NASA Contractor Report 177646

Growth of Potatoes for CELSS

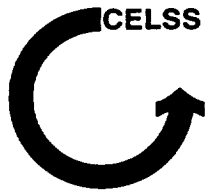
T. W. Tibbitts, W. Cao, and R. M. Wheeler

University of Wisconsin–Madison
Department of Horticulture
Madison, WI 53706

Prepared for
Ames Research Center
CONTRACT NCC2-301
August 1994

National Aeronautics and
Space Administration

Ames Research Center
Moffett Field, California 94035-1000



SUMMARY

The white potato (*Solanum tuberosum* L.) is one of eight plant species that has been proposed for inclusion in bioregenerative life support systems for space bases. The potato has several desirable characteristics for life support in space. The crop has a high productivity of digestible food per unit area per unit time, and a high ratio (0.80) of edible to inedible biomass (harvest index). The edible portions of potatoes, the tubers, are nutritious, consisting primarily of carbohydrates (82%), with a significant amount of protein (11%). These proteins have a reasonable balance of all required amino acids and are high in methionine and lysine. Potatoes require no special processing and can be prepared in a number of culinary forms which are palatable and acceptable to most people. Also, they can be stored for periods up to 6 months as fresh tubers or for longer periods as a frozen or dried product.

This report summarizes research on the utilization of potatoes for space life support systems undertaken at the University of Wisconsin-Madison over the period of 1984 to 1993 under Cooperative Agreement NCC 2-301. An extensive series of studies was conducted, first to establish cultural conditions guaranteeing consistently high yields in controlled environments, then to determine environmental conditions insuring both adequate and optimum growth of the crop, and finally to study growing procedures that would have usefulness in life support systems in space.

Potatoes for these research studies were propagated from stem cuttings maintained under sterile culture. This provided homogenous, disease-free, and insect-free plants. Similar pest-free plants could easily be maintained in space through use of small tubers. Plants could be easily started from small tubers (0.5- 1.0 cm) initially taken into space and then additional small tubers would become available from the mature plants at each harvest. A small number of tubers would be required (about 10 tubers for each square meter of growing area) because each plant branches and will fill the available space rapidly.

Successive harvests demonstrated that tuber production continued to increase until the last harvest at 147 days, but the productivity in grams per unit area per day was essentially level from 105 to 147 days. In an operational life support system, it would likely be an advantage to maintain plants for as long a growing period as possible to reduce the frequency of planting and

harvesting operations. At full maturity, a total plant dry weight was obtained of 5920 g m^{-2}, edible dry weight of 4352 g m^{-2}, tuber productivity of 37.5 g m^{-2} d^{-1}, and nutritional yield of 139 kcal m^{-2} d^{-1}. This production equates to a growing area requirement for 1 human (2800 kcal d^{-1}) of 20.1 m^2. In an operational CELSS, more area than this should be programmed to provide some leeway for yield variations and losses of tubers during storage.

Potatoes grow well and tuberize effectively in many different types of media. Effective growth has been obtained in commercial peat:vermiculite mixture (1:1), arcillite (baked montmorillonite clay) particles, and gravel particles. These media are effective because they maintain adequate aeration with different types of watering and nutrient feeding procedures. The arcillite and gravel media would be most useful in space because they could be sterilized with heat and would maintain their particle size over long periods of time.

Several different types of recirculating nutrient systems including solution culture, mist culture, and nutrient film technique were studied. The plants grew and expanded rapidly in all types of nutrient systems, however, plants tuberized normally and developed successfully only when the nutrient was provided as a nutrient film. In solution culture and mist culture, tuber initiation and enlargement was severely inhibited. Best potato growth and tuber yields were obtained with nutrient film provided in trays with a 2-3 cm layer of gravel or arcillite media with the media covered with a light-tight plastic film to maintain the rooting area at high humidity. The thin layer of media ensured that tuber formation and enlargement occurred above the mass of fine roots and thus avoided the problem of tubers enlarging and lifting roots out of the nutrient film.

A major portion of the research effort in this project was directed toward understanding the role of environmental factors controlling potato growth in order to establish the range of conditions for which tuber productivity would be high. Most studies included one early maturing cultivar, usually Norland, and one late maturing cultivar, either Denali or Russet Burbank. In certain studies evaluations were made with as many as 23 different cultivars obtained from different locations throughout the world.

The summary of these environmental research studies is that potato production in life support systems would be close to maximum under lighting levels of 400 μmol m^{-2} s^{-1} of photosynthetic photon flux (PPF) for 24 hours or 800 μmol m^{-2} s^{-1} for 12 hours, alternating diurnal temperatures of 22 C and 14 C, relative humidity of 85%, and carbon dioxide level of

1000 μmol mol^{-1}.

Light plays a major role in potato production. Long light periods ($\geq$ 16 hours) encouraged stem elongation and branching so that when photon levels were low (200 μmol m^{-2} s^{-1}), tuber production was delayed and allocation of photosynthates to tubers reduced compared to short photoperiods ($\leq$ 12 hours). However, when photon levels were $\geq$400 μmol m^{-2} s^{-1}, sufficient photosynthates were available for allocation to tubers even though photoperiods were long. Thus, potato yields were closely linked to the total quantity of photons obtained in each 24 hour period, irrespective of the length of the light period. Potato yield was essentially similar with 400 μmol m^{-2} s^{-1} of continuous lighting compared with 800 μmol m^{-2} s^{-1} of 12 hour lighting. A harvest index of 80% was obtained under both photoperiods although stem length was greatly increased under the long photoperiod. When the photoperiod was changed between 12 and 24 hours during growth, greater tuber yields were obtained with 12 h photoperiods during early vegetative growth and 24 h photoperiods during tuber enlargement than with the reverse treatments. Although greatest tuber yields were obtained with continuous 24 h lighting during the entire growth period. Continuous lighting (or longer than 16 h light periods) was found to produce severe stunting of certain cultivars as Kennebec and Superior, unless grown with diurnal temperature fluctuations of at least 8 C. The use of supplemental far red wavelength irradiation at the end of the photoperiod had no significant effects on plant morphology. The use of within-canopy light also had no significant effect on plant morphology and did not cause leaf epinasty. Problems with management of within-canopy systems during plant growth appear to limit their usefulness in CELSS.

Temperature is an extremely important environmental factor for regulating tuber production in potatoes. Tuberization requires cool temperatures and was found to be maximum between 16 and 20 C. At 24 C, tuberization was severely inhibited, and at 28 C no tubers formed on the plants, although shoot dry weight increased with increasing temperatures. Warmer temperatures (22 C) during the first three weeks of growth followed by 17 C were found to promote greater tuber growth than maintaining cool temperatures (average of 18 C) during the entire growth period. Diurnal fluctuations in temperatures, as 22 L:14 D, provided greater growth and tuber yields with some cultivars and no advantage with others. Fluctuations were of particular advantage to prevent injury to certain sensitive cultivars when grown under continuous light.

Tuber production of potatoes was greater at high relative humidity (85% RH) than at low (50% RH), particularly under 12 h light periods. Under 12 h light periods, RH increases from 50% to 85% at 18 C enhanced both total plant growth and tuber yield, whereas under continuous light, RH increases had no significant effect on total plant growth but encouraged allocation to tubers. These responses to humidity were more significant with Denali than with Norland cultivar.

Studies with elevated carbon dioxide levels to 1000 μmol mol^{-1} documented significant growth advantages, resulting from enhanced photosynthate production. Increases in carbon dioxide during dark periods showed no benefit. It appeared that increasing CO_2 above 1000 μmol mol^{-1} had little advantage at 16 C, but at 20 C tuber production would likely continue to increase with CO_2 up to 2000 μmol mol^{-1}. Also, relative effects of CO_2 enrichment on potato growth was found to be greater at low humidity than at high humidity. The advantages of elevated CO_2 were evident when PPF levels were below 34 moles PPF per day (this equates to a PPF of 800 μmol m^{-2} s^{-1} for 12 hours or 400 μmol m^{-2} s^{-1} for 24 hours), whereas when PPF was greater than 34 moles per day, elevated CO_2 levels were of no advantage and were found to decrease yield.

A series of studies was undertaken to establish the concentrations of each of the separate nutrients for effective potato growth under controlled environment. From these separate studies, the ranges of concentrations in mM for good growth were found to be (the value in parenthesis indicates the concentration for maximum growth): K = 0.5 to 6 (3), P = 0.5 to 1.4 (1), N (as nitrate) = 2 to 8 (5), N (as ammonium) = 2 to 4 (3)., Ca = 0.25 to 5 (1), Mg = 0.25 to 2 (1), Fe = 0.5 to 5 (2), and Mn = 0.1 to 10 (0.5). It was found that when total nutrient concentrations were increased, there was a slowing of vegetative growth and stimulation of tuber growth. Uptake of N, S, P, and K from the solution on a proportionate basis was similar and greater than the proportionate uptake of Ca and Mg. Nutrient uptake was about 50% greater during the light period than during the dark period.

Studies were made to determine if potato plants could use both the NO_3 and NH_4 forms of nitrogen effectively. Leaf area, total and tuber dry weights per plant were consistently higher with the NO_3 form than with the NH_4 form. However, plant growth and tuber yield were consistently higher with both forms present in the solution than with either nitrogen form alone. The presence of NH_4 in the solution decreased Ca and Mg uptake into the plant and greatly

increased chlorine uptake and accumulation in the tissues.

Experiments were conducted to determine potato responses to different solution pH levels. At solution pH levels between 3.5 and 7.5, the optimum pH level was closely linked to the form of nitrogen in the solution. Plant dry weight and tuber number were highest at pH 5 with NO_3 and highest at pH 6 with NH_4. However, with both nitrogen forms present in the solution, growth was vigorous for the entire pH range of 4.5 to 7.0.

Determinations were made of glycoalkaloid levels in the tubers of potatoes grown under the various conditions of temperature, light intensity, photoperiod, carbon dioxide, and relative humidity evaluated in this project. The results indicate that there is no unacceptable accumulation of glycoalkaloids in potatoes for CELSS under any particular controlled environment conditions.

Effort was made to establish if plant species recommended for growth in CELSS would have undesirable allelopathic reactions when grown with a common recirculating nutrient solution. Experiments maintained for 35 days with potato and wheat grown in a combined solution culture system demonstrated that there were no important negative effects of potatoes on wheat or wheat on potatoes. However, small differences in growth for the different treatments were seen and justify additional allelopathic study with these crops grown to full maturity.

The extensive studies with potatoes in this project have demonstrated that this crop has high productivity of nutritious tubers with a high harvest index in controlled environments, and thus can fulfill a significant portion of the energy and protein requirements for humans in space. Adequate information is now known to utilize potatoes effectively in space and this crop has distinct advantages that encourage its inclusion in space life support systems to provide food, supply oxygen, purify water, and removal of excess carbon dioxide.

CONTENTS

SECTION 1. INTRODUCTION

The white potato (*Solanum tuberosum* L.) is one of eight plant species that has been proposed for inclusion in bioregenerative life support systems for space bases (Tibbitts and Alford, 1982). The others are wheat, rice, peanut, soybean, sweetpotato, sugar beet, and lettuce. Potatoes are unique among these crop species in that the edible portions of the plant develop as tubers below the soil surface on underground, horizontally-growing stems.

The potato has several desirable characteristics for life support in space (Tibbitts and Alford, 1982; Tibbitts and Wheeler, 1987). The crop has a high productivity of digestible food per unit area per unit time, and a high ratio (0.80) of edible to inedible biomass (harvest index). This minimizes growing space for effective food production and reduces energy expenditure for recycling the inedible portions of the crop. The edible portions of potatoes, the tubers, are nutritious, consisting primarily of carbohydrates (82%), with a significant amount of protein (11%). These proteins have a reasonable balance of all required amino acids and are high in methionine and lysine (Desborough, 1985). Potatoes require no special processing and can be prepared in a number of culinary forms which are palatable and acceptable to most people. Also, they can be stored for periods up to 6 months as fresh tubers or for longer periods as a frozen or dried product.

This report summarizes research on the utilization of potatoes for space life support systems conducted at the University of Wisconsin over the period of 1984 to 1993 under Cooperative Agreement NCC 2-301. An extensive series of studies have been carried out, first to develop cultural conditions to insure consistently high yields in controlled environments, then to determine environmental conditions for both adequate and optimum growth of the crop, and finally to develop growing procedures that would have usefulness in life support systems in space.

A major portion of the research effort in this project has been directed toward understanding the role of environmental factors controlling potato growth and specifically toward encouraging tuber productivity. The effort was directed toward quantifying the effects of all different environmental conditions to establish the range of conditions under which potatoes could be grown successfully and to model the edible and inedible productivity under different

interacting conditions. Potatoes, and other crops with vegetative storage organs, have very dramatic responses to specific environmental levels that trigger or depress the accumulation of photosynthates in the storage organs, thus markedly affecting the productivity of the edible product. A major importance in this regard are factors as light intensity, light duration, temperature, nutrient levels, and pH.

The significant findings in this project for NASA CELSS have been partially summarized in previous reports (Tibbitts and Wheeler, 1986a, 1986b, 1987; Wheeler et al., 1988; Tibbitts et al., 1989; Tibbitts and Cao, 1992) and studies of general scientific interest have been reported in several different scientific journals. Here, presented is a comprehensive summary of all studies undertaken during this project. References of the published research are cited in the text and listed in Section 11 References.

The research being reported under this Cooperative Agreement has been the result of a large number of cooperating individuals assuming responsibilities for particular phases of the work. This includes Joseph Van Elbe and Anati Chungcharoen of the Food Science Department providing the glycoalkaloids determinations, Maria Teslik undertaking the allelopathy studies, Amina Najar and Prof Brian Yandell conducting the modeling investigations, and Alberto Villanaueva undertaking the continuous harvesting experiments. Special thanks are extended to the research specialists over the years, Laura Paine, Ann Fitzpatrick, and Laura Kao, and to the Electronics Technician, Thomas Frank, who have made special commitments to this project and insured precision and reliability in the many experiments. A special thanks to the staff of the Biotron in maintaining controlled environments for these studies and to the many staff in the Departments of Horticulture and Botany for the sharing of their facilities for particular investigations.

Theodore W. Tibbitts
February 1994

SECTION 2. CULTURAL STUDIES

PLANT PROPAGATION

Sterile propagated plantlets have been utilized for all research studies conducted in this project. These plantlets are produced from stem cuttings of sterile plants.

