropical highlands with mean daily temperatures between 15 and 18^{0}C (Haverkort, 1990). In the field, tuber dry matter production can be seen as a function of the cultivar and the length of the growing season (Kooman *et al.*, 1996b), where the length of the growing season is again determined by day length

and temperature. Short days at the time of plant emergence and high temperatures throughout the growing season will result in a shorter growing season (Haverkort, 1990; Kooman *et al.,* 1996b).

The optimum air temperature for sprout elongation is 18^{0}C, while haulm growth is optimum at about 25^{0}C (Struik & Wiersema, 1999). Tuberization will be enhanced at air temperatures between 18 and 20^{0}C and slow down at air temperatures above 20^{0}C (Kooman *et al.*, 1996a). Tuber bulking, the dry matter partitioning to the tubers, will be greatest at air temperatures between 15 and 20^{0}C (Struik & Wiersema, 1999).

Plant morphology is influenced by both air and root zone temperature, with plants grown under high temperatures (>20 / > 30^{0}C night / day temperatures) being taller with more internodes and more sympodial growth, the leaves are shorter and narrower with a more acute leaf to stem angle, and increased axillary branching at the base of the main stem. These plants also exhibit higher total leaf dry weights, total stem dry weights and a decrease in the leaf / stem ratio (Wheeler, Tibbits & Najar, 1986; Ewing & Struik, 1992). Low air temperatures after planting can increase the level of determinacy of the shoots (O'Brien *et al.*, 1998), signifying that more side branches will form, and thus a larger leaf area to intercept incoming radiation. Air temperatures above 30^{0}C will also shorten crop senescence (Midmore, 1990). Both heat sensitive and heat tolerant potato clones develop smaller root systems with a root zone temperature of 30^{0}C compared to a root zone temperature of 20^{0}C (Sattelmacher, Marschner & Kuhne, 1990). High soil temperatures (32 / 27^{0}C day night temperatures) also inhibit stolon development and may cause stolons to grow upwards and form aerial tubers, if the air temperature is cooler than the soil temperature (Reynolds & Ewing, 1989).

The dry matter allocation to tubers will start earlier at air temperatures less than 20^{0}C (Kooman *et al.*, 1996a; Struik & Ewing, 1992). However, O'Brien *et al.* (1998) found no effect on the onset of tuber initiation between soil temperatures of 12 and 19^{0}C, suggesting that in temperate areas, temperature does not significantly affect the onset of tuber initiation. In some cultivars high soil temperatures (28-30^{0}C) can delay or inhibit tuber formation (Ben-Khedher & Ewing, 1985), while for other cultivars tuber initiation was not significantly affected at high soil temperatures (Sale, 1976; Demagante & Vander Zaag, 1988). The interval from emergence to the onset of tuber initiation seems to be similar in crops grown at 25 – 30^{0}C in the hot tropics and those grown at 10 – 20^{0}C in more temperate areas (O'Brien *et al.*, 1998). The

duration of tuber initiation is however influenced by soil temperature, with a low soil temperature (<15^{0}C) being able to extend the period, while a soil temperature of 19^{0}C was able to shorten the initiation period with one week (O'Brien *et al.*, 1998). High mean daily temperatures (25 - 30^{0}C) will also reduce the number of tubers being retained (Sale, 1979).

The reduction in carbon assimilation rate that takes place at temperatures above 30^{0}C (Midmore & Prange, 1992) is due to the decrease in the net photosynthetic rate, the increase in dark respiration (Thornton, Malik & Dwelle, 1996) and the decline in starch accumulation since many enzymes involved in starch synthesis are not active at these high temperatures (Struik & Wiersema, 1999). Under controlled environments, the reduction in carbon assimilation rate under high temperatures correlates with the reductions in growth and yield (Midmore & Prange, 1992), but under field conditions the reduced carbon assimilation rate can not always explain the observed yield reductions (Sarquis, Gonzalez & Bernal-Lugo, 1996), possibly due to interacting effects such as low light intensity, long photoperiods or water- or nutrient stress. Increasing the soil temperature, while keeping the ambient temperature at a constant 20^{0}C, also result in a decrease in the net photosynthetic rate (Hammes & De Jager, 1990) and a reduction in the tuber dry weight is observable whenever the soil or air temperature is raised (Menzel, 1983). Struik, Geertsema & Custers (1989) found that increasing the temperature around the stolons and tubers led to an increase in tuber number. The increase in tuber number when increasing the stolon temperature to 28^{0}C was associated with a decrease in tuber size and final tuber yield (Struik *et al.*, 1989). Temperature during the tuberization phase has the most significant effect on the final number of tubers (Ewing & Struik, 1992).

The effect of temperature on growth and tuberization will be affected by other factors such as the light intensity, photoperiod and cultivar. Mean temperatures of 15 to 19^{0}C in combination with a 12 h photoperiod is most beneficial for early tuber growth, with both the onset of growth and the onset of bulking taking place earlier and the dry matter partitioning to the tubers increasing (Dam, Kooman & Struik, 1996).

As with short photoperiods, leaf starch accumulation during the light period is observed in plants grown at cool temperatures (Ewing & Struik, 1992). The resulting high C:N ratio was previously believed to be involved in bringing about tuberization. Although currently tuberization is believed to be controlled hormonally, assimilate

level may be involved in inducing tuberization through the effects of sucrose levels on genes involved in tuberization (Krauss & Marschner, 1982; Ewing & Struik, 1992).

Root zone temperatures can also influence growth and yield through its influence on oxygen supply, water and nutrient uptake and translocation (Anderson & McNaughton, 1973; Franklin, *et al.*, 2005). Decreasing soil temperatures can lead to a decrease in root growth, reduced shoot growth and a reduction in the photosynthetic rate due to a reduction in water and nutrient uptake at low soil temperatures (Franklin *et al.*, 2005). For tropical species such as cassava, low root zone temperatures can lead to mineral deficiencies (Forno, Asher & Edwards, 1979) but for the temperate oilseed rape (*Brassica napus*), low root zone temperatures (10^0C) did not affect boron uptake rates or plant biomass, although it did promote the partitioning of boron to actively growing leaves (Zhengqian *et al.*, 2002). The difference in day night temperature (DIF) is also known to affect stem and leaf development and mineral uptake and translocation for greenhouse grown tomatoes (Gent & Ma, 2000). Root zone temperature may also influence growth through its effect on plant growth regulators, since it has been found that the translocation of cytokinin and gibberellin is reduced when the root temperature is lowered (Atkin, Barton & Robinson, 1973).

Light intensity

Plants can modify their growth, development and physiology according to their environment. Environmental conditions can lead to modifications in the photosynthetic apparatus enabling plants to acclimatize photosynthetically to the reigning light environment (Walters, *et al.*, 2003). Together with temperature, light determines the growth rate of crops. Although light drives plant growth, an excess can lead to photoinhibition (Powles, 1984). Low light intensity can however limit yields when potato crops are grown in the winter, in order to escape the summer heat (Haverkort, 1990).

The most evident morphological response of potato plants grown under low light intensities is stem elongation and thinner leaves with lower specific leaf areas (Ewing & Struik, 1992). Low light intensities also result in a lower carbon exchange rate per unit leaf area (Ewing & Struik, 1992), a reduction in total biomass accumulation and tuber weight and a decrease in the percentage of biomass partitioning to the tubers

(Gawronska & Dwelle, 1989). Reduced light intensities are also associated with a decrease in tuber number (Sale, 1976; O'Brien *et al.*, 1998). Tuber initiation can be completed within two to three days under warm, high light conditions (O'Brien *et al.*, 1998) but under low light intensities the initiation of tubers seems to be delayed (Ewing & Struik, 1992). *In vitro* tuberization was accelerated and synchronized when a high light intensity treatment (111 μmol m^{-2} s^{-1}) under short days, was followed by darkness (Dobranski, Tabori & Ferenczy, 1999). The conclusion from this study was that a determined quantity of light is necessary to induce tuberization and that beyond this threshold the effect of light can become unfavourable (Dobranski, *et al.*, 1999).

The effect of light intensity on yield will be influenced by the growth stage, with the greatest yield reduction caused by lowering the light intensity during tuber initiation, while tuber bulking seems to be the least affected by shading (Ghosh *et al.*, 2002). Studying the effect of shading in controlled environment chambers, Chen & Setter (2003), showed that shade inhibited net biomass accumulation when applied from either tuber initiation or tuber bulking. Imposing shade early, from tuber initiation, led to a higher proportion of the biomass being allocated to the shoots, whereas a higher proportion of the biomass was allocated to the tubers when shade commenced from tuber bulking (Chen & Setter, 2003). Reducing the light intensity during tuber initiation will delay the termination of initiation, although this is cultivar dependent (O'Brien *et al.*, 1998). Plants being shaded from the tuber initiation phase have fewer and smaller tubers, whereas shading commencing from tuber bulking do not decrease the tuber number, but result in smaller tubers (Chen & Setter, 2003).

The effect of light intensity on tuberization and the relative growth rate is influenced by temperature. Radiation-use efficiency is negatively related to the radiation intensity perhaps since under high radiation intensities, a larger part of the foliage will be radiation saturated and hence less effective for a larger part of the season (Kooman *et al.*, 1996a). Therefore radiation interception is important for tuber dry matter production (Kooman *et al.*, 1996a). In hot tropical sites, reducing the light intensity during midday or in the afternoon can favour tuber yield, more than when plants are shaded in the morning (Midmore, Berrios & Roca, 2003). Plants are more efficient in converting solar energy into tuber fresh weight when shaded in these hot tropical sites (Midmore *et al.*, 2003). Under relatively low air temperatures (20 – 22^{0}C) the number of tubers formed is not influenced by low light intensities (3.4 MJ m^{-2} d^{-1}), but under high temperatures (28 - 30^{0}C), the same low light levels greatly

inhibits tuber formation (Menzel, 1985). At high temperatures and long photoperiods, shading can also delay tuber initiation (Demagante & Vander Zaag, 1988). Supporting these findings was results from a study by Midmore & Prange (1992) who found that low light intensities (250-280 μmol m^{-2} s^{-1}) and low temperatures (20 / 10^0C day / night temperatures) gave rise to high relative growth rates, possibly due to the large leaf surface area, while under low light intensities and high temperatures (33 / 25^0C day / night temperatures), the relative growth rate and net assimilation rate were low and the tuber number and tuber weight was also reduced. The limiting effect of high temperature on potato growth is thus aggravated by low light intensities.

Plants make adjustments in the composition and functioning of the photosynthetic system in response to varying light conditions (Walters, 2005). This photosynthetic adjustment improves the efficiency of resource utilization. Although plants grown under low light intensities may have higher leaf chlorophyll contents (Baily *et al.*, 2001), plants grown in high light intensities exhibit increased photosynthetic capacity and an increase in carbon assimilation (Walters, 2005). The rate of photosynthesis increases as the light intensity increases and the light saturation for CO_2 uptake is achieved at 400 W m^{-2}, with a net CO_2 uptake of 35-40 mg $dm^{-2}h^{-1}$ at this solar input (Sale, 1974) and saturation for maximum photosynthesis being reached at about 500 μmol m^{-2} s^{-1} (Gawronska, Dwelle & Pavek, 1990). High light intensities at short photoperiods result in high leaf starch concentrations (Stuttle *et al.*, 1996), although no correlation could be found between the A_{net} and starch concentrations in individual leaves (Stuttle *et al.*, 1996). They hypothesised that a physiological limit for the fixation and transport of carbon may exist, related to the sink activity, and that increasing the light intensity even under high CO_2 enrichment, may not maximize potato yield. Accordingly any photosynthesis promoting factor will be limited in the extent to which it can influence biomass accumulation and yield, by the sink capacity (Paul & Foyer, 2003).

The reduction in yield due to shading for field grown potatoes has been linked to a reduction in nitrate reductase (NR) activity in the leaves (Ghosh *et al.*, 2002).

Higher light intensities, being associated with higher temperatures and greater vapour pressure deficits, will lead to higher transpiration rates. Higher transpiration rates will lead to an increase in cytokinins being exported to the shoots, possibly explaining the enhanced shoot growth, noticeable in plants grown in shade (Pons & Bergkotte, 1996).

Light quality

Solar radiation is not only important for photosynthesis, but also drives water and nutrient transport and affect plant development through photomorphogenesis.

A low red to far-red (R:FR) ratio is associated with closed canopy shade where there is a reduction in the red and blue light and an increase in the far-red (FR) light (Smith 1982). Green plant parts also reflect FR light, lowering the R:FR light ratios of horizontally propagated light (Balleré & Casal, 2000). Removing some of the FR light through the use of spectral filters led to higher R:FR ratios that resulted in the reduction of stem height for chrysanthemum *(Dendranthema x grandiflorum*), bell pepper (*Capsicum annuum* L.) (Li *et al.*, 2000), cucumber (*Cucumis sativus* L.), tomato (*Lycopersicon esculentum* Mill.) and sunflower (*Helianthus annuus* L.) (Murakami, *et al.*, 1996a; Murakami, *et al.*, 1996b). Low R:FR light ratios can also reduce the rate at witch lateral roots emerge in young seedlings (Salisbury *et al.*, 2007). Li *et al.* (2000) suggest that the stage of development might influence the degree to which the filtered light will affect plant height. The FR filtering film also reduced the total leaf area and leaf size, shoot dry weights and the dry matter assimilation for both chrysanthemums and bell peppers (Li *et al.*, 2000). Dry matter partitioning was also affected suggesting that light quality can affect the translocation of photosynthates (Li *et al.*, 2000). Morphological attributes linked to low R:FR ratios are mediated by plant growth regulators (Vandenbussche *et al.*, 2005).

Photoselective greenhouse covering with dyes absorbing light from certain wavelengths are being introduced as a comparatively safer and less expensive method to control plant growth in the greenhouse (Li, *et al.*, 2000).

Light spectral quality can be used to control the growth and morphogenesis of potato plantlets *in vitro* avoiding the use of growth regulators. Increasing the red portion of the light reaching tissue cultured plantlets lead to enlarged leaf areas (Seabrook & Douglas, 1998). Other studies found that in *in vitro* grown potato plants, blue light activates the development of the underground storage organs (Drozdova *et al.*, 2001), whereas red light stimulates the development of the aboveground sink organs (Aksenova *et al.*, 1994). Blue light stimulate the formation of tubers and the accumulation of cytokinins in the underground parts of *in vitro* potato plants, while red light had no effect on either (Nauk & Langille, 1978). Blue light has also been shown to reduce plant height (Warpeha & Kaufman, 1989) and *in vitro* grown potato plantlets grown in a blue light deficient environment were reported to be longer and

showed an increase in haulm fresh and dry weight (Seabrook & Douglas, 1998). Britz and Sager (1990) demonstrated how under blue light deficient conditions the dry matter content of leaves increased due to a reduced amount of translocation of photosynthate out of leaves.

Light quality can also affect photosynthesis (Kim et al., 2004), stomatal regulation (Taylor & Assmann, 2001) and other processes such as flowering and germination (Taiz & Zeiger, 2002).

THE TUBERIZATION SIGNAL

Perception of environmental stimuli

Light is perceived by photoreceptors, including phytochrome, chryptochromes, blue-UVA photoreceptors and UVB photoreceptors. Phytochrome perceives the red and far-red wavelengths (600 – 750 nm) of the spectrum (Smith 1995) and is involved in various morphological and biochemical processes in the plant, including the photoperiodic response of flowering, shade avoidance and tuberization (Smith & Whitelam, 1990). Pr is the physiological inactive form that is responsible for absorbing red light, while Pfr is the far-red light absorbing active form of phytochrome. Upon absorption of red and far-red light, a balance, the phytochrome photoequilibrium (Ø) expressed as the ratio of Pfr to total phytochrome, is formed between the two forms (Smith & Holmes, 1977), determining the plants response. Environments with high R light relative to FR light result in establishing a high Ø and certain morphological responses to canopy shade such as stem elongation has been found to be inversely related to Ø (Morgan & Smith, 1979). It is the phytochrome photo equilibrium that determines the plants response. Phytochrome B has been found to affect the levels of a graft-transmissible factor that is involved in inhibiting tuberization (Jackson *et al.*, 1998) and in antisense PHYB plants, this factor is absent or ineffective since tuberization is possible both under long and short day conditions (Jackson *et al.*, 1998).

Signal Transduction

After the photoperiodic reception in the leaves, some kind of signal must be relayed to the stolons for the development of tubers. It has been shown that this signal is graft-transmissible (Kumar & Wareing, 1973). Plant growth regulators are more than likely involved in translating the leaf derived signal to the below ground parts. Both photomorphogenesis and plant hormones are involved in regulating the source sink-relationship within a plant (Ewing & Struik, 1992). For radish plants the morphogenic responses to light quality was closely related to the distribution of phytohormones between the different plant parts and not to a difference in photosynthetic activity (Drozdova *et al.*, 2001).

Gibberellins (GAs), abscisic acid (ABA), cytokinins (Cks) and jasmonic acid (JA), are the most likely candidates for involvement in tuberization (Fernie & Willmitzer, 2001). High endogenous GA levels appear to be involved in promoting shoot growth and inhibiting tuberization under non-inducing conditions such as long photoperiods (Simko, 1994; Xu *et al.*, 1998), whereas GA biosynthesis seems to be reduced under short day conditions, favouring tuberization (Amador *et al.*, 2001). High GA levels in the tuber can also inhibit the accumulation of tuber specific proteins (Vreugdenhill & Sergeeva, 1999). The application of the gibberellin biosynthesis inhibitor, paclobutrazol increases tuberization (Simko, 1994). The GA biosynthetic pathway is known to be controlled by photoperiod in amongst others, willow (Olsen *et al.*, 1995) and phytochrome B can have an effect on the levels or sensitivity of GA (Lopez-Juez *et al.*, 1995). Red light is known to stimulate the accumulation of GAs (Reid, Clements & Carr, 1968). Drozdova *et al.* (2001) found GA contents ten times higher in the aboveground parts of radish plants grown under red compared to blue light.

The ABA/GA ratio may also play an important role in tuberization, although no differences in tuberization were found between wild-type potato plants and an ABA-deficient mutant of potato (Quarrie, 1982). Exogenously applied ABA promotes tuberization, possibly by antagonising the effects of GA (Xu *et al.*, 1998). Internode elongation under low R:FR light, is regulated by gibberellins (Vandenbussche *et al.*, 2005). For *Brassica napus* seedlings, low R:FR ratios resulted in seedlings with longer petioles and reduced leaf areas (Kurepin, Shah & Reid, 2007).

Cytokinins play a central role in sink formation (Roitsch & Ehneb, 2000) and addition of cytokinins is necessary for *in vitro* tuberization (Palmer & Smith, 1999). Cytokinins are also believed to play a role in breaking dormancy. Early sprouting was observed

in potato plants overexpressing a gene responsible for the synthesis of cytokinins (Galas *et al.*, 1995).

Jasmonic acid and the chemically related tuberonic acid has also been shown to induce tuberization in *in vitro* assays (Jackson, 1999), but the application of JA onto potato leaves had no effect on potato tuberization (Koda *et al.*, 1991). Many plant responses that are also controlled by auxin are also regulated by light including root growth and development (Salisbury *et al.*, 2007). Phytochrome and auxin signalling are connected, and a recent study showed that phytochrome regulates auxin transport and thereby controls growth and development in *Arabidopsis* (Salisbury *et al.*, 2007). Ehylene has also been linked to shoot elongation under low R:FR ratios (Pierik *et al.*, 2003).

From studies using transgenic plants it has been shown that increasing sugar concentrations can promote tuber formation (Muller-Rober, Sonnewald & Willmitzer, 1992). The high sugar concentration in the antisense ADP-glucose phosphorylase plants lead to more but smaller tubers being formed. The effect of sucrose on promoting tuberization may be mediated through plant growth regulators (Simko, 1994). The glucose concentration in the cambial zone is a potential signal in response to the photosynthetic status of the plant, with glucose concentrations increasing under conditions that favour the allocation of biomass to tubers (Chen & Setter, 2003).

SEED POTATO PRODUCTION

Conventionally, potatoes are propagated vegetatively by using seed tubers. Seed tubers are prone to pathogen attack, have a low multiplication rate and a seeding rate of 2.0-2.5 t ha^{-1} (Nyende Schittenhelm, Mix-Wagner & Greef, 2005). Combining this with the fact that it is a bulky planting material that needs to be transported and stored, it is understandable that potato seed can comprise up to 30% (in the developed world) of the total input cost (Struik & Wiersema, 1999). Although according to a report by the South African National Department of Agriculture (NDA, 2003) seed comprise on average only 18.2% of the total input cost, it is still the largest input component compared to transport (10.9%), fertilizer (10.5%), chemicals (10.4%) and packaging (10.3%). High quality seed potatoes are necessary for the production of high yielding potatoes, but the yield potential of seed potatoes

deteriorates every year in the field and several bulking up generations in the field is necessary (Struik & Wiersema, 1999). To make a commercial planting of a new cultivar, five to seven field multiplications are necessary to obtain sufficient seed tubers, therefore by the time a commercial "ware" crop can be produced, there is a major decline in yield potential (Struik & Wiersema, 1999; Nichols, 2005). A key component for high quality seed is thus the reduction in the number of field generations needed. Reducing the number of field generations will not only improve the seed quality, but has the potential to also reduce costs. Different production systems have been researched with this in mind (Muro *et al.*, 1997; Ritter *et al.*, 2001; Nichols, 2005; Nyende *et al.*, 2005; Farran & Mingo-Castel, 2006; Lommen & Struik, 2006).

Production systems

In vitro propagated potato plantlets are generally used as a source of pathogen-free propagation material. The *in vitro* plantlets can be used for the production of minitubers in the greenhouse, or sometimes first raised to transplants before transplanting in the field (Lommen & Struik, 2006). Conventional methods of minituber production in the greenhouse seems to be hampered by the fact that only a limited number of tubers are produced per plantlet, and it's a fairly labour intensive method. With greenhouse raised transplants for field planting, a common problem is that tuberization commence too early, before the formation of a sufficient canopy and thereby limiting the final tuber yield (Lommen & Struik, 2006).

Different hydroponic culture systems are also used for the production of minitubers, including deep flow technique (DFT), nutrient film technique (NFT) and aeroponics. Advantages of these systems include solution recirculation, less water use and optimal supervision of nutrients and pH (Struik & Wiersema, 1999). Soil-less cultivation has been shown to increase the yield and number of tubers (Muro *et al.*, 1997) most probably due to the enhancement of water and nutrient availability. In an aeroponic system increased vegetative growth and delayed tuberization has been observed although final tuber yields were high since the crop cycle was extended to seven months and this production method allows sequential harvesting that allows initiation of new tubers (Ritter, *et al.*, 2001). Comparing an aeroponic system to a standard bark medium system, Nichols (2005) states that using the aeroponic

system, it is possible to obtain a similar yield, but an increase in tuber number. A productivity of 800 minitubers / m^2, with an average tuber size of 8g, is obtainable using an aeroponic system with a planting density of 60 plants / m^2 and weekly harvests (Farran & Mingo-Castel, 2006).

Alternative propagation techniques have been studied, such as the use of synthetic seeds (i.e., artificially encapsulated somatic embryos, shoot buds, cell aggregates or any other tissue that can be used for sowing as seeds) (Nyende *et al.*, 2005). The advantage of using synthetic seed would be planting material that is virus free, genetically identical and easy to handle, transport and store.

Seed potato production in South Africa

There are currently six companies with greenhouses accredited for minituber production in South Africa, of which four have their own tissue culture facilities (Thiart, 2004). The *in vitro* genebank at ARC-Roodeplaat provide the mother material, which is then further multiplied in the on-site tissue culture facilities (Thiart, 2004). The current laboratory capacity for the production of *in vitro* plants in these facilities is 1.6 million plants per year (Thiart, 2004).

The first nuclear seed production unit was established in the Long Tom pass in Lydenburg by the Potato Board in 1971 and in 1993 the first privately owned commercial facility was established in the North-West Province. Currently about 5.6 million certified minitubers are produced yearly in a greenhouse space that totals 17 352 m^2. According to figures given by producers, productivity ranges from 70 tubers m^{-2} harvest $^{-1}$ to 190 tubers m^{-2} harvest $^{-1}$. Greenhouse production of G0 minitubers is mostly on a solid medium, pine shavings or a mixture of vermiculite, perlite and coir allowing only a single harvest. *In vitro* plantlets are transplanted into trays or plant bags at high densities and grown for between 10 and 14 weeks before harvests. Most facilities produce two crops a year, one from September to December and the other from the end of January to April. Slightly larger minitubers, between 20 and 40 g, are generally preferred by the producers due to local agroclimatical conditions that require seed that can better stand stresses such as water and temperature stress. The G0 minitubers are then supplied to approximately 400 seed growers that will produce seed potatoes throughout the year. The seed potato production comprises approximately 13% of the total potato production in South Africa (National

Department of Agriculture, 2003). Local producers still express the need to increase the ratio of minitubers per *in vitro* plant.

DETERMINANTS OF POTATO SEED QUALITY

Potato seed quality is the most important yield determining factor that can be influenced by the producer (Struik & Wiersema, 1999) and poor seed quality is probably the main factor contributing to low productivity in many developing countries. Tuber quality can affect not only the number of stems that will be formed, but also the plant vigour, the length of the growing cycle and the number and growth rate of tubers formed (Struik & Wiersema, 1999). Apart from the effect of pests and diseases, potato seed quality is mainly determined by a few mutually related characteristics, namely the size of the tuber, its physiological age, the number of sprouts that will form per tuber and the proportion of sprouts that will develop into main stems (Struik & Wiersema, 1999).

Tuber size

The tuber size will determine the number of eyes because as the tuber grows, more lateral buds will be initiated. Tuber size is also related to the physiological age of the tuber, with larger tubers generally being further developed. Seed size will affect the number of stems per seed tuber (Struik & Wiersema, 1999). More stems per seed tuber will enhance early ground cover but may however reduce the plant vigour later in the growing season due to crowding (Struik & Wiersema, 1999). Planting smaller seed tubers at a higher density, will mean that fewer stems per seed is formed, but less clumping and a more uniform arrangement of stems can be achieved (Struik & Wiersema, 1999). In a study in Nepal, minitubers of 1-5 g produced almost twice as much as minitubers weighing less than 1g and tubers weighing more than 5g produced three times as much (Schulz *et al.*, 1998). Wiersema (1989), found that individual stems from seed tubers above 20g performed the same, however tubers smaller than 20 g had slower growth and lower yields. Seed tubers weighing between 1 and 5 g yielded 40 tons per hectare (t ha^{-1}), tubers weighing 5-10 g

yielded 47 t ha^{-1}, those weighing between 10 and 20 g yielded 50 t ha^{-1} and the large tubers weighing between 40 and 60 g yielded 54 t ha^{-1} (Wiersema, 1989). Locally, yields of 33 t ha^{-1} have been obtained using potato seed weighing 5 g (Hammes, 1985). Very small tubers will emerge slower and have a lower initial growth rate and will therefore require a longer growing period to reach their yield potential (Struik & Wiersema, 1999). Laboratory analysis has confirmed that the seed piece contribute to plant development up to at least a plant height of 20 cm when seed pieces of approximately 70 g were used (Bohl, Love & Thompson, 2001). Smaller tubers contain fewer reserves for the growing stems and would probably not contribute to plant development until this stage. Smaller tubers are also more severely affected by stress conditions, partly because water loss is higher from small tubers (Struik & Wiersema, 1999). A local study, however, concluded that although tubers weighing less than 10 g will lead to later emergence, the formation of fewer stems and a smaller canopy, tuber yields will not necessarily be higher if seed weighing more than 10 g is used (Kleingeld, Hammes & Beyers, 1996).

Physiological age

The physiological age of a tuber determines the quality in terms of planting material. It can be defined as "the stage of development of a tuber, which is modified progressively by increasing chronological age, depending on growth history and storage conditions" (Struik & Wiersema, 1999). Yield is affected by the physiological age of the seed tubers through effects on the sprout number, sprouting capacity and growth vigour of the sprouts (Reust, 1982; Struik & Wiersema, 1999; Caldiz, Fernandez & Struik, 2001). Sprouting capacity is determined by the sprout weight of sprouts developing on tubers of uniform size that is placed in the dark at 18-20^{0}C for four weeks after any sprouts already visible have been removed (Pieterse & Nel, 1999; Coleman, 2000). The effect of physiological age will also differ between cultivars (Struik & Wiersema, 1999; Coleman 2000).

Apart from sprouting capacity, degree days to sprouting are also sometimes an indicator of physiological age. Although temperature has a great effect on the biochemical and physiological processes determining the physiological age of the tuber, this can not be used as a reliable method of predicting physiological age since temperatures during production, transport and storage will have to be accurately

measured making it a very protracted process (Van der Zaag & Van Loon, 1987; Ewing & Struik, 1992; Pieterse & Nel, 1999; Struik & Wiersema, 1999). Usually the physiological age of tubers are determined visually with no sprouts indicating dormancy, then a single apical sprout, followed by several sprouts that will branch as the tubers age (Ewing & Struik, 1992; Pieterse & Nel, 1999). Physiologically old seed tubers may even initiate tubers on the sprouts (Pieterse & Nel, 1999).

Physiological young seed tubers will have fewer sprouts developing due to the presence of apical dominance, and plant emergence will be slow resulting in an uneven stand due to the lower sprouting capacity and growth vigour of the sprouts (Pieterse & Nel, 1999; Struik & Wiersema, 1999). Increasing the physiological age to a stage where apical dominance is lost and more sprouts start developing, will advance emergence, lead to more underground nodes being produced and accelerate the onset of tuber initiation and plant senescence (O'Brien *et al.*, 1998; Coleman 2000). The increase in number of sprouts that develop from these tubers will lead to a final yield of more tubers although the mean tuber size will be less (Theron & Pieterse, 1999). Physiological older seed will also increase the determinacy of the shoots, leading to a larger leaf area being formed (O'Brien *et al.*, 1998). At the other extreme, seed tubers that are physiologically too old will develop more sprouts, but they will produce weak multi-stemmed plants since the sprouting capacity and growth vigour starts declining after a certain time (Struik & Wiersema, 1999).

The physiological age of a tuber may also have an effect on the plant's response to its environment. Slow root development of young tubers may increase the plants susceptibility to soil moisture stress (Coleman, 2000).

Physiological disorders

Tuber quality can be influenced by abiotic stress factors, including heat stress, drought, salinity and air pollution. Such factors can influence the dry matter content of the tuber and lead to physiological disorders such as hollow heart and growth cracks (Struik & Wiersema, 1999; Theron & Pieterse, 1999).

In South Africa, the most important physiological disorders affecting potato seed quality mainly by affecting sprouting includes internal black spot, chilling injury and blackheart (Theron & Pieterse, 1999). Shatter bruises affect seed vigour and the

bruises can become infected with Fusarium dry rot (Burton, 1989; Rich, 1983), causing poor emergence. Mechanical damage of the seed tuber skin can also negatively affect sprouting by removing the eyes (Steyn, 1999).

Although not a disorder, mechanical damage can also significantly influence the seed tuber quality as these tubers will not only be subjected to high moisture loss and pathogen infections but may age physiologically faster due to the accumulation of reducing sugars (Theron & Pieterse, 1999).

INFLUENCES ON TUBER QUALITY

During production

Because potatoes are produced below ground, they are exposed to conditions different than those in the air and these are not always readily visible or easily measured. Conditions during crop production may influence tuber quality by affecting the growth rate of the tubers, influencing the number of eyes forming on the progeny tubers or lead to physiological disorders (Struik & Wiersema, 1999).

High soil and air temperatures can lead to internal black spot, while a low soil water availability or fluctuating soil water levels can result in tuber malformation or growth cracks and high soil moisture conditions can lead to enlarged lenticels that can increase the risk of infections (Davies, 1998; Theron & Pieterse, 1999).