Initially, potato shoots were obtained from tubers sprouted in a chamber under non-sterile conditions. A procedure described by Goodwin et al (1980) was utilized. The tips of shoots from tubers were excised, cut, and immediately dipped in molten (less than 60°C) paraffin wax (melting point 54°C) to prevent uptake of the sterilant. The excised shoot tips were then immersed in 1% $NaC10_4$, 0.1% Tween-20 solution for 7 minutes, with gentle shaking, and rinsed four times in sterile distilled water. The shoot tips were then cut to 10-20 mm and transferred to 17 mm x 150 mm test tubes containing 10 ml of agar medium and capped with plastic caps.

The agar medium contains inorganic salts (Murashige and Skoog, 1962), sucrose and vitamins as detailed in Table 2.1. The concentrations of inorganic salts are (mg/l) 1650 NH_4NO_3, 1900 KNO_3, 332.2 $CaCl_2$, 180.7 $MgSO_4$, 170 KH_2PO_4, 37.25 Na_2EDTA, 27.8 $FeSO_4 \cdot H_2O$, 6.2 H_3BO_3, 16.9 $MnSO_4 \cdot H_2O$, 5.37 $ZnSO_4 \cdot H_2O$, 0.83 KI, 0.25 $Na_2MoO_4 \cdot 2H_2O$, 0.016 $CuSO_4$, 0.014 $CoCl_2$. The concentrations of other constituents are sucrose 60 g/l, agar 16 g/l, thiamin 0.9 mg/l, nicotinic acid 0.1 mg/l, pyridoxine 0.1 mg/l, glycine 0.4 mg/l, and MYO-inositol 100 mg/l.

The test tubes with shoot tips were transferred to a culture room under continuous cool white fluorescent lighting at 60 μmol m^{-2} s^{-1} PPF and temperature of 20 C. Plantlets that developed free of disease were saved for use in experiments and those showing any fungal or bacterial growth on the media were discarded. Duplicate plant cultures were maintained in a second facility in a separate location to avoid technical problems with growth chambers or contamination by small insects which would cause loss of culture lines.

When the selected plantlets had a stem of $\approx$ 10 cm long between 26 and 30 days after transfer, they were utilized for regeneration of new plantlets (Figure 2.1). These plantlets were removed from the tubes within an aseptic transfer hood and 3-5 nodal cuttings were made. Each nodal cutting selected for use contained at least a 1 cm section of stem and a bud that was dormant (or lateral shoot less than 2 mm in length). If cuttings had a lateral shoot that was of

Table 2.1. Composition of culture medium utilized for sterile culture of potato plantlets.

Constituents	Conc.	Constituents	Conc.
	mg/l		mg/l
NH_4NO_3	1650	KI	0.83
KNO_3	1900	$Na_2Mo0_4 \cdot 2H_20$	0.25
$CaCl_2$	332.2	$CuSO_4 \cdot 5H_20$	0.016
$MgSO_4 \cdot 7H_20$	180.7	$CoCl_2 \cdot 6H_20$	0.014
KH_2PO_4	170	Thiamine · HCI	0.9
$Na_2 \cdot EDTA$	37.25	MYO-inositol	100
$FeS0_4 \cdot 7H_20$	27.8	Nicotinic acid	0.1
H_3BO_3	6.2	Pyridoxine · HC1	0.1
$MnSO_4 \cdot H_20$	16.9	Glycine	0.4
$ZnSO_4 \cdot 7H_20$	5.37		
Sucrose 60 g/l and agar 16 g/l			

larger size and developing rapidly, shoot production was often accelerated and root development depressed. The leaf was removed from the node cutting and then transferred to a fresh sterilized 17 mm x 150 mm test tube containing 10 ml of agar medium.

These micropropagated shoots were then grown in a tissue culture room at 20 C and continuous lighting of 60 μmol m^{-2} s^{-1}. When new plantlets were between 6-8 cm in length at 21-23 days after transfer, they were used for experiments. These plantlets were shorter than the plantlet shown in Figure 2.1, and the growing tip was slightly below the bottom of the cap.

When used for experimentation, the plant and agar were carefully lifted from each test tube using a thin spatula and then gently laid into a tray of distilled water. The agar was gently separated from the roots in the water. The plantlet was then transplanted to the experimental container being careful not to scrape or bend the tender stem of the plant. The plantlets were

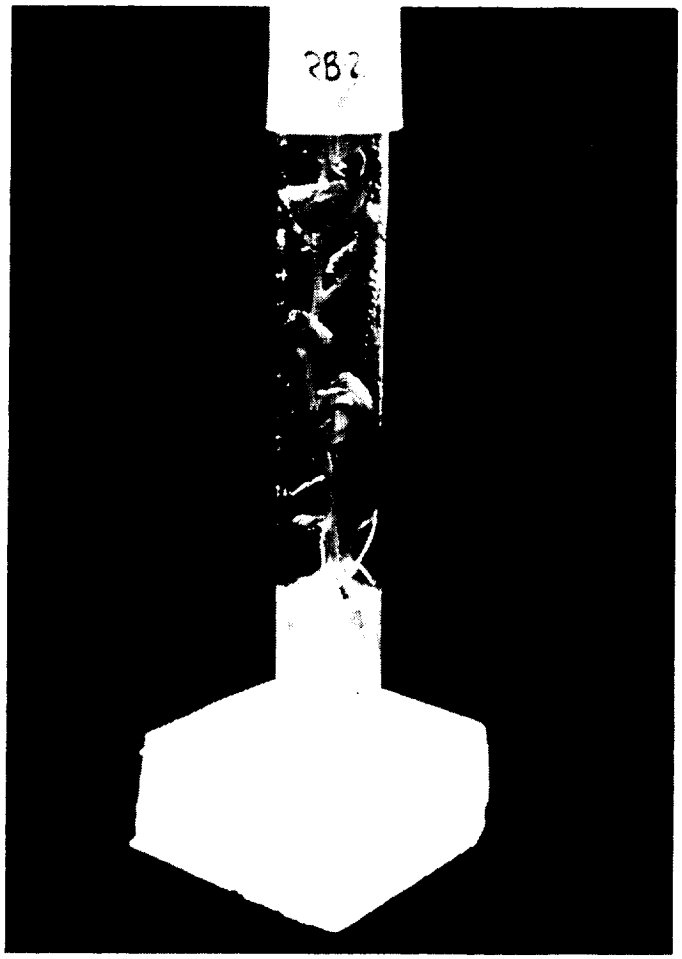


Figure 2.1. Sterile plantlet of potatoes used for regeneration of new plantlets.

planted to a depth of a 3-4 cm with 3-4 cm of stem protruding above the surface. After transplanting into containers, the plantlet was covered with a 200 ml glass beaker or transparent plastic cup for 3 days to maintain a high humidity around the shoot until roots became established.

GROWING SYSTEMS

In the field, potatoes are grown in soil in which the tuber is buried ten or more centimeters under the soil and commonly additional soil is 'hilled' around the plants to further

bury the roots and tubers. Thus, a large volume of soil is utilized for the production of potatoes. In contrast to these field procedures, when potatoes are grown for life support in space, there is a need to keep the mass of the tuber-bearing matrix to a minimum.

Several different growing systems have been evaluated involving different solid matrices in containers and various hydroponic systems including solution culture (containers filled with liquid), nutrient film procedures, and mist culture. Good plant growth has been obtained with all procedures, yet consistent tuber production has only been obtained when solid matrices were used with container and nutrient film growing systems.

For much of the research to establish the responses of potatoes to environmental conditions, studies have been conducted using large containers with a large quantity of media to insure that there were no interacting stresses on the root system. However, this type of culture would not be applicable to space growing systems.

Container Culture. For most experiments, plants in container culture were maintained in a peat-vermiculite (50:50 V:V) mix commercially prepared with additions of limestone and balanced nutrients. The medium was moistened with as much distilled water as possible without causing clumping and then loosely placed in containers to full. The containers were then gently tapped twice to settle the media 10%. Plants were transplanted into the media with light compaction. The containers were only filled to within 4 cm of the top. At 14 days after planting, the containers were filled to the top with additional peat-vermiculite mix.

The loose-filling of containers permitted the use of automatic drip watering systems with applications at frequent intervals, usually every 6 hours to keep the media close to saturation at all times. The duration of each watering was adjusted weekly so that leachate from the containers was about 50% of solution supplied to the containers. Each watering involved use of a dilute nutrient solution (Hammer et al, 1978) with nutrient concentrations as detailed in Table 2.2.

Container capacity varied between 1-38 liters depending on the length of the experiment and the expected, final size of the plants. Plants growing in 38-liter polyethylene containers are shown in Figure 2.2.

Two studies were undertaken to obtain information on potato growth versus container size. In one experiment involving successive harvests from 42 days to 148 days after planting,

Table 2.2. Composition of nutrient solution utilized for potato studies.

Macro-Nutrient	Concentration		Micro-Nutrient	Concentration	
	mmol/l	ppm		μmol/l	ppm
N[z]	7.5	104.9	B	23.0	0.25
K	3.0	117.4	Mn	4.57	0.25
P	0.5	15.5	Mo	0.055	0.005
Mg	1.0	32.0	Zn	0.38	0.025
Ca	2.5	100.2	Cu	0.16	0.010
Fe[y]	0.09	5.0	Cl	500.0	18.10
S	1.0	32.0			

[z] All as nitrate. [y] As sequestrene 330.

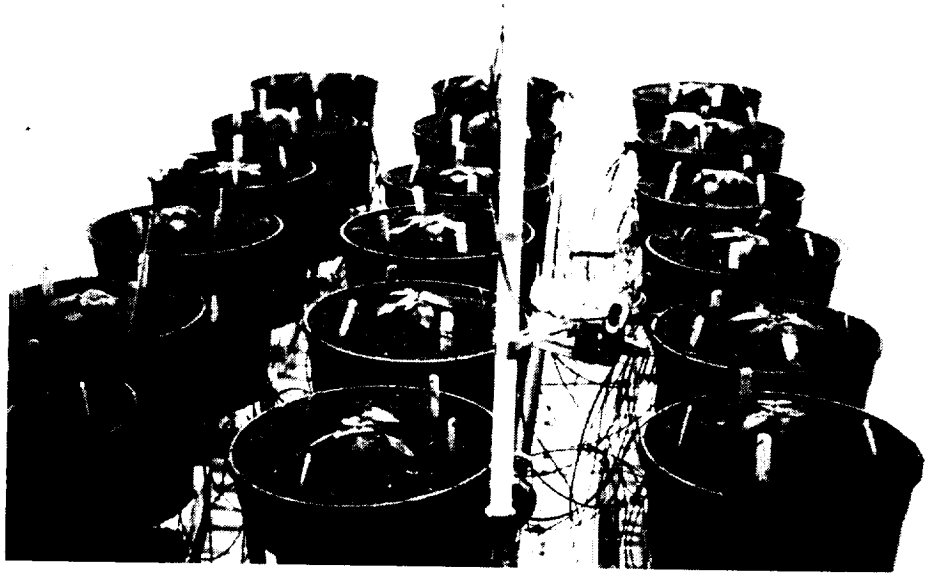


Figure. 2.2. Potato plants enlarging in a Biotron room in 38-liter polyethylene containers filled with peat-vermiculite and watered automatically with a drip irrigation system.

19 liter and 38 liter containers were utilized for separate plants at each harvest (Wheeler and Tibbitts, 1987). Plants in the 38 liter containers were consistently 15-25% larger than the plants in 19 liter containers even though the same area for canopy development was provided to each plant.

In another shorter term study of 64 days, the volume and depth of media was studied. Plastic containers of 20.3 and 30.5 cm diameter were utilized. Four of the 20.3 cm containers were filled with peat-vermiculite media. Four of the 30.5 cm containers were filled to the top with peat-vermiculite. Eight of the 30.5 cm containers were fitted with false bottoms, four with only the upper 17.8 cm filled with media and four with only the upper 7.6 cm filled with media Figure 2.3). Potatoes (cv Norland) were grown under continuous irradiance at 400 μmol m^{-2} s^{-1} PPF, 16°C and 70% RH.

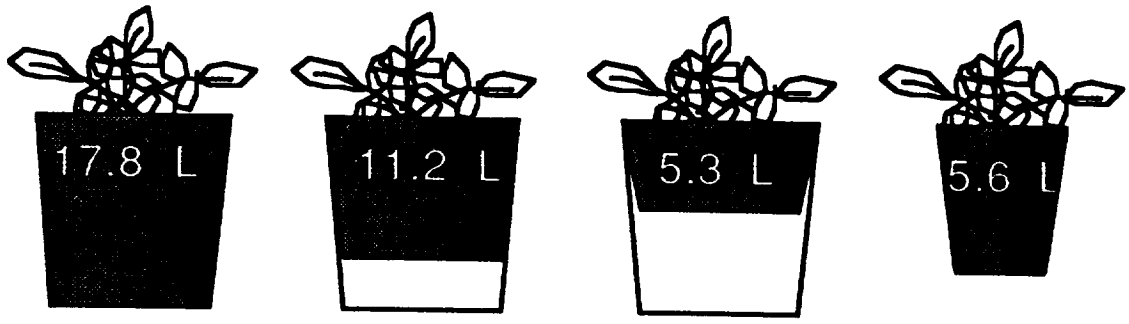


Figure 2.3. Configuration of containers with different size, shape, and capacity.

Harvests made at 64 days indicated that tuber and total plant production were proportional to the volume of media, with greatest production from plants that were provided with the largest quantity of media (Table 2.3). Although the differences in plant yield were not large at this early harvesting date, it would be expected that if the plants had been grown to maturity the difference in yield would be much greater. It was of considerable interest that container shape appeared to have little influence on plant productivity, for plants grown in 30.5 cm wide x 7.6 cm depth had similar yields to those grown in 20.3 cm wide x 17.8 cm depth (containers with similar volumes of media).

Table 2.3. Growth of Norland potatoes grown for 64 days in containers of different size, shape, and capacity.

Container			Tuber	Total
Diameter	Height	Volume	dry weight	dry weight
cm	cm	m^3	g $plant^{-1}$	
30.5	30.5	.022	93.7	198.4
30.5	17.8	.013	86.0	171.3
30.5	7.6	.006	79.5	152.2
20.3	17.8	.006	79.4	160.5

Solution Culture. Plants were grown in 15-30 liter containers of liquid with plants supported with 3 cm diameter foam plugs. A nutrient solution as detailed in Table 2.2 was utilized. The solution was aerated using aeration stones or by recirculating solution (about 1 liter min^{-1}) with a pump. Significant problems were found in obtaining good tuber development. When the solution was maintained at a high enough level so that the developing stolons were immersed, many stolons were initiated and they extended to long lengths, but there was no initiation of tubers until the container was completely filled with roots and stolons. When the container filled with the mass of tissue, apparently the restricted nutrient mixing and constriction of root growth permitted tuberization. Several studies were undertaken to maintain the solution level at the base of the stem to keep the stolons out of the liquid. However, when stolons extended above the solution in the air space, they developed necrotic tips and stopped elongation. This has been observed by other workers and found to result from insufficient calcium uptake by the stolons (Krauss, 1985).

We were able to produce tubers effectively by maintaining the solution level at the base of the stem, locating a plastic screen across the container at that level, and filling the area between the screen and the top of the container with moist sphagnum that is kept moist by contact with the

solution below. However, these containers were difficult to set up and maintain. The difficulties associated with making solution culture effective for potato production limit its potential for potato growth in CELSS.

It has been documented that certain stress conditions such as nitrogen deficiency can stimulate tuberization in solution culture (Krauss, 1985). We found that intermittent reductions of solution pH can induce tuberization without significant inhibition of plant growth as detailed in Wan et al. (1994). In this study, sterile plantlets of potatoes were transplanted into 15-liter containers with a recirculating solution at 120 ml min^{-1}. The pH and conductivity of the solution were carefully controlled. Each container was also fitted with an aerator. Treatments included a constant pH at 5.5 and two intermittent pH reductions to pH 3.5 and 4.0 for 10 hours on each of three dates: 30, 35, and 40 days after transplanting. In each treatment, three plants were grown in three separate solution containers. During each of the three 10 h periods, solution cycling through six containers was shut off, and pH was manually lowered to 3.5 in three containers and to 4.0 in the other three containers using 0.5 N H_2SO_4 solution. Additional H_2SO_4 solution was added as needed at hourly intervals. At the end of 10 h periods, pH was raised back to 5.5 in all containers with 0.5 N KOH. Environmental conditions were 12 L:12 D photoperiod with 400 μmol m^{-2} s^{-1} photon flux, 18/15°C light/dark temperature, and 75% relative humidity.

With the pH 3.5 treatment, tubers were first observed on day 42 and averaged 140 tubers per plant at harvest on day 54 (Figure 2.4). With the pH 4.0 treatment, tubers were observed first on day 48 and averaged 40 tubers per plant at harvest. At a constant pH 5.5, tubers were observed on day 52 and averaged only 2 tubers per plant at harvest. With the intermittent pH 3.5, plants had smaller shoots and roots with shorter and thicker stolons compared to a constant pH 5.5. With the intermittent pH 4.0, plants were of similar size as controls but stolons were shorter and slightly thickened. Mineral composition of leaf tissues at harvest did not change substantially for the three pH treatments.

The results indicate that short-term reductions of solution pH can significantly promote tuber initiation on potato plants grown with stolons immersed. The data also suggest that for rapid and consistent tuber induction, the intermittent pH levels need to be below 4.0. It appeared that with the reduced pH assimilate partitioning to shoots and roots was restricted and directed toward stolon development and tuber initiation. This procedure of solution pH control may be of particular use for producing large numbers of small tubers for use in propagating plants.

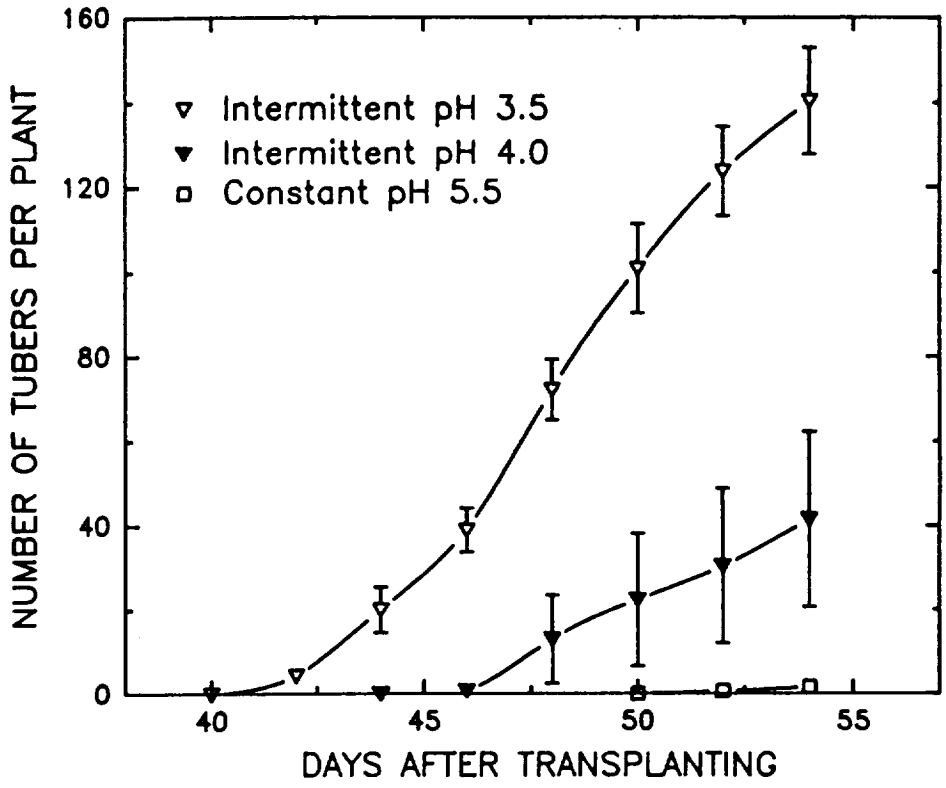


Figure 2.4. Time course response of tuber initiation with three pH treatments. For the intermittent pH treatments, plants were subjected to pH 3.5 or 4.0 for 10 h on each of three dates: 30, 35, and 40 d after transplanting. Vertical bars represent standard errors of treatment means at different times.

Aeroponic Culture. Efforts were directed toward providing nutrients and water to a suspended root system through use of a misting spray. This was studied because it had the potential of minimizing the mass of media and liquid needed for growth. It was found necessary to provide this spray at the top of the root compartment in order that the developing stolons were misted with the solution to prevent necrosis of the stolon tips (as also seen in solution systems). The system developed for use is shown in Figure 2.5.

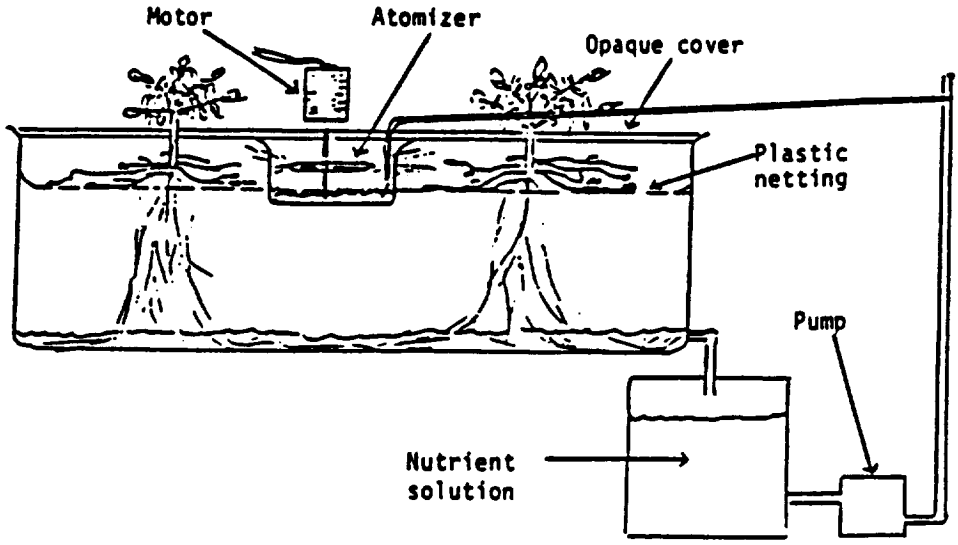


Figure 2.5. Diagram of mist culture system developed for potatoes utilizing a spinning atomizer with recirculating nutrient solution.

However, it was also found that aeroponic systems, as with solution systems, do not permit any tuber initiation or enlargement when the system is continuously misted unless there is some disruption in the misting or other stress is imposed. It was found that tubers were produced when the misting was stopped for a short period and plants wilted. We also obtained tuberization when nitrogen was removed for a long enough period to cause plants to yellow and slow growth. L. Peterson (person. commun.) has obtained good tuberization with alternate periods of on and off misting, however it is difficult to avoid varying amounts of water stress on plants as they enlarge exponentially and have increasing demands for water

It should also be recognized that plants in an aeroponic system, are subject to very quick wilting and death if there is a misting failure for there is no reserve of water and nutrients available to the plants. Thus aeroponics is not recommended as a useful procedure for growth of potatoes in CELSS.

Nutrient Film Technique. Significant effort has been directed toward using nutrient film techniques (NFT) for growing potatoes, for this procedure has been found to minimize the mass of media and water required for growth, and to permit good tuber development. This effort was directed both toward using NFT alone and also in combination with a shallow layer of solid matrix. This procedure involved providing a small stream (film) of nutrient solution continuously to the plants along the bottom in a sloping container. The thin film provided a constant supply of water and nutrients to plants with a continuous and adequate supply of oxygen for the root system. Sloping trays (3-5° slope), 35 to 50 cm in width and 50 to 100 cm in length were utilized. Nutrient solution was added through 3-5 drip tubes or a 'tee' header spread across the upper end of the tray and was drained through holes into a trough at the lower end of the tray. The trays had sides of 4-5 cm in height and were covered with opaque polyethylene film. The polyethylene cover was attached so it rested on the media but had sufficient flexibility to bulge upward as tubers enlarge.

When using only nutrient film without media, potato transplants were supported in 3 cm diameter foam plugs inserted through slits in each tray cover. The lower portion of the stem was laid along the bottom of the tray. Difficulty was experienced in obtaining good contact of the small roots with the solution, therefore the slant on the tray was reduced until good root spread was obtained so that some free water was present around the roots. Also it was found desirable to lay a piece of plastic screening in the bottom of the tray that covered the center half of the tray.

When media was utilized, a layer 2-4 cm in depth, was placed in the bottom of the tray (Figure 2.6). Various media have been utilized effectively including arcillite (a calcined clay of 2-3 mm particles), crushed quartz gravel (2-3 cm particles), and sphagnum moss. Plants were transplanted into the media so that at least 2 cm of the lower part of the stem was buried in the media. The slope of the tray was at least 5 degrees so that liquid could not accumulate to any significant extent in the lower part of the tray. It was not necessary to place a plastic screen in the bottom of the tray and the tray was maintained with the indicated slant from the time of transplanting. Advantages and disadvantages of these growing systems are discussed in the following experiments.

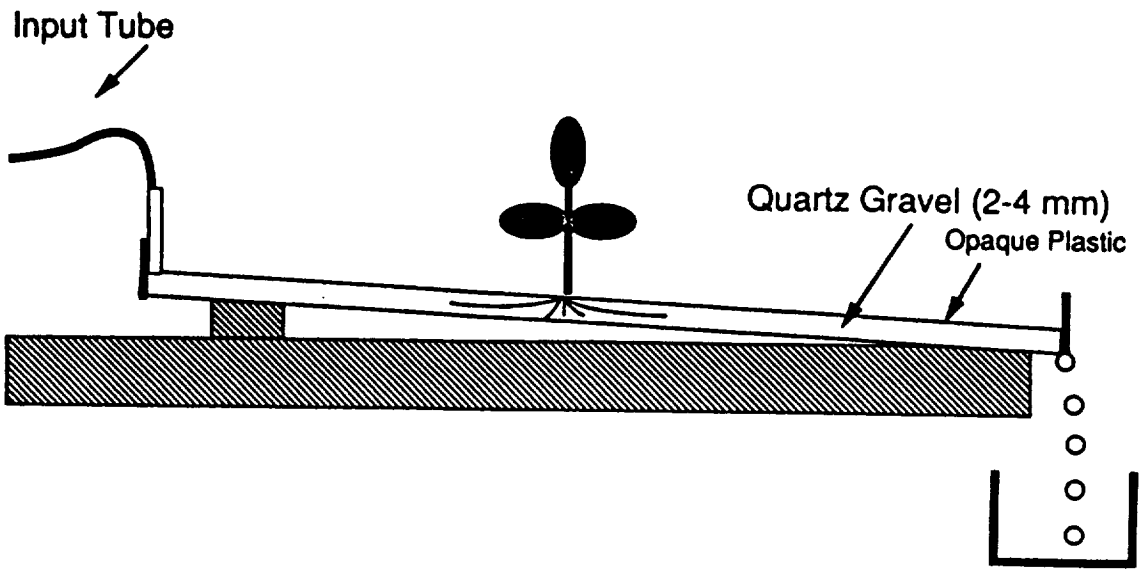


Figure 2.6. Nutrient film system for growing potatoes in a non-recirculating nutrient solution.

Comparison Studies. Two studies were conducted in a walk-in growth room to compare NFT, NFT with a shallow layer of arcillite (NFT-ARC), and pot culture with a deep bed of peat-vermiculite as detailed in Tibbitts and Cao (1993). In these studies, the NFT and NFT-ARC plants were grown in trapezoidal-shaped plastic trays, 18 and 41 cm wide on the ends, 84 cm long, and 5 cm deep as utilized in the Breadboard chamber at the Kennedy Space Center (Wheeler et al., 1990). For NFT-ARC treatment, trays were provided with a 1 cm layer of arcillite particles (2-3 mm in diameter). The wide ends of the trays were elevated 4 cm in NFT treatment and 8 cm in NFT-arc treatment. In the first study, a small plastic screen was laid on the tray bottom in the center half of the NFT trays to help support the seedlings. In the second study, the NFT trays were kept flat for the first two weeks as utilized at KSC in Breadboard experiments. This maintained a layer of solution in the trays and thus a plastic screen was not provided across the bottom of the tray. Nutrient solution was continuously pumped from two 200-liter reservoir tanks to each of the trays at a flow of 500 ml min^{-1} in the first study and 250 ml min^{-1} in the second study, and recycled back to the tanks. The pH was automatically controlled at 5.5 with addition of sulfuric acid solution. Conductivity was controlled at

1.1 ± 0.1 dS m^{-1} by adding stock solutions twice a week and replacement of 50% of the solution at 4, 6 and 8 weeks after the start of the experiment. For pot culture, plants were grown in 19 liter pots containing peat-vermiculite mix, and watered to excess four times daily (excess discarded), using the same nutrient formulation as used with NFT and NFT-ARC, but mixed and supplied from a separate reservoir.