Calcium ions are transported within the plant in the xylem stream and since the potato tuber is likely to receive most of its water along with sucrose from the phloem it is susceptible to calcium related disorders that can be exacerbated by high rates of transpiration experienced in hot climates (Davies, 1998). An insufficient calcium supply to the tubers can also lead to internal black spot (Barnard 2001; Busse & Palta, 2006)

During storage

The harvested tubers have an active metabolism that needs to be controlled in order to control the quality of the tuber. Once disconnected from the mother plant a seed

tuber displays an independent physiological behaviour starting with dormancy (Burton 1989; Struik & Wiersema 1999). The physiological properties change over time and is affected by environmental conditions including photoperiod, temperature, light, relative humidity and the CO_2 / O_2 ratio of the air (Struik & Wiersema, 1999).

Temperature is an important factor influencing the rate at which the intensity of dormancy will decrease. At 28^0C dormancy is lost at maximum speed (Struik & Wiersema, 1999). At 4^0C no sprout growth will occur and storage of tubers at low temperature is employed to extend dormancy and is essential for the release of apical dominance (Struik & Wiersema, 1999; Theron & Pieterse, 1999). Cold storage is thought to decrease dormancy and improve sprouting due to increase in endogenous levels of GA (Struik & Wiersema, 1999; Claassens & Vreugdenhill, 2000). Breaking or shortening the dormancy period of tubers will make it possible to plant the tubers soon after harvest, thereby improving their performance (Burton, 1989). Storage temperatures below 10^0C can increase the risk of mechanical damage to tubers, while storage temperatures below 1^0C can lead to chilling injury that can negatively affect sprouting (Theron & Pieterse, 1999). High storage temperatures in combination with poor ventilation resulting in a high CO_2 / O_2 ratio of the air which can lead to blackheart (Burton, 1989; Theron & Pieterse, 1999).

The presence of light during storage will result in shorter, thicker and green sprouts that will not easily break off during handling and will ease the planting process. It is also possible that the presence of light during storage can delay the maximum sprouting capacity (Pieterse & Nel, 1999).

Removal of the apical sprout can facilitate the release of apical dominance leading to the development of lateral sprouts that will ensure more shoots per tuber and a better ground cover (Pieterse & Nel, 1999). Tubers treated with ethylene during storage were also found to release apical dominance and more and longer stems and stolons were produced resulting in higher final yields (Pruski, *et al.* 2003).

CONCLUSION

The potato is a temperate climate crop and growth and yield is strongly influenced by climatic factors, with relatively cool temperatures and high light conditions resulting in high yields. Attainable yield can also be influenced by the availability of water, nutrients, crop protectants, seed quality and the level of technology. Being clonally

propagated, the build-up and transfer of pathogens is one of the most important disadvantages of the potato. The reduction of the number of field generations is therefore a key component in supplying high quality seed and can facilitate a reduction in the cost of seed potatoes. The yields and quality of G0 minitubers produced in the greenhouse could be increased and possibly better controlled by applying the knowledge of how light and temperature in the greenhouse affect plant growth, tuberization and assimilate partitioning.

Conditions that will benefit rapid plant growth and a short, synchronized tuberization period will be beneficial to the potato seed industry. A more synchronized tuberization period will lead to more minitubers in the preferred size classes being harvested and a shorter growing period may reduce the risk against pathogens, can limit expenses and possibly facilitate an extra production cycle. This will also lead to a reduced number of field plantings that will eventually increase the quality of tubers used in commercial plantings.

According to Struik (2006), many challenges still lie ahead for potato research, including better size distribution and increasing the resource use efficiency of the crop. Tuber quality is another topic that will have to be addressed in future research. Problems with bruising, reducing sugars, after cooking darkening, hollow heart and internal rust spots need to be further studied by physiologists, agronomists and breeders.

OBJECTIVES

The main objective of this study was to determine the effect of light intensity, light quality and root zone temperature on the potato plant growth, tuberization, assimilate distribution, tuber size distribution and tuber dormancy in order to improve conditions within the greenhouse to increase yield and possibly also tuber quality. This was achieved by comparing different levels of light intensity, different levels of light quality and different levels of root zone temperature for different cultivars and determining the effect of above-mentioned treatments on plant growth, minituber yield and tuber dormancy. To achieve this, the main objective was divided into more specific objectives:

Objective 1: Determining the effect of reduced light intensity on growth, yield and dormancy.

Objective 2: Determining the effect on plant growth, yield and dormancy of filtering light from specific wave lengths on minituber production of two different local cultivars.

Objective 3: Determining the effect of root zone temperature on minituber production.

REFERENCES

AKSENOVA, N.P., KONSTANTINOVA, T.N., SERGEEVA, L.I., MACHACHKOVA, I., & GOLYANOVSKAYA, S.A., 1994. Morphogenesis of potato plants *in vitro*: 1. Effect of light quality and hormones. *J. Plant Growth Regul.* 13, 143-146.

AMADOR, V., BOU, J., MARTINEZ-GARCIA, J., MONTE, E., RODRIGUEZ-FALCON M., RUSSO, E., & PRAT, S., 2001. Regulation of potato tuberization by day length and gibberellins. *Int. J. Dev. Biol.* 45(S1), S37-S38.

ANDERSON, J.E., & MCNAUGHTON, S.J., 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. *Ecology* 54, 1220-1233.

ATKIN, R.K., BARTON, G.E., & ROBINSON, D.K., 1973. Effect of root growing temperature on growth substances in xylem exudates of *Zea mays*. *J. Exp. Bot.* 24, 475-487.

BAILEY, S., WALTERS, R.G., JANSSON, S., & HORTON, P., 2001. Acclimation of *Arabidopsis thaliana* to the light environment: the existence of separate low light and high light responses. *Planta* 213, 794-801.

BALAMI, V., VELUTHAMBI, K., & POOVAIAH, B.W., 1986. Effects of calcium on tuberization in potato (*Solanum tuberosum* L.). *Plant Physiol.* 80, 856-858.

BALARE, C.L., & CASAL, J.J., 2000. Light signals perceived by crop and weed plants. *Field Crops Res.* 67, 149-160.

BARNARD, R., 2001. Verbeterde metodes vir miniknol produksie by aartappels (*Solanum tuberosum* L.). MSc thesis, University of Stellenbosch, South Africa.

BEN KHEDHER, M., & EWING E.E., 1985. Growth analyses of eleven potato cultivars grown in the greenhouse under long photoperiods with and without heat stress. *American Potato J.* 62, 537-554.

BOHL, W.H., LOVE, S.L., & THOMPSON, A.L., 2001. Effect of seed piece removal on yield and agronomic characteristics of Russet Burbank potatoes. *Amer. J. of Potato Res.* 78, 397-402.

BREMNER, P.M., & RADLEY, R.W., 1966. Studies in potato agronomy. II. The effects of variety and time of planting on growth, development and yield. *J. Agric. Sci., Cambridge* 66, 253-262.

BRITZ, S.J., & SAGER, J.C., 1990. Photomorphogenesis and photoassimilation in soybean and sorghum grown under broad spectrum or blue-deficient light sources. *Plant Physiol.* 94, 448-454.

BURTON, W.G., 1989. The potato, 3rd edn. Harlow: Longman Scientific & Technical.

BUSSE, J.S., & PALTA, J.P., 2006. Investigating the *in vivo* calcium transport path to developing potato tuber using ^{45}Ca: a new concept in tuber calcium nutrition. *Physiol. Plant.* 128, 313-323.

CALDIZ, D.O., FERNANDEZ, L.V., & STRUIK, P.C., 2000. Physiological age index: a new, simple and reliable index to asses the physiological age of seed potato tubers based on haulm killing date and length of the incubation period. Field Crops Res. 69, 69-79.

CHAPMAN, H.W., 1958. Tuberization in the potato plant. *Physiol. Plant.* 11, 215-224

CHEN, C., & SETTER, T.L., 2003. Response of potato tuber cell division and growth to shade and elevated CO_2. *Ann. Bot.* 91, 373-381.

COLEMAN, W.K., 2000. Physiological ageing of potato tuber: A review. Ann. Appl. Biol., 137, 189-199.

DAM, J.V., KOOMAN, P.L., & STRUIK, P.C., 1996. Effects of temperature and photoperiod on early growth and final number of tubers in potatoes (*Solanum tuberosum* L.). *Potato Res.* 39, 51-*62.*

DAVIES, H.V., 1998. Physiological mechanisms associated with the development of internal necrotic disorders of potato. *Amer. J. of Potato Res.* 75, 37-44.

DEMAGANTE, A.L., & VAN DER ZAAG, P., 1988. The response of potato (*Solanum* spp.) to photoperiod and light intensity under high temperatures. *Potato Res.* 31, 73-83.

DOBRANSKI, J., TABORI, K.M., & FERENCZY , A., 1999. Light and genotype effects on *in vitro* tuberization of potato plantlets. *Potato Res.* 42, 483-488.

DROZDOVA, I.S., BONDAR, V.V., BUKHOV, N.G., KOTOV, A.A., KOTOVA, S.N., MAEVESKAYA S.N., MOKRONOSOV, A.T., 2001. Effects of light spectral quality on morphogenesis and source-sink relations in radish plants. *Russian J.Plant Physiol.* 48, 285-490.

DURANT, M.J., LOVE, B.J.G., MESSEEN, A.B., & DRAYCOT, A.P., 1973. Growth of crop roots in relation to soil moisture extraction. *Ann. Appl. Biol.* 74, 387-394.

EWING, E.E., & STRUIK, P.C., 1992. Tuber formation in Potato: Induction, Initiation, and growth. *Hortic Rev.* 14, 89-197.

EWING, E.E., & WAREING, P.F., 1978. Shoot, stolon, and tuber formation on potato (*Solanum tuberosum* L.) cuttings in response to photoperiod. *Plant Physiol.* 61, 348-353.

FARRAN, I., & MINGO-CASTEL, A.M., 2006. Potato minituber production using aeroponics: Effect of plant density and harvesting intervals. *Amer. J. of Potato Res.* 83, 47-53.

FERNIE, A.R., & WILLMITZER, L., 2001. Molecular and biochemical triggers of potato tuber development. *Plant Physiol.* 127, 1459-1465.

FORNO, D.A., ASHER, C.J., & EDWARDS, D.G., 1979. Boron nutrition of cassava, and the boron-temperature interaction. *Field Crop Res.* 2, 265-279.

FRANKLIN, J.A., KAV, N.N.V., YAJIMA, W., & REID, D.M., 2005. Root temperature and aeration effects on the protein profile of canola leaves. *Crop Science* 45, 1379-1386.

GALAS, I., MACAS, J., VLASAK, J., ONDREJ, M., & VAN ONCKELEN H.A.,1995. The effect of an elevated cytokinin level using the *ipt* gene and N-6 benzyladenine on a singe node and intact potato plant tuberization *in vitro. Plant Growth Regul.* 14, 143-150.

GAWRONSKA, H., & DWELLE, R.B., 1989. Partitioning of assimilates by potato plants (*Solanum tuberosum* L.) as influenced by irradiance I. Partitioning patterns in cultivar Russet Burbank grown under high and low irradiance. *Am. Potato J.* 66, 201-213.

GAWRONSKA, H., DWELLE, R.B., & PAVEK, J.J., 1990. Partitioning of photoassimilates by potato plants (*Solanum tuberosum* L.) as influenced by irradiance II. Partitioning patterns by four clones grown under high and low irradiance. *Am Potato J.* 67, 163-176.

GEIGENBERGER, P., GEIGER, M., & STITT, M., 1998. High temperature inhibition of starch synthesis is due to inhibition of ADPGlc pyrophosphorylase by decreased levels of 3PGA in growing potato tubers. *Plant Physiol.* 117, 1307-1317.

GENT, M.N., & MA, Y., 2000. Mineral nutrition of tomato under diurnal temperature variation of root and shoot. *Crop Sci.* 40, 1629-1636.

GHOSH, S.C., ASANUMA, K., KUSUTANI, A., & TOYOTA, M., 2002. Effects of shading on dry matter production, yield, and nitrate reductase activity of potato under two levels of spacing. *Env. Control in Biol.* 40, 259-268.

HAMMES, P.S., 1985. The effect of stem population on tuber yield in a trial with single-stem seed pieces. *Potato Res.* 28, 119-121.

HAMMES, P.S., & DE JAGER, J.A., 1990. Net photosynthetic rate of potato at high temperatures. *Potato Res.* 33, 515-520.

HAVERKORT, A.J. 1990. Ecology of potato cropping systems in relation to latitude and altitude. *Agric. Syst.* 32, 251-272.

HENDRIKS, T., VREUGDENHIL, D., & STIEKEMA, W., 1991. Patatin and four serine protease inhibitor genes are differently expressed during potato tuber development. *Plant Mol. Biol.* 17, 385-394.

JACKSON, S.D., JAMES, P., PRAT, S., & THOMAS, B., 1998. Phytochrome B affects the levels of a graft-transmissible signal involved in tuberization. *Plant Physiol.* 117, 29-32.

JACKSON, S.D., 1999. Multiple signalling pathways control tuber induction in potato. *Plant Physiol.* 119:1-8.

KAHN, B.A., EWING, E.E., & SENESAC, A.H., 1983. Effects of leaf age, leaf area, and other factors on tuberization of cuttings from induced potato (*Solanum tuberosum* L.) shoots. *Canadian J. Bot.* 61, 3193-3201.

KIM, S.J., HAHN, E.J., HEO, J-W., PAEK, K.Y., 2004. Effects of LEDs on net photosynthetic rate, growth and leaf stomata of chrysanthemum plantlets in vitro. *Sci. Hort.* 101, 143-151.

KLEINGELD, C.F., HAMMES, P.S., & BEYERS, E.A., 1996. Die invloed van knol grootte en plantestand op die opbrengspotensiaal van miniknolle in Suid-Afrika In: Aartappelkortkursus, Roodeplaat Instituut vir groente en sierplante. pp 10-15.

KODA, Y., KIKUTA, Y., TAZAKI, H., TSUJINO, Y., SAKAMURA, S., & YOSHIHARA, T., 1991. Potato tuber-inducing activities of jasmonic acid and related compounds. *Phytochem.* 30, 1435-1438.

KOOMAN, P.L., FAHEM, M., TEGERA, P., & HAVERKORT, A.J., 1996a. Effects of climate on different potato genotypes 1. Radiation interception, total and tuber dry matter production. *European J. Agron.* 5, 207-217.

KOOMAN, P.L., FAHEM, M., TEGERA, P., & HAVERKORT, A.J., 1996b. Effects of climate on different potato genotypes 2. Dry matter allocation and duration of the growth cycle. *European J. Agron.* 5, 207-217.

KRAUSS, A., & MARSCHNER, H., 1982. Influence of nitrogen, day length and temperature on contents of gibberellic and abscisic acid and on tuberization in potato plants. *Potato Res*. 25, 13-21.

KUMAR, D., & WAREING, P.F. 1973. Studies on tuberization in *Solanum andigena*. I. Evidence for the existence and movement of a specific tuberization stimulus. *New Phytol.* 72, 283-287.

KUREPIN, L.V., SHAH, S., & REID, D.M., 2007. Light quality regulation of endogenous levels of auxin, abscisic acid and ethylene production in petioles and leaves of wild type and ACC deaminase transgenic *Brassica napus* seedlings. *Plant Growth Regul.* 52, 53-60.

LI, S., RAJAPAKSE, N.C., YOUNG, R.E., & OI, R., 2000. Growth responses of chrysanthemum and bell pepper transplants to photoselective plastic film. *Sci. Hort*. 84, 215-225.

LOMMEN, W.J.M., & STRUIK, P.C., 2006. Tuber induction and initiation during production and early field growth of transplants from *in-vitro* derived potato plants. *Ann. Appl. Biol.* 149, 281-290.

LOPEZ-JUEZ, E., KOBAYASHI, M., SAKURAI, A., KAMIYA, Y., & KENDRICK,R.E., 1995. Phytochrome, gibberillins and hypocotyl growth. *Plant Physiol.* 107, 131-140.

LORENZEN, J.H., & EWING, E.E., 1992. Starch accumulation in leaves of potato (*Solanum tuberosum* L.) during the first 18 days of photoperiod treatment. *Ann. Bot*., 69, 481-485.

MACKERRON, D.K.L., & JEFFERIES, R.A., 1986. The influence of early soil moisture stress on tuber numbers in potato. *Potato Res.* 29, 299-312.

MENZEL, C.M., 1983. Tuberization in potato (*Solanum tuberosum* cultivar Sebago) at high temperature: interaction between shoot and root temperatures. *Annu. Bot*. 52, 65-70.

MENZEL, C.M., 1985. Tuberization of potato under high temperatures: Interaction between temperature and irradiance. *Ann. Bot*. 55, 35-39.

MIDMORE, D.J., 1990. Influence of temperature and radiation on photosynthesis, respiration and growth paramaters of the potato. *Potato Res.* 33, 293-294.

MIDMORE, D.J., BERRIOS, D., & ROCA, J., 2003. Potato (*Solanum* spp.) in the hot tropics V. Intercropping with maize and the influence of shade on tuber yields. *Field crops res*. 18, 159-176.

MIDMORE, D.J., & PRANGE, R.K., 1992. Growth responses of two *Solanum* species to contrasting temperatures and irradiance levels: relations to photosynthesis, dark respiration and chlorophyll fluorescence. *Ann. Bot.* 69, 13-20.

MORGAN, D.C., & SMITH, H., 1979. A systemic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145, 210-212.

MULLER-ROBER, B., SONNEWALD U., & WILLMITZER, L., 1992. Inhibition of the ADP-glucose pyrophosphorylase in transgenic potatoes leads to sugar-storing tubers and influences tuber formation and tuber storage protein genes. *EMBO Journal* 11, 1229-1238.

MURAKAMI, K., CUI, H., KIYOTA, M., YAMANE, T., & AIGA, I., 1996a. The effects of covering materials for greenhouses to control plant growth by changing spectral distribution of daylight. *Acta Hort.* 435, 123-130.

MURAKAMI, K., CUI, H., KIYOTA, M., TAKEMURA, Y., OI, R. & AIGA, I., 1996b. Covering materials to control plant growth by modifying the spectral balance of daylight. *Plasticulture* 110, 2-14.

MURO, J., DIAZ, V., GONI, J.L., & LAMSFUS, C., 1997. Comparison of hydroponic culture and culture in peat/sand mixture and the influence of nutrient solution and plant density on seed potato yields. *Potato Res.*40, 431-438.

NATIONAL DEPARTMENT OF AGRICULTURE, 2003. Food pricing monitoring committee, Final Report. Available online at http://www.nda.agric.za/docs/fpmc/part4_chapter_8.pdf Accessed on 15 September 2007.

NAUK, C.S., & LANGILLE, A.R., 1978. Physiology of tuberization in *Solanum tuberosum* L. *Cis*-Zeatin in the potato plant: Is identification and changes in endogenous levels influenced by temperature and photoperiod. *Plant Physiol,* 62, 438-443.

NICHOLS, M.A. 2005. Aeroponics and potatoes. *Acta Hort.* 670, 201-206.

NYENDA, A.B., SCHITTENHELM, S., MIX-WAGNER, G., & GREEF, J.M., 2005. Yield and canopy development of field grown potato plants derived from synthetic seeds. *Europ. J. Agronomy* 22, 175-184.

O'BRIEN, P.J., ALLEN, E.J., & FIRMAN, D.M., 1998. A review of some studies into tuber initiation in potato (*Solanum tuberosum*) crops. *J. Agric. Sci.* 130, 251-270.

OLSEN, J.E., JENSEN, E., JUNTTILA, O., & MORITZ, T. 1995. Photoperiodic control of endogenous gibberillins in seedlings of *Salix pentandra*. *Physiol. Plant.* 93, 639-644.

OPARKA, K.J., & DAVIES, H.V., 1985. Translocation of assimilates within and between potato stems. *Ann. Bot.* 56, 45-54.

PALMER, C.E., & SMITH O.E., 1999. Cytokinins and tuber initiation in the potato *Solanum tuberosum* L. *Nature* 221, 279-280.

PAUL, M.J., & FOYER, C.H., 2001. Sink regulation of photosynthesis. *J. Exp. Bot.*. 52, 1383-1400.

PIERIK, R., VISSER, E.J.W., DE KROON, H., VOESENEK, L.A.C.J., 2003. Ethylene is required in tobacco to successfully compete with proximate neighbours. *Plant Cell Environ.* 26, 1229-1234.

PIETERSE, B.J., & NEL, J.J., 1999. Die invloed van fisiologiese ouderdom van aartappelmoere en plantestand op die opbrengs van aartappels . In:Handleiding vir aartappelverbouing in Suid-Afrika. pp 14-24.

PONS, T.L., & BERGKOTTE, M., 1996. Nitrogen allocation in response to partial shading of a plant: possible mechanisms. *Physiol Plant.* 92, 636-644.

POWLES, S.B., 1984. Photoinhibition of photosynthesis induced by visible light. *Annu. Rev. Plant Physiol.* 35, 14-44.

PRUSKI, K., ASIEDU, S., PRANGE, R., DANIELS-LAKE, B., & NOWAK, J., 2003. Tuber size control in Shepody and Russet Burbank potatoes via modification of seed tuber storage conditions. Acta Hort. 619, 351-369

QUARRIE, S.A., 1982. Droopy: a wilty mutant of potato deficient in abscicic acid. *Plant Cell Environ.* 5, 23-26.

REID, D.M., CLEMENTS, J.B., & CARR, D.J., 1968. Red light induction of gibberellin synthesis in leaves. *Nature*, 217, 580-582.

REUST, W. 1986. EAPR working group physiological age of the potato. *Potato Res.* 29, 268-271.

REUVENI, R., & RAVIV, M., 1997. Control of downy mildew in greenhouse-grown cucumbers using blue photoselective polyethylene sheets. *Plant Dis.* 81, 999-1004.

REYNOLDS, M.P., & EWING, E.E., 1989. Effects of high air and soil temperature stress on growth and tuberization in *Solanum tuberosum*. *Ann. Bot.*. 64, 241-247.

RICH, A.E., 1983. In: Potato diseases. Academic Press, New York.

RITTER, E., ANGULO, B., RIGA, P., HERRAN, C., RELLOSO, J., & SAN JOSE, M., 2001. Comparison of hydroponic and aeroponic cultivation systems for the production of potato minitubers. *Potato Res.* 44, 127-135.

ROITSCH, T., & EHNEB, R., 2000. Regulation of source/sink relations by cytokinins. *Plant Growth Reg.* 32, 359-367.

SALE, P.J.M., 1974. Productivity of vegetable crops in a region of high solar input. III. Carbon balance of potato crops. *Aust. J. Plant Physiol.* 1, 283-296.

SALE, P.J.M., 1976. Effect of shading at different times on the growth and yield of the potato. *Aust. J. Agric. Res.* 27, 557-566.

SALE, P.J.M., 1979. Growth of potatoes (*Solanum tuberosum* L.) to the small tuber stage as related to the soil temperature. *Aust. J. Agric. Res.* 30, 667-675.

SALISBURY, F.J., HALL, A., GIERSON, C.S., & HALLIDAY, K.J., 2007. Phytochrome coordinates *Arabidopsis* shoot and root development. *The Plant Journal* 50, 429-438

SARQUIS, J.I., GONZALEZ, H., & BERNAL-LUGO, I., 1996. Response of two potato clones (S tuberosum L.) to contrasting temperature regimes in the field. *Am. Potato Res.* 73, 285-300.

SATTELMACHER, B., MARSCHNER, H., & KUHNE, R., 1990. Effects of the temperature of the rooting zone on the growth and development of roots of potato (*Solanum tuberosum*). *Ann. Bot.* 65, 27-36.

SEABROOK, J.E.A., & DOUGLAS, L.K., 1998. Prevention of stem growth inhibition and alleviation of intumescence formation in potato plantlets *in vitro* by yellow filters. *Amer. J. of Potato Res.* 75, 219-224.

SCHULZ, S., WELLS, G.J., BANIYA, B.K., BARAKOTI, T.P., KHAREL, G., SAHA, B., THAPA, B.V., & OJHA, D.N., 1998. Decentralized on-farm seed potato production from pre-basic minitubers: A case study from Nepal. *Expl Agric.* 34, 487-495.

SIMKO, I., 1994. Sucrose application causes hormonal changes associated with tuber induction. *J. Plant growth regul.*13, 73-77.

SMITH, H., 1982. Light quality, photoreception, and plant strategy. *Ann Rev. Plant Physiol.* 33, 481-518.

SMITH, H., 1995. Physiological and ecological function with in the phytochrome family. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 46, 289-315.

SMITH, H., & HOLMES, M.G., 1977. The function of phytochrome in the natural environment: III. Measurement and calculation of phytochrome photoequilibrium. *Photochem and photobiol.* 25, 547-550.

SMITH, H., & WHITELAM G.C., 1990. Phytochrome, a family of photoreceptors with multiple physiological roles. *Plant Cell Environ.* 13, 695-707.

STEYN, P.J., 1999. Die herkoms en groeistadiums van die aartappelplant. In: Handleiding vir aartappelverbouing in Suid-Afrika. pp 2-6.

STITT, M., 1991. Rising the carbon dioxide levels and their potential significance for carbon flow in photosynthetic cells. *Plant cell env.* 14, 741-762.

Statistics South Africa : LEHOHLA, P., 2002. Report on the survey of large and small scale agriculture. Available online at http://www.statssa.gov.za/publications/LargeSmallScaleAgri/LargeSmallScaleAgri.pdf Accessed on 16 September 2007.

STRUIK, P.C., 2006. Trends in agricultural science with special reference to research and development in the potato sector. *Potato Res.* 49, 5-18.

STRUIK, P.C., & VAN VOORST, G., 1986. Effects of drought on the initiation, yield, and size distribution of tubers of *Solanum tuberosum* L. cv. Bintje. *Potato Res.* 29, 487-500.

STRUIK, P.C., & WIERSEMA, S.G., 1999. Control and manipulation of physiological seed tuber quality. In: Seed potato technology. Wageningen pers. pp95-131.

STRUIK, P.C., GEERRTSEMA, J., & CUSTERS, C.H.M.G., 1989. Effects of shoot, root and stolon temperature on the development of the potato (*Solanum tuberosum* L.) plant. III. Development of tubers. *Potato Res.* 32, 143-150.

STRUIK, P.C., HAVERKORT, A.J., VREUGDENHIL, D., BUS, C.B., & DANKERT, R., 1990. Manipulation of tuber-size distribution of a potato crop. *Potato Res.* 33, 417-432.

STUTTLE, G.W., YORIO, N.C., & WHEELER, R.M., 1996. Interacting effects of photoperiod and photosynthetic photon flux on net carbon assimilation and starch accumulation in potato leaves. *J. Am. Soc. Hortic. Sci.* 121,264-268

TAYLOR, A.R., & ASSEMANN S.M., 2001. Apparent absence of a redox requirement for blue light activation of pump current in broad bean guard cells. *Plant Physiol.* 125, 329-338.

TAIZ, L., & ZEIGER, E., 2002. Plant physiology, 3rd edn. Sinauer Associates, Sutherland, MA.

THERON, D.J., & PIETERSE, B.J., 1999. Moerkwaliteit en faktore wat dit beinvloed. In: Handleiding vir aartappelverbouing in Suid-Afrika. pp 7-13.

THIART, S., 2004. Maxi growers for mini tubers. *Chips* November/Desember, 35-40.

THORTON, M.K., MALIK, N.J., & DWELLE, R.B., 1996. Relationship between leaf gas exchange characteristics and productivity of potato clones grown at different temperatures. *Am. Potato J.* 73, 63-77.

VANDENBUSSCHE, F., PIERIK, R., MILLENAAR, F.F., VOESENEK, L.A., & VAN DER STRAETEN, D., 2005. Reaching out of the shade. *Cur. Opin. Plant Biol.* 8, 462-468.

VAD DER ZAAG, D.E., & VAN LOON, C.D., 1987. Effect of physiological age on growth vigour of seed potatoes of two cultivars. 5. Review of literature and integration of some experimental results. *Potato Res.* 30, 452-472.

VREUGDENHIL, D., and SERGEEVA, L.I., 1999. Gibberellins and tuberization in potato. *Potato Res.* 42,471-481.

WALWORTH, J.L., CARLING, D.E., 2002. Tuber initiation and development in irrigated and non-irrigated potatoes. *Am. J. potato Res. 79, 387-395.*

WALTERS, R.G., 2005. Towards an understanding of photosynthetic acclimation. *J. Exp. Bot.* 56, 435-447.

WALTERS, R.G., SHEPHARD, F., ROGERS, J.J.M., ROLFE, S.A.,& HORTON, P., 2003. Identification of mutants of *Arabidopsis* defective in acclimation of photosynthesis to the light environment. *Plant physiol.* 131, 472-481.

WARPEHA, K.M., & KAUFMAN, L.S., 1989. Blue light regulation of epicotyl elongation in *Pisum sativus*. *Plant Physiol.* 89, 544-548.

WHEELER, R.M., TIBBITS, W., & NAJAR, A., 1986. Interactions of irradiance, temperature, and CO_2 in growth and tuberization of potato. *Hort. Science* 21, 741.

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

XU, X., VAN LAMERREN, A.A., VERMEER, E., & VREUGDENHIL, D., 1998. The role of gibberellin, abscicic acid and sucrose in the regulation of potato tuber formation *in vitro*. *Plant Physiol.* 117, 575-584.

ZHENGQIAN, Y., HUANG, L., BELL, R.W., & DELL, B., 2003. Low root zone temperature favours shoot B partitioning into young leaves of oilseed rape (*Brassica napus*). *Physiol. Plant*. 118, 213-220.

CHAPTER 2

The effect of light intensity on the growth, tuber formation and tuber dormancy of potato (*Solanum tuberosum* L.) during the production of G0 minitubers

ABSTRACT

In South Africa an accelerated production of seed potatoes is achieved through the production of minitubers from tissue cultured plantlets in the greenhouse, but current yields for minituber production are relatively low. As commercial growers start to prefer earlier generation seed, G0 minituber production systems need to be re-evaluated in order to maximize yields.

Plantlets of two South-African cultivars, BP1 and VanderPlank, raised in tissue culture, were grown in a closed greenhouse with an evaporative cooling system. Different shade treatments (plants covered by 20%, 40% and 50% shade nets) were compared to an un-shaded control to asses the effect of light intensity on plant growth, tuber induction and growth, and biomass accumulation as well as assimilate distribution between the plant parts. Tubers were harvested and evaluated twelve weeks after planting. Decreasing light intensity levels caused an increase in plant height and shoot dry mass, while tuber fresh mass was only reduced under the 50% shade treatment. A greater percentage of the total biomass was distributed to the shoots under the lower light intensities. The dry matter percentage of the shoots and tubers were reduced by a decrease in light intensity. The total number of tubers was not affected by the shade treatments, but VanderPlank had significantly more tubers weighing more than 40 g compared to BP1. The duration of dormancy and the number of sprouts formed were not affected by the light intensity during crop growth but were determined by cultivar and tuber size.

These results indicated that light intensity in the greenhouse is an important factor affecting potato tuber yield and tuber size distribution and should be considered when producing minitubers in the greenhouse. Some shading will be beneficial but care should be taken not to lower the light intensity to the point were the harvest index becomes too low.

INTRODUCTION

Potatoes contributed to approximately 47% of the total gross value of vegetables produced in South Africa in 2004 (NDA report, 2003). The potato has a high production efficiency and is the most important vegetable product in South Africa (NDA report, 2003). Potato seed production in South Africa makes use of meristem culture, repetitive cycles of nodal cutting and the production of minitubers in a greenhouse to facilitate an increase in the number of individuals of the first year clones. Worldwide the trend is to reduce the number of field plantings as much as possible in order to reduce cost and risk of disease and pests and allowing new or improved cultivars to enter the market soon after development. Fewer field generations will also guarantee a higher tuber health and will be more environmentally friendly, since fewer pesticides will be used.