In both studies, temperature was a constant 18°C and relative humidity 70%. Photon flux was 470 μmol m^{-2} s^{-1}, with 12 h light period in the first study and 24 h light period in the second study. CO_2 concentrations were ambient at about 350 μmol mol^{-1} (ppm).

Plants of 'Norland' potatoes were raised from micropropagated stem cuttings grown in sterile agar culture. Uniform single plantlets were transplanted into the centers of the trays and pots. Each study was a randomized complete block design with three replications (Figure 2.7). Plants were harvested on day 66 after transplanting in the first study, and on day 54 in the second study.

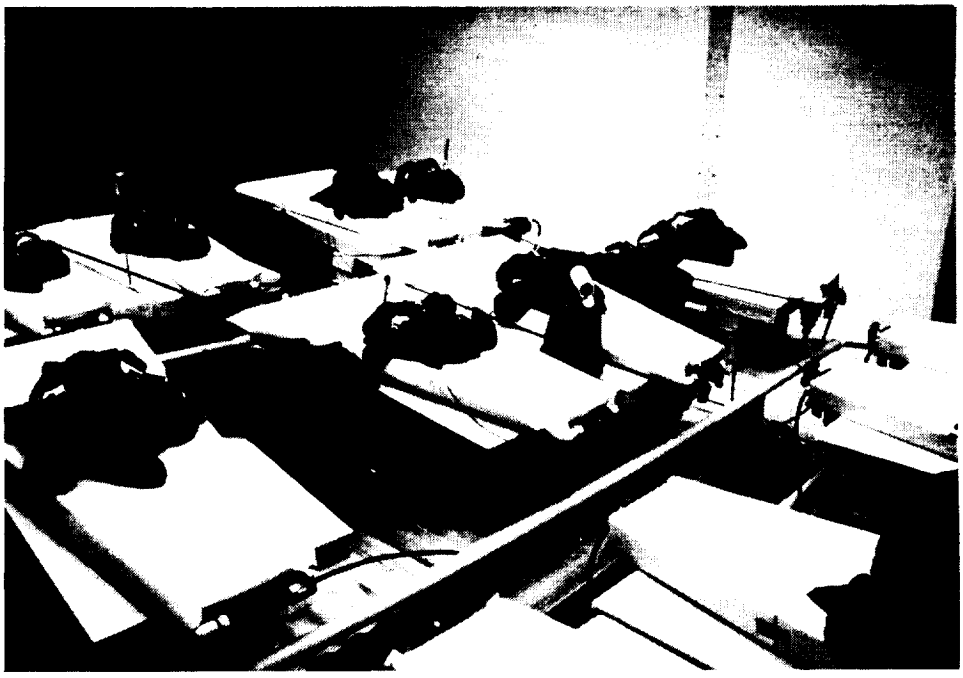


Figure 2.7. Potato plants growing in trapezoidal-shaped trays and pots in a Biotron room for comparison of nutrient film and pot culture growing procedures.

The growth of potatoes with all three cultural procedures in both studies was vigorous, but there were some significant differences in tuberization and biomass partitioning to tubers.

The total plant growth for the cultural procedures followed a similar pattern under the 12 and 24 h photoperiods in the separate studies. Total plant growth was greatest in NFT-ARC and less with NFT and pot culture with these two treatments of similar weight (Tables 2.4, 2.5).

The tuber weight was good in pot culture under both 12 and 24 hr photoperiods (Tables 2.4, 2.5). In contrast, the tuber weight of NFT was only one-half of the tuber weight of pot culture under 12 h photoperiods and only about 20% of the pot culture yield under 24 h photoperiods. The NFT-ARC produced a high tuber weight under 12 h photoperiod, about 30% greater than pot culture, but under 24 h photoperiod the tuber weight was reduced to only about 20% of the pot culture weight.

The number of tubers in pot culture was small, whereas in NFT and NFT-ARC, particularly NFT, a large number of tubers were produced (Table 2.4, 2.5). This effect was greater under 24 h than under 12 h photoperiods. Under continuous irradiation, the tuber number was 3 times higher with NFT-ARC, and 7 times higher with NFT than with pot culture.

Table 2.4. Potato growth with different cultural procedures under 12 h photoperiod for 66 days.

	Dry weight				
	Total	Shoot	Tuber	Harvest index[z]	Tuber number
	g			%	
NFT	230±3[y]	143±44	83±40	36	45±23
NFT-ARC	410±24	190±17	213±29	52	33±4
Pot	266±7	100±5	165±4	62	21±3

[z]Percentage of total dry weight that is tuber dry weight.

[y]Mean and SD of three plants.

Table 2.5. Potato growth with different cultural procedures under 24 h photoperiod for 54 days.

	Dry weight				
	Total	Shoot	Tuber	Harvest index[z]	Tuber number
	g			%	
NFT	368±56[y]	312±38	29±17	8	242±39
NFT-ARC	434±9	387±4	30±6	7	127±27
Pot	352±6	182±6	165±15	47	33±2

[z]Percentage of total dry weight that is tuber dry weight.

[y]Mean ± SD of three plants.

The growth of plants in the different cultural systems also exhibited unique differences that are not shown in the tabular data. Plants grown in NFT culture under 12 h photoperiod developed a large number of tubers (up to 1 cm in diameter) in the axils of leaves and the base of the lower leaves became swollen. A few stem tubers were also evident in the NFT-ARC culture under 12 h photoperiod, but none in the pot culture. There were never any stem tubers on plants in culture systems under 24 h photoperiod.

Another undesirable response of plants in NFT and NFT-ARC culture was that the initial stolons that developed from the stem frequently developed a necrotic area of 0.5 to 1.0 cm over the tip area that stopped the terminal elongation of the stolon and prevented tuber formation (Figure 2.8). This apparently resulted from lack of calcium (Krauss, 1985) because the stolon tips were not in contact with nutrient solution. The necrosis was seen to initiate about 0.3 cm back from the tip but quickly involved the entire tip, and developed only on stolons that were elongating in air space without contact of the tip with media or nutrient solution. This injury was more serious under 24 h photoperiod than under 12 h photoperiod. The use of media minimized this problem because the lower stem could be buried beneath the surface and stolons below the

surface were in constant contact with the nutrient solution.

Figure 2.8. Stolons of potatoes with necrotic tips resulting from lack of calcium. Stolons elongating in air space with no contact with media or nutrient solution frequently develop this injury and the tip collapses.

Another problem was with tubers. In NFT, and occasionally in NFT-ARC, the tubers were found to have cracks and/or blackish necrotic areas on the apical end as shown in Figure 2.9. This injury was also assumed to result from a lack of calcium at the tip of the enlarging stolon.

In NFT culture, the lack of media encouraged stolons to develop and extend under the developing mass of fine roots. Thus the tubers that enlarged under the root mass would lift it up from the tray bottom and the root mass no longer contacted the flowing solution. Although there would be some capillary movement of nutrient solution through the root mass, it was suspected that this would lead to reduced tuber yields during the later stages of potato growth.

Figure 2.9. Blackish necrotic area developing on the tip of a tuber apparently from lack of calcium during early development.

In summary, unique growing procedures are needed to effectively utilize tuber crops in life support systems. These procedures must ensure that stolons are kept dark and in contact with nutrient supply, although stolons can not be totally submerged or continuously sprayed with mist culture. The work has shown that NFT systems have the potential for providing a good tuber yield with a minimum volume and weight for a CELSS system. This research has also shown that there are advantages to the use of a thin layer of solid media to ensure a supply of calcium to developing stolons and to minimize separation of the root systems from the nutrient solution as tubers enlarge. However, additional work is needed to ensure high tuber production under long photoperiods. It also must be recognized that NFT systems can not operate without gravity, but membrane or tubular nutrient supply systems providing nutrients and water under negative pressures have been shown to have potential to satisfying this need (Morrow et al, 1992).

SPACING AND PLANT SUPPORT

Spacing for potatoes is not as critical a factor as for many plants because potatoes branch as needed to fill available spaces. Potato plants produce a vine-like plant with stems extending more than 2 meters under certain growing conditions. As shown in Figure 2.10, potato stems quickly extend and fill the open areas so that the area appears covered in 40 days after planting and essentially complete light interception is obtained by 50 days after planting. From 60 days on, a leaf area index of 4-5 is consistently present in the canopy. This data suggests that closer spacing would make more effective use of space only during the first 30 days of growth.

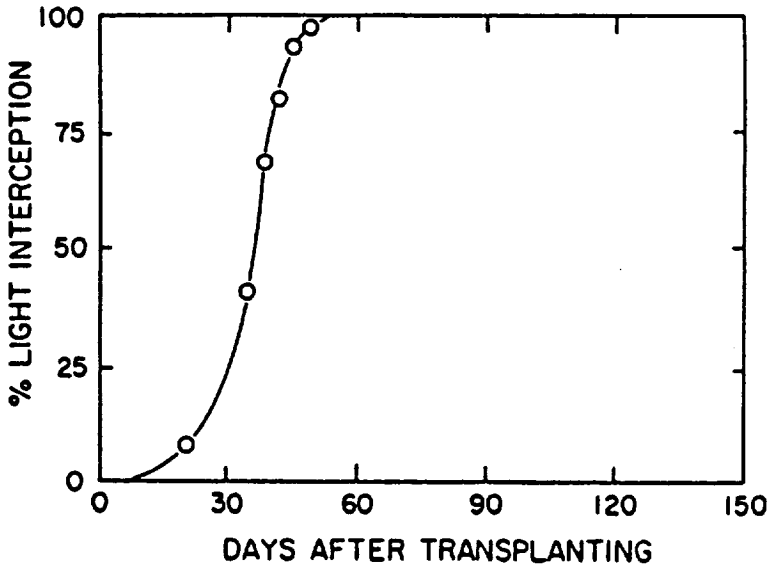


Figure 2.10. Light interception as measured on surface below potato plants spaced 0.5 m apart to provide 0.25 m^2 for each plant.

It is possible that with closer spacing production of tubers per unit area would be increased slightly and that production per plant would be reduced and likely be more variable. Studies were undertaken to determine the effects of spacing on both canopy and tuber development.

In a study to determine the effects of plant spacing, Denali, a late maturing cultivar, was grown for 87 days under 400 μmol m^{-2} s^{-1} PPF of 24 h duration, 16°C and 70% RH. Plastic trays (54 cm wide and 83 cm long and 11 cm deep) were filled with a peat-vermiculite medium and planted with two, four and eight potato plants which provided .224, .112 and .056 m^2 (respectively) of growing area for each plant. Duplicate trays at each spacing were used. Wire fencing was placed around each tray to contain the shoots to the tray area. The nutrient solution detailed in Table 2.2 was provided to the plants four times daily in excess.

The trays with eight plants developed a solid canopy that appeared to cover the surface of the trays in 20 days, whereas with four plants it required 25 days and with two plants 35 days. The shoot and tuber dry weights increased with increasing numbers of plants in the trays with about a 40% greater yield at the close spacing (Table 2.6).

It should be noted that this harvest was made 87 days after planting and did not permit plants to reach full maturity. Thus this growth duration magnified the gains for close spacing compared to wide spacing and likely overestimated the gains that would be anticipated at 140 days with full maturity of the plants. Additional study is needed with plants grown to full maturity and with both early and late cultivars. Early maturing plants have less branching than late maturing cultivars and may gain more from closer spacing.

Table 2.6. Effect of plant spacing on tuber weight, shoot weight, and plant height of Denali cultivar grown for 87 days.

Area per plant (m^2)	Tuber dry weight ($g\ m^{-2}$)[z]	Shoot dry weight ($g\ m^{-2}$)[z]
.224	907±25	830±29
.112	1020±5	882±34
.056	1285±190	952±5

[z] ± weight of plants in duplicate trays.

The significance of containment of stolons and roots on growth and tuber yield was studied by growing multiple plants in large tray containers with and without dividers. The trays were constructed of 0.3 cm thick polyvinyl chloride sheeting to provide growing areas that were 96 cm x 96 cm by 20 cm high. Two trays were constructed with dividers that partitioned the tray area into 9 separate compartments, each 32 cm x 32 cm. Two trays were constructed with no compartmentation. The trays were filled with peat-vermiculite media within 2 cm of the top. Nine potato plants (cv Denali) were planted in each tray with a single plant positioned in the center of each compartment or in similar locations in the open tray. An automatic watering tube was installed by each plant. Wire fencing was placed around each tray to contain the shoots to the tray area. Plants were grown under continuous light of 700 μmol m^{-2} s^{-1} PPF, 16°C, and 70% RH. Harvest of plants at 59 days showed no difference in potato growth or tuber yield between the two types of trays. The total plant dry weight and tuber dry weight from the compartmented trays were 351 and 101 g respectively and from the open trays were 347 and 86 g respectively.

For long term experiments (over 6 weeks), plant support was provided to insure separation of plants so that uniform growth of individual plants could be obtained. 'Chicken' wire netting, 1.2 m wide with 6 cm openings, was shaped into a circle to surround the plant, and it was rigidly attached to the bench surface. As branches grew through the openings, daily effort was required to keep the elongating stems within the fencing. To avoid this complication, hardware cloth with 0.5 cm openings was utilized. However, the cloth had to be kept slightly below the top of the canopy to avoid shading, and thus additional cloth had to be installed at regular intervals to contain the plants. This hardware cloth had the advantage that it did restrict most sideways lighting and thus plants at the edge of the growing area received nearly equal amount of total lighting as compared to plants shaded in the center of the growing area.

HARVESTING

The usual procedure for harvesting plants was to sever the shoot from the lower part of the plant at the media surface. The roots, stolons, and tubers were separated from the matrix, first by light vibration, and then placed under a stream of water to remove remaining media. Tubers were grouped into size categories dictated by the largest dimensions of the tuber. They were separated into different sizes by passing between upright pegs positioned at desired distances

apart. All swellings twice the width of connecting stolon were counted as tubers. For dry weight determination, the tubers were sliced from tip to base in thin sections <0.5 cm thick. A minimum of four tubers were sampled from each experimental unit, with a proportionate amount from the different sized tubers. The leaves were separated from the stems and all petiole tissue was included with the stems. Leaf areas were determined with a leaf area meter. All plant materials were dried in oven at 70°C for at least two days before dry weights were taken.

Analysis by ANOVA was made for different measurements when treatments were repeated in separate growth rooms or when replicate plants were randomized in a particular room. When treatments were not repeated, as with two humidity levels in two separate rooms, and the experiments only undertaken once, then plants for each humidity level were considered subsamples and the standard deviation for plants in each treatment is provided.

SECTION 3. PRODUCTIVITY

TIME COURSE OF TUBER YIELD

Of significant importance for utilizing potatoes effectively in CELSS is a knowledge of the productivity of this crop in g m^{-2} day^{-1} at different harvest dates to establish the optimum harvest period. In this study, plants were grown under 12 h photoperiod in one room and under continuous light in another room (Wheeler and Tibbitts, 1987). Norland plantlets were used and grown for the first 16 days in 1-liter pots and then one-half of the plants transplanted to 19-liter containers and one half to 38-liter containers filled with peat-vermiculite. The 19- and 38-liter containers for each treatment were uniformly spaced on 50-cm centers in the growth rooms. We had intended to harvest plants grown in the smaller (19-liter) containers for the initial three harvests at 42, 63, and 84 days, but plants grown in the larger containers appeared noticeably larger by 40 days after transplanting. Consequently, to avoid inconsistencies between early and late harvests, two large and two small containers were selected for harvest at each date throughout the experiment. All containers were watered to excess four times daily with the complete nutrient solution. Lighting was provided by cool white fluorescent lamps with the average PPF at 403 and 408 μmol s^{-1} m^{-2} for the 24-h and 12-h photoperiod treatments, respectively. Temperatures for both photoperiod treatments averaged 16.1 C ($\pm$0.1 C) and relative humidities averaged 70% ($\pm$ 5%).

Six weeks after planting, the individual plants were encaged in wire fence cylinders of 122 cm high and 46 cm in diameter. This provided a cross-sectional area of approximately 0.2 m^2 for each plant. As plants grew, any branches or leaves that emerged through the holes in the fencing were gently pushed back to confine lateral growth to the diameter of the cylinder. At 63 days after planting, individual plants were arranged around the center of the growth room in an elliptical design in an attempt to equalize peripheral lighting effects.

Beginning at 42 days after planting, four plants (two 19-liter and two 38-liter containers) were harvested from each room. Five additional harvests followed at approximately 21-day intervals up to 148 days after planting. Shoots were cut at soil level and dried at 70C for dry weight determination. Tuber fresh and dry weights were also taken. Dry weights of large tubers (tubers $\geq$ 100 g) were determined by drying a subsample of 100 g fresh weight from three

representative tubers from each plant. The subsequent percent dry weight was then applied to the total fresh yield to determine total dry weight.

Average dry weights of tubers and whole plant along with harvest index and tuber productivity are shown through time for the 24- and 12-h treatments in Tables 3.1 and 3.2. Although there was significantly greater tuber production (15-25%) in the large containers at each harvest date, this difference was consistent for both light treatments throughout the experiment. Total plant dry weight and tuber dry weight continued to increase under both photoperiods throughout the experiment. Total plant dry weights of 24-h plants (Table 3.2) always exceeded those of 12-h plants (Table 3.1), and with the exception of the 42-day harvest, 24-h tuber dry weights always exceeded 12-h tuber yields. After 148 days, individual 24-h plants yielded an average of 4.3 kg fresh tuber weight (791 g dry weight), while 12-h plants yielded 3.4 kg fresh tuber weight (572 g dry weight). Harvest index of plants under 24 h increased from 21% at 42 days to 80% at 126 days.

Beginning at 20 to 30 days and lasting until the final harvest at 148 days after planting, leaves of plants under the 12-h photoperiod were consistently larger and oriented nearly

Table 3.1. Production of Norland potatoes grown under a 12 h photoperiod.

Plant age	Tuber dry wt	Total dry wt	Harvest Index	Tuber productivity
days	g plant^{-1}		%	g m^{-2} d^{-1}
42	6±1[z]	28±1	22±4	0.76±0.25
64	62±9	121±9	51±5	4.92±1.39
84	207±16	283±21	73±2	12.33±1.95
105	318±16	410±23	78±1	15.14±1.53
126	465±18	574±25	81±1	18.44±1.41
148	572±28	704±39	81±1	19.33±1.89

[z]Mean ± SD of 4 plants.

Table 3.2. Production of Norland potatoes grown under a 24 h photoperiod.

Plant age	Tuber dry wt	Total dry wt	Harvest Index	Tuber productivity
days	g plant^{-1}		%	g m^{-2} d^{-1}
42	$<1\pm1$	61 ± 8	0	0.23 ± 0.04
64	114 ± 7	228 ± 17	50 ± 3	9.02 ± 1.12
84	337 ± 6	475 ± 14	71 ± 2	20.06 ± 0.68
105	599 ± 34	756 ± 49	79 ± 1	28.52 ± 3.20
126	740 ± 51	906 ± 64	82 ± 1	29.37 ± 4.02
148	791 ± 89	972 ± 107	81 ± 1	26.74 ± 6.02

[z]Mean $\pm$ SD of 4 plants.

horizontally in comparison to leaves on plants under the 24-h photoperiod, which showed an upward inclination. In addition, the undersides (abaxial surface) of exposed leaves of the 24-h plants nearly always showed reddish-purple coloration but this was seldom noted on the 12-h plants' leaves. By 90 days, exposed leaves on the 24-h plants began to show rusty necrotic spotting. These symptoms intensified with age and appeared to be a natural senescence. By 148 days approximately 90% of the exposed leaves were necrotic. In contrast, 12-h plants remained relatively green and healthy for the first 126 days after which leaves began to show some necrotic spotting. At the final harvest at 148 days, about 30% of the exposed leaf surface was necrotic on the 12-h plants.

A comparison of tuber productivities (Figure 3.1) indicates that under continuous light, a 15- to 18-week cropping cycle would be the most efficient approach for growth of potatoes for a CELSS. Although total tuber yields per plant continued to increase throughout the 21 weeks, the productivity in terms of g m^{-2} day^{-1} decreased after 18 weeks. In contrast, under the 12-h photoperiod productivity continued to increase throughout the experiment, indicating that 21 weeks might be insufficient for achieving maximum productivity under this photoperiod.

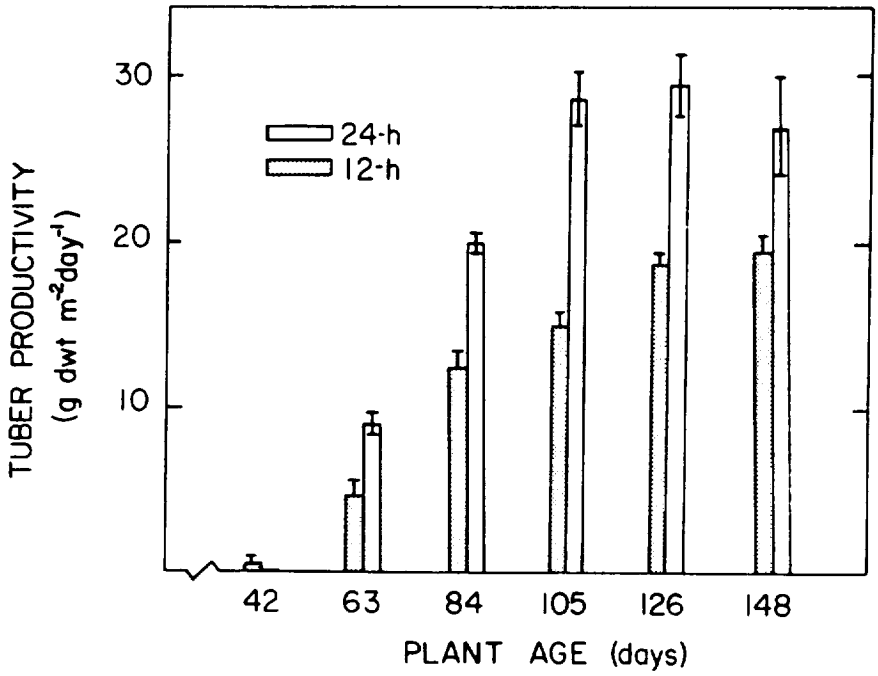


Figure 3.1. Tuber productivity over time of Norland potatoes grown under 12 h and 24 h photoperiod.

However, it is likely that with higher temperature during early growth, maturity would be advanced.

The plants grown under the 24-h photoperiod received twice the radiation, i.e., 100% more than that given to the 12-h plants, and total plant dry weight under 24-h at each harvest was always greater than that under 12-h. Yet, the data indicate that the difference between the two treatments became less with age. Plants from the 24-h treatment produced nearly 100% more total biomass at 42 days but only 38% more biomass at 148 days. This apparent change in utilization of light energy with age of the plants results from the fact that plants develop and accumulate dry weight exponentially and thus during any time during early growth, the faster growing plants will be found to have higher efficiencies. This is discussed in page 37.

MAXIMUM PRODUCTIVITY

A study was undertaken to maximize yield productivity in terms of grams per unit area per day (g m^{-2} d^{-1}). Plants were grown in 24 closely spaced containers to develop a solid stand of 3.0 m x 2.0 m (Figure 3.2). The area was enclosed by a wire mesh fence to contain the plants. The sides were further enclosed by opaque but reflective siding to prevent side lighting of the plants. This siding was gradually raised during growth to be just below the top most part of the plants. Sixteen plants, excluding the rows of plants on each end, were harvested for productivity calculations. To maximize growth and tuber production, temperature and photoperiod were changed during growth (Table 3.3) whereas PPF was held constant at 725 μmol m^{-2} s^{-1}, carbon dioxide at 1000 μmol mol^{-1}, and relative humidity at 70%.

Figure 3.2. Potato plants being maintained in a closed canopy in a Biotron room for determination of maximum tuber productivity.

Table 3.3. Temperature and photoperiod conditions during growth of potatoes.

	0-37 days	38-41 days (Transition)	42-132 days
Temperature	20D:16N	——————>	16D:16N
Light period	12 h	——————>	24 h

A peat:vermiculite medium was used and plants watered to excess four times daily using a nutrient solution detailed in Table 2.2. Plants were raised from tissue culture plantlets and grown for 18 days after transplanting in 1-liter plastic containers to minimize the growing area when plants were small. Plants were then transferred to 19-liter polyethylene containers until harvest at 132 days. Spacing of each plant was 0.02 m^2 $plant^{-1}$ for day 0-18 and 0.25 m^2 $plant^{-1}$ for day 19-132, averaging 0.22 m^2 $plant^{-1}$ during the entire study.

Table 3.4 shows the yields from the sixteen center plants, excluding the 8 plants in the two side rows, and the nutritional values as obtained by proximate analysis. The average tuber yield of 4.9 kg fresh weight from a single plant is shown in Figure 3.3. The data demonstrate the size and composition of these potatoes to be within the range of field grown potatoes.

Table 3.4. Tuber productivity and nutritional values.

Tuber production		Tuber nutrition	
Total dry matter	5920 g m^{-2}	Protein	9%
Edible dry matter	4352 g m^{-2}	Carbohydrate	82%
Harvest index	73.5%	Fat	0.6%
Tuber productivity	37.5 g m^{-2} d^{-1}	Energy content	3.7 kcal/g dw

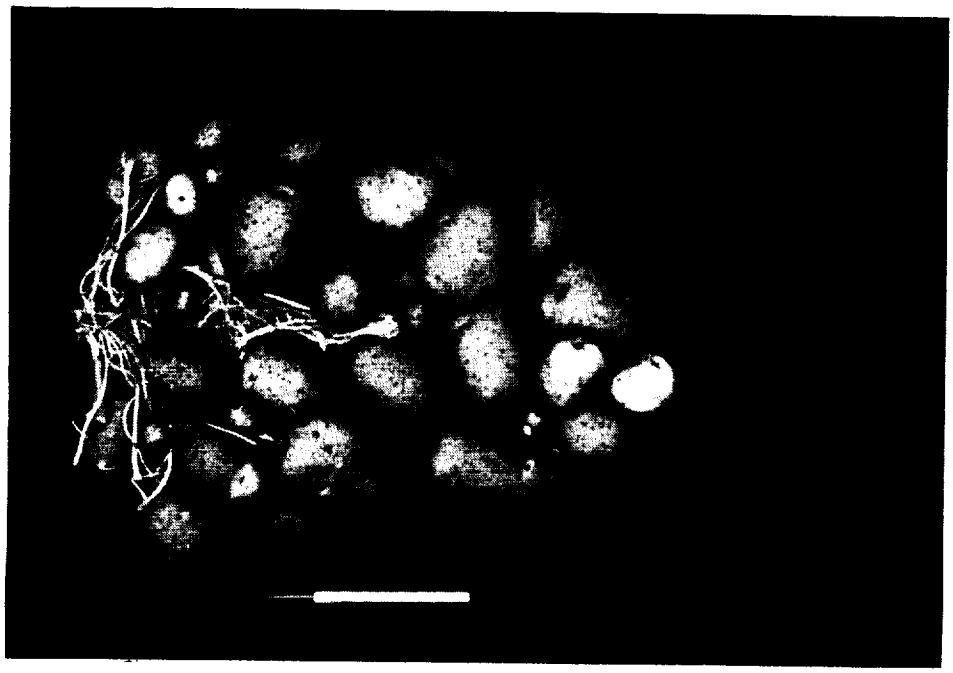


Figure 3.3. Yield of 4.9 kg fresh weight of potatoes from a single plant growing for 132 days.