The potato is a temperate climate crop and high temperatures are associated with lower yields (Morpurgo & Oritz, 1988). Haulm growth is optimal at about 25^0C (Struik & Wiersema, 1999) and tuberization is enhanced at temperatures between 18 and 20^0C. Above 29^0C tuber growth will be completely inhibited (Levy, 1992 as cited by Tekalign & Hammes, 2005).

Temperatures above 25^0C are not uncommon in the minituber greenhouses in South Africa. In order to reduce the temperature, evaporative cooling and shade netting is used although shade netting can lead to a substantial decrease in the amount of light reaching the plants. In hot tropical sites, a reduction in the light intensity during midday or in the afternoon was found to favour tuber yield (Midmore, Berrios & Roca, 2003), suggesting that potato plants are more efficient in converting solar energy into tuber fresh mass when shaded in these hot tropical sites (Midmore *et al.*, 2003).

Along with temperature, light energy plays a dominant role in the regulation of plant growth and development in the greenhouse. Solar radiant energy drives photosynthesis, influences plant morphology and will have an effect on irrigation and fertilization frequency as it affects leaf and air temperature, the rate of evapotranspiration and thus the rate of plant growth (Taiz & Zeiger, 2002).

Low light levels have similar effects on tuber formation as high temperature (Ewing & Struik, 1992). Potato plants grown under low light intensities show evidence of stem elongation, a reduction in total biomass accumulation, reduced tuber mass and a decrease in the percentage of biomass partitioning to the tubers (Gawronska & Dwelle, 1989).

Low light intensities during the day were also shown to decrease the induction to tuberize (Demagante & Van der Zaag 1988) and prolong the tuber induction phase (Ewing & Struik, 1992). Dobranski, Taborti and Ferenczy (1999), found that a high light intensity during the induction phase followed by a period of darkness, can accelerate and synchronize tuberization. According to these authors, a fixed quantity of light illumination is necessary to induce tuberization, beyond which additional light can be unfavourable. Shading during tuber initiation, leads to more biomass being accumulated in the shoots, compared to a higher accumulation of biomass in the tubers when shading occurs during the tuber bulking stage (Chen & Setter, 2003). In a study providing short days for the first 40 days in order to initiate strong tuber sinks, followed by continuous high light conditions (PAR of 52.4 mol m^{-2} day^{-1}) for 92 days to promote tuber bulking, final yields reached 197 t ha^{-1}, twice that of record field yields (Wheeler, 2006). Yield may thus be optimized if strong induction could be combined with high total light during tuber bulking (Wheeler & Tibbits, 1997).

Tests by the United States' National Aeronautics and Space Administration (NASA) to study potato growth and development in controlled environment chambers, demonstrated that greater total light levels could override the tendency in some cultivars to tuberize only under short day conditions (Wheeler, 2006) and tuber yield increased with total irradiance, regardless of photoperiod or other environmental conditions (Wheeler, Tibbits & Fitzpatrick, 1991; Wheeler, 2006). Radiation-use efficiency (RUE) was however found to be negatively related to the light intensity since under high light intensities, a larger part of the foliage will be light saturated and hence less effective for a larger part of the season (Kooman *et al.*, 1996). Accordingly, high light will not be beneficial if the radiation interception is not optimal, in other words a high leaf area index (LAI) for a large part of the season is necessary (Kooman *et al.*, 1996).

The effect of light intensity on tuberization and the relative growth rate is influenced by temperature. Relatively low temperatures (20 – 22^{0}C) in combination with low light intensities (3.4 MJ m^{-2} day^{-1}) will not affect the number of tubers formed, but under high temperatures (28 - 30^{0}C), the same low light levels inhibits tuber formation (Menzel, 1985). A possible hypothesis is that the effect of low light levels will lower photosynthesis, causing reduced sucrose levels. Plants grown in high light intensities have an increased photosynthetic capacity and increased carbon assimilation (Walters, 2005). However, any photosynthesis promoting factor will be

limited in the extent to which it can influence biomass accumulation and yield, by the sink capacity (Paul & Foyer, 2003).

The effect of low light intensity may also be linked to an increased production of growth substances, most likely gibberellins (GA), which inhibit tuberization (Menzel, 1985). High levels of endogenous GA's are associated with increased vegetative growth and the delay or inhibition of tuber formation (Menzel, 1980; Vandam, Kooman & Struik, 1996). Under low light intensities the GA levels in potato leaves increase (Woolley & Wareing, 1972). Tuberization can be induced by blocking GA biosynthesis as happens when applying paclobutrazol (Tekalign & Hammes, 2005). Applying paclobutrazol to potato plants grown under non-inductive conditions, favoured assimilation to the tubers, suppressed excessive vegetative growth, increased tuber size (with a reduction in tuber number), improved tuber quality and extended the tuber dormancy period (Tekalign & Hammes, 2005).

Claassens & Vreugdenhill (2000) found that environmental conditions during crop growth will not only influence tuber initiation, but also tuber dormancy. Potatoes cultivated under short-day conditions have a shorter dormancy period than those cultivated under long day conditions (Claassens & Vreugdenhill, 2000). Shading during tuber growth can also shorten the dormancy period (Struik & Wiersema, 1999). High endogenous levels of GA in the tubers are not only involved in regulating dormancy, but can also affect the accumulation of tuber specific proteins and starch in the tuber (Vreugdenhil & Sergeeva, 1999). High levels of GA in the tuber tissue will reduce the sink strength and thus the specific gravity of the tuber (Booth & Lovell, 1972).

With the growing environmental concern, a trend originated to move away from the use of plant growth regulators and there is a continual interest in searching for ways to reduce the use of chemical growth regulators (Khattak, Pearson & Johnson, 2004). Researchers are increasingly looking at regulating plant growth through altering the environmental stimuli. *In vitro* tuberization has received much attention in this regard (Charles, Rossignol & Rossignol, 1992; Dobranski *et al.,* 1999), but more research on environmental regulation during the greenhouse production phase can uncover methods whereby less chemicals are used that can possibly also benefit plant health and tuber quality.

The objective of this study was to determine the effect of various light intensities on plant growth, tuber formation, dry matter partitioning and tuber dormancy for two commonly used South African cultivars.

Material and Methods

Plant material and production technique

Experiments were conducted in a closed greenhouse with evaporative cooling at Welgevallen, the experimental farm of the University of Stellenbosch, in the Western Cape of South Africa.

Potato (*Solanum tuberosum* L.) plantlets of cultivars BP1 and VanderPlank were used in this study. BP1 is a medium maturing (90 to 110 days) cultivar with a high yield potential and a short dormancy period (50 to 70 days). VanderPlank is an early maturing (70 to 90 days) cultivar, more sensitive to sub-optimal growing conditions, with a dormancy period of 90 to 110 days.

In vitro plantlets obtained from Agricultural Research Council (ARC) Roodeplaat were used. The *in vitro* plantlets were transplanted into troughs, containing a seedling mixture of peat, vermiculite and perlite on 8 September 2006, and allowed to acclimatize in a fully temperature controlled glasshouse at 18/22^{0}C night/day temperatures and a relative humidity (RH) above 60%. The acclimatized plantlets were transplanted in a closed polyethylene covered greenhouse with an evaporative cooling system on 21 September 2006. Pine shavings were used as growing medium and one plantlet was transplanted into each 5L growing bag. The greenhouse is equipped with a fan and pad cooling system, which starts as soon as the temperature reaches 20^{0}C. The midday air temperature inside the greenhouse increased between 20 and 25^{0}C during the start of the growing season to temperatures approaching 30^{0}C near the end of the growing season (Figure 2.1). The temperature in the growth medium was above 25^{0}C for most of the first 4 weeks, but decreased to an average of about 22^{0}C for the remainder of the trial.

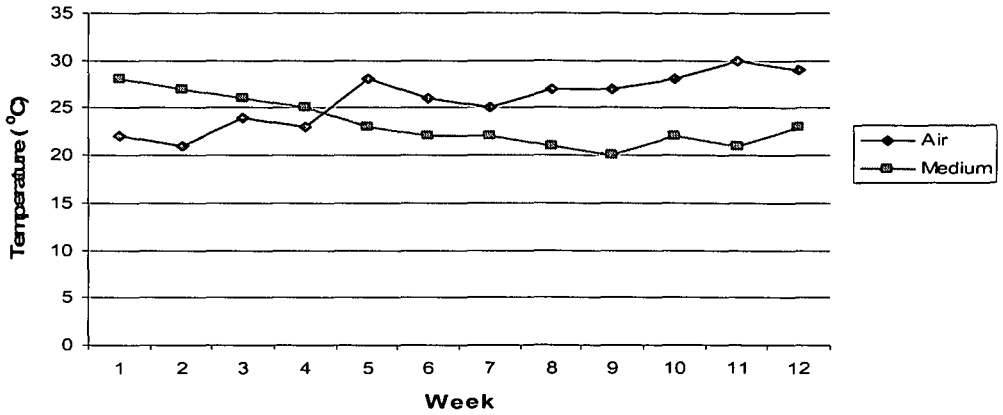


Figure 2.1 Mean weekly air and root zone temperatures for the control measured at midday inside the greenhouse.

A drip fertigation system was used with a standard Steiner nutrient solution (Steiner, 1984) at an Electrical Conductivity (EC) of 1.5 mS cm^{-1} (Table 2.1). The initial irrigation volume per plant was 160 ml per pulse, four times per day. The irrigation volume was adjusted throughout the experiment to ensure drainage of 20%.

Table 2.1 Composition of the standard Steiner nutrient solution used for fertigation at an EC of 1.5 mS cm^{-1}.

Macro nutrients	**Application (g $1000L^{-1}$)**
KNO_3	227.25
K_2SO_4	195.75
KH_2PO_4	102.00
$Ca(NO_3)_2.2H_2O$	675.00
$MgSO_4.7H_2O$	369.00

Micro nutrients	**Application (g $1000L^{-1}$)**
Fe-EDTA	6.60
Boric acid	1.45
NH_4 molybdate	0.10
$MgSO_4$	2.00
$CuSO_4$	0.20
$ZnSO_4$	1.44

Treatments

Shade nets of 20%, 40% and 50% were used, giving an effective shading percentage of 24%, 43% and 52%. To facilitate this, wire structures of 1.6m high and 1m wide were constructed and covered with the shade net. Each structure covered one plant and structures were placed 1.5 m apart to prevent additional shading from neighbouring structures. Plants were placed under the shade nets from the time the plantlets were transplanted into the closed polyethylene covered greenhouse on 21 September 2006 until harvest on 22 December 2006.

Data collected

The pH and EC of the irrigation and drainage water was monitored weekly. Air temperature, growth medium temperature and relative humidity readings were recorded weekly (3 random readings per treatment) with a thermohygrometer (model HI 9161C, Hanna instruments). Photosynthetically Active Radiation (PAR) within the 400 – 700 nm range was measured twice a week outside the greenhouse as well as above and inside the experimental units inside the greenhouse, using a ceptometer (model LP-80 PAR/LAI Ceptometer, AccuPAR). Light intensity in this study refers to these PAR values. Temperature, light intensity and air humidity readings were taken between 13:00 and 14:00. Plant growth characteristics were recorded twice a week and included plant height and internode length. Plant height was measured as the vertical length between the apical growing point of the plant and the growing medium. Internode length was taken as the average of 5 random measurements per plant.

At harvest, plant height and internode length was measured again before determining the fresh mass of the shoots (stems and leaves). Shoots were oven dried at 80^0C for 72 hours before determining the dry mass and shoot dry mass percentage, calculated as the percentage of shoot dry mass to shoot fresh mass. Any swelling of the stolon to twice its diameter was considered a tuber (Ewing & Struik, 1992). Total tuber number and fresh mass were determined per plant and tubers were separated into 7 different size classes according to mass (<5 g, 5-10 g, 10-20 g, 20-40 g, 40-60 g, 60-80 g and >80 g) for all treatments and the number and fresh mass of the tubers in each size class were recorded (Addendum 2.1). For analysis of tuber number and tuber fresh mass per size class only three size classes were used, <20 g, 20-40 g and >40 g since BP1 yielded too few large tubers. The total fresh mass was calculated per plant as the sum of the shoot and tuber fresh mass.

Two tubers from each of two size classes (< 20 g, 20–60 g an >60 g) were selected per treatment combination, and placed in a dark room with daily mean temperature between 17 and 20 ^{0}C to determine the time to sprouting and the number of sprouts developing. Tubers were monitored twice a week to determine the dormancy period. Due to the lack of tubers from cultivar BP1 weighing more than 60 g from the 50 % shade treatment, only two size classes were used for the tuber dormancy study, namely tubers weighing less than 20 g and tubers weighing between 20 and 60 g. The rest of the tubers were cut in pieces and oven dried at 80^{0}C for 72 hours and the dry mass and dry mass percentage, as the percentage of tuber dry mass to tuber fresh mass, was determined.

Experimental design and statistical analysis

The trial was conducted using a completely randomized factorial design with four shading levels and two cultivars. A single plant was considered as an experimental unit and the treatments were replicated four times. Analyses of variance (ANOVA) were performed to test treatment effects on vegetative plant growth, tuber number, mean tuber mass and tuber number and tuber fresh mass per size class using the general linear model procedure of STATISTICA version 7.1 (StatSoft Inc., 2006). Significant levels (Pr >F) of the main effects were calculated at the 5% probability level.

RESULTS

Photosynthetic Active Radiation

The PAR readings showed a steady increase in light intensity over the growing period (Table 2.2). From table 2.2 the greenhouse light transmission was calculated at 72%.

Table 2.2 Average PAR values in μmol m^{-2} s^{-1} as measured at plant level twice a week.

	Outside greenhouse	Un-shaded control	20% shade	40% shade	50% shade
Week 1-4	452.08	319.90	243.83	182.93	155.17
Week 4-8	567.86	412.01	308.41	228.84	196.23
Week 8-12	824.25	586.77	448.31	331.70	284.68

Plant height, internode length, shoot fresh mass, shoot dry mass and shoot dry mass percentage

Results of the Analysis of Variance (ANOVA) done on data with regard to plant growth parameters are summarized in Table 2.3.

Table 2.3 Significant levels (Pr > F) of main effects, namely light intensity and cultivar as well as interactions with regard to plant height (PH), internode length (IL), shoot fresh mass (ShFW), shoot dry mass (ShDW) and the shoot dry mass percentage (ShDW%).

	DF	PH (Pr > F)	IL (Pr > F)	ShFW (Pr > F)	ShDW (Pr > F)	ShDW% (Pr > F)
Light intensity	3	0.000000	0.000000	0.000276	0.011069	0.000003
Cultivar	1	0.000811	0.003810	0.000020	0.000000	0.000114
Light intensity*cultivar	3	0.734471	0.069061	0.725227	0.811333	0.331933

Light intensity and cultivar significantly influenced the plant height, internode length, fresh and dry mass of the shoots and the shoot dry mass percentage (Table 2.3).
There was no significant interaction between light intensity and cultivar on the plant height, internode length, shoot fresh mass, shoot dry mass or shoot dry mass percentage.

Plant height and internode length

Plant height and internode length increased as light intensity decreased (Table 2.4). The difference in plant height and internode length was significant between the unshaded control and all the shaded treatments. Plant height and internode length of the 20 % shading was significantly larger compared to the 40% and 50% treatments, but it did not differ significantly between the 40% and 50% shade treatments (Table 2.4).

Plants of BP1 were significantly higher than plants of VanderPlank (93.38 cm compared to 73.79 cm), while VanderPlank had longer internodes (6.1 cm compared to 5.5 cm for BP1) (Table 2.4).

Table 2.4 Effect of different shading levels and cultivars on the vegetative growth of potato plants.

Treatments	Plant growth parameters				
	Plant height (cm)	**Internode length (cm)**	**Shoot fresh mass (g)**	**Shoot dry mass (g)**	**Shoot dry mass percentage**
Shading %					
0	53.25a	4.13a	530.19a	78.72a	14.7a
20	82.13b	5.81b	702.95ab	83.88a	11.9b
40	103.57c	6.71c	858.44b	105.65b	12.6b
50	102.71c	6.71c	844.74b	96.83ab	11.8b
LSD (P = 0.05)	16.99	0.83	174.58	21.29	1.7
Cultivars					
BP1	93.38a	5.5a	849.07a	112.84a	13.4a
VanderPlank	73.79b	6.1b	585.88b	69.71b	12.0b
LSD (P = 0.05)	8.97	0.44	92.19	11.24	1.1

Means followed by the same letters are not significantly different at the 5% probability level.

Shoot mass

A decrease in light intensity caused an increase in the fresh and dry mass of the shoots but a reduction in the shoot dry mass percentage (Table 2.4).

Shoot fresh and dry mass did not increase significantly when the light intensity was reduced by 20% from the control, but reducing the light intensity by 40% and 50% did lead to a significant increase in shoot fresh mass compared to the control. Shoot dry mass was significantly higher than the control only for the 40% shade treatment, while no significant difference in shoot dry mass was observed between the control, 20 % and 50% shade treatments (Table 4.2).
BP1 had a significantly higher shoot fresh mass, dry mass and dry mass percentage compared to VanderPlank (Table 2.4).

Tuber formation and yield

Results of the ANOVA done on data with regard to tuber formation and yield are summarized in Table 5.

Table 2.5 Significant levels (Pr > F) of main effects, namely light intensity and cultivar as well as interactions with regard to the number of tubers, the tuber fresh mass per plant, total plant fresh mass and tuber dry mass percentage.

	Tuber number (Pr > F)	**Tuber fresh mass** (Pr > F)	**Total fresh mass** (Pr > F)	**Tuber dry mass percentage** (Pr > F)
Light intensity	0.404994	0.020282	0.024746	0.000002
Cultivar	0.614108	0.001066	0.236988	0.000000
Light intensity*cultivar	0.691050	0.970478	0.764967	0.238671

There were no significant interaction between light intensity and cultivar on the tuber number, tuber fresh mass per plant, total plant fresh mass or the tuber dry mass percentage (Table 2.5). Light intensity significantly affected the tuber fresh mass per plant, the total plant fresh mass and the tuber dry mass percentage, while significant cultivar differences in total tuber fresh mass and tuber dry mass percentage were also observed (Table 2.5).

Table 2.6 Effect of different shading levels and cultivars on the tuber number and yield per plant.

Treatments	Tuber formation and yield			
	Tuber number	Tuber fresh mass (g)	Total fresh mass (g)	Tuber dry mass percentage
Shading %				
0	19.88a	537.54ab	1171.5a	19.21a
20	22.63a	678.48a	1500.1b	16.09b
40	16.50a	449.91ab	1353.9ab	15.44b
50	20.04a	310.41b	1176.8ab	14.53b
LSD (P = 0.05)	9.38	291.40	313.06	2.93
Cultivars				
BP1	19.13a	348.76a	1252.6a	14.83a
VanderPlank	20.5a	655.46b	1353.4a	18.21b
LSD (P = 0.05)	4.95	153.88	165.3	1.55

Means followed by the same letters are not significantly different at the 5% probability level.

The total tuber fresh mass per plant generally decreased as the light intensity decreased. Although it was highest under 20% shade, the only significant difference in tuber fresh mass was between the 20% and 50% shade treatments (Table 2.6). The tuber fresh mass of VanderPlank (655.46 g) was significantly higher than that of BP1 (348.76 g) (Table 2.6).

The total fresh mass per plant was significantly higher under the 20% treatment compared to the control, but not significantly different under the 40% and 50% shade treatments which in turn did not differ from the control (Figure 2.6). The total fresh mass was not significantly different between the two cultivars (Table 2.6).

The tuber dry mass percentage decreased as the light intensity decreased with all shade treatments differing significantly from the control, but not from each other (Table 2.6). Tubers from VanderPlank had significantly higher dry mass percentages compared to tubers from BP1 (Table 2.6).

Tuber size distribution

Results from the ANOVA done on data with regard to tuber size distribution are summarized in Table 2.7.

Table 2.7 Significant levels (Pr > F) of main effects, namely light intensity, cultivar and tuber size as well as interactions with regard to the number of tubers in the different size classes and the total tuber mass in the different size classes.

	Tuber number			Tuber fresh mass		
	< 20 g (Pr > F)	20–40 g (Pr > F)	> 40 g (Pr > F)	< 20 g (Pr > F)	20–40 g (Pr > F)	> 40 g (Pr > F)
Light intensity	0.204147	0.584356	0.156966	0.558702	0.636318	0.154945
Cultivar	0.153086	0.394624	0.032690	0.247637	0.369294	0.009962
Light intensity*cultivar	0.350630	0.877603	0.863568	0.161196	0.874717	0.756161

There was no significant interaction between light intensity and cultivar for tuber number per size class or total fresh mass per size class (Table 2.7). Light intensity did not significantly affect the number of tubers per size class or the fresh weight per size class and the number of tubers per size class and tuber fresh mass per size class was only significantly different between the cultivars for tubers weighing more than 40 g (Table 2.7).

For tubers weighing more than 40 g, VanderPlank had a higher total fresh mass and a higher number of tubers than BP1 (Figure 2.2). The average fresh mass per tuber for tubers weighing more than 40 g was 58.88 g for BP1 and 84.80 g for VanderPlank.

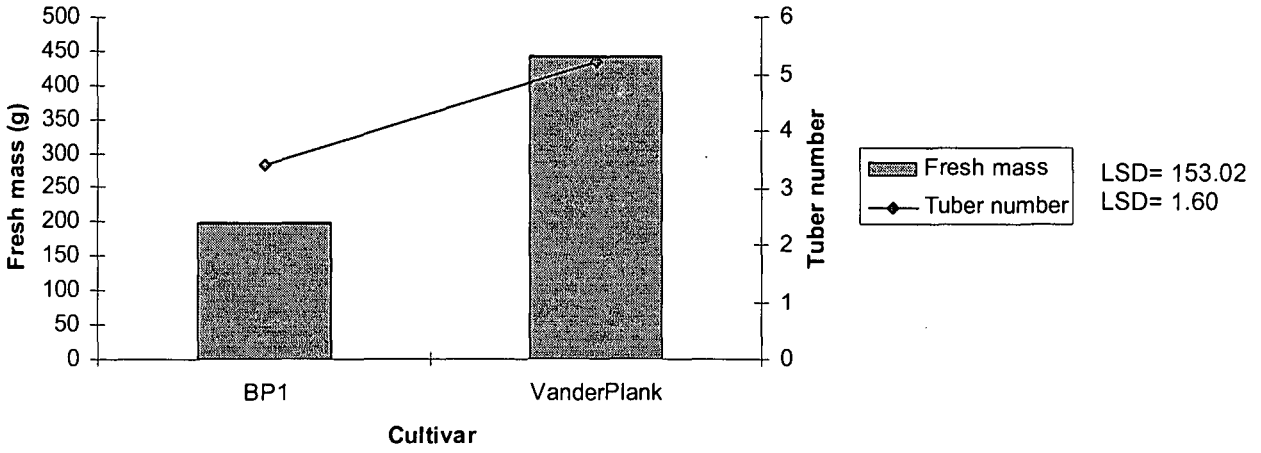


Figure 2.2 The fresh mass and tuber number for tuber weighing more than 40 g for cultivars BP1 and VanderPlank.

Tuber dormancy

Results of the ANOVA done on data with regard to tuber dormancy are summarized in Table 2.8.

Table 2.8 Significant levels (Pr > F) of main effects, namely light intensity, cultivar and tuber size as well as interactions with regard to the dormancy duration and number of sprouts developed.

	Dormancy duration		Sprout formation	
	< 20 g (Pr > F)	20–40 g (Pr > F)	< 20 g (Pr > F)	20–40 g (Pr > F)
Light intensity	0.198538	0.129927	0.677966	0.801809
Cultivar	0.000011	0.000000	0.289672	0.080516
Light intensity*cultivar	0.198538	0.204399	0.677966	0.595719

The duration of tuber dormancy and the number of sprouts formed after 150 days were not significantly influenced by any interactions between light intensity and cultivar (Table 2.8). Cultivar differences with regards to the dormancy period were apparent for tubers weighing less than 20 g and between 20 and 60 g (Table 2.8).

The number of sprouts that developed differed significantly between the cultivars only for tubers weighing between 20 and 60 g (Table 2.8).

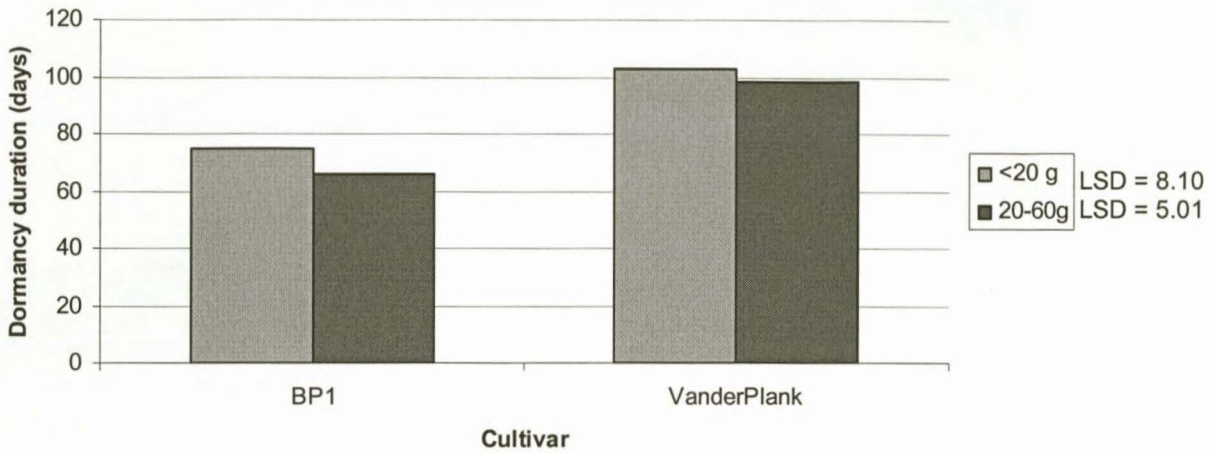


Figure 2.3 The difference in time to dormancy break for tubers weighing less than 20 g and between 20 and 60 g for cultivars BP1 and VanderPlank.

Although not significant, tubers of BP1 weighing between 20 and 60 g tended to develop more sprouts than tubers of VanderPlank in the same size class.

DISCUSSION

Results from this study indicated that on average shading can increased plant height (Table 2.4). Shade-avoiding plants will allocate more resources to extension growth in order to acquire more light when shaded (Taiz & Zeiger, 2002). Internode expansion is however usually at a cost to leaf area and branching. Shaded leaves are typically thinner with lower specific leaf areas and lower carbon exchange rates per unit leaf area (Ewing & Struik, 1992). The most important role of light in plant growth is as energy supplier for carbon assimilation through photosynthesis. Under low light intensities a reduction in the rate of photosynthesis can be expected, decreasing sucrose levels and lowering final yields. Gawronska & Dwelle (1989) found that for the potato shading during plant growth favoured vegetative growth but reduced total biomass accumulation, reduced tuber mass and decreased the

percentage of biomass partitioning to the tubers. Results from this study demonstrated that shoot mass increased to more than 800 g under the 40% and 50% shade treatments, compared to 530 g for the control plants (Table 2.4), but tuber number averaged 20 tubers per plant for all treatments (Table 2.6). Total plant fresh mass and tuber fresh mass tended to increase under the 20% shade and this contributed resulted in the biomass being relatively equally distributed between the shoots and tubers. The 40 and 50% shade tended towards a decrease in tuber fresh mass, while the total plant fresh mass did not differ from the control (Table 2.6). This resulted in a greater percentage of the total biomass being allocated to the shoots under 40% and 50% shade, and thus a decrease in the harvest index. Shading of 20% would thus not have a negative impact on the potato plants' growth, net assimilation or distribution of biomass within the plant and might in fact have resulted in adaptations both morphological (like the increase in internode length) and biochemical, so that the area for light interception as well as the efficiency of light utilization is increased as is common for shaded plants (Barbour, Burk & Pitts, 1987). By decreasing the light intensity even further, these adaptations could probably not increase the rate of carbon assimilation enough to offset the high rate of photorespiration, which would have been present at the high temperatures present in the greenhouse (Figure 2.1).

The dry mass percentage as the ratio of dry mass to fresh mass, of both shoots and tubers were lower for all shade treatments compared to the control (Table 2.4 & Table 2.6). The decrease of between 15 and 20% in the shoot dry mass percentage could indicate that the transpiratory moisture loss was less for plants grown under shade, possibly due to a reduction in air temperature although recorded temperature readings under the different shade treatments did not differ. The higher dry mass percentage (14.7% for control plants compared to a mean of 12% for the shade treatments) of the shoots in the higher light intensity (Table 2.2) of the control could in addition be in part accounted for by the higher turnover of leaves. High light intensities increased the growth rate and thus earlier senescence of older leaves. Rapid growth of sink organs can also compete with leaves for remobilizable nitrogen, which could lead to leaf senescence (Salisbury & Ross 1992), Furthermore, the higher dry mass percentage of the shoots of plants grown under higher light intensities could also be caused by higher levels of photosynthesis in combination with the accumulation of starch in the leaves, which has been observed when the source activity is higher than the sink activity (Stutte *et al.*, 1996). The sink activity

could have been suboptimal due to the high air temperatures in the greenhouse that can reduce the tuber growth rate (Vandam *et al.*, 1996). Tuber yield and plant dry mass is greatest under a combination of high irradiance, 550 μmol m^{-2} s^{-1}, and cool temperatures, 16 ^{0}C (Wheeler *et al.*, 1986). According to Menzel (1985) the inhibitory effect of low irradiance on yield can be modulated by other environmental factors, of which high temperature seems to be the most restraining.

The dry mass percentage of the tubers was lower for plants grown under shade, decreasing from 19.21% for the control to 14.53% under the 50% shade treatment (Table 2.6), and could indicate that the accumulation of tuber specific proteins and starch in the tuber was affected by the low light intensity. Low light intensities may thus increase the level of endogenous GAs in the tubers which can decrease the accumulation of tuber specific proteins and starch in the tuber (Vreugdenhil & Sergeeva, 1999).

The light intensity did not affect the number of tubers significantly (Table 2.6), indicating that the light intensity did not necessarily affect the induction to tuberize. Results from this study thus found that under low light intensities the induction to tuberize will not necessarily be affected. Earlier studies in the Philippines did show that low levels of irradiance (26% shading) during the day decreased the induction to tuberize (Demagante & Vander Zaag, 1988). However in Australia, 34% shade had no effect on the timing of tuberization (Sale 1976). Struik (1986) states that low light conditions can cause a delay in stolon initiation and prolong the period of stolon elongation. This could have resulted in the formation of more potential sites for tuberization during this study, possibly explaining why the final number of tubers was not negatively affected under low light intensities.

Tuber number at a mean of 20 tubers per plant over all treatments (Table 2.6) was noticeably higher than what is reported by local producers and abroad (Struik & Wiersema, 1999) using this production system. This may be due to the low plant density, since our experimental units consisted of only one plant per bag. Since light intensity did not significantly affect the number of tubers per plant, but more tubers per plant are produced when a lower planting density is used, it is possible that the number of tubers will be influenced by the light quality rather than the light quantity, since shade from neighbouring plants will lead to a decrease in red light (Vandenbussche *et al.*, 2005)

Light intensity had no effect on the number of tubers in the different size classes or the tuber fresh weight per size class (Table 2.7). This may indicate that neither tuber

initiation nor the rate of tuber bulking was decreased by lowering the light intensity. This is in contract to Menzel (1985) who found that under low light intensity the partitioning of assimilates to tubers decrease even when photosynthesis is not limiting (Menzel 1985).

The two cultivars differed significantly with regard to tuber growth. VanderPlank is an early maturing cultivar and it would be expected to yield larger tubers upon harvest compared to the medium maturing cultivar BP1. This was the case in this study with VanderPlank that had significantly more biomass in tubers weighing more than 40 g than BP1 and the average tuber fresh weight for tubers in this size class was also significantly higher for VanderPlank (Figure 2.2).

The results also indicated that the duration of dormancy and the sprout growth is affected to a greater degree by the cultivar and tuber size than by light intensity during the greenhouse production phase. However, the plant establishment, which was not studied here, might be affected since the tubers from plants grown at lower light intensities had much lower dry mass percentages. Light intensity in the greenhouse may, though indirectly, influence the seed quality through its effect on tuber dry matter content.

Conclusion

Light intensity in the greenhouse during the production of minitubers will have an effect on plant morphology, with low light intensities leading to prolific shoot growth. Tuber number, therefore tuber initiation, was not affected by light intensity, but the harvest index was lower for plants grown under low light levels. The increase in the vegetative growth and decrease in tuber growth, associated with a decrease in light intensity, was perceptible both cultivars BP1 and VanderPlank, although these cultivars differ in their plant growth characteristics. These results indicated that for the cultivars BP1 and VanderPlank, tuber yield was determined by tuber dry matter allocation and not tuber number, as is the case with various other *Solanum* tuber-genotypes (Victorio, Moreno, & Black, 1986).

Tuber yield can be affected by light intensities in the greenhouse and these effects can not be attributed to the effect of light on photosynthesis alone, but light intensity probably also acts as a signal to control the distribution of carbohydrates in the plant, possibly through endogenous plant growth regulators. Therefore shading may

decrease the dry matter concentration of the tubers during the greenhouse production phase although this may need to be explored further as these results may hold considerable value for the potato seed industry.

In production areas with high temperatures, some degree of shading may be beneficial in terms of lowering temperatures without necessarily affecting tuber yields. The excessive foliar growth, which can hinder effective disease control, may however be problematic.

It is possible that in production areas with low light levels and high temperatures during the production cycle, an increase in the light intensity inside the greenhouse may be able to compensate for the inhibitory effect of high temperatures on tuber yield and this must be explored in future studies.

It is necessary to define more exactly and in more physiological terms than 'shading percentage' the light responses of greenhouse grown potato plants. Current experiments do not provide that detail, but the results are valuable for designing experiments to resolve mechanisms for greenhouse light management. Future studies should work towards determining the optimal daily light integral (DLQI) during different growth stages for the greenhouse production of minitubers at the high temperatures experienced locally.

REFERENCES

BALBOUR, M.G., BURK, J.H., & PITTS, W.D., 1987. Environmental factors and photosynthetic response In: Terrestrial Plant ecology 2nd edn. The Benjamin/Cummings Publishing Company. pp366-381.

BOOTH, A. & LOVELL, P.H., 1972. The effect of pre-treatment with gibberellic acid on the distribution of photosynthates in intact and disbudded plants of *Solanum tuberosum*. *New Phytol.* 71,795-804.

BURTON, W.G., 1978. The physics and physiology of storage. In: P.M. Harris (Ed.), The potato crop. Chapman and Hall, London, pp545-606.

CHARLES, G., ROSSIGNOL, L., & ROSSIGNOL, M., 1992. Environmental effects on potato plants *in vitro*. *J. Plant Physiol.* 139(6),708-713.

CHEN, C., & SETTER, T.L., 2003. Response of potato tuber cell division and growth to shade and elevated CO_2. *Ann.Bot.* 91, 373-381.

CLAASSENS, M.M.J., & VREUGDENHIL, D., 2000. Is dormancy breaking of potato tubers the reverse of tuber initiation? *Potato Res.* 43, 347-369.

DEMAGANTE, A.L., & VAN DER ZAAG, P., 1988. The response of potato (*Solanum* spp.) to photoperiod and light intensity under high temperatures. *Potato Res.* 31, 73-83.

DOBRANSKI, J., TABORTI, K.M., & FERENCZY, A., 1999. Light and genotype effects on in vitro tuberization of potato plantlets. *Potato Res* 42, 483-488.

EWING, E.E., & STRUIK, P.C., 1992. Tuber formation in Potato: Induction, Initiation, and growth. *Hortic. Rev.* 14, 89-197.

GAWRONSKA, H., & DWELLE, R.B., 1989. Partitioning of assimilates by potato plants (*Solanum tuberosum* L.) as influenced by irradiance I. Partitioning patterns in cultivar Russet Burbank grown under high and low irradiance. *Am. Potato J.* 66, 201-213.

JACKSON, S.D., 1999. Multiple signalling pathways control tuber induction in potato. *Plant Physiol.* 119:1-8.

KATTAK, A.M., PEARSON, S., & JOHNSON, C.B., 2004. The effect of far red spectral filters and plant density on the growth and development of chrysanthemums. Sci. Hort. 102, 335-341.

KOOMAN, P.L., FAHEM, M., TEGERA, P., & HAVERKORT, A.J., 1996a. Effects of climate on different potato genotypes 1. Radiation interception, total and tuber dry matter production. *European J. Agron.* 5, 207-217.

LEVY, D., 1992. Potato in hot climates-could we do more? In: Proceedings of Advanced Potato Production in the Hot Climates Symposium, 24-28 May 1992, Nahal-OZ, Israel, p3-7.

MENZEL, C.M., 1980. Tuberization in potato (*Solanum tuberosum* cultivar Sebago) at high temperature: response to gibberellin and growth inhibitors. *Ann.Bot.* 46,259-266.

MENZEL, C.M., 1985. Tuberization of potato under high temperatures: Interaction between temperature and irradiance. *Ann. Bot.* 55, 35-39.

MORPURGO, R., & ORITZ, R., 1988. Morphological variation in potato (*Solanum* spp.) under contrasting environments. *Environ. Exp.Bot.* 28,165-169.

NATIONAL DEPARTMENT OF AGRICULTURE(NDA), 2003. Food pricing monitoring committee, Final Report, Chapter 8: The potato supply chain. Available online at http://www.nda.agric.za/docs/fpmc/part4_chapter_8.pdf Accessed on 15 September 2007.

O'BRIEN, P.J., ALLEN E.J., & FIRMAN, D.M., 1998. A review of some studies into the tuber initiation in potato (*Solanum tuberosum*) crops. *J. Agricultural Science, Cambridge.* 130, 251-270.

PAUL, M.J., & FOYER, C.H., 2001. Sink regulation of photosynthesis. *J. Exp. Bot.* 52, 1383-1400 SALE, P.J.M., 1976. Effect of shading at different times on the growth and yield of the potato. *Aus. J. Agr. Res.* 27: 557-566.

SALISBURY, F.B., & ROSS, C.W. 1992. Transport in the phloem. In: Plant Physiology. 4th edn. Wadsworth Publishing Company, Belmont, California. pp 161 - 187.

StatSoft, Inc. (2006). STATISTICA (data analysis software system), version 7.1. www.statsoft.com.

STEINER, A.A., 1984. The Universal nutrient solution. Proc. Int. Soc. Soilless Culture, 633-649.

STRUIK, P.C., 1986. Effects of shading during different stages of growth and development, yield and tuber size distribution of Solanum tuberosum L. Am. Potato . 63, 457. (Abstr.)

STRUIK, P.C., & WIERSEMA, S.G., 1999. Control and manipulation of physiological seed tuber quality. In: Seed potato technology. Wagenin the Netherland, Wagenin pers. Pp95-31.

STUTTE, G.W., YORIO, N.C., WHEELER, R.M., 1996. Interacting effects of photoperiod and photosynthetic photon flux on net carbon assimilation and starch accumulation in potato leaves. *J. Am. Soc. Hort. Sci.* 121, 264-268.

TAIZ, L., & ZEIGER, E., 2002. Plant physiology, 3rd edn. Sinauer Associates, Sutherland, MA.

TEKALIGN, T., & HAMMES, P.S., 2005. Response of potato to paclobutrazol and manipulation of reproductive growth under tropical conditions. Ph.D. Thesis, University of Pretoria, Pretoria, South Africa.

VANDENBUSSCHE, F., PIERIK, R., MILLENAAR, F.F., VOESENEK, L.A., & VAN DER STRAETEN, D., 2005. Reaching out of the shade. *Cur. Opin. Plant Biol.* 8, 462-468.

VANDAM, J., KOOMAN, P.L., & STRUIK, P.C. 1996. Effects of temperature and photoperiod on early growth and final number of tubers in potato (*Solanum tuberosum* L.) *Potato Res.* 39,51-62.

VICTORIO, R.G., MORENO, U., & BLACK, C.C., 1986. Growth, partitioning, and harvest index of tuber-bearing *Solanum* genotypes grown in two contrasting Peruvian environments. *Plant Physiol.* 82, 103-108.

VREUGDENHIL, D., and SERGEEVA, L.I., 1999. Gibberellins and tuberization in potato. *Potato Res.* 42,471-481.

WALTERS, R.G., 2005. Towards an understanding of photosynthetic acclimation. *J. Exp. Bot.* 56, 435-447.

WHEELER, R.M., 2006. Potato and human exploration of space: some observations from NASA-sponsored controlled environment studies. *Potato Res.* 49, 67-90.

WHEELER, R.M., & TIBBITS, T.W., 1997. Influences of changes in daylenght and carbon dioxide on the growth of potato. *Ann. Bot.* 79,529-533.

WHEELER, R.M., TIBBITS, T.W., & NAJAR, A., 1986. Interactions of irradiance, temperature, and CO_2 in growth and tuberization of potato. *Hort Science* 21, 741.

WHEELER, R.M., TIBBITS, T.W., & FITZPATRICK, A.H., 1991. Carbon dioxide effects on potato growth under different photoperiods and irradiance. *Crop Sci* 31, 209-1213.

WOOLLEY, D.J., & WAREING, P.F., 1972. Environmental effects on endogenous cytokinins and gibberellin levels in *Solanum tuberosum*. *New Phytol* 71: 1015-1025.

CHAPTER 3

The effect of light quality on the growth, tuber formation and tuber dormancy of potato (*Solanum tuberosum* L.) during the production of G0 minitubers

ABSTRACT

The effect of excluding light with certain wavelengths on potato was examined in a greenhouse. Two potato (*Solanum tuberosum* L.) cultivars, namely Buffelspoort and Shepody, were grown under a clear cover, a red light absorbing cover (blue cellophane), a blue light absorbing cover (red cellophane) or a far-red light absorbing cover ("Solatrol'). Plant height and internode length increased under the red and blue light absorbing covers while internodes were significantly shorter under the far-red filter. Plants under the red absorbing cover had the highest leaf dry mass, leaf dry mass percentage, stolon mass, tuber number and total tuber mass and most of these tubers fell in the preferred size class of between 20 and 60 g. The tuber fresh mass per plant and tuber number per plant was affected to a greater degree for cultivar Buffelspoort than for Shepody. Under the red absorbing cover a very high percentage of total biomass was allocated to the tubers. A higher leaf dry mass percentage, higher stem : leaf ratio and an increase in stolon growth were observed under the blue absorbing filter. Tuber fresh mass per plant and tuber number per plant was not significantly affected under the blue filter. The most distinctive effect the far-red filter had was a decrease in tuber number but an increase in the average tuber fresh mass. These results indicated that by limiting red light irradiancy, the plants' efficiency in dry matter production, biomass distribution to the tubers and the number of tubers initiated can be increased.

INTRODUCTION

Minituber producers in South Africa produce yearly about 5.6 million certified minitubers in greenhouse space totalling 17 352 m^2 with productivity ranging from 70 tubers m^{-2} harvest $^{-1}$ to 190 tubers m^{-2} harvest $^{-1}$ (Thiart, 2004). *In vitro* plantlets are transplanted into solid media in the greenhouse at high densities to maximize production. The effect of these high planting densities may however affect productivity through the effect on the light environment. Light intensity as well as light quality, or the composition of light from different wavelengths, can affect plant growth, development and physiology through effects on photosynthesis, water and nutrient uptake as well as transport and photomorphogenesis (Taiz & Zeiger, 2002). The excessive shoot growth observed by some minituber producers is most likely an effect of not only light quantity but also the light quality reaching the plants.

Light conditions can lead to modifications in the photosynthetic apparatus enabling plants to acclimatize photosynthetically to the reigning light environment (Walters *et al.,* 2003; Kim *et al.,* 2004). Light quality can also affect stomatal regulation (Taylor & Assemann, 2001) and other processes such as flowering and germination (Taiz & Zeiger, 2002).

The most well known effects of light spectral quality are on plant development through photomorphogenesis. Increasing the red (600-700nm) portion of the light reaching the tissue cultured plantlets, can lead to enlarged leaf areas (Seabrook & Douglas, 1998) and may stimulate the development of the aboveground sink organs (Aksenova *et al.,* 1994), while blue (400-500nm) light activates the development of the underground storage organs (Drozdova *et al.,* 2001). Blue light has been shown to reduce plant height (Warpeha & Kaufman, 1989) and *in vitro* grown potato plantlets grown in a blue light deficient environment are longer and show an increase in haulm fresh- and dry mass (Seabrook & Douglas, 1998). Britz and Sager (1990) demonstrated that under blue light deficient conditions the dry mass percentage of leaves increased due to a reduced amount of translocation of photosynthates out of leaves. Blue light, or a high ratio of blue to UV light, has been effective in inhibiting the sporulation of the phytopathogen that causes downy mildew in greenhouse cucumbers (Reuveni & Raviv, 1997).

A low red to far-red (R:FR) ratio is associated with closed canopy shade where there is a reduction in the red and blue light and an increase in the far-red (FR) light (700-800nm) (Smith, 1982). Green plant parts also reflect FR light, lowering the R:FR light

ratios of light reflected between plants (Ballaré & Casal, 2000). Low R:FR light ratios, enhance stem elongation, reduce branching, accelerate leaf senescence and reduce the rate at witch lateral roots emerge in young seedlings (Balleré & Casal, 2000; Salisbury *et al.,* 2007). For *Brassica napus* seedlings, low R:FR ratios resulted in seedlings with longer petioles and reduced leaf areas (Kurepin, Shah & Reid, 2007). Removing some of the FR light through the use of spectral filters lead to higher R:FR ratios that resulted in the reduction of stem height for chrysanthemum *(Dendranthema x grandiflorum*), bell pepper (*Capsicum annuum* L.) (Li *et al.,* 2000), cucumber (*Cucumis sativus* L.), tomato (*Lycopersicon esculentum* Mill.) and sunflower (*Helianthus annuus* L.) (Murakami *et al.,* 1995; Murakami *et al.,* 1996a; Murakami *et al.,* 1996b). Li *et al.* (2000) suggest that the stage of development might influence the degree to which the filtered light will affect plant height. Dry matter partitioning was affected, suggesting that light quality can affect the translocation of photosynthates (Li *et al.*, 2000).

Light is absorbed by photoreceptors, phytochrome absorbs the red and far-red wavelengths (600 – 750 nm) of the spectrum and chryptochrome absorbs the blue wavelength (400 – 450nm) (Smith 1982). Phytochrome exists in one of two states, Pr the physiological inactive form that is responsible for absorbing red light, and Pfr the far-red light absorbing active form of phytochrome. Upon absorption of red and far-red light, a balance, the phytochrome photoequilibrium (Ø) expressed as the ratio of Pfr to total phytochrome, is formed (Smith & Holmes, 1977), which determines the plants' response. Phytochrome is involved in various morphological and biochemical plant processes, including the photoperiodic response of flowering, shade avoidance and tuberization (Smith & Whitelam, 1990). The *lh* mutant of cucumber deficient in phytochrome B exhibits enhanced stem growth and a decrease in leaf and root growth (Lopéz Juez, 1992). Environments with high red light relative to far-red light result in establishing a high Ø and stem elongation has been found to be inversely related to Ø (Morgan & Smith, 1979).

For the potato, it was shown that after the environmental reception in the leaves, some kind of graft-transmissible signal is relayed to the stolons for the development of tubers (Kumar & Wareing, 1973). Phytochrome B affects the levels of this graft-transmissible factor, involved in inhibiting tuberization since antisense PHYB plants are able to tuberize both under long and short day conditions (Jackson *et al.*, 1998). This could indicate that Ø may also be involved in tuber formation in the potato.

Morphological attributes linked to low R:FR ratios are now known to be mediated by plant growth regulators (Vandenbussche *et al.,* 2005).

Gibberellins (GAs), Abscisic acid (ABA), cytokinins (Cks) and jasmonic acid (JA), are the most likely canditiates for involvement in tuberization (Fernie & Willmitzer, 2001). High endogenous GA levels appear to stimulate shoot growth and inhibit tuberization and are affected by environmental conditions (Simko, 1994; Xu *et al.*, 1998; Amador *et al.,* 2001). Red light is known to stimulate the accumulation of GAs (Reid, Clements & Carr, 1968) and Drozdova *et al.* (2001) found GA contents ten times higher in the aboveground parts of radish plants grown under red compared to blue light. Internode elongation under low R:FR light, is also regulated by gibberellins (Vandenbussche *et al.*, 2005).

Cytokinins play a central role in sink formation (Roitsch & Ehneb, 2000) and the accumulation of cytokinins in the underground parts of potato plants and consequent stimulation of tuber formation is observed in *in vitro* plants under blue light but not under red light (Nauk & Langille, 1978). Many plant responses that are controlled by auxin are also regulated by light, including root growth and development (Salisbury *et al.*, 2007). Phytochrome and auxin signalling are connected, and a recent study showed that phytochrome regulates auxin transport and thereby controls growth and development in Arabidopsis (Salisbury *et al.*, 2007). Ethylene has also been linked to shoot elongation under low R:FR ratios (Pierik *et al.,* 2003).

It thus seems likely that the formation of an underground storage organ is influenced by a morphogenic response to light quality by affecting the biosynthesis or transport of one or more plant growth regulators or by affecting photosynthesis and thereby altering the source-sink relationship. For radish plants the morphogenic responses to light quality was closely related to the distribution of phytohormones between the different plant parts and not to a difference in photosynthetic activity (Drozdova *et al.*, 2001). The FR light reflected by neighbouring plants has been found to alter the pattern of assimilate distribution before photosynthesis is altered through shading (Ballaré & Casal, 2000).

Photoselective greenhouse covering with dyes absorbing light from certain wavelengths are being introduced as a comparatively safer and less expensive method to control plant growth in the greenhouse (Li *et al.,* 2000). The aim of this study was to examine the effect of different light spectral qualities on potato plant morphology, tuber formation and yield and dry matter distribution to ascertain if these photoselective covers could be of value for local minituber production.

Material and Methods

Plant material

Experiments were conducted in a closed greenhouse with evaporative cooling at Welgevallen, the experimental farm of the University of Stellenbosch, in the Western Cape of South Africa. Potato (*Solanum tuberosum* L.) *in vitro* plantlets of the cultivars Shepody and Buffelspoort were obtained from Ceres Potatoes. The *in vitro* plantlets, were transplanted into troughs, containing a seedling mixture of peat, vermiculite and perlite on 15 January 2007 and allowed to acclimatize in a fully temperature controlled glasshouse at 18/22^{0}C night/day temperatures and a relative humidity (RH) above 60% for 14 days. The plantlets were then transplanted to a closed polyethylene covered greenhouse with an evaporative cooling system on 29 January 2007. Pine shavings were used as growing medium and one plantlet was transplanted into each 5L growing bag. The greenhouse is equipped with a fan and pad cooling system, which starts as soon as the temperature rises to 20^{0}C. A drip fertigation system was used with a standard Steiner nutrient solution as detailed in Chapter 2, and an electrical conductivity (EC) of 1.5 mS cm^{-1} was maintained The initial irrigation volume per pulse was 160 ml, with a frequency of five times per day. The irrigation volume was adjusted throughout the experiment to ensure drainage of 20%.

Treatments

Round wire structures of 1.6m high and 1m in diameter were constructed and covered with coloured plastic filters filtering out a specific part of the light spectrum reaching the plants. The top and bottom 15 cm was not covered by the film to facilitate some air movement preventing excessive heat and humidity build up. A lid, slightly larger than the cage covered with film and overlaying the gap at the top, ensured that most of the light reaching the plants was filtered (Plate 1). As the aim of this study was to determine the effect on plant growth and tuberization through an altered light environment and not necessarily the complete exclusion of light from certain wavelengths, these structures were deemed sufficient for this study. The control consisted of clear cellophane, blue cellophane was used as red light filter, red cellophane as blue light filter and a commercially available film, 'Solatrol' as the far-red filter. Figure 3.1 shows the transmission spectra of the different films used in this study. The spectral transmissions between 300 and 800 nm for each of the films

were measured on an optical bench using a spectroradiometer as described by Pearson *et al* (1995).

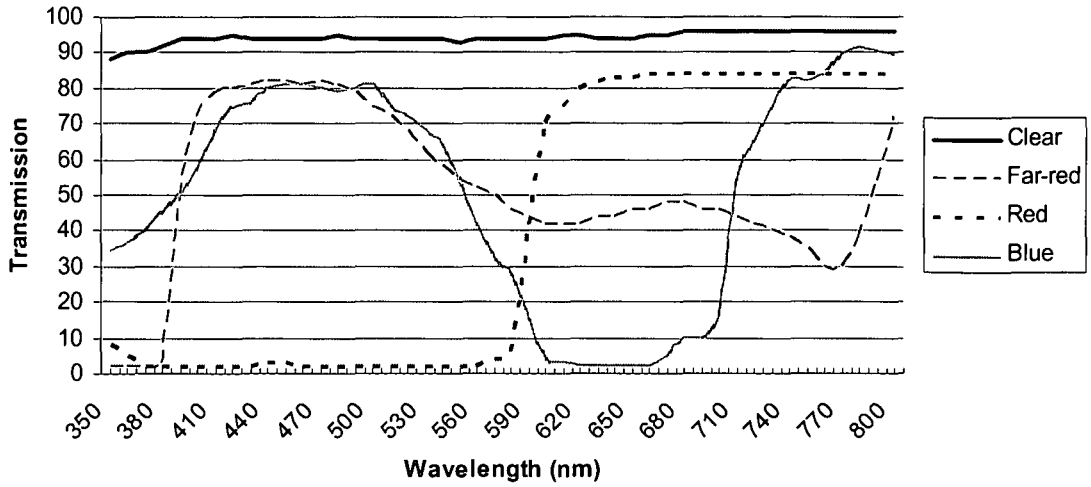


Figure 3.1 Transmission spectra of the clear, red and blue cellophane and the photo-selective film.

Each structure covered two plants and structures were placed 1.5 m apart to prevent additional shading from neighbouring structures. Plants were placed under the colour filters from the time the plantlets were transplanted to the closed polyethylene covered greenhouse on 29 January 2007 until the first harvest on 12 March 2007 and the second harvest on 9 April 2007.

Data collected

The pH and EC of the irrigation and drainage water was monitored weekly to ensure that pH and EC were constant throughout the experiment. Air temperature, medium temperature and relative humidity readings were recorded weekly (3 random readings per treatment) with a thermohygrometer (model HI 9161C, Hanna instruments) but because no significant differences occurred due to the treatments this data was not shown. Temperature and air humidity readings were taken between 13:00 and 14:00. Plant growth characteristics were recorded upon harvest and included plant height and internode length. Plant height was measured as the

vertical length between the apical growing point of the plant and the growing medium. Internode length was taken as the average of 5 random measurements per plant.

Six weeks after plants were transplanted to the greenhouse; one plant per treatment was harvested and separated into leaves, stems, tubers, roots and stolons. Leaf area was measured with a leaf area meter before determining the fresh mass of all the different plant parts separately. Plant tissue was then oven dried at 72 ^{0}C for 3 days. Dry mass percentage of the different plant parts were calculated as the ratio of dry mass to fresh mass for each part. Dry matter distribution was determined from the dry mass of the individual plant parts as a percentage of the total plant dry mass.

At harvest, tuber fresh mass and total number and fresh mass per size class (<20 g, 20-60 g and >60 g) was recorded per plant. Three tubers, weighing between 20 and 25 g from each plant were selected at the second harvest to test the effect of light spectral quality during plant growth on the duration of dormancy. Each treatment of the dormancy test had four replicates and the samples were distributed randomly in a dark room with daily mean temperatures between 17 and 20^{0}C. A sprout of at least 2 mm signified the end of dormancy.

Experimental design and statistical analysis

The trial was conducted using a completely randomized design with four light qualities and two cultivars as factors in a 4x2 factorial experiment. A single plant was considered as an experimental unit and the treatments were replicated four times. Analyses of variance (ANOVA) were performed to test light quality effects on vegetative plant growth, tuber number, mean tuber mass, dry mass distribution between the plant parts, tuber number and tuber mass per size class using the general linear model procedure of STATISTICA (StatSoft Inc., 2006). Significant levels (Pr > F) of the main effects were calculated at the 5% probability level with the Bonferonni test.

Plate 1 Layout and design of trial to determine the effect of filtering light from certain wavelengths on minituber production.

Plate 2 Plants from cultivar Buffelspoort grown under the red filter showing the increase in plant height and internode length.

Plate 3 Plants from cultivar Shepody grown under the blue filter showing the increase in plant height , internode length and leaf area.

Plate 4 The formation of aerial tubers on the stems of cultivar Shepody for plants grown under the far-red filter.

RESULTS

Plant height, internode length, leaf and stem mass

Results of the Analysis of Variance (ANOVA) done on data with regard to plant height, internode length, leaf and stem mass are summarized in Table 3.1.

Table 3.1 Significant levels (Pr > F) of main effects, namely light quality and cultivar for two harvest dates as well as interactions with regard to plant height (PH), internode length (IL), leaf dry mass (LDW), leaf dry mass percentage (LDW%), stem dry mass (SDW) and stem dry mass percentage(SDW%) for both harvest dates.

A First harvest date

	PH	IL	L DW	L DW%	S DW	S DW%
Light quality	0.000000	0.000000	0.000054	0.125254	0.005452	0.012767
Cultivar	0.000000	0.769645	0.055946	0.121435	0.005180	0.000570
Light quality*Cultivar	0.015760	0.000000	0.003590	0.005189	0.000444	0.019319

B Final harvest date

	PH	IL	L DW	L DW%	S DW	S DW%
Light quality	0.000000	0.000000	0.000252	0.000000	0.000000	0.598023
Cultivar	0.007444	0.002241	0.185697	0.169537	0.014409	0.059617
Light quality*Cultivar	0.070988	0.707236	0.282565	0.366645	0.059931	0.498043

First harvest date

For the first harvest date, there was a significant interaction between light quality and cultivar for all the parameters tested (Table 3.1A). Since there were no interactions between light quality and cultivar for the final harvest date (Table 3.1B), it is assumed that these were temporary interactions that occurred due to differences in the early vegetative development stages of the respective cultivars. Interpretation of the results will therefore focus on the significant (Pr > F) main effects of the final harvest. Means from the analysis of variance for the effect of light quality and cultivar on the

vegetative growth parameters for the first harvest date are summarized in Addendum 3.1.

Final harvest date

Light quality had a significant influence on the plant height, internode length, leaf and stem dry mass and leaf dry mass percentage, while plant height, internode length and stem dry mass differed significantly between the two cultivars (Table 3.1B).

Plants under the far-red filter (42 cm) were not significantly shorter than the control plants (43 cm) while plants under the red and blue filters did not differ significantly from each other (82 cm and 83 cm for red and blue respectively) with regard to plant height but they were almost twice the height of the control plants and plants under the far-red filter (Table 3.2).

Internode length was significantly different for all light quality treatments with the shortest internodes for plants under the far-red filter (2.42 cm), followed by the control plants (3.00 cm), plants under the blue filter (5.25 cm) and lastly the internodes of the plants under the red filter (6.16 cm) (Table 3.2).

The leaf dry mass and leaf dry mass percentage was significantly higher for plants under the red filter than for plants from other light quality treatments. For leaf dry mass percentage, the control did not differ significantly from plants under the blue filter, but both treatments were significantly lower than that of plants grown under the far-red and red filter (Table 3.2).

Stem dry mass was significantly lower under the far-red filter (10.86 g) compared to plants under the red and blue filters (13.83 g & 22.96 g respectively), while the stem dry mass of the control (11.73 g) was only significantly lower than that of plants under the blue filter (Table 3.2).

Buffelspoort plants were significantly higher than that of Shepody with significantly longer internodes and had a significantly lower stem dry mass than Shepody, while the stem dry mass percentage was lower, although not significantly (Table 3.2).

Table 3.2 Effect of different light quality and cultivars on the vegetative growth of potato plants for the final harvest date.

Treatments	PH	IL	L DW	L DW %	S DW	S DW %
Light filter						
Control	43.25a	3.00a	19.77a	11.41ad	11.73ab	15.65a
Far-red filter	42.00a	2.42b	19.25a	13.15b	10.86a	15.08a
Red filter	82.88b	6.16c	23.09b	14.50c	13.83b	14.96a
Blue filter	83.25b	5.25d	19.73a	11.07d	22.96c	14.82a
LSD (P = 0.05)	4.12	0.33	2.25	0.70	3.53	1.78
Cultivars						
Shepody	61.31a	4.06a	20.85a	12.41a	16.03a	15.58a
Buffelspoort	64.38b	4.35b	20.07a	12.66a	13.66b	14.68a
LSD (P = 0.05)	2.18	0.17	1.19	0.37	1.86	0.94

Means followed by the same letters are not significantly different at the 5% probability level.

PH = plant height, IL = internode length, L DW = leaf dry mass, L DW% = leaf dry mass percentage, S DW = stem dry mass, S DW% = stem dry mass percentage.

Stem leaf ratio and specific leaf area (SLA)

Results of the Analysis of Variance (ANOVA) done on data with regard to the stem to leaf ratio and ratio of leaf area to leaf dry mass (Specific leaf area (SLA)) are summarized in Table 3.3.

Table 3.3 Significant levels (Pr > F) of main effects, namely light quality and cultivar for two harvest dates as well as interactions with regard to the ratio between stem dry mass and leaf dry mass (S : L) and the ratio of total leaf area to leaf dry mass (SLA) for both harvest dates.

	First harvest date		*Final harvest date*	
	S : L	**SLA**	**S : L**	**SLA**
Light quality	0.000343	0.004836	0.000000	0.000038
Cultivar	0.000087	0.028135	0.098222	0.462049
Light quality*Cultivar	0.002367	0.000414	0.068060	0.508145

First harvest date

For the first harvest date, there was a significant interaction between light quality and cultivar for both S : L and SLA (Table 3.3). Since there were no significant interactions between light quality and cultivar for the final harvest date (Table 3.3), it is assumed that these were temporary interactions that occurred due to differences in the early vegetative development stages of the respective cultivars. Interpretation of the results will therefore focus on the significant (Pr > F) main effects of the final harvest date. Means from the analysis of variance for the effect of light quality and cultivar on the S : L and SLA for the first harvest date are summarized in Addendum 3.2.

Final Harvest date

Light quality had a significant influence on the S : L ratio and the SLA but these parameters did not differ between the cultivars (Table 3.3).

Although not significant there was a trend towards Shepody having higher S : L ratios, except under the far-red filter, where Buffelspoort had a slightly higher S : L ratio compared to Shepody.

Removing far-red light or blue light did not affect the S : L ratio, whereas a removal of blue light caused a significant increase in the S : L ratio (Figure 3.2). Under the blue filter stem mass increased concomitantly to plant height, but not leaf mass, leading to a high S : L ratio. This indicated that the increase in stem mass was proportionally greater than that of the leaves for plants under the blue filter (Figure 3.3) compared to plants from the control and other treatments.