The area and number of plants required to produce the dietary energy for one human can be calculated from this data set. With one g of tuber dry matter containing 3.7 kcal, the tuber productivity of 37.5 g m^{-2} day^{-1} (x 3.7) provides 139 kcal m^{-2} day^{-1}. Assuming a daily dietary need of 2800 kcal for one human, then 20.1 m^2 (2800/139) of potatoes would be sufficient to provide the dietary energy requirements for one person on a continuous basis. This 20.1 m^2 area would require a total of 100 plants spaced at 0.2 m^2 per plant. Thus a 5 m x 4 m area containing 100 plants that is harvested and immediately replanted at 132 day intervals could sustain one person. This assumes 100% utilization of the harvested product and that no storage losses occur. Therefore, somewhat more area than this should be provided for each person. We proposed an area of 4.9 m x 4.9 m (15 feet by 15 feet) with a 1 meter height for maintaining a crop of potatoes for one person (Figure 3.4).

Another significant factor in the productivity calculation is the energy into lamps to provide PPF for the plants and hence also the amount of cooling required to remove this lamp

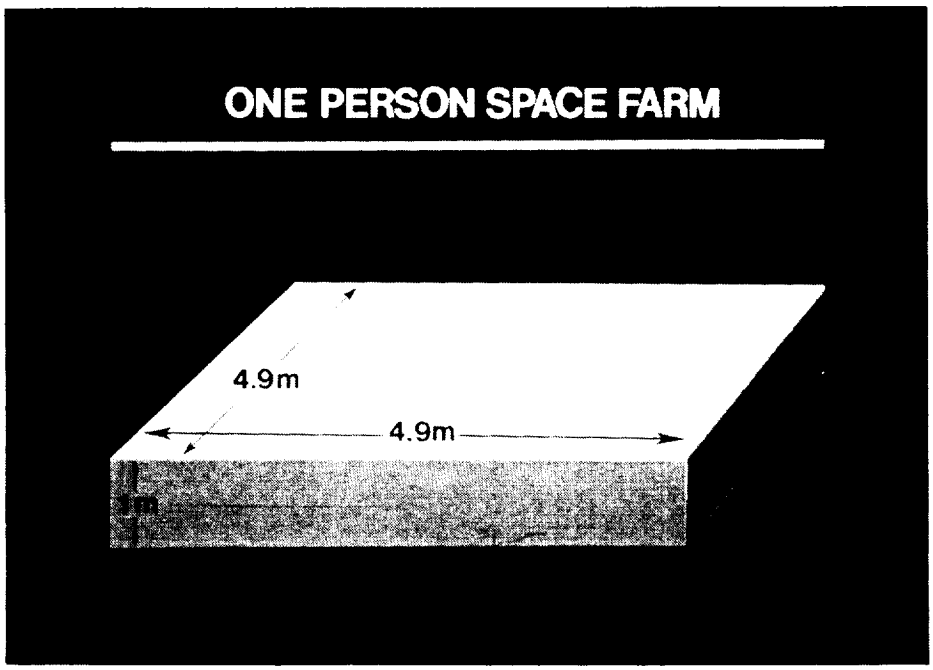


Figure 3.4. Estimated growing volume for potatoes to produce energy requirements for one person in space.

energy. In a commercial plant growing facility in the United States, a level of 400 μmol m^{-2} s^{-1} was provided by 304 lamp watts m^{-2}. Thus the photon level of 725 μmol m^{-2} s^{-1} in this study would equate to 551 lamp watts m^{-2}. Using this lamp output efficiency, the growing area of 20.1 m^{-2} would require continuously 11.1 kw of electricity to produce the requirements for each person.

CONTINUOUS HARVESTING

It was hypothesized that if tubers were removed from the plants as soon as they reached a useful size, plant productivity could be increased because plants could be kept in high photosynthetic rates and avoid, or slow, maturation of the plants. This is nearly impossible to study under field conditions because of the interacting effects of disease and insects, along with changing photoperiods over time in the outside environment. An experiment was undertaken to test this hypothesis by continuously harvesting from the same plants at weekly intervals and

comparing this harvest to a single harvest at plant maturity. Potatoes were grown with the nutrient film technique using a 1 cm layer of arcillite, as described in Section 2. Trays of 83 cm long, 54 cm wide and 54 cm deep were used. A total of four trays were utilized, two that were continuously harvested and two that were harvested only on the final date of the experiment. Two plants were transplanted into each tray. Plants were grown under 600 μmol m^{-2} s^{-1} PPF of 12 h duration, a light:dark temperature of 22:16°C and 70% RH. At weekly intervals from week 8 to week 16, enlarged tubers over 5 cm in diameter were removed by reaching under the cover (with the room dark) and separating the tuber from the stolon. At 16 weeks, tubers were also harvested from trays that were undisturbed.

The yield for the treatments is shown in Figure 3.5. No yield advantage was obtained with the continuous harvesting practice, and there was no evidence that senescence of the plants

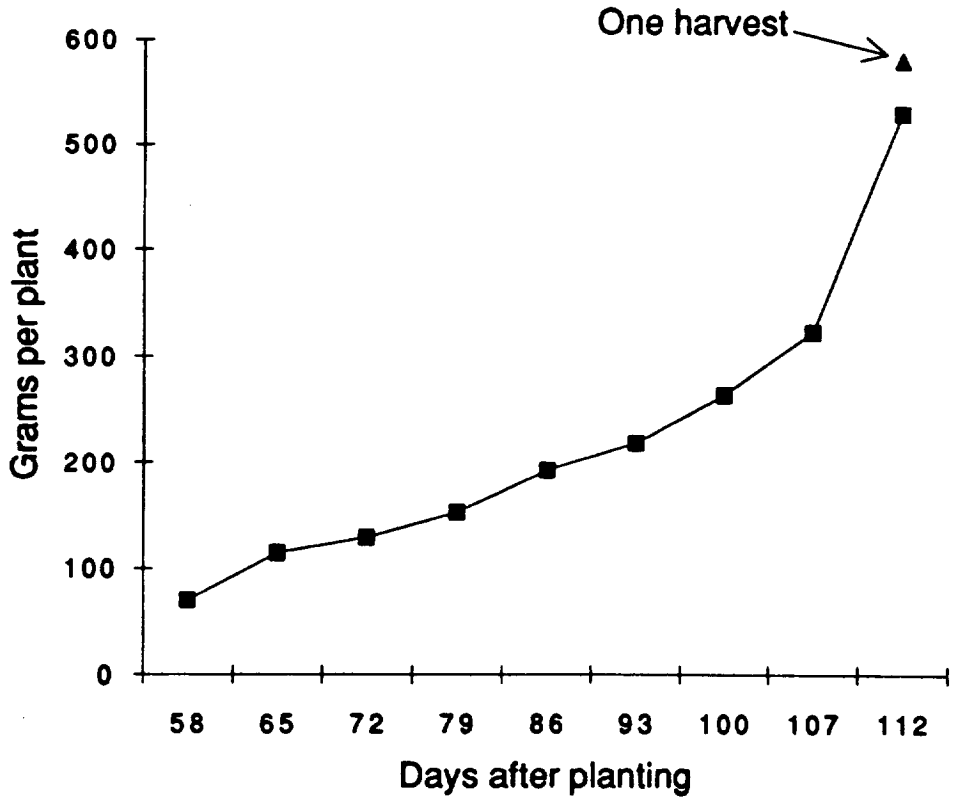


Figure 3.5. Average tuber yield per plant harvested continuously during a 16 week growth period.

was delayed. However, tuber removal disturbed the source-sink balance in the plants as evidenced by the collapse of small areas of tissue on exposed leaflets within 24-h after the removal of the first tubers at 58 days after transplanting. Damage to stolons was also apparent in trays subjected to successive harvesting. The stolons collapsed and rotted back to the main stem or back to where another tuber was enlarging on the stolon.

SECTION 4. LIGHT

DURATION AND INTENSITY

Both photoperiods and light intensity have major controlling effects on productivity of potatoes. It has long been accepted and demonstrated that short photoperiods, e. g. less than 12 hours, encourage tuberization of potatoes (Ewing and Struik, 1992; Gregory, 1965), and it is also recognized that low light levels produce more photosynthesis per unit of light than high light levels (Bodlaender, 1963). Thus, in an attempt to reduce light intensity without reducing the total amount of light received by plants, a significant effort was undertaken to utilize continuous lighting for potatoes. This approach has the added advantage to gain efficiency in electrical use and also hopefully to reduce the quantity of lighting that would have to be installed in a CELSS. Early in this research it was found that potatoes, or at least some cultivars, would tolerate and develop a high production under continuous light. As the studies progressed, it was found that tuberization was initiated quite rapidly under continuous light if light was maintained at a high enough level. The work has documented that long light periods encourage shoot growth, but if enough light is provided with long light periods, tuberization will occur at a high rate in essentially the same period of time as under short light periods.

Duration & Intensity Interactions. In a study utilizing Norland potatoes, continuous lighting was compared to 12 h light and 12 h dark. Plants were grown at a temperature of 16 C and 70% RH for 21 weeks in peat-vermiculite. The photosynthetic photon flux level (PPF) was 400 μmol m^{-2} s^{-1} for both photoperiod treatments. Successive harvests were made at two week intervals. Complete data on these harvests is presented in Table 3.1 of Section 3 and the experiment detailed in Wheeler and Tibbitts (1987). The continuous lighting (24 h light) produced 38% more tuber yield than the 12 h light and 12 h dark each day with the same instant PPF level (Table 4.1). Only at a 6 weeks harvest, tuber weight was slightly greater with the 12 L:12 D than under continuous light indicating that tuber development may have begun slightly sooner with 12 h light period. In all succeeding harvests, tuber production was significantly greater under continuous light than under 12 h light. At 21 weeks, the harvest index of plants under continuous light was essentially the same as under 12 h light (Table 4.1).

Table 4.1. Dry weight and harvest index of Norland potato plants grown for 21 weeks under 12 h and continuous lighting.

Light (h)	Dark	Dry weight			Harvest index (%)
		Tubers	Shoots (g/plant)	Total	
12	12	572	130	704	81
24	0	791	174	972	81

16°C at PPF level of 400 μmol m^{-2} s^{-1} for 21 weeks.

In this study, the total photosynthetically active radiation received each day with continuous lighting was double (100% greater) the amount obtained under the 12 h photoperiod, yet final tuber production under continuous irradiation was only about 40% greater than under 12 h irradiation. This comparison documents that the conversion efficiency of electrical energy to plant dry matter is greater with 12 hour light periods than with continuous lighting when plants are grown for the same duration of 21 weeks. However, a more accurate comparison of conversion efficiency was made by comparing the amount of plant growth over the time period for maximum productivity of plants in each light period treatment. The productivity of plants was determined using the data of Tables 3.1 and 3.2. The maximum productivity under 12 h light period was 19.33 g m^{-2} day^{-1} at 148 days, and under continuous light was 29.37 g m^{-2} day^{-1} at 126 days, only about 50% gain compared to the 12 h plants. The calculation of weight gain for the whole plant was also $\approx$50%. Thus although there is greater production under continuous lighting than under 12 h lighting with the same PPF level, there is a significant loss in electrical conversion efficiency for plants grown under continuous light compared to under 12 h light.

Evidence that long photoperiods do suppress tuberization was found in an experiment comparing plants grown at 400 μmol m^{-2} s^{-1} PPF for 12 h to plants grown at 200 and 400 μmol m^{-2} s^{-1} for 24 h as detailed in Wheeler and Tibbitts (1986b). In this experiment the same total

amount of irradiation was provided over each 24 h period for two of the treatments, the treatment at 12 h photoperiod with 400 μmol m^{-2} s^{-1} PPF and the treatment at 24 h photoperiod with 200 μmol m^{-2} s^{-1}. Plants of the Norland cv were grown for 6 weeks at 20 C and 70% RH. There was essentially no tuberization under the continuous light treatment at 200 μmol m^{-2} s^{-1} and good tuberization with a 12 h light treatment at that instant PPF level (Table 4.2). However, this long photoperiod suppression of tuberization was shown to be overcome by increasing the irradiance level of the continuous light from 200 to 400 μmol m^{-2} s^{-1} as shown in the middle treatment of Table 4.2. It is noteworthy that when total plant growth was compared between 400 μmol m^{-2} s^{-1} PPF for 12 h and 200 μmol m^{-2} s^{-1} d for 24 h (treatments with the same daily photon amounts), there was more total dry weight and thus higher conversion efficiency of electrical energy to dry weight with the 24 h treatment (Table 4.2). This results because plants have increasing efficiency in capturing and converting photons to photosynthates with decreasing photon levels.

Table 4.2. Dry weight of Norland potato plants grown at different irradiance durations and levels.

Irradiance (PPF)		Dry weight per plants	
Duration (h)	Level (μmol m^{-2} s^{-1})	Total biomass (g)	Tubers (g)
12	400	53	12.2
24	400	125	19.6
24	200	80	0.4

20°C for 6 weeks.

When total plant growth was compared between 12 h and 24 h photoperiods with the same PPF levels of 400 μmol m^{-2} s^{-1}, there was also a higher conversion efficiency with the 24 h

treatment than with the 12 h treatment. The 24 h plants received double light but had more than double the dry weight of the 12 h plants. However, this comparison was biased because plant growth increases exponentially and comparison made before maturity of the plants provided an exaggerated conversion efficiency for the faster developing plants. As seen with Table 4.1, at full maturity the conversion efficiency would be lower under the 24 h photoperiod than under the 12 h photoperiod.

A series of studies were undertaken in large rooms at the Biotron to study intensity and duration interactions utilizing a high PPF level of 800 μmol m^{-2} s^{-1} in combination with 400 μmol m^{-2} s^{-1} at both ambient and elevated carbon dioxide levels. These studies documented the significant interactions of PPF level, light duration and carbon dioxide level for growth and tuber production and provided data on the upper PPF level for maximum productivity.

The studies were undertaken in rooms of the Biotron at 16 C and 70% RH. Three cultivar, Norland (early maturing), Russet Burbank (late maturing), and Denali (late maturing) were grown for 90 days and harvested. Details of the study are provided in Wheeler et al. (1991).

The dry weight data indicates increasing tuber weight for all cultivars with increasing PPF from 400 to 800 μmol m^{-2} s^{-1} under light of 12 h duration but gains only for Denali cultivar with light of 24 h duration (Table 4.3). It can be seen that a PPF of 800 μmol m^{-2} s^{-1} for 12 h and a PPF of 400 μmol m^{-2} s^{-1} for 24 h, treatments with similar total daily PPF, produced similar tuber yields for Norland and Denali, but greater tuber yields were produced with the 24 h than with the 12 h for Russet Burbank.