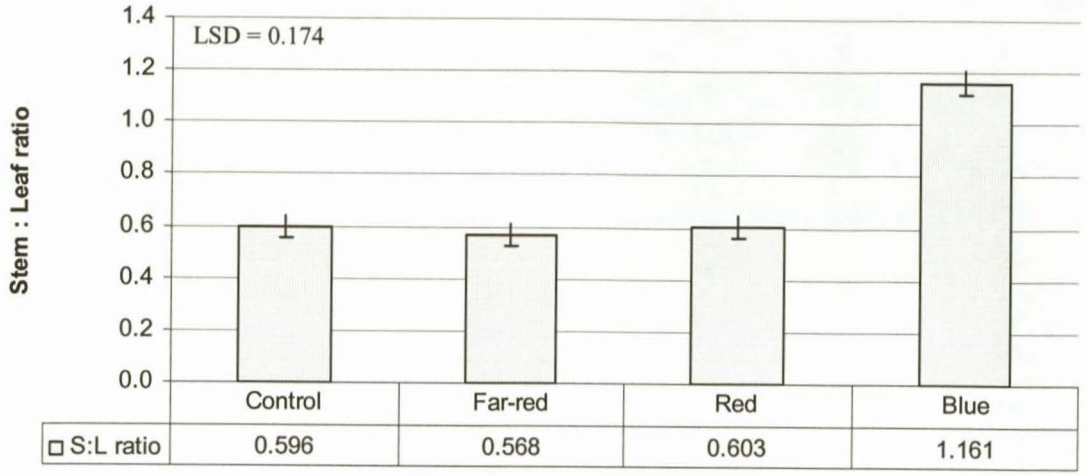


Figure 3.2 The influence of light spectral quality on the stem : leaf ratio, of plants from both potato cultivars combined, at the final harvest.

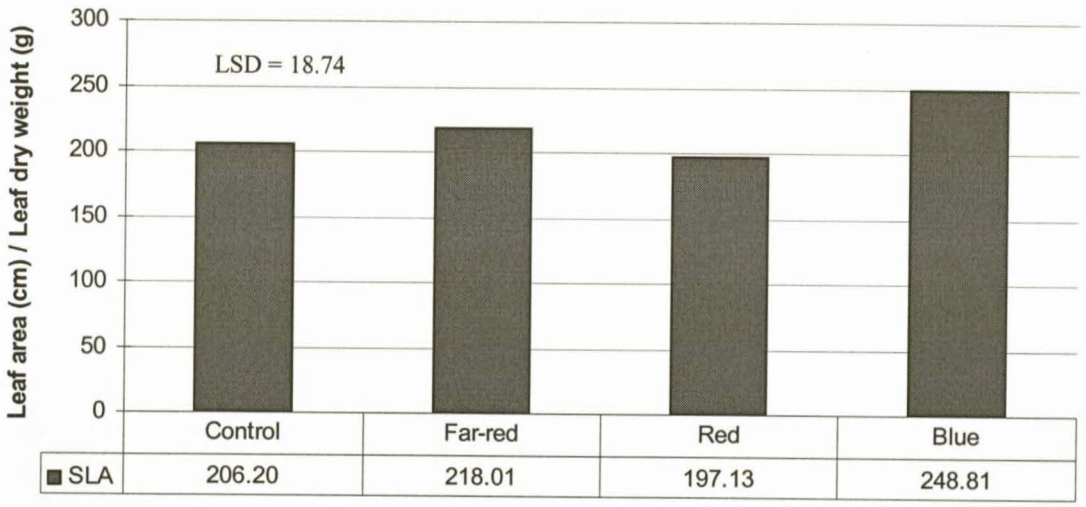


Figure 3.3 The influence of light spectral quality on the specific leaf area (SLA), of plants from both potato cultivars combined, at the final harvest.

The SLA was not significantly affected under the far-red and red filters but was significantly higher under the blue light filter (Figure 3.3). Since the leaf dry mass was not significantly higher under the blue filter this indicated that leaves were thinner and thus had a larger leaf area per leaf dry mass.

Root-, stolon- and tuber mass

Results of the Analysis of Variance (ANOVA) done on data with regard to root-, stolon- and tuber mass are summarized in Table 3.4.

Table 3.4 Significant levels (Pr > F) of main effects, namely light quality and cultivar for two harvest dates as well as interactions with regard to root fresh mass (RFW), root dry mass (RDW), stolon fresh mass (StFW), stolon dry mass (StDW), tuber fresh mass (TFW) and tuber dry mass (TDW).

A First harvest date

	RFW	RDW	StFW	StDW	TFW	TDW
Light quality	0.309157	0.130677	0.000000	0.000000	0.000007	0.000011
Cultivar	0.816813	0.076659	0.000006	0.000000	0.002194	0.003430
Light quality*Cultivar	0.178525	0.093373	0.000691	0.000081	0.021597	0.043322

B Final harvest date

	RFW	RDW	StFW	StDW	TFW	TDW
Light quality	0.043736	0.204825	0.000000	0.000000	0.000038	0.000009
Cultivar	0.780680	0.175080	0.000000	0.000000	0.028195	0.021003
Light quality*Cultivar	0.468102	0.023784	0.000000	0.000000	0.001482	0.001378

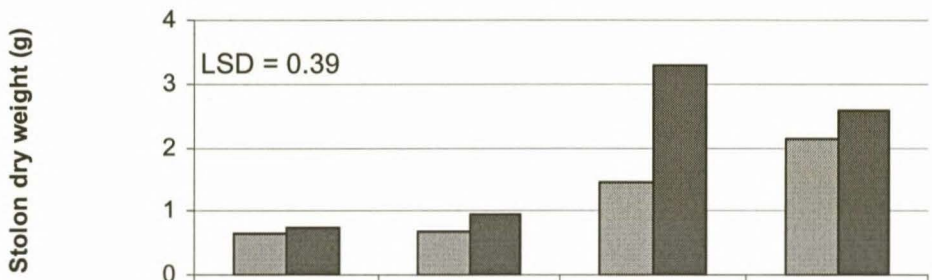
Since the interactions were valid for the same parameters at both harvest dates, only the significant (Pr > F) results of the final harvest date will be discussed. Means from the analysis of variance for the effect of light quality and cultivar on the sub-soil parameters for the first harvest date are summarized in Addendum 3.3.

Interactions between the light quality and cultivar had a significant effect on the stolon and tuber fresh and dry mass and the root dry mass, but not the root fresh mass (Table 3.4B). Root fresh mass was significantly influenced by the light quality, but did not differ between the two cultivars (Table 3.4B).

The interaction between the light quality and cultivar for the RDW occurred due to the significantly higher root dry mass for cultivar Buffelspoort under the control film

(2.39 g) compared to the lower root dry mass of the plants of the same cultivar under the blue filter (2.01 g), while root dry mass of Shepody plants did not differ due to the light quality treatments (results not shown).

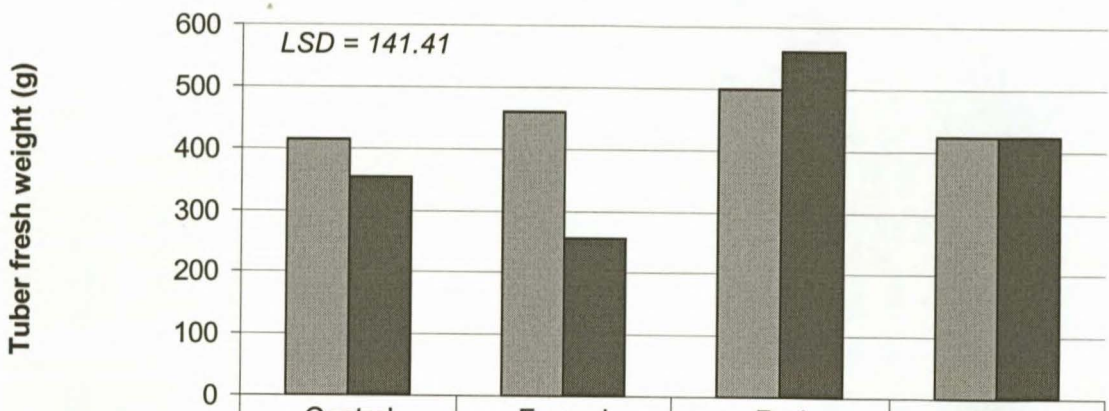
The effect of the light quality treatments on the fresh and dry mass of the stolons was found to be similar and the rest of the discussion will therefore only refer to the stolon dry mass, but may also be applied to stolon fresh mass. Stolon dry mass was significantly higher for plants grown under the red light- and blue light filters compared to the control and far-red filter, especially for the cultivar Buffelspoort (Figure 3.4). The stolon dry mass of Buffelspoort was significantly higher compared to Shepody under the far-red, blue and red filters but the largest difference between the two cultivars was under the red filter (Figure 3.4). Under the control film there was no difference in stolon dry mass between the cultivars.



	Control	Far-red	Red	Blue
Shepody	0.64	0.70	1.44	2.13
Buffelspoort	0.74	0.94	3.29	2.57

Figure 3.4 The effect of light quality on the stolon dry mass for potato cultivars Shepody and Buffelspoort.

For cultivar Buffelspoort the total tuber fresh mass under the red filter was significantly higher than the total tuber fresh mass under the control, far-red and blue film (Figure 3.5). There were no differences in the total tuber fresh mass per plant between the different light qualities for cultivar Shepody (Figure 3.5), but the red film also tend to result in the highest total tuber fresh mass.



	Control	Far-red	Red	Blue
Shepody	413.41	458.66	498.19	424.44
Buffelspoort	353.38	256.33	561.10	424.24

Figure 3.5 The effect of light quality on the total tuber fresh mass per plant for potato cultivars Shepody and Buffelspoort.

Cultivar responses to different light quality treatments with regard to tuber dry mass were found to be similar to that of tuber fresh mass (data not shown). Dry mass of the tubers were therefore found to be higher under the red filter (86.66 g and 99.14 g for Shepody and Buffelspoort respectively) compared to the tuber dry mass under the blue filter (67.35 g and 68.63 g for Shepody and Buffelspoort respectively) and the control (73.21 g and 56.04 g for Shepody and Buffelspoort respectively).

Tuber formation, -growth and efficiency of production

Results of the analysis of variance (ANOVA) done on the data with regard to the total number of tubers, the average tuber fresh mass and the ratio between tuber fresh mass and leaf area are summarized in Table 3.5.

Table 3.5 Significant levels (Pr > F) of main effects, namely light quality and cultivar as well as interactions with regard to the total number of tubers per plant, the average tuber fresh mass (ATFW) and the ratio between the tuber fresh mass and total plant leaf area (TFW / LA).

A First harvest date

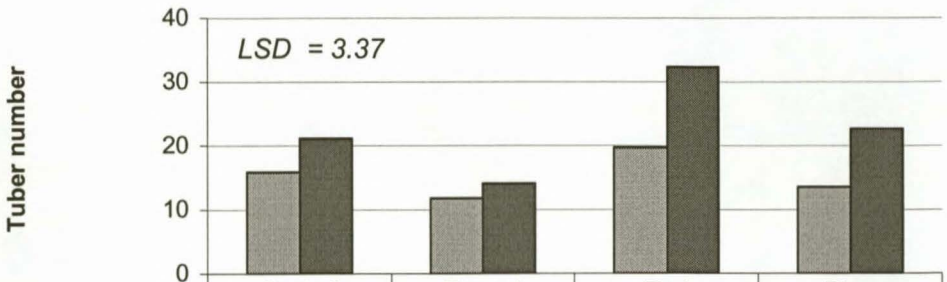
	Tuber Number	ATFW	TFW / LA
Light quality	0.000000	0.277587	0.000000
Cultivar	0.003052	0.000040	0.006797
Light quality*Cultivar	0.000045	0.368486	0.000160

B Final harvest date

	Tuber Number	ATFW	TFW / LA
Light quality	0.000000	0.000216	0.001235
Cultivar	0.000000	0.000000	0.060384
Light quality*Cultivar	0.000030	0.001470	0.000417

Interactions between light intensity and cultivar influenced the total number of tubers per plant as well as the ratio between tuber fresh mass and leaf area at both the first and final harvests, while the significant interaction between the main effects for the average tuber fresh mass in the final harvest incorporate the difference between cultivars in the first harvest date (Table 3.5). Therefore, only the significant (Pr > F) results of the final harvest date will be discussed. Means from the analysis of variance for the effect of light quality and cultivar on the tuber number, average tuber fresh mass and tuber fresh mass per leaf area for the first harvest date are summarized in Addendum 3.4.

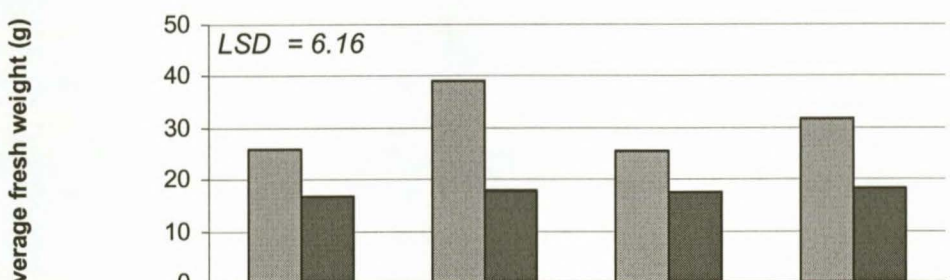
Compared to the control, both cultivars had a significantly higher number of tubers per plant for plants grown under the red filters, significantly fewer tubers per plant for plants grown under the far-red filters and no significant difference in the number of tubers per plant for plants grown under the blue filter (Figure 3.6). Cultivar Buffelspoort had significantly more tubers per light quality treatment compared to Shepody, except under the far-red filter where it was not significantly higher (Figure 3.6). The mean tuber number over all the light quality treatments was significantly higher for Buffelspoort (22.63) compared to Shepody (15.25).



	Control	Far-red	Red	Blue
Shepody	16.00	11.75	19.75	13.50
Buffelspoort	21.25	14.25	32.25	22.75

Figure 3.6 The number of tubers per plant as affected by different light qualities for cultivars Buffelspoort and Shepody.

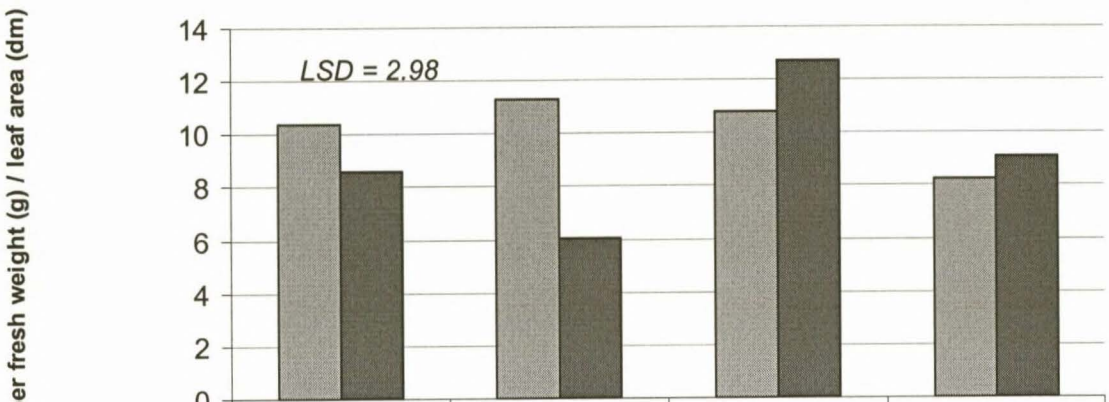
For cultivar Buffelspoort the average fresh mass per tuber was not significantly affected by light quality, while it was significantly higher for cultivar Shepody under the far-red filter compared to the control, but not significantly different under the red filter as compared to the control (Figure 3.7). Although not significant, the average tuber fresh mass per tuber tended to be higher for Shepody under the blue filter compared to the control (Figure 3.7). For all the treatments, the average fresh mass per tuber was significantly lower for Buffelspoort than for Shepody (Figure 3.7).



	Control	Far-red	Red	Blue
Shepody	25.91	39.22	25.49	31.81
Buffelspoort	16.65	18.04	17.42	18.35

Figure 3.7 The average fresh mass per tuber as affected by the different light quality treatments for cultivars Shepody and Buffelspoort.

The efficiency of biomass production and distribution to the tubers, expressed as the ratio between tuber fresh mass and leaf area at the final harvest, was significantly affected by an interaction between the light quality and cultivar (Table 3.4). For cultivar Shepody there was no significant difference in the T FW / LA between the different light quality treatments although it was lowest under the blue filter (Figure 3.8). Cultivar Buffelspoort had a significantly higher T FW / LA under the red filter and a significantly lower TFW / LA under the far-red filter compared to the other light quality treatments (Figure 3.8). The difference in TFW / LA between the cultivars was highly significant under the far-red filter with Buffelspoort having a very low T FW / LA (Figure 3.8).



	Control	Far-red	Red	Blue
Shepody	10.38	11.32	10.80	8.21
Buffelspoort	8.59	6.06	12.71	9.10

Figure 3.8 Tuber fresh mass per leaf area as affected by light quality for cultivars Shepody and Buffelspoort.

Tuber size distribution

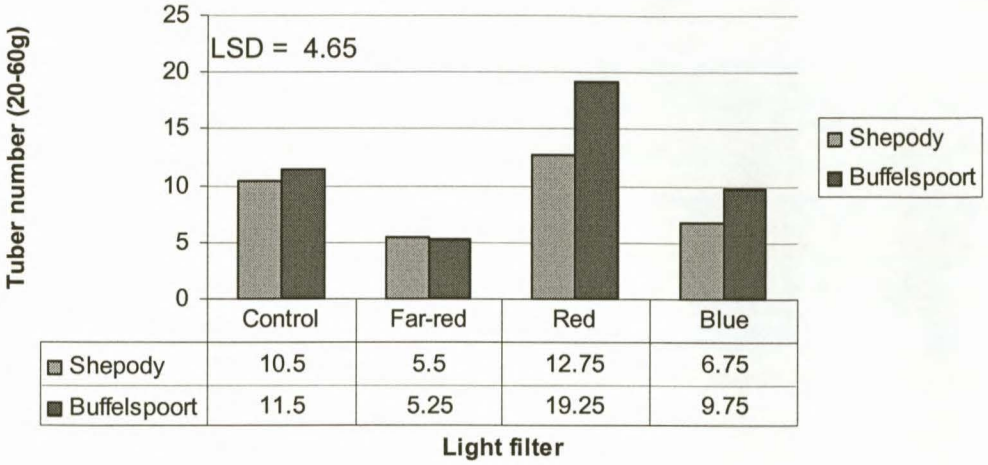
Results of the analysis of variance (ANOVA) done on the data of the second harvest with regard to the tuber size distribution are summarized in Table 3.6.

Table 3.6 Significant levels (Pr > F) of main effects, namely light quality and cultivar as well as interactions with regard to the number of tubers weighing less than 20 g (TNo <20 g), the average tuber fresh mass for tubers weighing less than 20 g (ATFW <20 g), the number of tubers weighing between 20 and 60 g (TNo 20-60 g), the average tuber fresh mass for tubers weighing between 20 and 60 g (ATFW 20-60 g), the number of tubers weighing more than 60 g (TNo >60 g) and the average tuber fresh mass for tubers weighing more than 60 g (ATFW >60 g).

	TNo <20 g	ATFW < 20 g	TNo 20-60 g	ATFW 20-60 g	TNo >60 g	ATFW > 60 g
Light quality	0.001992	0.113618	0.000000	0.040330	0.007802	0.433630
Cultivar	0.000000	0.000038	0.001276	0.136744	0.000002	0.007974
Light quality*cultivar	0.171546	0.367790	0.013326	0.973989	0.112130	0.407092

There was a significant interaction between light quality and cultivar on the number of tubers weighing between 20 and 60 g while the total number of tubers in each of the size categories was significantly influenced by the light quality and cultivar (Table 3.6). The average tuber fresh mass for tubers weighing less than 20 g and tubers weighing more than 60 g was significantly influenced by cultivar but not by light quality, while the average tuber fresh mass for tubers weighing between 20 and 60 g was significantly affected by light quality but did not differ between cultivars (Table 3.6).

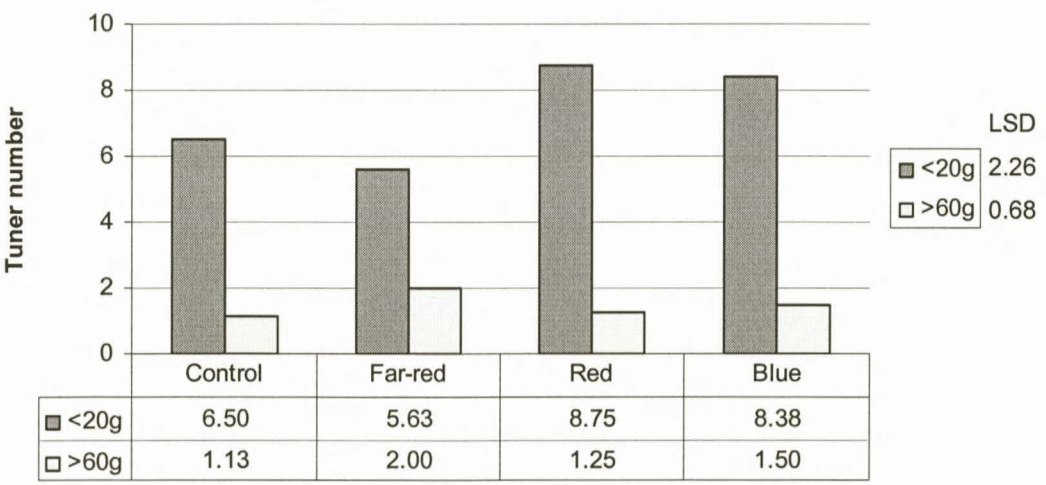
The interaction between light quality and cultivar on the number of tubers weighing between 20 and 60 g was due to a significant difference found in tuber numbers between cultivars grown under a red filter while the number of tubers for different cultivars grown under a far-red, blue and the control treatment did not differ (Figure 3.9)



	Control	Far-red	Red	Blue
Shepody	10.5	5.5	12.75	6.75
Buffelspoort	11.5	5.25	19.25	9.75

Figure 3.9 The interaction between light quality and cultivar on the number of tubers weighing between 20 and 60 g.

Significantly more tubers weighing less than 20 g were produced under the red filters compared to the control and far-red filters although the difference was not significant, more tubers weighing less than 20 g were also harvested from plants under the blue filter compared to the control (Figure 3.10). Significantly more tubers weighing more than 60 g were harvested from plants under the far-red filter compared to the control and red filter (Figure 3.10).



	Control	Far-red	Red	Blue
<20g	6.50	5.63	8.75	8.38
>60g	1.13	2.00	1.25	1.50

Figure 3.10 The effect of different light qualities on the mean number of tubers for tubers weighing less than 20 g and more than 60 g.

All treatments had a higher number of tubers weighing less than 20 g than tubers weighing more than 60 g (Figure 3.10 & Figure 3.11). Shepody had significantly fewer tubers weighing less than 20 g and significantly more tubers weighing more than 60 g compared to Buffelspoort (Figure 3.11).

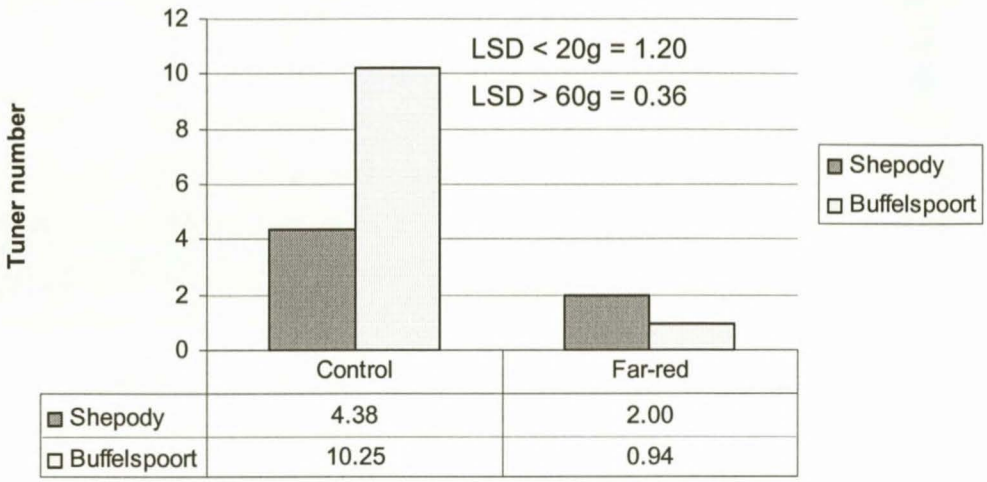


Figure 3.11 The variation in the number of tubers per size class between cultivars Shepody and Buffelspoort.

The average tuber fresh mass for tubers weighing between 20 and 60 g was significantly higher under the blue filter (31.04 g) compared to the control (24.59 g) and red filter (24.74 g) but not significantly different from the far-red filter (28.26 g) (Figure 3.12).

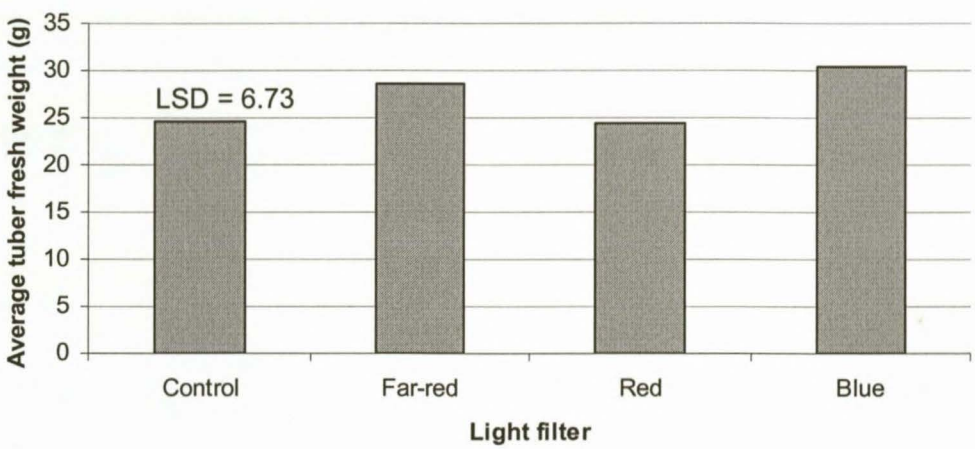


Figure 3.12 The average tuber fresh mass for both cultivars for tubers weighing between 20 and 60 g as affected by the light quality.

Buffelspoort had significantly fewer tubers weighing less than 20 g and tubers weighing more than 60 g compared to Shepody (Figure 3.13)

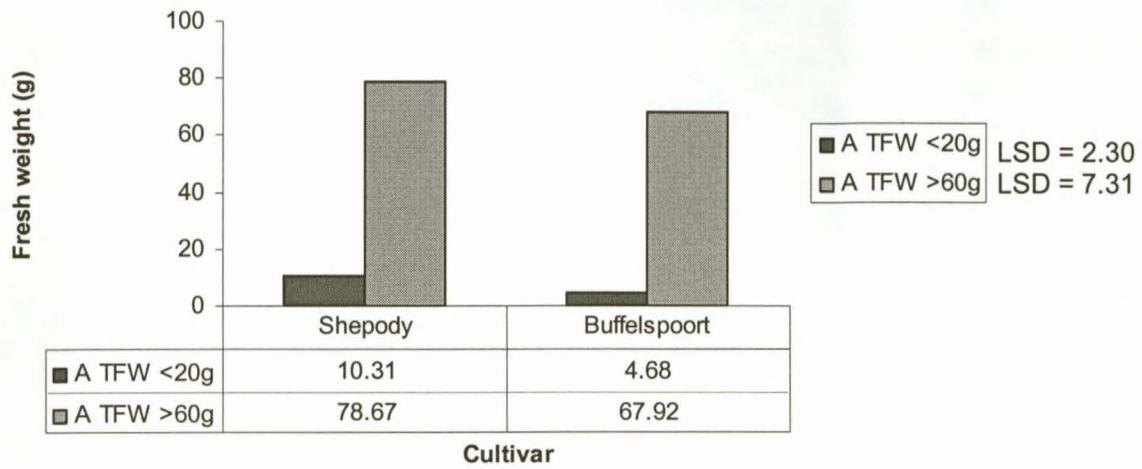


Figure 3.13 The average fresh mass per tuber for tubers weighing less than 20 g and more than 60 g for cultivars Shepody and Buffelspoort.

Dry matter partitioning

Results of the analysis of variance (ANOVA) done on the data from the first harvest with regard to the dry matter partitioning are summarized in Table 3.7.

Table 3.7 Significant levels (Pr > F) of main effects, namely light quality and cultivar as well as interactions with regard to the percentage of total dry mass allocated to the leaves, stems, roots, stolons and tubers.

	Leaves	Stems	Roots	Stolons	Tubers
Light quality	0.000020	0.000021	0.000598	0.000000	0.000025
Cultivar	0.149128	0.000003	0.009862	0.000000	0.001074
Light quality*Cultivar	0.095811	0.007554	0.195766	0.000004	0.046401

Dry matter distribution between the different plant parts were analyzed for the first harvest date only since tubers from the second harvest were used in the dormancy study and the dry mass of all tubers could not be determined.

There was a significant interaction between the light quality and cultivar with regard to the percentage of total dry mass allocated to the stems, stolons and tubers (Table 3.7). Light quality affected the dry matter partitioning to all the plant parts and cultivar differences were seen in the dry matter allocation to the stems, roots, stolons and tubers (Table 3.7).

The percentage of the total dry mass allocated to the tubers of cultivar Shepody were not significantly affected by the light quality, but for Buffelspoort the tubers under the red filter contained a significantly larger portion of the total dry mass compared to the control, far-red- and blue filters, although tubers under the blue- and far-red filter did not differ from the control in the percentage of total dry mass being allocated to them (Figure 3.14). The only significant difference between the cultivars in the total dry mass allocated to the tubers was under the blue filter, where tubers from Shepody contained a significant larger percentage of the total dry mass compared to Buffelspoort (Figure 3.14).

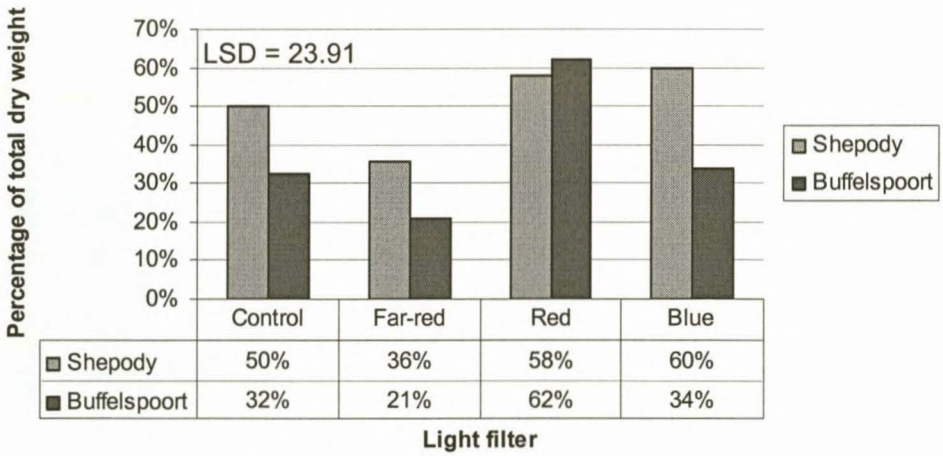
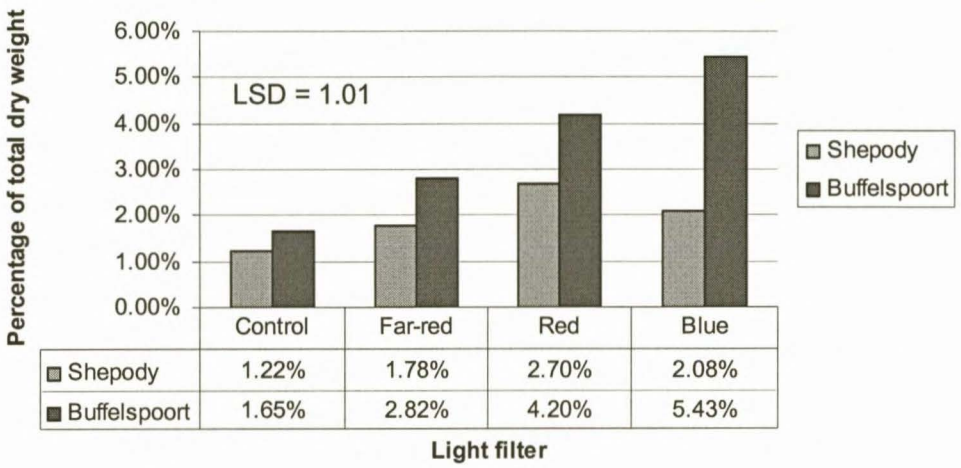


Figure 3.14 The interaction between light quality and cultivar on the percentage of total dry mass allocated to the tubers for cultivars Shepody and Buffelspoort.

For Shepody the percentage of the total dry mass allocated tot the stolons was significantly higher under the red filter compared to the control, blue- and far-red filter, while for Buffelspoort the percentage was significantly higher for all colour filters compared to the control, with the highest allocation to the stolons under the blue filter (Figure 3.15). Dry mass allocation to the stolons was also significantly higher under the red filter for Buffelspoort compared to the control and far-red filter (Figure 3.15). Buffelspoort allocated a significantly larger percentage of the total dry mass to the stolons under the red- and blue filters compared to Shepody (Figure 3.15).



	Control	Far-red	Red	Blue
Shepody	1.22%	1.78%	2.70%	2.08%
Buffelspoort	1.65%	2.82%	4.20%	5.43%

Figure 3.15 The interaction between light quality and cultivar on the percentage of total dry mass allocated to the stolon.

The stems contained a significantly lower percentage of the total dry mass for Buffelspoort under the red filter compared to the control, far-red and blue filter, while there was no significant difference in the percentage of dry mass allocated to the stems under the different filters and control film for Shepody (Figure 3.16).
Buffelspoort allocated a significantly higher percentage of the total dry mass to the stems under the control and far-red filter compared to Shepody, while under the red and blue filter there was no significant difference between the cultivars (Figure 3.16).

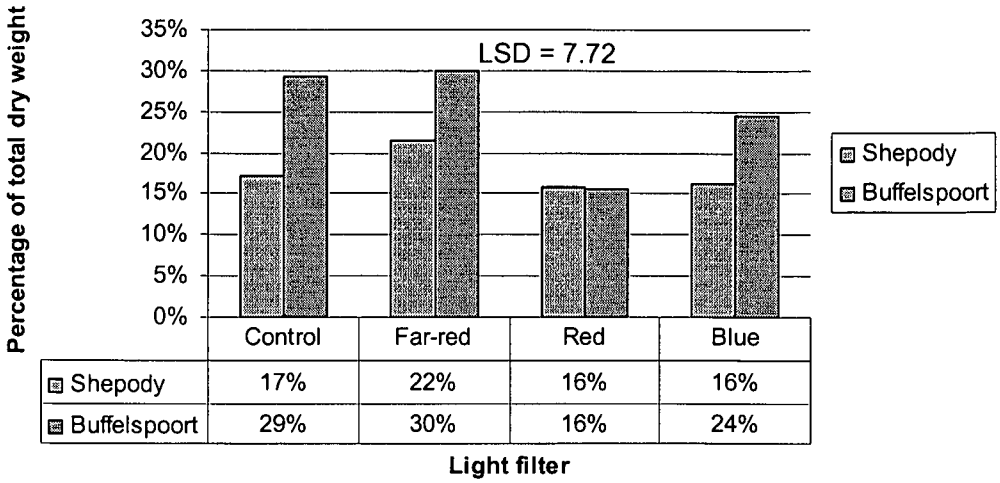


Figure 3.16 The interaction between light quality and cultivar on the percentage of total dry mass allocated to the stems.

The dry matter partitioning to the leaves were significantly lower under the red filter compared to the control and far-red filter, and the dry matter partitioning to the roots were higher under the far-red filter compared to the control (Table 3.8).

The dry matter allocation to the leaves did not differ between the cultivars, but Buffelspoort had a higher dry matter allocation to the roots compared to Shepody.

Table 3.8 Effect of different light qualities and cultivars on the dry matter allocation (%) to the leaves and roots at the first harvest

Treatments	Leaves	Roots
Light filter		
Control	28.60ac	5.44a
Far-red light	35.78c	7.88b
Red light	16.23b	4.51a
Blue light	23.55ab	5.36a
LSD (P = 0.05)	8.66	1.97
Cultivars		
Shepody	24.38a	5.09a
Buffelspoort	27.69a	6.51b
LSD (P = 0.05)	4.58	1.04

Means followed by the same letters are not significantly different at the 5% probability level.

Dormancy

Results of the analysis of variance (ANOVA) done on the data from the final harvest with regard to the time to and degree of dormancy break are summarized in Table 3.9.

Table 3.9 Significant levels (Pr > F) of main effects, namely light quality and cultivar as well as interactions with regard to the time to sprouting and the number of sprouts per tuber.

	Time to sprouting	Number of sprouts
Light quality	0.897567	0.984000
Cultivar	0.533342	0.401835
Light quality*Cultivar	0.692577	0.870655

There was neither a significant interaction between the light quality and cultivar nor an effect of light quality or cultivar on the number of days to the appearance of a sprout or on the number of sprouts that developed per tuber (Table 3.9).

DISCUSSION

High planting densities can lead to low R:FR light ratios, which in turn are associated with enhanced stem elongation, reduced branching (Balleré & Casal, 2000) and reduced leaf areas (Kurepin *et al.*, 2007). Conditions under the red light removing filter would simulate these conditions. The obtained results indicate that filtering part of the red light resulted in plants with an increase in plant height through internode elongation and an increase in leaf growth but did not have an effect on the stem:leaf ratio (Table 3.2, Figure 3.2 & Plate 2).

This is in contrast to Wilson & Rajapakse (2001) who found no effect on plant height or leaf area for three salvia species grown under red-absorbing film. In this potato trial, for plants under the red filter there was no effect on the SLA (Figure 3.3), although there was an increase in the dry mass percentage of the leaves (Table 3.2), which could indicate that although leaf morphology was not necessarily affected by the reduction in red light (or low R:FR ratio), the rate of photosynthesis or the photosynthetic efficiency could have been increased or the translocation of photosynthate out of the leaves decreased. Conditions leading to a reduction in red light reaching plants, such as canopy shade, can lead to a shade-avoidance response in plants that is characterized by a plant phenotype that will maximize light capture (Ballare, 1999) and can lead to a reduction in the generation time (Cerdan & Chory, 2003). The combination of these two responses caused by a decrease in the R:FR ratio could explain the fact that the plants under the red filters did not only exhibit an increase in vegetative growth, but also had an increase in tuber mass and number (Figure 3.5 & Figure 3.6). If the vegetative growth rate was enhanced from early on in the season and the leaves were placed to optimize light interception, a high starch accumulation rate could be achieved from the time of tuber initiation. An escape mechanism to low R:FR conditions could also lead to earlier tuber initiation, in order to shorten the generation time. Stolon growth was also enhanced, especially for cultivar Buffelspoort (Figure 3.4 & Figure 3.15), providing more sites for tuber

formation and tuber number were in fact also higher for cultivar Buffelspoort (Figure 3.6). The results obtained in this study thus indicate that stolon growth is closely related to the number of tubers initiated and that conditions leading to enhanced stem growth can lead to an increase in stolon growth. Results from the dry matter partitioning at the first harvest date, six weeks after transplanting indicate that although the leaf and stem mass of the plants under the red filters were higher than those of the control plants, an increase in dry matter partitioning to the stolons and tubers from relatively early on (Figure 3.14, Figure 3.15, Figure 3.16 & Table 3.8). This would also point to earlier tuber initiation under the red filters, but this did not necessarily inhibit leaf and stem growth since leaf dry mass was higher at the second harvest compared to the control whereas leaf dry mass was lower at the first harvest for plants under the red filter compared to the control (Table 3.2 & Addendum 3.1).

In addition there is some evidence that the tuber sink can influence photosynthesis and carbon partitioning (Basu *et al.*, 1999) and for carbon to be available for storage, the rate of assimilation in the light must be sufficient to not only support the immediate demand for growth but also to accumulate storage compounds in the leaf to be mobilized during the night. It is therefore possible that the increase in leaf dry mass percentage under the red filter (Table 3.2) could be due to an increase in the assimilation rate due to the demand from tubers. Under the red filter the plants of cultivar Buffelspoort were very efficient in allocating biomass to the storage organs (Figure 3.8 & Figure 3.14). More tubers weighing between 20 and 60 g were harvested from plants under the red filter, especially for cultivar Buffelspoort that yielded 19.25 tubers per plant in this size class (Figure 3.9) while the number of tubers in the other size classes was not affected by filtering the red light (Figure 3.10). A possible explanation could be that filtering of the red light increased tuber growth rate, resulting in an increase in the number of tubers weighing between 20 and 40 g compared to tubers weighing less than 20 g, and the initiation of more tubers therefore not affecting the number of tubers weighing less than 20 g. Shepody in general yielded more tubers weighing more than 60g, with a higher average fresh mass, and Buffelspoort yielded more tubers weighing less than 20 g, with a lower average fresh mass than Shepody (Figure 3.11 & Figure 3.13), possibly due to the fact that Shepody is an earlier maturing cultivar.

High yields are not usually associated with high planting densities and the difference from normal canopy shade and the conditions under the red removing filter in this trial was the presence of blue light, which is also reduced in canopy shade.

Drozdova *et al.* (2001) found that a lower ratio of red to blue light can activate the development of the underground storage organs in radish plants, while in *in vitro* grown potato plants a decrease in blue light led to longer plants with an increase in haulm fresh and dry mass (Seabrook & Douglas, 1998). In this study, the blue light filter resulted in an increase in plant height and internode length (Table 3.2, Plate 3), coinciding with an increase in stem mass, but a higher leaf area developed, resulting in the high S : L ratio and high SLA for these plants (Figure 3.2, Figure 3.3 & Figure 3.18).

Stolon growth was also promoted by the blue light filter but not tuber number or fresh mass (Figure 3.4, Figure 3.5 & Figure 3.6). No change in the leaf dry mass percentage (Table 3.2) or tuber fresh mass per leaf area (Figure 3.8) indicates that even though the leaf area was higher it did not result in a higher carbon assimilation rate and filtering of the blue light did not result in adaptations to increase the efficiency of biomass production or distribution to the tubers.

The number of tubers in the different size classes for plants grown under the blue filter was not affected but the average tuber fresh mass for tubers weighing between 20 and 60 g was slightly higher than the control (Figure 3.12). For the two potato cultivars used in this study the blue light deficient environment did not lead to a significant change in dry matter allocation at the first harvest, except for the stolons of plants from cultivar Buffelspoort that was significantly higher (Figure 3.15). In conclusion it can be said that under the blue light filters the total biomass assimilation increased, but not assimilate partitioning to the tubers.

The R:FR ratio can be increased by removing some of the far-red light reaching the plant and thereby reducing the stem height (Murakami *et al.*, 1996). For the two potato cultivars in this trial, decreasing the far-red portion of the light reaching the plants did not lead to a decrease in plant height, leaf or stem dry mass, but did decrease the internode length and increased the leaf dry mass percentage (Table 3.2). While stolon growth was not significantly affected, fewer tubers were formed and the total tuber fresh mass was significantly lower for Buffelspoort than Shepody, leading to the lower efficiency of biomass production for plants of this cultivar (Figure 3.5 & Figure 3.6). The average tuber fresh mass was significantly higher for cultivar Shepody under the far-red filter (Figure 3.7) and both cultivars yielded fewer tubers weighing between 20 and 40 g and more tubers weighing more than 60 g (Figure 3.10). This is a good indication that filtering the far-red light reduced tuberization and instead whatever assimilates were available were allocated to existing tubers. Total

leaf area and specific leaf area was also not affected under the far-red filters (Figure 3.3) as has been reported for both chrysanthemums and bell peppers (Li *et al.*, 2000). Li *et al.* (2000) suggested that the stage of development might influence the degree to which the filtered light will affect plant height, but in their experiments the height reduction was more pronounced later in the growing season. It is possible that the absence of a decrease in plant height under the far-red filter relative to the control could be due to the reduction in transmission of photosynthetic photon flux (PPF). A follow-up trial where the PPF of every treatment is adjusted using shade would be insightful.

The dry matter partitioning indicated a much greater percentage of biomass being allocated to the leaves, roots and stolons and less to the tubers under the far-red filter(Figure 3.14, Figure 3.15 & Figure 3.16). R:FR ratios are known to affect certain plant responses through its effects on GA regulation and/or transport (Ewing & Struik, 1992), with red light stimulating the accumulation of GAs (Reid et al., 1968) while high endogenous GA levels inhibit tuberization. The development of aerial tubers at the nodes of plants from the cultivar Shepody (Plate 4) also indicated that the tuberization signal is affected under the far-red filter (increased R:FR ratio).

Dry matter assimilation and distribution within the plant are key factors determining crop productivity. It is believed that the source-sink relationship is important in tuber formation, since factors that promote tuber formation will inhibit or reduce shoot growth (Ewing & Wareing, 1978; Ewing & Struik, 1992). Both photomorphogenesis and plant hormones are involved in regulating the source sink-relationship within a plant and photomorphogenic responses can influence the assimilate partitioning and the plants ability to accumulate biomass. These results indicate that for the potato it seems that yield is not solely dependent on radiation interception and photosynthesis but is intricately controlled by endogenous plant growth regulators. These results also contradict the opinion that for the potato crop whatever promotes shoot growth will inhibit tuber formation and vice versa, since the plants grown under the red filters had an increase in shoot growth and an increase in tuber growth, both in number and total fresh mass.

Removing some of the red light reaching the plants will result in a low R:FR ratio, or low Ø with phytochrome in the active Pfr form. If Pfr is involved in the translocation of GA from the shoots to the stolons, less Pfr would thus lead to more GA in the stems, leading to stem elongation, and less GA below ground that can inhibit tuberization

leading to more tubers being formed. This seems to be a likely explanation except that stolon growth was also promoted.

Although light quality or cultivar did not significantly affect the duration of dormancy or the degree of sprouting upon dormancy break, the tubers selected for the dormancy study were relatively uniform in size. Since tuber size will have an effect on these factors and the light quality did affect the tuber size distribution, the conclusion is that light quality will indirectly affect the duration of dormancy and the degree of sprouting upon dormancy break.

CONCLUSION

The excessive shoot growth observed by some minituber producers, which they sometimes control by applying chemical growth retardants, is most likely an effect of not only light quantity but also the light quality reaching the plants. The use of these chemical growth retardants is falling out of favour and this study indicates that it would be possible to regulate plant growth in the greenhouse by altering the light environment. Spectral filters can be used to alter the greenhouse light quality inexpensively and several companies have started the commercialization of photoselective greenhouse covering with dyes absorbing certain wavelengths (Reuveni & Raviv, 1997; Li et al., 2000; Wilson & Rajapakse, 2001), as an alternative to chemical growth regulation or the use of expensive artificial light sources. Photoselective greenhouse covers could reduce costs for growth regulating chemicals, reducing health risks and environmental pollution. Reducing the amount of red light reaching the plants may be able to increase tuber number and yields for minituber producers, although plant height will also be increased. A combination of increased light intensity or decreased temperatures, which has been shown to decrease plant height and filtering part of the red light, should be investigated further as a method of enhancing minituber yields and quality.

Further investigation into the rate of photosynthesis and respiration as well as the endogenous levels and distribution of plant growth regulators under the different spectral filters may help explain the results obtained in this study.

REFERENCES

AKSENOVA, N.P., KONSTANTINOVA, T.N., SERGEEVA, L.I., MACHACHKOVA, I., & GOLYANOVSKAYA, S.A., 1994. Morphogenesis of potato plants *in vitro*: 1. Effect of light quality and hormones. *J. Plant Growth Regul.* 13, 143-146.

AMADOR, V., BOU, J., MARTINEZ-GARCIA, J., MONTE, E., RODRIGUEZ-FALCON M., RUSSO, E., & PRAT, S., 2001. Regulation of potato tuberization by day length and gibberellins. *Int. J. Dev. Biol.* 45(S1), S37-S38.

BALLARÉ, C.L., 1999. Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. *Trends Plant Sci.* 4, 97-102.

BALLARÉ, C.L., & CASAL, J.J., 2000. Light signals perceived by crop and weed plants. *Field Crops Res.* 67, 149-160.

BASU, P.S., SHARMA, A., GARG, I.D., & SUKUMARAN, N.P., 1999. Tuber sink modifies photosynthetic response in potato under water stress. *Env. Exp. Bot.* 42, 25-39.

BRITZ, S.J., & SAGER, J.C., 1990. Photomorphogenesis and photoassimilation in soybean and sorghum grown under broad spectrum or blue-deficient light sources. *Plant Physiol.* 94, 448-454.

CERDAN, P.D., & CHORY, J., 2003. Regulation of flowering time by light quality. *Nature*, 423, 881-885.

CHEN, C., & SETTER, T.L., 2003. Response of potato tuber cell division and growth to shade and elevated CO_2. *Ann. Bot.* 91, 373-381.

DROZDOVA, I.S., BONDAR, V.V., BUKHOV, N.G., KOTOV, A.A., KOTOVA, S.N., MAEVESKAYA S.N., MOKRONOSOV, A.T., 2001. Effects of light spectral quality on morphogenesis and source-sink relations in radish plants. *Russian J.Plant Physiol.* 48, 285-490.

EWING, E.E., & STRUIK, P.C., 1992. Tuber formation in Potato: Induction, Initiation, and growth. *Hortic Rev.* 14, 89-197.

EWING, E.E., & WAREING, P.F., 1978. Shoot, stolon, and tuber formation on potato (*Solanum tuberosum* L.) cuttings in response to photoperiod. *Plant Physiol.* 61, 348-353.

FERNIE, A.R., & WILLMITZER, L., 2001. Molecular and biochemical triggers of potato tuber development. *Plant Physiol.* 127, 1459-1465.

GALAS, I., MACAS, J., VLASAK, J., ONDREJ, M., & VAN ONCKELEN H.A., 1995. The effect of an elevated cytokinin level using the *ipt* gene and N-6 benzyladenine on a singe node and intact potato plant tuberization in vitro. *Plant Growth Regul.* 14, 143-150.

JACKSON, S.D., JAMES, P., PRAT, S., & THOMAS, B., 1998. Phytochrome B affects the levels of a graft-transmissible signal involved in tuberization. *Plant Physiol.* 117, 29-32.

KIM, S.J., HAHN, E.J., HEO, J-W., PAEK, K.Y., 2004. Effects of LEDs on net photosynthetic rate, growth and leaf stomata of chrysanthemum plantlets *in vitro*. Sci. Hort. 101, 143-151.

KUMAR, D., & WAREING, P.F. 1973. Studies on tuberization in *Solanum andigena*. I. Evidence for the existence and movement of a specific tuberization stimulus. *New Phytol.* 72, 283-287.

KUREPIN, L.V., SHAH, S., & REID, D.M., 2007. Light quality regulation of endogenous levels of auxin, abscisic acid and ethylene production in petioles and leaves of wild type and ACC deaminase transgenic Brassica napus seedlings. *Plant Growth Regul.* 52, 53-60.

LI, S., RAJAPAKSE, N.C., YOUNG, R.E., & OI, R., 2000. Growth responses of chrysanthemum and bell pepper transplants to photoselective plastic film. *Sci. Hort.* 84, 215-225.

LOPEZ-JUEZ, E., KOBAYASHI, M., SAKURAI, A., KAMIYA, Y., & KENDRICK,R.E., 1995. Phytochrome, gibberellins and hypocotyl growth. *Plant Physiol.* 107, 131-140.

MORGAN, D.C., & SMITH, H., 1979. A systemic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145, 210-212.

MURAKAMI, K., CUI, H., KIYOTA, M., & AIGA, I., 1995. The design of special covering materials for greenhouses to control plant elongation by changing spectral distribution of daylight. *Acta Hort.* 399, 135-142.

MURAKAMI, K., CUI, H., KIYOTA, M., YAMANE, T., & AIGA, I., 1996a. The effects of covering materials for greenhouses to control plant growth by changing spectral distribution of daylight. *Acta Hort.* 435, 123-130.

MURAKAMI, K., CUI, H., KIYOTA, M., TAKEMURA, Y., OI, R. & AIGA, I., 1996b. Covering materials to control plant growth by modifying the spectral balance of daylight. *Plasticulture* 110, 2-14.

NAUK, C.S., & LANGILLE, A.R., 1978. Physiology of tuberization in *Solanum tuberosum* L. *Cis*-Zeatin in the potato plant: Is identification and changes in endogenous levels influenced by temperature and photoperiod. *Plant Physiol,* 62, 438-443.

PEARSON, S., WHELDON, A.E., HADLEY, P., 1995. Radiation transmission and fluorescence of nine greenhouse cladding materials. *J. Agri. Eng. Res.* 62, 61-70

PIERIK, R., VISSER, E.J.W., DE KROON, H., VOESENEK, L.A.C.J., 2003. Ethylene is required in tobacco to successfully compete with proximate neighbours. *Plant Cell Environ.* 26, 1229-1234.

POWLES, S.B., 1984. Photoinhibition of photosynthesis induced by visible light. *Annu. Rev. Plant Physiol.* 35, 14-44.

REID, D.M., CLEMENTS, J.B., & CARR, D.J., 1968. Red light induction of gibberellin synthesis in leaves. *Nature*, 217, 580-582.

REUVENI, R., & RAVIV, M., 1997. Control of downy mildew in greenhouse-grown cucumbers using blue photoselective polyethylene sheets. *Plant Dis.* 81, 999-1004.

ROITSCH, T., & EHNEB, R., 2000. Regulation of source/sink relations by cytokinins. *Plant Growth Reg.* 32, 359-367.

SALISBURY, F.J., HALL, A., GIERSON, C.S., & HALLIDAY, K.J., 2007. Phytochrome coordinates Arabidopsis shoot and root development. *Plant Journal* 50, 429-438.

SEABROOK, J.E.A., & DOUGLAS, L.K., 1998. Prevention of stem growth inhibition and alleviation of intumescence formation in potato plantlets *in vitro* by yellow filters. *Amer. J. of Potato Res.* 75, 219-224.

SIMKO, I., 1994. Sucrose application causes hormonal changes associated with tuber induction. *J. plant growth regul.* 13, 73-77.

SMITH, H., 1982. Light quality, photoreception, and plant strategy. *Ann Rev. Plant Physiol.* 33, 481-518.

SMITH, H., & HOLMES, M.G., 1977. The function of phytochrome in the natural environment: III. Measurement and calculation of phytochrome photoequilibrium. *Photochem and photobiol.* 25, 547-550.

SMITH, H., & WHITELAM G.C., 1990. Phytochrome, a family of photoreceptors with multiple physiological roles. *Plant Cell Environ.* 13, 695-707.

TAYLOR, A.R., & ASSEMANN S.M., 2001. Apparent absence of a redox requirement for blue light activation of pump current in broad bean guard cells. *Plant Physiol.* 125, 329-338.

TAIZ, L., & ZEIGER, E., 2002. Plant physiology, 3rd edn. Sinauer Associates, Sutherland, MA.

VANDENBUSSCHE, F., PIERIK, R., MILLENAAR, F.F., VOESENEK, L.A., & VAN DER STRAETEN, D., 2005. Reaching out of the shade. *Cur. Opin. Plant Biol.* 8, 462-468.

VREUGDENHIL, D., and SERGEEVA, L.I., 1999. Gibberellins and tuberization in potato. *Potato Res.* 42,471-481.

WALTERS, R.G., SHEPHARD, F., ROGERS, J.J.M., ROLFE, S.A.,& HORTON, P., 2003. Identification of mutants of Arabidopsis defective in acclimation of photosynthesis to the light environment. Plant Physiol. 131, 472-481.

WARPEHA, K.M., & KAUFMAN, L.S., 1989. Blue light regulation of epicotyl elongation in *Pisum sativus*. *Plant Physiol.* 89, 544-548.

WILSON, S.B., & RAJAPAKSE, N.J., 2001. Use of photoselective plastic films to control growth of three perennial salvias. *J. Appl Hort.* 3, 71-74.

XU, X., VAN LAMERREN, A.A., VERMEER, E., & VREUGDENHIL, D., 1998. The role of gibberellin, abscicic acid and sucrose in the regulation of potato tuber formation *in vitro*. *Plant Physiol.* 117, 575-584.

CHAPTER 4

The effect of root zone temperature on the growth, dry matter accumulation and dry matter distribution of potato (*Solanum tuberosum* L.) during the production of G0 minitubers

ABSTRACT

Two cultivars of potato (*Solanum tuberosum* L., cvs. Shepody and Buffelspoort) were grown in coarse washed sand cooled by the circulation of cold water through glass spirals in the medium to study the effect of root zone temperature on growth, assimilate partitioning and yield of tubers during minituber production. A root zone temperature of less than 15^0C resulted in plants with a reduced height, lower leaf-, stem- and stolon mass and reduced leaf areas compared to plants grown at root zone temperatures above 15^0C. Total growth was reduced but assimilate partitioning was shifted to the tubers under the lower root zone temperature although this did not have a significant effect on the final tuber number or yield for both cultivars. The plants grown in the cooler root medium were more efficient in accumulating dry matter in the tubers since a reduced leaf area resulted in tuber dry mass similar to plants grown in the un-cooled medium. The dry mass percentage of the leaves was not affected by the root zone temperature and therefore transpiration and photosynthesis was probably not affected. Lower root zone temperature could have affected assimilate partitioning through a reduction in the translocation of cytokinin and gibberellin. The results indicated that cooling of the root medium may facilitate a decrease in stem growth without affecting tuber formation and final tuber yield.

INTRODUCTION

The potato (*Solanum tuberosum* L.) is the most important non-cereal crop in the world, and yearly covers about 18 million hectares worldwide (Struik & Wiersema, 1999). The potato has a high production efficiency (Struik & Wiersema, 1999) and a high use efficiency in terms of land and energy. Potential yields are highest in temperate regions, in areas where the length of the growing season is not restricted by high temperatures (Struik & Wiersema, 1999).

In South-Africa, temperatures inside the greenhouse during the production of G0 minitubers often reach 30^{0}C, while the growing medium can easily reach temperatures above 25^{0}C early in the production season before a sufficient leaf canopy has formed.

This is unfavourable since the potato is best adapted to cool climates with mean daily temperatures between 15 and 18^{0}C (Haverkort, Van de Waart & Bodleander, 1990). The optimum temperature for sprout elongation is 18^{0}C, while haulm growth is optimum at about 25^{0}C (Struik & Wiersema, 1999). Plant morphology is influenced by temperature and low temperatures can increase the level of determinacy of the stems (O'Brien, Allen & Firman, 1998), signifying that more side branches will form, and thus a larger leaf area to intercept incoming radiation. Plants grown under high temperatures (>20 / >30 ^{0}C night / day temperatures) are taller with more internodes and more sympodial growth, they have shorter and narrower leaves, a more acute leaf to stem angle, and increased axillary branching at the base of the main stem. These plants also exhibit higher total leaf dry mass, total stem dry mass and a decrease in the leaf / stem ratio (Wheeler, Tibbits & Najar, 1986; Ewing & Struik, 1992). Smaller root systems develop when the root zone temperature is 30^{0}C compared to a root zone temperature of 20^{0}C (Sattelmacher, Marschner & Kuhne, 1990). Increasing the soil temperature, while keeping the ambient air temperature at a constant 20^{0}C, lead to a decrease in the net photosynthetic rate (Hammes & De Jager, 1990). Decreasing soil temperatures can lead to a decrease in root growth, reduced stem growth and a reduction in the photosynthetic rate due to a reduction in water and nutrient uptake at low soil temperatures (Franklin *et al.*, 2005).

Tuberization will be enhanced at temperatures between 18 and 20^{0}C and slow down at temperatures above 20^{0}C (Kooman *et al.*, 1996). In some cultivars high soil temperatures (28-30^{0}C) can delay or inhibit tuber formation (Khedher & Ewing, 1985), while for other cultivars tuber initiation was not significantly affected at high

soil temperatures (Sale, 1976; Demagante & Vander Zaag, 1988). Stolon branching can be increased by higher soil temperatures and the number of tubers initiated is known to be closely related to the number of stolons (Haverkort *et al.*, 1990). Struik, Geertsema and Custers (1989) found that increasing the temperature around the stolons and tubers led to an increase in tuber number. The increase in tuber number when increasing the stolon temperature to 28^0C was associated with a decrease in tuber size and final tuber yield (Struik *et al.*, 1989). Very high soil temperatures (32 / 27^0C day / night temperatures) can however inhibit stolon development and may cause stolons to grow upwards and form aerial tubers, if the air temperature is cooler than the soil temperature (Reynolds & Ewing, 1989). Aerial tubers on orthotropic stolons, aerial tubers on main stems and swellings above the attachment of side branches is not uncommon under circumstances where the tuberization signal cannot be translocated to or expressed in the stolon tips (Ewing & Struik, 1992). Although the onset of tuber initiation is not influenced by soil temperature (O'Brien *et al.*, 1998), the duration of tuber initiation is influenced by soil temperature, with a low soil temperature (<15^0C) being able to extend the period, while a soil temperature of 19^0C was able to shorten the initiation period with 1 week (O'Brien *et al.*, 1998). Ambient temperature during the tuberization phase has the most significant effect on the final number of tubers (Ewing & Struik, 1992), with high mean daily temperatures (25 - 30^0C) reducing the number of tubers being retained (Sale, 1979).

Tuber bulking and dry matter partitioning to the tubers will be greatest at temperatures between 15 and 20^0C (Struik & Wiersema, 1999). It is also expected that the dry matter allocation to tubers will start earlier at temperatures less than 20^0C (Kooman *et al.*, 1996; Struik & Ewing, 1992). A reduction in tuber dry mass is observable whenever the soil or air temperature is raised (Menzel, 1983).

At temperatures above 30^0C, a reduction in the carbon assimilation rate takes place (Midmore & Prange, 1992) due to a decrease in the net photosynthetic rate, an increase in dark respiration (Thornton, Malik & Dwelle, 1996) and a decline in starch accumulation since many enzymes involved in starch synthesis are not active at these high temperatures (Struik & Wiersema, 1999). As with short photoperiods, increased leaf starch accumulation during the light period is observed in plants grown at cool temperatures (Ewing & Struik, 1992). The resulting high C:N ratio was previously believed to be involved in bringing about tuberization. Although currently tuberization is believed to be controlled hormonally, the assimilate level may be involved in inducing tuberization through the effects of sucrose levels on genes

involved in tuberization (Ewing & Struik, 1992). The translocation of cytokinin and gibberellin is reduced when the root temperature is lowered (Atkin, Barton & Robinson, 1973) and are likely involved in relay the tuberization signal. Under controlled environments, the reduction in carbon assimilation rate under high temperatures correlates with the reductions in growth and yield (Midmore & Prange, 1992), but under field conditions the reduced carbon assimilation rate can not always explain the observed yield reductions (Sarquis, Gonzalez & Bernal-Lugo, 1996), possibly due to interacting effects such as low light intensity, photoperiod or water stress.

High temperature and low light intensity conditions (due to location or shading to reduce temperature) in local minituber greenhouses, often lead to excessive vegetative growth that not only divert resources away from the developing tubers, but also create conditions favorable for disease outbreak.

The aim of this experiment was to study the effect of lowering the root zone temperature on potato plant growth, dry matter production and -distribution and final minituber yield in terms of number and size distribution.

Material and Methods

Plant material

Experiments were conducted in a fully temperature controlled glasshouse at Welgevallen, the experimental farm of the University of Stellenbosch, in the Western Cape of South Africa.