When CO_2 supplementation at 1000 μmol mol^{-1} was provided, maximum yields were obtained with all cultivars at 400 μmol m^{-2} s^{-1} for 24 h and 800 μmol m^{-2} s^{-1} for 12 h. This is detailed, along with data on total dry weights for these treatments in Section 7 - Carbon Dioxide research studies.

The significant effect of long photoperiods on shoot growth is documented in the data of Table 4.4. All levels of continuous light produced essentially twice as much shoot growth as with 12 h light. There was only a small increase in shoot growth with increasing PPF with 12 h photoperiod and actually a small decrease in shoot growth with increasing PPF under continuous light. This response was similar for all cultivars.

Table 4.3. Tuber dry weight of potatoes grown with different durations and intensities of light.

Cultivar	Photoperiod	PPF (μmol m^{-2} s^{-1}) 400	800
		g/plant	
Norland	12 h	248	307
	24 h	304	317
Russet Burbank	12 h	225	262
	24 h	339	311
Denali	12 h	253	334
	24 h	334	488

Table 4.4. Shoot dry weight of potatoes grown with different durations and intensities of light.

Cultivar	Photoperiod	PPF (μmol m^{-2} s^{-1}) 400	800
		g/plant	
Norland	12 h	79	88
	24 h	155	142
Russet Burbank	12 h	95	110
	24 h	243	189
Denali	12 h	97	117
	24 h	217	185

Thus the data indicate that a photon flux of 800 μmol m^{-2} s^{-1} for 12 h or 400 μmol m^{-2} s^{-1} for 24 h is close to being sufficient for maximum productivity of potatoes. This PPF need may vary with particular cultivars, but obviously energy conversion efficiency of PPF to tubers will decrease significantly at higher PPF amounts.

A detailed series of interaction studies were undertaken with light intensities using continuous light at PPF's of 250, 400, and 550 μmol m^{-2} s^{-1} with varied levels of temperature and carbon dioxide with two cultivars, Norland and Russet Burbank. Plants were grown for 56 days at temperatures of 16, 20, and 24 C and 400, 1000, and 1600 μmol mol^{-1} CO_2. A series of 4 studies with 5 separate chambers in each study were utilized using response surface methodology to develop models of the interaction effects of light intensity with these other environmental factors as detailed in Yandell et al. (1988). This study found that maximum yields of Russet Burbank cv were obtained with 455 μmol m^{-2} s^{-1} of PPF continuously at optimum temperatures and elevated CO_2 levels, whereas with Norland cv, maximum yields were obtained at a PPF of 550 μmol m^{-2} s^{-1} continuously. This paper compares techniques for conducting experiments to model the interacting effects of environmental factors on potato growth.

These several studies with different cultivars of potatoes appear to document that the effect of photoperiods has a direct controlling effect on stem growth and an indirect effect on tuber initiation and enlargement. That is, when the light period is 12 h the vegetative growth of potatoes is slowed and allocation of photosynthates to tubers is promoted. This slowed growth involves terminal growth of stems, growth of axillary (branch) buds, and initiation and extension of stolons. In contrast, when the light period is greater than 12 h these vegetative activities are not slowed and photosynthates are allocated to maximize the shoot and stolon growth of the plants. Therefore when light periods are greater than 12 h, but total daily irradiation is limited, most of the available photoassimilates are allocated to vegetative growth. However, when daily irradiation is great enough to exceed vegetative demands with high PPF levels and short dark periods, the excess photosynthates are allocated for tuber production. Thus, the apparent photoperiod effects on tuber development vary with amount of daily irradiation received by plants. This conclusion suggests that the previous research studying long light periods (Gregory, 1956, Bodlaender, 1963) was undertaken with limiting light levels so that tuberization was greatly reduced or delayed when long light periods were used, which led to the assumption that tuberization is controlled directly by photoperiod. The research of this present project therefore

contradicts this assumption and provides evidence that a high tuber yield and high harvest index can be obtained with 24 h lighting. A critical experiment to sort the effects of photoperiod and total irradiation would be to provide high PPF (e.g. 800 μmol m^{-2} s^{-1}) for a short photoperiod (e.g. 12 h) and then to interrupt the dark period with dim light. If tuberization is slowed by this treatment, then photoperiod would also be having a direct effect on tuberization.

A study of different photoperiods was undertaken with 12, 16, and 20 h light periods with four different cultivars, Norland, Superior, Norchip, and Kennebec as detailed in Wheeler & Tibbitts (1986a) and Wheeler et al. (1988). The plants were grown for 15 weeks in Biotron rooms under a PPF of 400 μmol m^{-2} s^{-1}, 20 C, RH of 70%, and ambient CO_2. At 6 weeks each plant was fenced to contain it within a 46 cm diameter area. Plants were harvested at 105 days after planting. Tuber, shoot, and total dry matter production per unit area for the four cultivars is shown in Table 4.5.

Tuber yields of Norland plants (Table 4.5) increased slightly with increasing photoperiod, while Norchip and Superior yields were similar under 12 h and 20 h treatments and slightly depressed under 16 h photoperiod. Kennebec plants produced high tuber yields under 12 h but low yields under 16 h and 20 h treatments. It can be seen that there were large increases in shoot dry weight with increasing light periods for all cultivars, again documenting the increasing shoot growth with light periods greater than 12 h. The light level was high enough, 400 μmol m^{-2} s^{-1} so that there was significant tuber production in all treatments. However, at 16 h, the total light per day was at a marginal level to satisfy both the shoot and tuber demands, for three of the four cultivars showed less tuber yields than with 12 h lighting. On the other hand, with 20 h lighting, the total light per day was sufficient to satisfy shoot requirements and provide additional assimilates to tubers for a higher tuber weight was obtained than at 12 h except with the cv Kennebec. This cultivar was found to be sensitive to long light periods and begin to show slowed growth by 60-70 days after planting. At harvest the Kennebec plants had compact stunted shoot growth and diminutive, upright leaves with mild 'rusty' flecking on the surfaces of the leaflets. These symptoms also began to appear under 16 h after the 85th day. This injury is discussed in detail in a succeeding part of this section.

Table 4.5. Dry weights per unit area[z] of 15-week old potatoes grown under different photoperiods.

Cultivar		Photoperiod (h) 12	16	20
			kg m^{-2}	
Norland	Tuber	1.62±0.14[y]	1.80±0.10	2.18±0.39
	Shoot	0.71±0.02	1.48±0.05	1.82±0.23
	Total	2.36±0.16	3.31±0.05	4.07±0.16
Superior	Tuber	1.29±0.05	1.12±0.09	1.46±0.31
	Shoot	0.81±0.13	1.43±0.10	1.87±0.02
	Total	2.11±0.17	2.60±0.03	3.39±0.33
Norchip	Tuber	1.29±0.16	0.97±0.15	1.52±0.30
	Shoot	0.97±0.04	1.63±0.21	1.99±0.08
	Total	2.28±0.16	2.65±0.09	3.55±0.39
Kennebec	Tuber	1.69±0.17	0.16±0.02	0.56±0.15
	Shoot	0.95±0.13	2.06±0.60	1.91±0.04
	Total	2.67±0.23	2.21±0.47	2.54±0.21

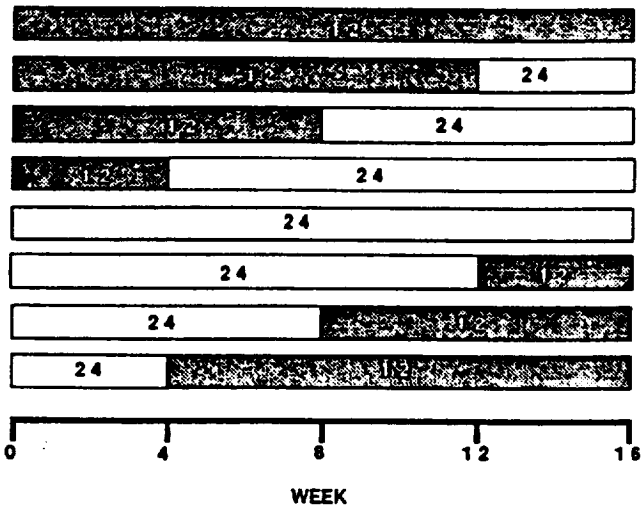
[z]Values calculated assuming 0.2 m^2 area available for each plant.

[y]Means±SD of three replicate plants.

Light Period Changes during Growth. The significant effect of photoperiod on stem growth led to studies to determine if changes in photoperiods at different stages of growth could be utilized to increase tuber production of plants. In these studies, two rooms of the Biotron

were utilized, one maintained at 12 L:12 D photoperiod (12 h) and the other under continuous (24 h) light as detailed in Tibbitts et al. (1989). At 4, 8, and 12 weeks after planting, 3 plants were switched from each room to the opposite room (plants were not switched back to the starting room) providing 8 treatment combination as shown in Figure 4.1. The cultivar Denali was utilized and plants were grown for 16 weeks under 16 C, 70% RH, a PPF of 400 μmol m^{-2} s^{-1} and ambient CO_2 ($\approx$ 350 μmol mol^{-1}). The experiment was repeated with similar treatments and conditions except that the CO_2 was elevated to 1000 μmol mol^{-1}.

At 16 weeks old, plants grown with 24 h light gave the highest tuber yields and those grown at 12 h light produced the lowest yields (Figure 4.1). Plants which were switched between light treatment gave intermediate yields. Plants grown first with 12 h of light followed by 24 h of light gave higher tuber yields than plants given the reverse treatment. This response can be seen for the two treatments that were switched at 8 weeks and thus had equal photosynthetic flux over the growth period.



Light duration	Tuber dry wt (g plant^{-1})	Energy efficiency (g tuber/h light)
12	582	3.03
12 → 24	832	3.47
12 → 24	1043	3.62
12 → 24	1019	3.03
24	1177	3.06
24 → 12	853	2.53
24 → 12	711	2.46
24 → 12	749	3.12

Figure 4.1. Effect of light duration changes during growth on tuber yield and light energy requirement (light energy use per unit weight of tubers).

The most efficient treatment, in terms of light energy use per unit weight of tubers, was the treatment which began with 8 weeks at 12 h and finished with 8 weeks at 24 h (Figure 4.1). Nearly as efficient was the treatment with 12 weeks at 12 h and finishing with 4 weeks at 24 h.

With CO_2 supplementation in the repeat experiment, tuber dry weights for each treatment were quite similar to the yields obtained without CO_2 enrichment although the shoot growth was substantially stimulated in all treatments (Tibbitts et al., 1989).

Thus this study demonstrated that total yield is greatest with the entire growth under continuous light but that energy efficiency would be improved if plants are started under short light periods for 8-12 weeks and then transferred to continuous light.

CONTINUOUS LIGHT INJURY

A significant concern in the use of continuous light is that only about one half of the cultivars we have tested developed and tuberized normally under continuous light. This includes the cultivars Norland, Russet Burbank, Denali, Atlantic, and Snowchip. Other cultivars have become chlorotic after two weeks of growth, producing small leaves and greatly stunted growth. This serious injury response has been found with Kennebec and Superior cultivars. A partial chlorosis and stunting also has been found with Norchip cultivar.

Cultivar Screening. In a comprehensive screening under continuous light, 23 cultivars were grown for 8 weeks. Included were five cultivars developed at a northern Norway research station under very long days. The cultivars were evaluated at 600 μmol m^{-2} s^{-1} PPF, 1000 μmol mol^{-1} CO_2, 18°C, and 70% RH. Twelve of the cultivars with good shoot growth and high tuber initiation were selected at 35 days after transplanting and grown for an additional 21 days. Data for tuber and dry weights were obtained for these selected cultivars. All cultivars are listed in Table 4.6 with the 12 selected cultivars in ranked order by tuber weight at the first harvest.

It can be noted that the cultivars which were bred at high latitudes under long days in Norway, The Netherlands, and Alaska, consistently grew and tuberized well under continuous light.

Table 4.6. Evaluation of selected cultivars with continuous irradiation.

Cultivar	Country of origin	Stunting and/or chlorosis	Dry weight (g plant^{-1})	
			Tubers	Total plant
Desiree	Netherlands	None	164a	300a
Ottar	Norway	None	129b	277ab
Haig	US	None	99c	176ef
Rutt	Norway	Slight	94c	187def
Denali	US (Alaska)	Slight	91c	243bc
Snogg	Norway	Slight	83cd	215cde
Atlantic	US	None	78cd	187def
Alaska 114	US (Alaska)	None	74cd	164f
Snowchip	US (Alaska)	Medium	61de	219cd
Troll	Norway	Slight	88de	239c
Binje	Netherlands	Slight	43ef	193def
New York 81	US	Slight	27f	191def
Norland	US	None		
R. Burbank	US	None		
Bake King	US	None		
Alpha	Netherlands	slight		
Gulauge	Netherlands	None		
Stately	US (Alaska)	Medium		
Spunta	Holland	Slight		
Kennebec	US	Medium		
Superior	US	Severe		
ND 860	US	Severe		
NY 72	US	Severe		

Physiological Responses. We have investigated the physiological responses of cultivars to continuous light utilizing two resistant cultivars, Denali and Haig, and two sensitive cultivars, Kennebec and Superior, as detailed in Cao and Tibbitts (1991a). Plants were grown for 56 days at 18°C, 71% RH and PPF of 470 μmol m^{-2} s^{-1}. Specific analyses were undertaken to determine whether carbohydrate accumulation in leaves was high, thus providing potential for feedback inhibition of CO_2 assimilation in sensitive cultivars.

The long-photoperiod-tolerant Denali and Haig cultivars grew well, but the long-photoperiod-sensitive Kennebec and Superior cvs were chlorotic and stunted within 14 days. The plants of Kennebec and Superior showed slight recovery before harvest. Dry weights of shoots, roots plus stolons, and tubers were much lower for Kennebec and Superior than for Denali and Haig (Table 4.7). Kennebec and Superior had only a few small tubers, weighing

Table 4.7. Plant dry weight and leaflet characteristics of potato cultivars grown under continuous irradiation.