Potato (*Solanum tuberosum* L.) plantlets of the cultivars Shepody and Buffelspoort were used in this study. Both Shepody and Buffelspoort are medium-short maturing cultivars with a medium to long dormancy period. *In vitro* plantlets were obtained from Ceres Potatoes and transplanted into troughs, containing a seedling mixture of peat, vermiculite and perlite on 5 January 2007 and allowed to acclimatize in the glasshouse at 18/22^{0}C night/day temperatures and a relative humidity (RH) averaging above 60%. The plantlets were watered with a 50% diluted (0.7 mS cm^{-1}) nutrient solution (Steiner, 1984). The acclimatized plantlets were each transplanted to a 5L pot filled with coarse washed sand as growing medium after 10 days on 15 January 2007. The pots were placed on a bench in the glasshouse at a density of 12 plants m^{-2}. A drip fertigation system was used and a standard Steiner nutrient

solution with an electrical conductivity (EC) of 1.5 mS cm^{-1} (Steiner, 1984) applied. The initial irrigation volume was 100 ml per irrigation pulse, with a frequency of six times per day.

Treatments

Glass spirals were placed in the pots and linked to each other and a cooling bath with plastic tubing through which cooled water was constantly circulated in order to cool the growing medium. The cooling bath was set at 10^0C and the growth medium temperature readings were taken hourly for a period of 24 hours, several times during the trial, with a thermohygrometer (model HI 9161C, Hanna instruments).

The difference in root zone temperature between the non-cooled control and the cooled treatment was on average twice as large during the first 4 weeks, than during the last 6 weeks of the trial due to the greater effect of solar radiation on heating of the growth medium when the leaf canopy was still very small. During the first four weeks the root zone temperature of the control reached 23.5^0C while the root zone temperature of the cooled medium stayed below 14.5^0C. During the last 6 weeks of the trial the root zone temperature of the control stayed below 17.5^0C and the root zone temperature of the cooled medium below 13.0^0C.

Data collected

Air temperature was recorded daily and relative humidity readings were recorded weekly with a thermohygrometer (model HI 9161C, Hanna instruments). Plant growth characteristics were recorded twice a week and included plant height and internode length. Plant height was measured as the vertical length between the apical growth point of the main stem and the growing medium. Internode length was taken as the average of 5 random measurements per plant.

After harvest, plant height and internode length was measured again before determining the fresh mass of the leaves, stems, stolons, roots and tubers and tuber number per plant. The relative chlorophyll content of three fully expanded leaves per plant was measured using a chlorophyll content meter (model CCM-200, Optiscience) and the leaf area per plant was determined using a leaf area meter (model LI 3100, Li-Cor).

Plant parts were oven dried separately at 80^{0}C for 72 hours and the dry mass and dry mass percentage determined for the different plant parts. Dry matter content was calculated as the percentage of dry mass to fresh mass. Dry matter distribution between the plant parts was calculated as the percentage dry mass of each plant part to the total plant dry mass. Any swelling of the stolon to twice its diameter was considered a tuber (Ewing & Struik, 1992). Tuber number and fresh mass were determined and tubers were separated into 3 different size classes according to mass, namely <20 g, 20-40 g and >40 g. These size classes were chosen since few large tubers were present at harvest. The number and fresh mass of the tubers in each size class was recorded. The tubers were chopped up and oven dried at 80^{0}C for 72 hours and the dry mass and dry mass percentage (the percentage of tuber dry mass to tuber fresh mass) as well as the harvest index (the ratio of tuber dry mass to total dry mass) was determined.

Experimental design and statistical analysis

The trial was conducted using a completely randomized design in a 2 x 2 factorial experiment with temperature and cultivar as factors. A single plant was considered an experimental unit and each treatment combination was replicated six times. Analyses of variance (ANOVA) were performed to test treatment effects on vegetative plant growth, tuber number per plant, mean tuber mass per plant and tuber size distribution using the general linear model procedure of STATISTICA (StatSoft Inc., 2006). Bonferoni significant levels (Pr > f) of the main effects were calculated at the 5% probability level.

RESULTS

Root zone temperatures

Figure 4.1 shows the average hourly readings of the root zone temperatures during the first four weeks of the trial and Figure 4.2 the root zone temperatures during the remainder of the trial. The mean difference in root zone temperature between the

non-cooled and cooled treatment were 6^0C and 9^0C for the night and day respectively during the first 4 weeks of the trial and 4^0C and 5^0C for the night and day respectively during the last 6 weeks of the trial (Figure 4.1 & Figure 4.2).

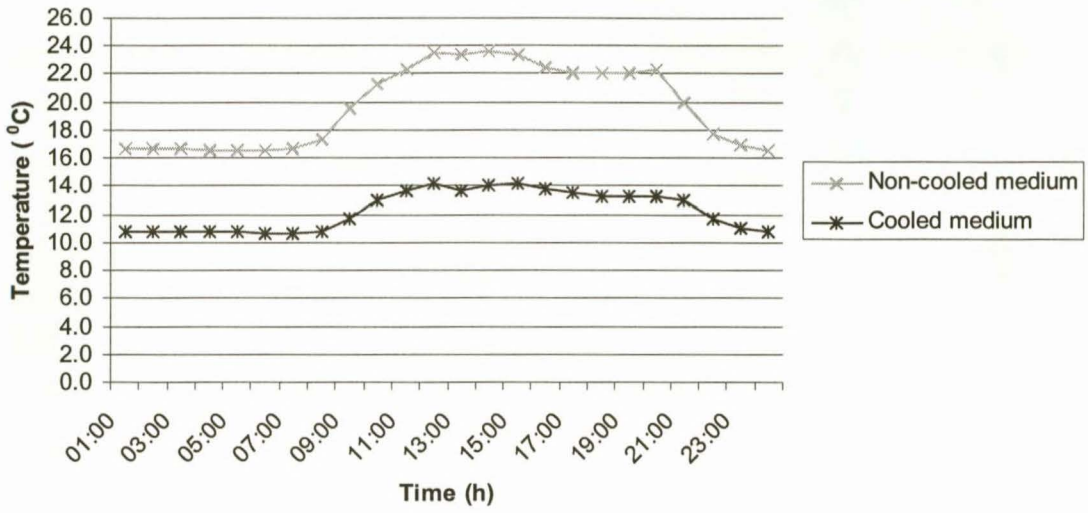


Figure 4.1 Average diurnal root zone temperatures over the growing period for the control and cooled treatments during the first 4 weeks of the trial.

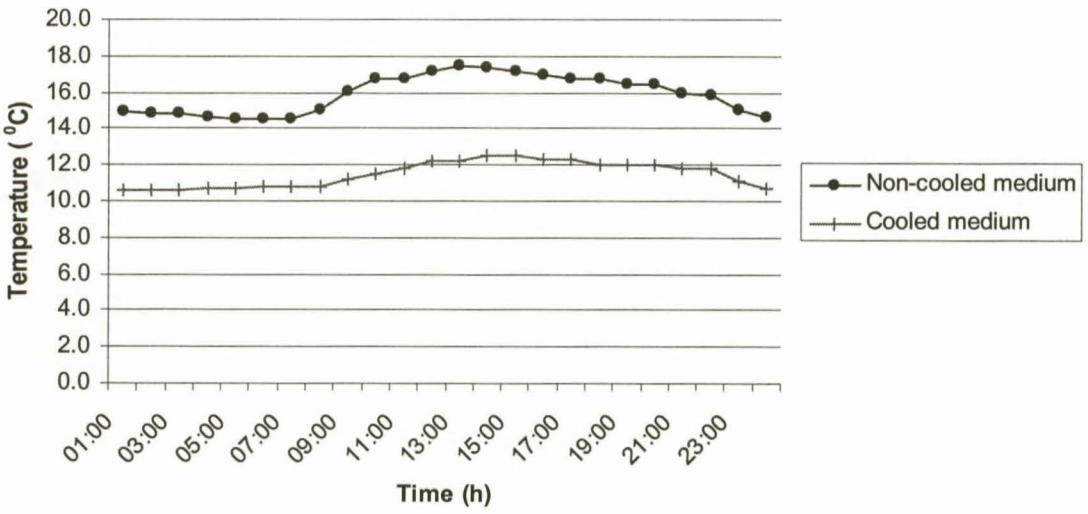


Figure 4.2 Average diurnal root zone temperatures over the growing period for the control and cooled treatments during the last 6 weeks of the trial.

Plant height, internode length, chlorophyll content and leaf area

Results of the ANOVA done on data with regard to plant growth factors are summarized in Table 4.1.

Table 4.1 Significant levels (Pr > f) of main effects, namely root zone temperature and cultivar as well as interactions with regard to plant height, internode length, relative chlorophyll content and leaf area.

	Plant height	Internode length	Chlorophyll content	Leaf area
Temperature	0.032176	0.229800	0.921418	0.001091
Cultivar	0.088460	0.047687	0.492417	0.314087
Temperature*cultivar	0.614477	0.620306	0.767498	0.601088

There was no significant interaction between root zone temperature and cultivar for the plant height, internode length, chlorophyll content and leaf area (Table 4.1). Root zone temperature significantly influenced the plant height and leaf area, but had no significant effect on the internode length and leaf chlorophyll content (Table 4.1). Significant differences in internode length was observed between the cultivars, but plant height, chlorophyll content and leaf area did not differ significantly between the cultivars.

Cooling of the root zone led to a significant reduction in the plant height for both cultivars, decreasing from a mean of 32.9 cm for the control to 28.4 cm for the cooled medium (Figure 4.3). Mean leaf area for both cultivars was also significantly reduced from 2356.2 cm^2 for the control to 1531.0 cm^2 for the cooled medium (Figure 4.3).

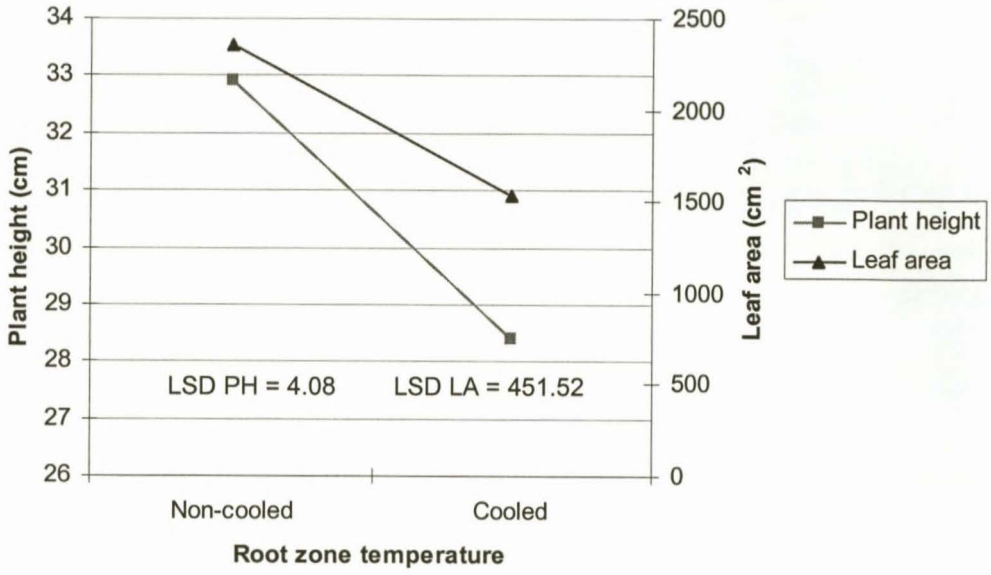


Figure 4.3 The effect of root zone cooling on the mean plant height (PH) and total leaf area (LA) for cultivars Buffelspoort and Shepody.

Internode length differed significantly between the two cultivars with longer internodes observed for cultivar Buffelspoort (2.0 cm) as compared to cultivar Shepody (1.7 cm) (Figure 4.4). Although not significant, plants from the cultivar Buffelspoort were taller (32.42 cm) than plants from the cultivar Shepody (28.92 cm).

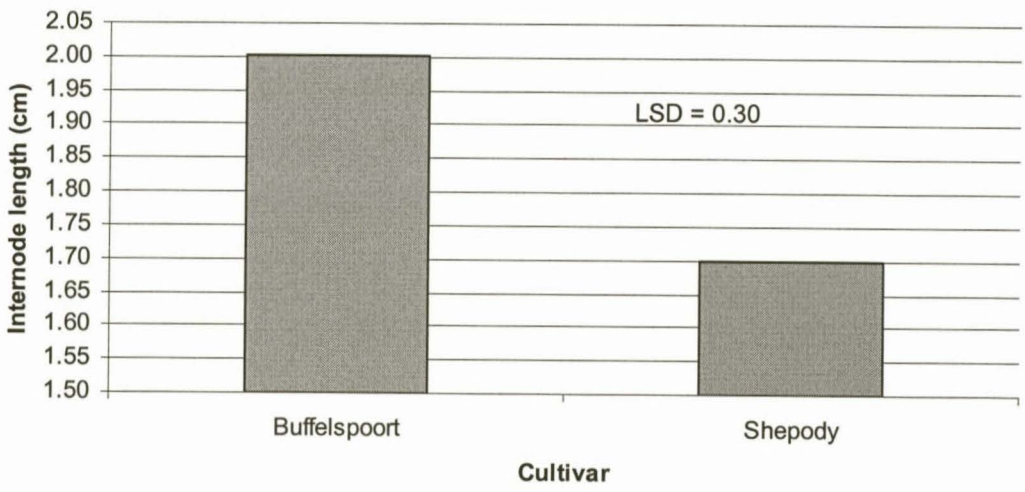


Figure 4.4 The difference in mean internode length for cultivars Buffelspoort and Shepody.

Fresh and dry mass of different plant parts

Results of the Analysis of Variance (ANOVA) done on data with regard to the fresh and dry mass of plant parts are summarized in Table 4.2.

Table 4.2 Significant levels (Pr > f) of main effects, namely root zone temperature and cultivar as well as interactions with regard to the leaf fresh mass (LFW), leaf dry mass (LDW), stem fresh mass (SFW), stem dry mass (SDW), stolon fresh mass (StFW), stolon dry mass (StDW), root fresh mass (RFW), root dry mass (RDW), tuber fresh mass (TFW) and tuber dry mass (TDW).

Above ground

	LFW (g)	LDW (g)	SFW (g)	SDW (g)
Temperature	0.003998	0.000586	0.000173	0.000117
Cultivar	0.989255	0.350478	0.251927	0.083536
Temperature*cultivar	0.370905	0.203718	0.002070	0.001410

Below ground

	StFW (g)	StDW (g)	RFW (g)	RDW (g)	TFW (g)	TDW (g)
Temperature	0.002678	0.003841	0.247304	0.134241	0.116983	0.100509
Cultivar	0.323610	0.441918	0.039610	0.188406	0.189689	0.575969
Temperature*cultivar	0.289299	0.153950	0.082784	0.152225	0.935383	0.931190

There was a significant interaction between the root zone temperature and cultivar for the stem fresh and dry mass (Table 4.2). Root zone temperature had a significant effect on the LFW, LDW, SFW, SDW, StFW and StDW while cultivar significantly affected RFW. Root zone temperature did not have a significant effect on the root- or tuber fresh or dry mass and no significant differences in the leaf, stem, stolon or tuber fresh and dry mass were observed between the cultivars (Table 4.2).

The root zone temperature and cultivar had a significant and similar effect on the stem fresh and dry mass and thus only the data for the stem dry mass will be discussed. The decrease in stem dry mass when the root zone was cooled was not significant for cultivar Buffelspoort but stem dry mass was significantly lower for cultivar Shepody when the root medium was cooled (Figure 4.5). Shepody had a

significantly higher stem dry mass than Buffelspoort when the growing medium was not cooled (Figure 4.5).

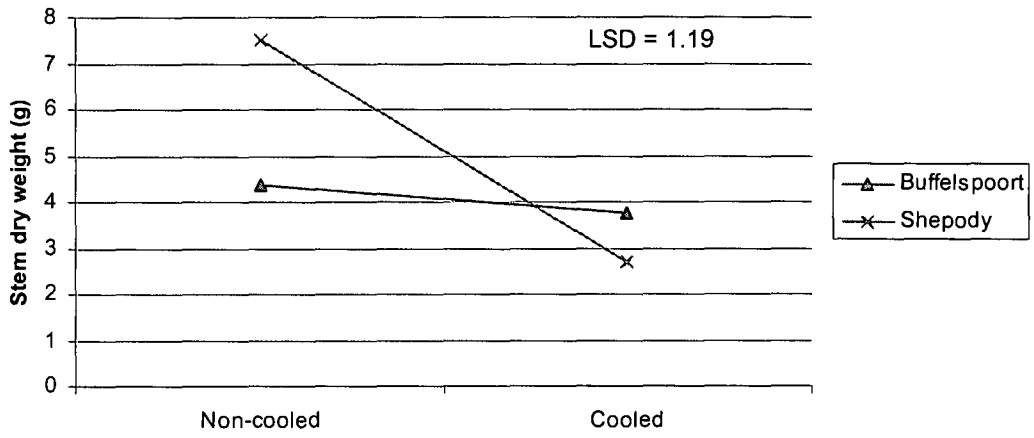


Figure 4.5 The interaction between root zone temperature and cultivar on the stem dry mass for cultivars Buffelspoort and Shepody.

The lower root zone temperature also resulted in a lower fresh and dry weight for both leaves and stolons (Table 4.3).

Table 4.3 Effect of different root zone temperature shading levels and cultivars on the leaf fresh mass (LFW), leaf dry mass (LDW), stolon fresh mass (StFW) and stolon dry mass (StDW).

Treatments	**LFW (g)**	**LDW (g)**	**StFW (g)**	**StDW (g)**
Root zone temperature				
Non-cooled	70.68a	9.96a	4.18a	0.66a
Cooled	55.18b	7.51b	2.54b	0.41b
LSD (P = 0.05)	9.94	1.25	1.00	0.16

Means followed by the same letters are not significantly different at the 5% probability level.

The two cultivars differed significantly with regard to root fresh weights, with a higher root fresh mass for Shepody (14.26 g) as opposed to Buffelspoort (11.29 g) (Figure 4.6).

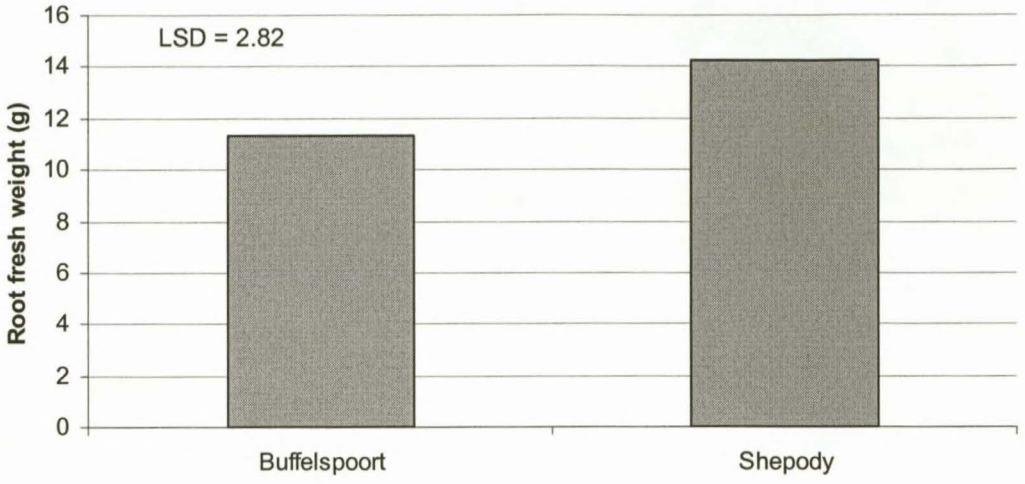


Figure 4.6 The difference in mean root fresh mass (RFW) for cultivars Buffelspoort and Shepody.

Dry mass percentage of plants

Results of the ANOVA done on data with regard to dry mass percentage of plant parts are summarised in Table 4.4.

Table 4.4 Significant levels (Pr > f) of main effects, namely root zone temperature and cultivar as well as interactions with regard to the leaf dry mass percentage (LDW%), stem dry mass percentage (SDW%), stolon dry mass percentage (StDW%), root dry mass percentage (RDW%) and tuber dry mass percentage (TDW%).

	LDW%	SDW%	StDW%	RDW%	TDW%
Temperature	0.060260	0.050120	0.371788	0.482549	0.511840
Cultivar	0.002257	0.140058	0.607084	0.043458	0.000009
Temperature*cultivar	0.141764	0.138938	0.143099	0.372394	0.641390

No interaction between the root zone temperature and cultivar was found with regard to the dry mass percentage of the leaves, stems stolons, roots or tubers (Table 4.4).

The root zone temperature did not influence the dry mass percentage of the leaves, stems, stolons, roots or tubers significantly but cultivar differences in the leaf, root and tuber dry mass percentage was significant (Table 4.4).

Although not significant there was a trend towards a decrease in the dry mass percentage of the leaves and stems for plants grown in the cooled root medium (Figure 4.7). Leaf and stem dry mass percentage decreased from 14.16% and 24.81% respectively in the control to 13.61% and 22.90% when the root zone was cooled (Figure 4.7).

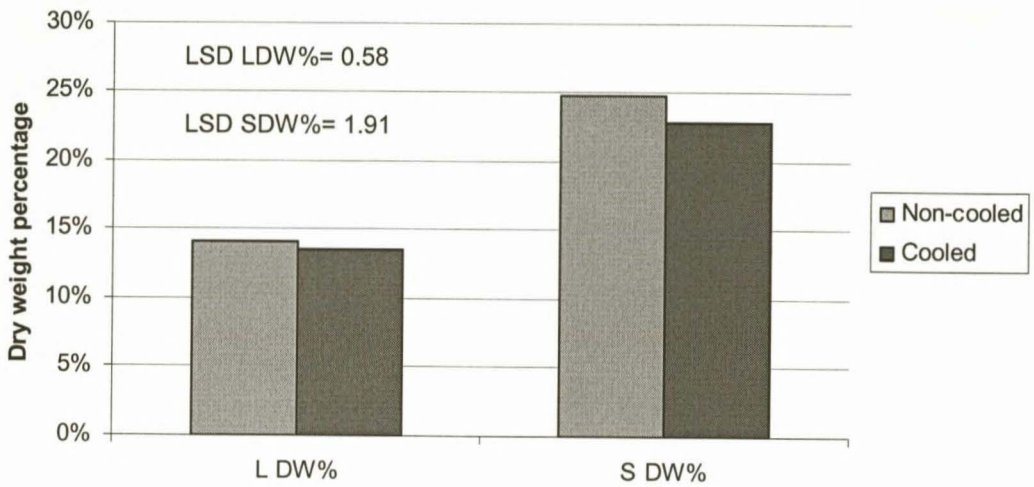


Figure 4.7 The mean dry mass percentage of the leaves and stems of cultivars combined as affected by cooling of the root zone.

The leaf and root dry mass percentage of Buffelspoort (14.37% and 15.65% for LDW% and RDW% respectively) was higher than that for Shepody (13.39% and 13.89% for LDW% and RDW% respectively); while the tuber dry mass percentage was higher for Shepody (20.21%) than for Buffelspoort (19.22%) (Table 4.5).

Table 4.5 Effect of different root zone temperatures and cultivars on the leaf dry mass percentage (LDW%), root dry mass percentage (RDW%) and tuber dry mass percentage (TDW%).

Treatments	LDW%	RDW%	TDW%
Buffelspoort	14.37a	15.65a	19.22a
Shepody	13.39b	13.89b	20.21b
LSD (P = 0.05)	0.58	1.69	0.35

Means followed by the same letters are not significantly different at the 5% probability level.

Dry matter distribution

Results of the ANOVA done on data with regards to the dry matter distribution are summarized in Table 4.6.

Table 4.6 Significant levels (Pr > f) of main effects, namely root zone temperature and cultivar as well as interactions with regard to the total dry mass and dry mass distribution between the leaves, stems, roots and stolons and the tubers.

	Total DW (g)	Leaves	Stems	Roots & stolons	Tubers
Temperature	0.000605	0.158507	0.002528	0.785984	0.004804
Cultivar	0.997133	0.196384	0.131337	0.370401	0.531190
Temperature*cultivar	0.125929	0.808241	0.003490	0.374198	0.016912

The interaction between temperature and cultivar was significant for the percentage of dry mass invested in stems and tubers, but no significant interaction between temperature and cultivar on the total plant dry mass or the percentage of dry mass invested in the leaves and stolons & roots was observed (Table 4.6). Root zone temperature significantly influenced the total dry mass, the percentage of the total dry mass allocated to the stems and tubers, while no significant differences in the percentage of the total dry mass allocated to the leaves and roots & stolons were observed (Table 4.6). There were no significant differences in total dry mass or the

percentage of dry mass allocated to the leaves, stems, roots & stolons or tubers between the two cultivars (Table 4.6).

For cultivar Shepody, cooling of the root medium resulted in a smaller percentage of the total dry mass being allocated to the stems and a larger percentage of the total dry mass being allocated to the tubers, while for cultivar Buffelspoort cooling of the root medium did not affect the percentage of the total dry mass being allocated to the stems or tubers (Figure 4.8). The result was that when the medium was not cooled, Shepody had a smaller percentage of the total dry mass invested in the tubers and a larger part of the total dry mass invested in the stems, compared to Buffelspoort (Figure 4.8). However, when the root medium was cooled, Shepody had a larger percentage of the total dry mass invested in the tubers and a smaller part of the total dry mass invested in the stems, compared to Buffelspoort, since the dry mass distribution was not significantly different for Buffelspoort when the root medium was cooled. The percentage of the total dry mass invested in the tubers is also referred to as the harvest index.

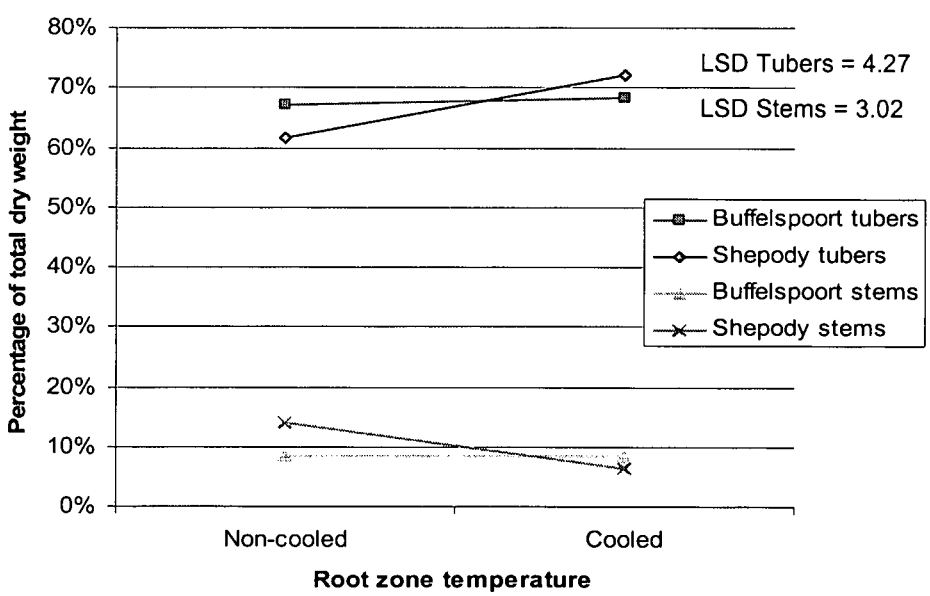


Figure 4.8 The interaction between the root zone temperature and the percentage of the total dry mass allocated to the tubers and stems for cultivars Shepody and Buffelspoort.

Cooling of the root medium caused a significant decline in the total dry mass per plant (leaves stems, roots, stolons and tubers) (Figure 4.9).

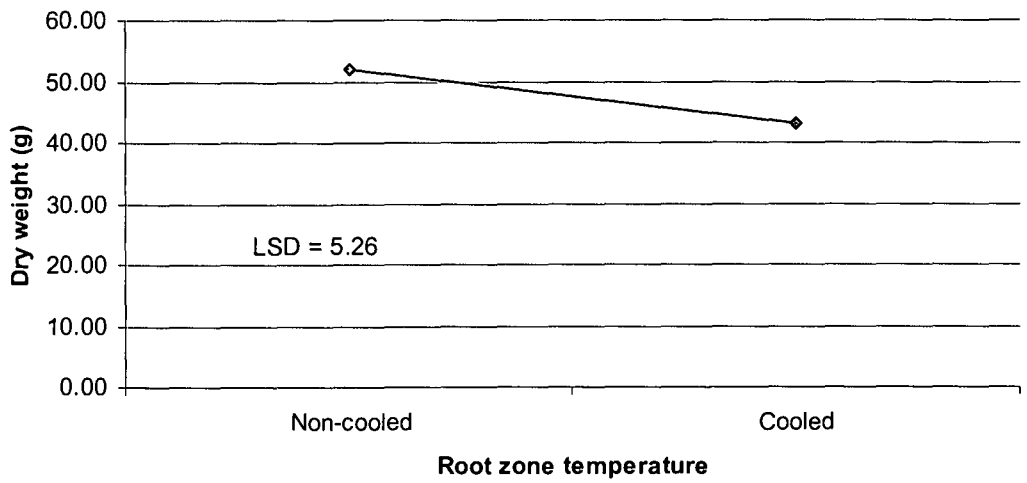


Figure 4.9 Mean total dry mass of plants from both cultivars grown with or without cooling of the growing medium.

Efficiency of dry matter production

Results of the ANOVA done on data with regards to the efficiency of dry matter production are summarized in Table 4.7.

Table 4.7 Significant levels (Pr > f) of main effects, namely root zone temperature and cultivar as well as interactions with regard to the tuber dry mass per leaf area (TDW / LA), the tuber dry mass per leaf dry mass (TDW / LDW) and the specific leaf area (SLA)(leaf area per leaf dry mass).

	TDW / LA (g cm $^{-2}$)	TDW / LDW (g g $^{-1}$)	SLA (cm^2 g^{-1})
Temperature	0.024955	0.064414	0.075611
Cultivar	0.277095	0.403568	0.443939
Temperature*cultivar	0.272796	0.261462	0.875450

There was no significant interaction between the root zone temperature and cultivar with regard to the TDW / LA, TDW / LDW or the SLA (Table 4.7). The root zone temperature had a significant effect on the TDW / LA while TDW / LDW and SLA were not significantly affected by the root zone temperature (Table 4.7). No significant differences in the TDW / LA, TDW / LDW or the SLA were observed between the cultivars (Table 4.7).

Cooling of the growing medium resulted in an increase in the TDW / LA (Figure 4.10). This effect can be ascribed to the decrease in leaf area when cooling the growing medium while the tuber dry mass was not significantly influenced.

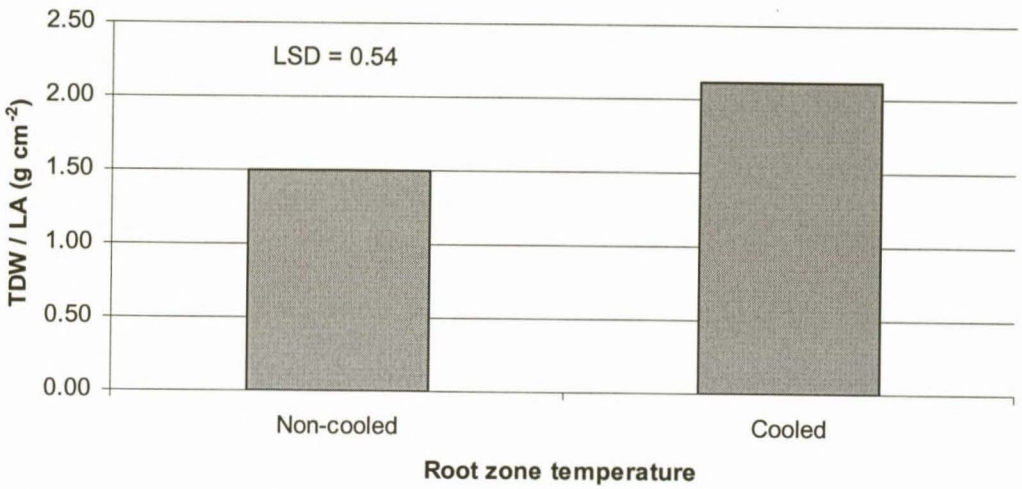


Figure 4.10 The tuber dry mass (TDW) per leaf area (cm^2) of a combination of the cultivars as affected by cooling of the growing medium.

The TDW / LDW was lower for plants grown in the non-cooled growing medium, although this effect was not significant (Figure 4.11). This can also be explained by the decrease in leaf dry mass when cooling the growing medium since tuber dry mass was not significantly influenced by the root zone temperature (Figure 4.11).

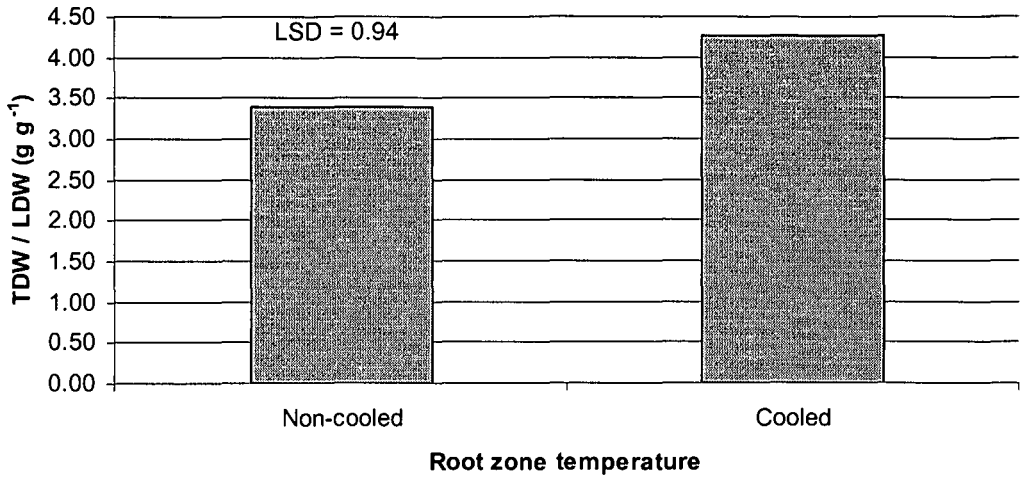


Figure 4.11 The mean tuber dry mass (TDW) per leaf area (cm^2) for plants from both cultivars with or without cooling of the growing medium.

Tuber number, size distribution and dry matter percentage

Results of the ANOVA done on data with regard to the tuber number per size class are summarized in Table 4.8.

Table 4.8 Significant levels (Pr > f) of main effects, namely temperature and cultivar as well as interactions with regard to the number of tubers in the different size classes.

	<20 g	20-40 g	>40 g
Temperature	0.965113	0.868945	0.329257
Cultivar	0.213683	0.413220	0.742352
Temperature*cultivar	0.050437	0.868945	0.742352

There was neither any significant interaction between temperature and cultivar nor any effect of temperature or cultivar on the number of tubers in any of the three size classes (Table 4.8).

Although not significant at $p < 0.05$, the number of tubers weighing less than 20 g for cultivar Buffelspoort was higher when the root was cooled compared to the un-cooled

control whereas cultivar Shepody had fewer tubers weighing less than 20 g when the root zone was cooled.
On average for both cultivars and both root zone temperatures the number of tubers per plant harvested were 3 for tubers weighing between 20 and 40 g and 0.5 for tubers weighing more than 40 g.

There was no significant interaction between temperature and cultivar on the tuber fresh or dry mass per size class or the average tuber fresh mass per size class and no effect of temperature or cultivar on either the tuber fresh or dry mass per size class or the average tuber fresh mass per size class (Addendum 4.1).

Average tuber fresh mass per plant for both cultivars and root zone temperatures were 4.3 g, 29.5 g and 54.3 g for the three size classes respectively.

Table 4.9 Significant levels (Pr > f) of main effects, namely temperature and cultivar as well as interactions with regard to tuber dry matter percentage for tubers in the different size classes.

	<20 g	20-40 g	>40 g
Temperature	0.932354	0.245051	0.689195
Cultivar	0.004934	0.355324	0.133429
Temperature*cultivar	0.603810	0.632122	0.849722

There were no interactions between root zone temperature and cultivar on the tuber dry matter percentage for tubers in any of the size classes (Table 4.9). Root zone temperature did not affect the tuber dry matter percentage for tubers in any of the three size classes and between the cultivars, except for the tuber dry matter percentage of tubers weighing less than 20 g (Table 4.9).

For tubers weighing less than 20 g at harvest, the tubers from cultivar Buffelspoort had a much lower dry mass percentage compared to the tubers from cultivar Shepody (Figure 4.13).

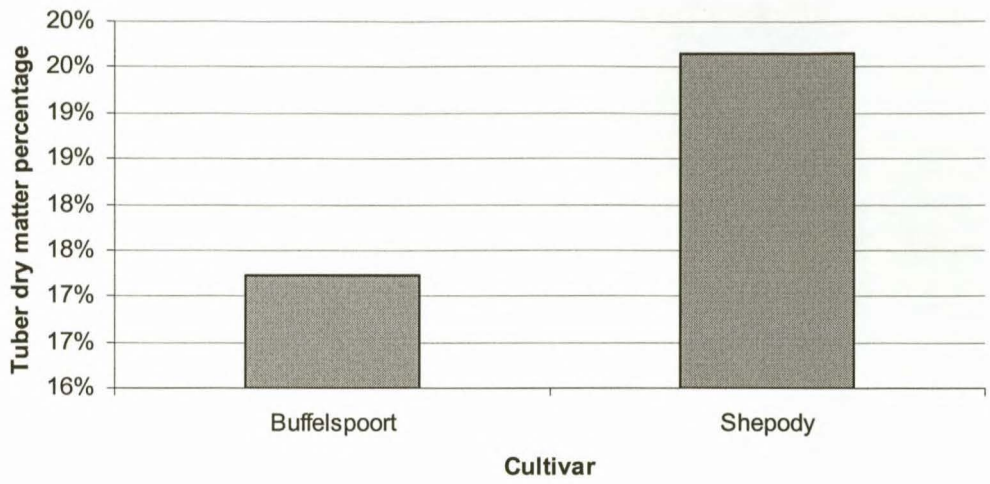


Figure 4.13 The mean dry matter percentage of tubers from both root zone temperatures weighing less than 20 g for cultivars Buffelspoort and Shepody.

Discussion

Crop morphology, the pattern of assimilate partitioning and yield can be influenced by environmental factors with yield being largely determined by the partitioning of carbon and nitrogen to the part of the plant that is utilized (Gifford & Evans, 1981). Ewing & Struik (1992) found that high temperatures lead to more assimilates being partitioned to the leaves and stems and less to the root system (Sattelmacher *et al.*, 1990) and tubers (Menzel, 1983). This study indicates that lowering the root zone temperature can cause a decrease in the total plant height and mass with the most noticeable effect being a decreased leaf, stem and stolon growth (Figure 4.3, Figure 4.5 & Table 4.3). Stems were shorter, with thicker leaves since the SLA was not significantly affected. This suggested that the growth rate of the plants was slowed down by cooling of the root medium, and could be due to a reduction in water and nutrient uptake and translocation under the lower temperatures (Franklin *et al.*, 2005) or a decrease in photosynthesis, although no decrease in transpiration and net photosynthesis was observed by Anderson & McNaughton (1973) when lowering the root zone temperature for various temperate species. Since the dry matter percentage and thus the water content of the leaves and stems were not significantly influenced by the cool root zone (Figure 4.7), it is possible that lowering the root zone

temperature did not cause a reduction in water and nutrient uptake. Potatoes are temperate climate crops and therefore would be expected to be more tolerant to root zone temperatures below 15^{0}C. For tropical species such as cassava, low root zone temperatures can lead to mineral deficiencies (Forno, Asher & Edwards, 1979) but for the temperate oilseed rape (*Brassica napus*), low root zone temperatures (10^{0}C) did not affect boron uptake rates or plant dry mass but it did promote the partitioning of boron to actively growing leaves (Zhengqian *et al.*, 2002). These results indicate that for temperate crops, such as the oilseed rape, a lower root zone temperature can actually facilitate the avoidance of boron, and possibly other nutrient deficiencies. The same may be true for the potato, as a temperate crop and further studies into the uptake and distribution of mineral elements as affected by different root zone temperatures can be useful to determine if temperature will have an effect on the mineral uptake and tuber quality of hydroponically grown minitubers. The lack of a temperature effect on the root growth in this study may also indicate that the potato is relatively cold tolerant and that water and mineral uptake was not negatively affected by the lower root zone temperature.

The results of this study suggest that a reduction in the root zone temperature to 10 to 15^{0}C as compared to a normal root zone temperature of 15 to 24^{0}C resulted in not only a decrease in biomass accumulation but a shift in assimilate partitioning from the stems to the tubers (Figure 4.8). According to Anderson & McNaughton (1973) low soil temperature can reduce leaf growth through inducing water stress which will reduce turgidity and thereby affect processes other than photosynthesis and transpiration resulting in reduced leaf expansion. The percentage of the total dry mass allocated to the tubers, also referred to as the harvest index, was higher when the root zone was cooled, especially for the cultivar Shepody. The larger harvest index of Shepody can also be ascribed to the fact that the stem mass of Shepody was reduced by a greater degree than Buffelspoort' due to cooling of the root medium. Since low temperatures are believed to extend the growing season (Tegara & Haverkort, 1996) it is possible that if harvesting took place at a later date the harvest index would be even higher.

The shift in assimilate partitioning from the stems to the tubers when the root zone is cooled could also have been facilitated by the reduction in the translocation of cytokinin and gibberellin (Atkin, Barton & Robinson, 1973).

The tuber mass per plant and tuber number per plant was not affected by cooling of the root zone. In effect the plants grown in the cooler root medium were more

efficient in accumulating dry matter in the tubers (Figure 4.10 & Figure 4.11) since a reduced leaf area resulted in the same tuber dry mass.

It is generally believed that the early initiation of tubers leads to a reduction in growth of the stems and roots (Ewing & Struik, 1992) and therefore tubers might have initiated earlier in the plants grown at the lower root zone temperatures. The lower stolon dry mass also indicated that tuberization may have commenced earlier when the root zone was cooled. If tuber initiation leads to a shift of assimilates away from the stems towards the tubers, early tuber initiation would thus result in small plants with smaller leaf surfaces and lower final tuber yield, while late tuber initiation will lead to larger plants with larger leaf surfaces and higher final yields (Bremner & Radley, 1966). However, more recent trials suggested that tuber initiation does not affect leaf and root growth and that leaves and roots are produced at a constant rate from emergence until after tuber initiation (O' Brien *et al.*, 1998).

In a review by O'Brien *et al.* (1998) it is stated that in their earlier research they found no effect on the onset of tuber initiation between soil temperatures of 12 and 19^{0}C but the duration of tuber initiation was however influenced by soil temperature, with a low soil temperature (<15^{0}C) being able to extend the period, while a soil temperature of 19^{0}C was able to shorten the initiation period with 1 week (O'Brien *et al.*, 1998). The results from this study do not indicate that root zone temperature affected the timing or duration of tuber initiation since no difference in the mean number or mean fresh and dry mass of tubers per size class was observed (Table 4.8). The number of tubers weighing less than 20 g was higher at the cooler root zone for Buffelspoort and higher at the warmer root zone for Shepody (Figure 4.12). The decrease in stem mass and leaf area was not necessarily brought about by earlier tuber initiation. If tuber initiation did take place earlier at the lower root zone temperature, the relative growth rate of the tubers must also have been reduced for final yields to be similar at the different root zone temperatures. It is possible however that extending the growing period by lowering the root zone temperature, could lead to an increased number of smaller tubers but a lower total yield in terms of tuber mass per plant.

The daily fluctuation in the root zone temperature of especially the un-cooled root medium and the difference in root zone temperature during the first half and second half of the trial period (Figure 4.1 & Figure 4.2) possibly caused an interacting effect not measured in this study. This should also be considered, since the difference in

ambient day and night temperature is known to affect stem and leaf development and mineral uptake and translocation (Gent & Ma, 2000).

Cultivars seem to differ in the ability to retain initiated tubers, in that for some cultivars the final tuber number at plant maturity may be only 60% of the tubers present earlier in the season (Walworth & Carling, 2002). Tuber reabsorption is considered by some to be more important in establishing tuber size distribution than tuber initiation (Struik *et al.*, 1990). This should be kept in mind when concluding on yield when conducting trials where tubers are harvested before full maturity. Earlier studies on the tuber inititation and development of Shepody revealed that this cultivar retain most of the tubers formed early on in the season (Walworth & Carling, 2002).

Studying the effect of local greenhouse conditions and altered temperature conditions on the assimilate partitioning in local potato cultivars can assist with optimizing production of G0 greenhouse minitubers.

Conclusion

The results indicate that cooling of the root medium may facilitate a decrease in foliage growth without affecting tuber formation and final tuber yield. As a temperate climate crop the lower root zone temperature might also benefit root metabolism and nutrient uptake. During the first few weeks of the crop growth, before a sufficient canopy has developed, the high light intensities can lead to considerable increases in root zone temperatures. Cooling of the root medium during the first few weeks after transplanting could result in a reduction in plant height, while not affecting tuber yields.

REFERENCES

ANDERSON, J.E., & MCNAUGHTON, S.J., 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. *Ecology* 54, 1220-1233.

ATKIN, R.K., BARTON, G.E., & ROBINSON, D.K., 1973. Effect of root growing temperature on growth substances in xylem exudates of *Zea mays*. *J. Exp. Bot.* 24, 475-487.

DEMAGANTE, A.L., & VAN DER ZAAG, P., 1988. The response of potato (*Solanum* spp.) to photoperiod and light intensity under high temperatures. *Potato Res.* 31, 73-83.

EWING, E.E., & STRUIK, P.C., 1992. Tuber formation in Potato: Induction, Initiation, and growth. *Hortic. Rev.* 14, 89-197.

FORNO, D.A., ASHER, C.J., & EDWARDS, D.G., 1979. Boron nutrition of cassava, and the boron-temperature interaction. *Field Crop Res.* 2, 265-279.

FRANKLIN, J.A., KAV, N.N.V., YAJIMA, W., & REID, D.M., 2005. Root temperature and aeration effects on the protein profile of canola leaves. *Crop Sci.* 45, 1379-1386.

GENT, M.N., & MA, Y., 2000. Mineral nutrition of tomato under diurnal temperature variation of root and stem. *Crop Sci.* 40, 1629-1636.

GIFFORD, R.M., & EVANS, L.T., 1981. Carbon partitioning and yield. *Ann. Rev. Plant Physiol.* 32, 485-509.

HAMMES, P.S., & DE JAGER, J.A., 1990. Net photosynthetic rate of potato at high temperatures. *Potato Res.* 33, 515-520.

HAVERKORT, A.J., VAN DE WAART, M., & BODLEANDER, K.B.A., 1990. The effect of early drought stress on numbers of tubers and stolons of potato in controlled and field conditions. *Potato Res.* 33, 89-96.

BEN KHEDHER, M., & EWING, E.E., 1985. Growth analysis of eleven potato cultivars grown in the greenhouse under long photoperiods with and without heat stress. *Am. Potato J.* 62,537-554.

KOOMAN, P.L., FAHEM, M., TEGERA, P., & HAVERKORT, A.J., 1996. Effects of climate on different potato genotypes 2. Dry matter allocation and duration of the growth cycle. *Eur.J.Agric.* 5, 207-217.

MENZEL, C.M., 1983. Tuberization in potato (*Solanum tuberosum* cultivar Sebago) at high temperature: interaction between stem and root temperatures. *Annu. Bot.* 52, 65-70.

MENZEL, C.M., 1985. Tuberization of potato under high temperatures: Interaction between temperature and irradiance. *Ann. Bot.* 55, 35-39.

MIDMORE, D.J., & PRANGE, R.K., 1992. Growth responses of two Solanum species to contrasting temperatures and irradiance levels: relations to photosynthesis, dark respiration and chlorophyll fluorescence. *Ann.Bot.* 69, 13-20.

O'BRIEN, P.J., ALLEN, E.J., & FIRMAN, D.M., 1998. A review of some studies into tuber initiation in potato (*Solanum tuberosum*) crops. *J.Agric. Sci.* 130, 251-270.

REYNOLDS, M.P., & EWING, E.E., 1989. Effects of high air and soil temperature stress on growth and tuberization in *Solanum tuberosum*. *Ann. Bot.* 64, 241-247.

SALE, P.J.M., 1979. Growth of potatoes (*Solanum tuberosum* L.) to the small tuber stage as related to the soil temperature. *Aust. J. Agric. Res.* 30, 667-675.

SARQUIS, J.I., GONZALEZ, H., & BERNAL-LUGO, I., 1996. Response of two potato clones (*S tuberosum* L.) to contrasting temperature regimes in the field. *Am. Potato Res.* 73, 285-300.

SATTELMACHER, B., MARSCHNER, H., & KUHNE, R., 1990. Effects of the temperature of the rooting zone on the growth and development of roots of potato (*Solanum tuberosum*). *Ann. Bot.* 65, 27-36.

StatSoft, Inc. (2006). STATISTICA (data analysis software system), version 7.1. www.statsoft.com.

STRUIK, P.C., & WIERSEMA, S.G., 1999. Control and manipulation of physiological seed tuber quality. In: Seed potato technology. Wagenin pers. pp. 95-131.

STRUIK, P.C., GEERRTSEMA, J., & CUSTERS, C.H.M.G., 1989. Effects of stem, root and stolon temperature on the development of the potato (*Solanum tuberosum* L.) plant. III. Development of tubers. *Potato Res.* 32, 143-150.

THIART, S., 2004. Maxi growers for mini tubers. *Chips* November/December, pp. 35-40.

THORTON, M.K., MALIK, N.J., & DWELLE, R.B., 1996. Relationship between leaf gas exchange characteristics and productivity of potato clones grown at different temperatures. *Am. Potato J.* 73, 63-77.

WALWORTH, J.L., CARLING, D.E., 2002. Tuber initiation and development in irrigated and non-irrigated potatoes. *Am. J. potato Res. 79, 387-395.*

WHEELER, R.M., TIBBITS, W., & NAJAR, A., 1986. Interactions of irradiance, temperature, and CO_2 in growth and tuberization of potato. *Hort. Science* 21, 741.

ZHENGQIAN, Y., HUANG, L., BELL, R.W., & DELL, B., 2003. Low root zone temperature favours stem B partitioning into young leaves of oilseed rape (*Brassica napus*). *Physiol. Plant.* 118, 213-220.

CHAPTER 5

General conclusions

For potato seed producers worldwide the trend is to reduce the number of field plantings since commercial growers prefer earlier generation seed in order to reduce the risk of disease and pests and because it will allow new or improved cultivars to enter the market sooner after development. Fewer field generations will also guarantee a higher tuber health and will be more environmentally friendly, since fewer pesticides will be used. In South Africa potato seed production makes use of meristem culture, the production of minitubers in a greenhouse, followed by several field multiplications. The *in vitro* plantlets are transplanted to a growth medium at high densities in the greenhouse to produce the minitubers used as starting material for the field multiplications. Current yields for minituber production are however relatively low. The growth, development and yield of the potato are largely dependent on environmental conditions, e.g. low light intensities as well as high temperatures are usually associated with lower tuber yields. Shade netting is used in many of the minituber greenhouses to reduce the air temperatures that can often reach between 25-30^{0}C during the production period. The high temperature and low light intensity could result in conditions sub-optimal for high minituber yields. The main objective of this study was to determine the effects of light intensity, light quality and root zone temperature on the potato plant growth, tuberization, assimilate distribution, tuber size distribution and tuber dormancy in order to improve conditions within the greenhouse to increase yield and possibly also tuber quality.

The light intensity study was conducted in a greenhouse from September 2006 to December 2006 in which the effect of three levels of shading (20%, 40% and 50%) was compared to an un-shaded control for two cultivars (BP1 and VanderPlank). From the results it became clear that shading can increase plant height and shoot weight but tuber number was not affected and the total tuber fresh weight per plant was only significantly reduced under the 50% shade treatment while there was actually a slight increase in the total tuber fresh weight per plant under the 20% shade. The distribution of biomass was only affected under the 40% and 50% shade treatments with more fresh weight being allocated to the shoots. However, shoot and tuber dry weight percentages were lower for all shade treatments

compared to the control. More of the tubers harvested from plants under the 50% shade treatment weighed less than 20g. The results also indicated that the duration of dormancy and the sprout growth is affected to a greater degree by the cultivar and tuber size than by light intensity, although light intensity will have an affect on tuber size and therefore indirectly influence the duration of dormancy and sprout growth.

These results indicate that shading of the potato plants in the greenhouse will result in morphological adaptations that are typical of shade avoidance and can lead to plants increasing the area available for light interception and / or making biochemical adjustments that will facilitate an increase in the efficiency of light capture and utilization. This would explain why plants under the 20% shade net actually showed evidence of an increase in total biomass accumulation. By decreasing the light intensity further, the increase in photosynthetic efficiency could probably not compensate for the high respiratory losses due to the high temperatures in the greenhouse and assimilate translocation to the tubers decreased, resulting in a slower tuber bulking evident in the smaller tubers harvested from the shaded plants and the lower dry matter content. Since tuber number was not affected by the light intensity and tuberization is thought to be reduced by high endogenous GA levels, it is unlikely that the low dry matter content of the tubers was due to high endogenous GA levels. Therefore, reducing the light intensity by 20% may be able to decrease temperatures in the greenhouse while increasing the efficiency of biomass accumulation, but will not affect the induction to tuberization that is considered to be brought about by a decrease in the level of endogenous GA.

Photoreceptors absorb light from different wavelengths and are known to affect the level or activity of plant growth regulators and possibly GA. Therefore, the second study conducted was to test the effect of three different colour filters, absorbing partly the blue, red or far-red light reaching the plants from two potato cultivars (Shepody and Buffelspoort) and compared to a control. The light quality study was conducted from January 2007 to April 2007 in the greenhouse.

The obtained results indicated that filtering part of the red light resulted in plants with an increased plant height, stem and leaf growth, an increased dry weight percentage of the leaves, increased stolon growth and an increased tuber weight and -number. The blue light filter resulted in an increased plant height, stem- and stolon growth but fewer and thinner leaves developed and tuber number and -fresh weight was not affected. Total biomass assimilation increased, but not assimilate partitioning to the tubers. Decreasing the far-red portion of the light reaching the

plants did not lead to a decrease in plant height, leaf or stem dry weight, but did decrease the internode length and increased the leaf dry weight percentage. Fewer tubers were formed and the total tuber fresh weight was significantly lower for Buffelspoort than for Shepody, leading to the lower efficiency of biomass production for plants of this cultivar. The dry matter partitioning indicated that less biomass was partitioned to the tubers under the far-red filter. The development of aerial tubers at the nodes of plants from the cultivar Shepody also indicated that the tuberization signal is affected under the far-red filter (increased R:FR ratio).

An increase in the leaf dry weight percentage could indicate a high starch accumulation rate in the leaves. Under the red filter it seemed that this was due to an increase in the assimilation rate, probably caused by an increase in the demand from the tubers, while under the far-red filters the increase in leaf dry weight percentage was more likely due to and inhibition in the transport of assimilates to the developing tubers. The formation of aerial tubers also supports this hypothesis. These results also indicate that stolon growth is closely related to the number of tubers and therefore any factor that will enhance stolon growth, should increase tuber number, unless tuber initiation is inhibited. Also a large leaf area is necessary to sustain a high carbon assimilation rate since under the blue filter, although stolon growth was enhanced, and the leaf area increased, tuber number and weight did not increase.

Dry matter assimilation and distribution within the plant are key factors determining crop productivity. Both photomorphogenesis and plant hormones are involved in regulating the source-sink relationship within a plant and photomorphogenic responses can influence the assimilate partitioning and the plants' ability to accumulate biomass. Therefore, for the potato plant, it seems that yield is not solely dependent on radiation interception and photosynthesis, but is intricately controlled by endogenous plant growth regulators. Further investigation into the rate of photosynthesis and respiration as well as the endogenous levels and distribution of plant growth regulators under the different spectral filters may help explain the results obtained in this study and enable us to investigate further the effect light will have on tuber quality.

Temperature is another key factor known to affect tuberization and dry matter allocation and the growth medium temperature, which can be very high at the beginning of the season in the greenhouse, should play a key role in yield and quality. The root zone temperature study was conducted from January 2007 to April

2007 in the glasshouse, using cultivars Buffelspoort and Shepody. Results indicated that lowering the root zone temperature can cause a decrease in the total plant height and weight with the most noticeable effect being a decreased leaf, stem and stolon growth. The lower root zone temperature not only resulted in a decrease in biomass accumulation but a shift in assimilate partitioning from the stems to the tubers, with the end result being that plants grown in the cooler root medium were more efficient in partitioning of dry matter to the tubers resulting in an increased harvest index. This effect was not observed to the same degree for both cultivars and cooling of the root medium may thus be more beneficial to certain cultivars. These results suggest that cooling of the root zone resulted in earlier tuberization and the relative growth rate of the tubers was probably also reduced since final yields were similar at the different root zone temperatures. The lack of a temperature effect on the root growth in this study may indicate that the potato is relatively cold tolerant and that water and mineral uptake was not negatively affected by the lower root zone temperature. Further studies into the uptake and distribution of mineral elements as affected by different root zone temperatures can be useful to determine if temperature will have an effect on the mineral uptake and tuber quality of hydroponically grown minitubers.

In conclusion, results from these studies indicate that the potato plant growth, tuberization and dry matter distribution within the plant can be controlled in the greenhouse by regulating the light quantity, light quality and root zone temperature, resulting in increased yields. High light intensities as well as a cool root zone can reduce the excessive foliar growth. In areas where the light intensity is low during the production period, supplemental lighting with the addition of a red light filter may enhance tuber yield. Additional research could possibly lead to the development of models that can be implemented in the greenhouse to precisely manage different crops and cultivars in terms of light and temperature requirements.

ADDENDUM

Addendum 2.1 Number and fresh weight of tubers in each of the seven size categories for plants from cultivars BP1 and Van der Plank grown at different light intensities.

		No tubers						
		< 5g	**5-10g**	**10-20g**	**20-40g**	**40-60g**	**60-80g**	**>80g**
Control	BP1	7.50	3.33	3.75	3.00	2.00	1.00	1.00
Control	VDP	4.00	3.33	2.00	5.25	3.00	1.50	1.75
20% intensity	BP1	6.25	3.00	5.00	5.25	3.75	1.00	1.00
20% intensity	VDP	7.25	1.75	2.00	5.50	3.00	2.00	2.00
40% intensity	BP1	5.50	3.75	3.67	2.75	1.50	1.00	0.00
40% intensity	VDP	3.33	1.00	3.33	4.00	2.00	1.00	2.33
50% intensity	BP1	7.50	3.50	2.50	4.00	1.00	0.00	0.00
50% intensity	VDP	6.67	4.33	5.00	4.00	1.67	2.00	1.00
		Tuber Fresh weight						
		< 5g	**5-10g**	**10-20g**	**20-40g**	**40-60g**	**60-80g**	**>80g**
Control	BP1	19.30	26.80	58.90	85.67	97.60	88.50	121.63
Control	VDP	7.23	29.73	32.90	158.78	149.03	103.58	183.53
20% intensity	BP1	11.58	24.50	78.60	156.33	184.88	70.30	85.80
20% intensity	VDP	13.03	15.73	28.60	155.35	158.37	136.67	412.58
40% intensity	BP1	12.95	30.30	61.80	82.38	73.85	64.53	0.00
40% intensity	VDP	6.57	5.20	49.03	112.03	99.17	70.75	289.90
50% intensity	BP1	14.50	27.90	36.58	108.60	48.90	0.00	0.00
50% intensity	VDP	14.47	30.30	75.33	129.17	76.27	142.00	83.90

Addendum 3.1 Means from the analysis of variance for the effect of light quality and cultivar on the vegetative growth parameters for the first harvest date.

First harvest

Treatments	PH	IL	L DW	L DMC	S DW	S DMC
Light filter						
Control	17.25a	2.54a	7.22a	9.23a	5.85a	11.85a
Far-red light	13.38b	1.68b	6.37b	9.77a	4.64b	11.97a
Red light	35.88c	3.72c	5.51c	9.91b	5.36a	10.95b
Blue light	40.25d	5.13d	6.58b	9.56a	5.75a	12.48a
LSD (P = 0.05)	2.45	0.36	0.80	0.80	0.92	1.19
Cultivars						
Shepody	24.19a	3.25a	6.62a	9.78a	5.04a	11.21a
Buffelspoort	29.19b	3.28a	6.21a	9.46a	5.76b	12.41b
LSD (P = 0.05)	1.29	0.19	0.42	0.42	0.49	0.63

Means followed by the same letters are not significantly different at the 5% probability level.

Addendum 3.2 Means from the analysis of variance for the effect of light quality and cultivar on the stem : leaf ratio and the specific leaf area.

First harvest

Treatments	S : L	SLA
Light filter		
Control	0.806a	179.55ab
Far-red light	0.743a	207.61a
Red light	1.000b	210.12a
Blue light	0.872ab	173.61b
LSD (P = 0.05)	0.144	31.22
Cultivars		
Shepody	0.769a	202.07a
Buffelspoort	0.941b	183.51b
LSD (P = 0.05)	0.076	16.48

Means followed by the same letters are not significantly different at the 5% probability level.

Addendum 3.3 Means from the analysis of variance for the effect of light quality and cultivar on the sub-soil parameters for the first harvest date.

First harvest

Treatments	R FW	R DW	St FW	St DW	T FW	T DW
Light filter						
Control	15.28a	1.36a	4.37a	0.36a	56.58ac	10.61ac
Far-red light	16.04a	1.40a	4.76a	0.42a	33.73a	6.21a
Red light	16.57a	1.54a	13.19b	1.18b	110.21bc	21.03bc
Blue light	15.84a	1.49a	11.23b	1.01b	80.05c	15.08a
LSD (P = 0.05)	1.87	0.22	1.99	0.16	32.48	6.78
Cultivars						
Shepody	15.88a	1.40a	6.92a	0.59a	84.31a	16.02a
Buffelspoort	15.99a	1.50a	9.86b	0.89a	55.97b	10.44b
LSD (P = 0.05)	0.99	0.11	1.05	0.08	17.15	3.51

Means followed by the same letters are not significantly different at the 5% probability level.

Addendum 3.4 Means from the analysis of variance for the effect of light quality and cultivar on the tuber number, average tuber fresh weight and tuber fresh weight per leaf area.

First harvest

Treatments	Tuber Number	ATFW	TFW / LA
Light filter			
Control	6.38a	9.24a	4.37a
Far-red light	3.13b	8.84a	2.58a
Red light	14.25c	8.46a	9.63b
Blue light	6.88a	11.47a	7.14c
LSD (P = 0.05)	2.46	4.54	2.24
Cultivars			
Shepody	6.63a	12.49a	6.77a
Buffelspoort	8.69b	6.60b	5.09b
LSD (P = 0.05)	1.30	2.40	1.18

Means followed by the same letters are not significantly different at the 5% probability level.

Addendum 4.1 Significant levels (Pr > f) of main effects, namely temperature and cultivar as well as interactions with regard to the tuber fresh weight and dry weight per plant for and average tuber fresh weight for each of the three size classes.

Tuber fresh weight

	<20g	20-40g	>40g
Temperature	0.828713	0.877245	0.169785
Cultivar	0.310338	0.221545	0.239745
Temperature*cultivar	0.532264	0.980953	0.238691

Tuber dry weight

	<20g	20-40g	>40g
Temperature	0.663289	0.752661	0.220727
Cultivar	0.096334	0.271331	0.684725
Temperature*cultivar	0.372909	0.904854	0.614090

Average tuber fresh weight

	<20g	20-40g	>40g
Temperature	0.657309	0.183938	0.445976
Cultivar	0.850762	0.554945	0.588581
Temperature*cultivar	0.410311	0.723886	0.586570