					Leaflets[y]		
	Plant dry wt[z] (g)				Area	Dry wt	Specific leaf area
Cultivar	Shoots	Roots	Tubers	Total	(cm^2)	(mg)	(cm^2 g^{-1})
Denali	170a	11.2a	162a	343a	11.6a	76.0b	154c
Haig	117b	4.2b	155a	276b	12.7a	96.7a	134d
Kennebec	27c	0.7c	0.1b	28c	8.0c	46.1c	176b
Superior	31c	0.8c	0.6b	33c	9.8b	43.7c	226a

[z]Means of six replicate plants. Mean separation in columns by Duncan's multiple range test, P =0.05.

[y]Data for terminal and adjacent paired leaflets of the leaves used for chlorophyll and carbohydrate analyses. Averages of leaf samples from each of six replicate plants.

< 1 g dry weight/plant, while Denali and Haig produced > 150 g/plant. These differences between the cultivars are consistent with previous observations (Tibbitts et al., 1989; Wheeler and Tibbitts, 1986).

Denali produced 50% more shoot and root plus stolon dry weights than Haig, but similar tuber dry weight (Table 4.7). The harvest index was 0.47 for Denali, but 0.56 for Haig. Thus, Denali developed more vegetative growth than Haig. Shoots were responsible for > 95% of the total dry weight of Kennebec and Superior.

Kennebec and Superior produced smaller (27%) leaflets, but higher (40%) specific leaf area (SLA) than Denali or Haig (Table 4.7). This difference in SLA suggests that there was significantly less dry matter accumulation per unit leaf area in Kennebec and Superior than in Denali and Haig.

Net CO_2 assimilation rates per unit leaf area in Kennebec and Superior were about 30% of rates in Denali and Haig (Fig. 4.2). The pattern among cultivars was similar for CO_2 assimilation expressed on the basis of leaf chlorophyll concentration. Leaf stomatal conductance did not differ consistently between the four cultivars (Fig. 4.2). It was highest for Kennebec, lowest for Haig, and intermediate for Denali and Superior. Kennebec and Superior maintained high stomatal conductance, while net CO_2 assimilation was very low in the leaves. As a result, the intercellular CO_2 partial pressure in the leaves was significantly higher in the two sensitive cultivars than in the two tolerant cultivars (Fig. 4.2). The results indicate that photosynthetic inhibition in Kennebec and Superior under continuous irradiation was not due to a limiting amount of CO_2. Therefore, the reduced CO_2 assimilation in these cultivars apparently resulted from reduced photosynthetic activity within the leaf tissues. A similar observation was reported by Wolf et al. (1990) with high temperature effect on photosynthesis in potatoes.

In leaflets of Kennebec and Superior, chlorophyll concentrations on a dry -weight basis were greater than in those from Denali and Haig (Fig. 4.3A). In contrast, chlorophyll concentrations on a leaf-area basis did not differ consistently between these four cultivars. The higher chlorophyll concentration per leaf dry weight for Kennebec and Superior apparently resulted from the higher SLA for these two cultivars.

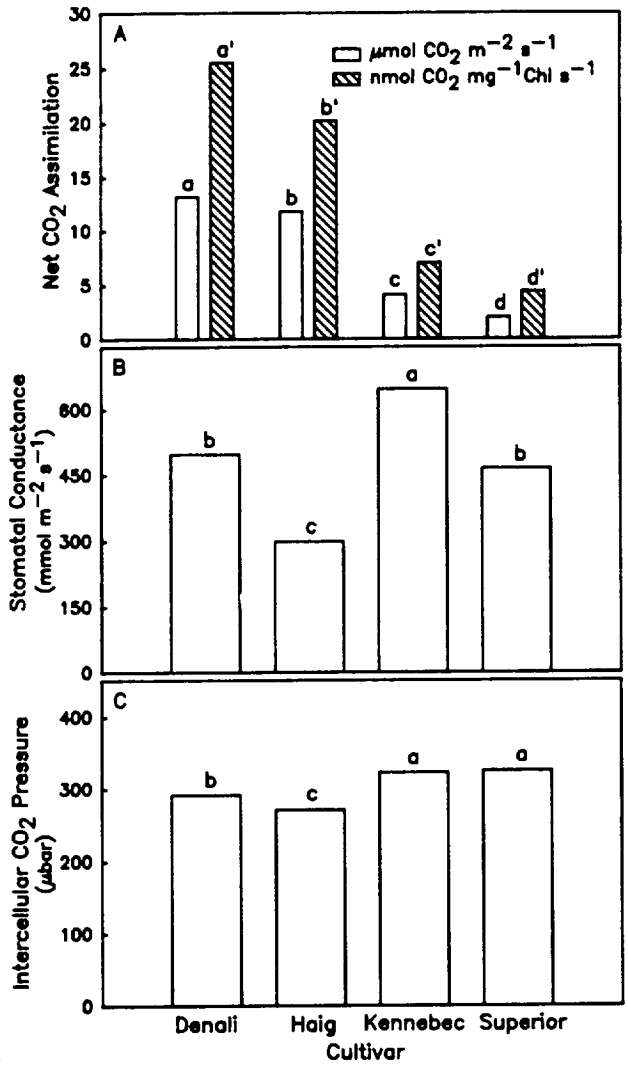


Figure 4.2. Net CO_2 assimilation (A), stomatal conductance (B), and intercellular CO_2 partial pressure (C) in the leaflets of potato cultivars grown under continuous irradiation. Values are means of six replicate plants. Mean separation in each data set by Duncan's multiple range test, P=0,05.

Starch concentrations in leaflets of Kennebec and Superior were only 10% of those for Denali and Haig (Fig. 4.3B). However, total soluble sugar concentrations were similar for all four cultivars. The high starch concentrations in leaves of Denali and Haig, in excess of 25% of the dry weight, were apparently related to high photosynthetic activity under continuous

irradiation. With CO_2 enrichment studies, a similar high level of starch accumulation was observed in potato leaves (Cao and Tibbitts, 1994d).

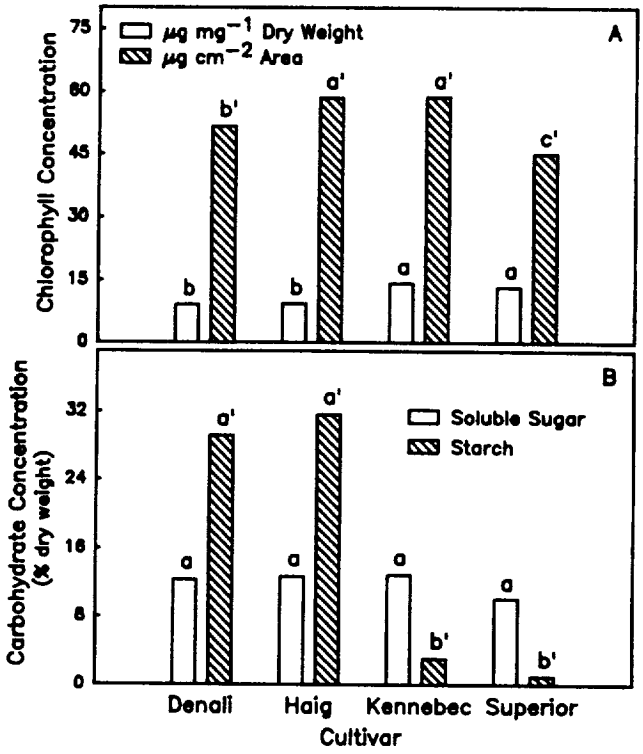


Figure 4.3. The concentration of chlorophyll (A) and starch and total soluble sugars (B) in the leaflets of potato cultivars grown under continuous irradiation. Values are means of six replicate plants. Mean separation in each data set by Duncan's multiple range test, P=0,05.

In conclusion, plant dry weights, CO_2 assimilation rates, and leaf starch concentrations under continuous irradiation were significantly lower in cultivars sensitive to long photoperiods, Kennebec and Superior, than in the tolerant cultivars, Denali and Haig. The results demonstrate that the lower CO_2 assimilation rates and stunted growth in Kennebec and Superior were not associated with an excess carbohydrate accumulation in the leaves. Thus, feedback inhibition from starch accumulation apparently was not a cause of the injury in these cultivars.

Continuous Light and Temperature Interaction. Tomato plants are also subject to continuous light injury, however it had been shown that a daily fluctuation in temperature produced healthy plants (Hillman, 1956). Thus studies were undertaken with potatoes to determine if daily temperature cycling could prevent injury on sensitive cultivars and permit normal growth and development as detailed in Tibbitts et al. (1990). Two potato cultivars, Kennebec and Superior, both sensitive to continuous light were utilized in duplicated experiments using two rooms of the Biotron. One room was maintained at a constant 18°C and 70% RH. Another room was kept at 22°C and 77% RH for 12 h and 14°C and 61% RH for 12 h. Thus the VPD was same at 0.60 kPa for all temperature levels. The PPF was 400 μmol m^{-2} s^{-1} provided with cool white fluorescent lamps on continuously. The same treatments were undertaken in each of two experiments, but the treatments were reversed in the two growth rooms in the second experiment. Each treatment consisted of four plants of each cultivar in each experiment. The plants were grown for 4 weeks after transplanting in the first experiment, and for 6 weeks in the second experiment to obtain information on tuber initiation.

In both Kennebec and Superior cultivars, the fluctuating temperature regime produced much greater growth than constant temperatures (Table 4.8). Under the alternating temperatures, the total dry weight of Kennebec plants was about 10 times greater, and for Superior was about 6 times greater than for the plants grown under constant temperature. Most of the dry weight was in above-ground shoots, with little in roots, stolons or tubers at these short growth periods of 4 and 6 weeks. The difference in dry matter between temperature treatments was somewhat greater after 6 weeks than after 4 weeks.

The plants grown under constant temperature developed small, chlorotic leaves. The lower leaves of Kennebec plants abscised in 3 weeks. Under fluctuating temperatures, the plants of both Kennebec and Superior cultivars grew vigorously and were compact and bushy with dark green leaves (Figure 4.4). The 4 and 6 week growing periods in this study were insufficient to obtain any significant tuber weights. With alternating temperatures, small tubers were initiated by 4 weeks, and tubers reached 2 cm in diameter at the 6 week harvest. Under constant temperatures, tuber initiation was observed, but it was delayed and no enlarged tubers were present at 6 weeks (Table 4.8).

Table 4.8. Dry weights of two potato cultivars grown in two separate experiments under continuous lighting with constant and alternating temperatures.

Cultivar	Exper. duration	Temperature	Dry weight			
			Shoots	Tubers	Roots/stolons	Total
	weeks	°C		g		
Kennebec	4	18	1.9±0.4[z]	<0.1	0.1±0.1	2.0±0.4
		22/14	16.2±1.1	<0.1	1.2±0.3	17.1±1.6
	6	18	7.3±3.5	<0.1	0.3±0.1	7.5±3.6
		22/14	85.8±6.3	0.2±0.2	3.3±0.3	89.4±6.4
Superior	4	18	2.6±1.1	0.0	0.1±0.1	2.7±1.1
		22/14	12.3±0.4	0.5±0.3	0.6±0.3	13.3±0.3
	6	18	12.5±2.2	<0.1	0.3±0.1	12.9±2.2
		22/14	79.3±5.6	9.4±3.0	3.1±2.1	91.9±8.1

[z]Means±SD.

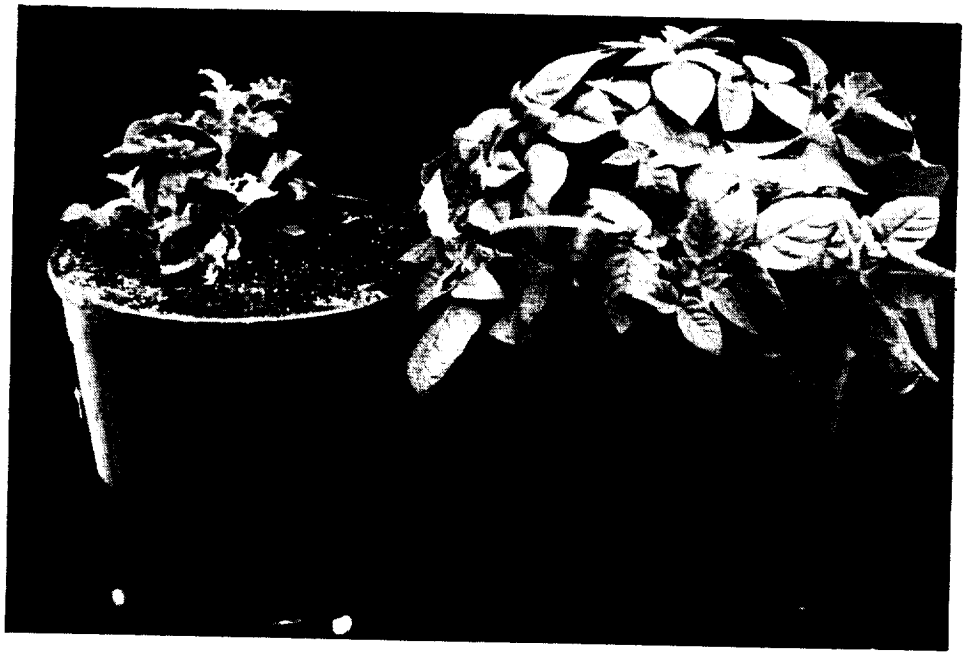


Fig. 4.4. Pictures of continuous light injury and injury prevention with temperature alternations.

An additional experiment was undertaken to determine if gradual temperature changes, that closely simulated the temperature changes in the natural environment would prevent injury as effectively as abrupt temperature changes.

Three potato cultivars, Denali, Superior, and Kennebec, were grown under four different temperature regimes with continuous irradiation at 380 μmol m^{-2} s^{-1} of PPF. The four temperature regimes were constant 18°C and fluctuating 20/16, 22/14, 24/12°C as detailed in Cao and Tibbitts (1990). The fluctuating temperature treatments were set with a gradually changing pattern that simulated the natural daily fluctuation and each averaged 18°C. Relative humidity was also fluctuated to maintain a constant vapor pressure deficit of 0.60 kPa. A representative graph for the temperature change of 22/14°C and associated humidity change is depicted in Figure 4.5.

Denali plants showed essentially similar growth under the different temperature regimes (Table 4.9). The plants of Superior and Kennebec showed severe continuous light injury under

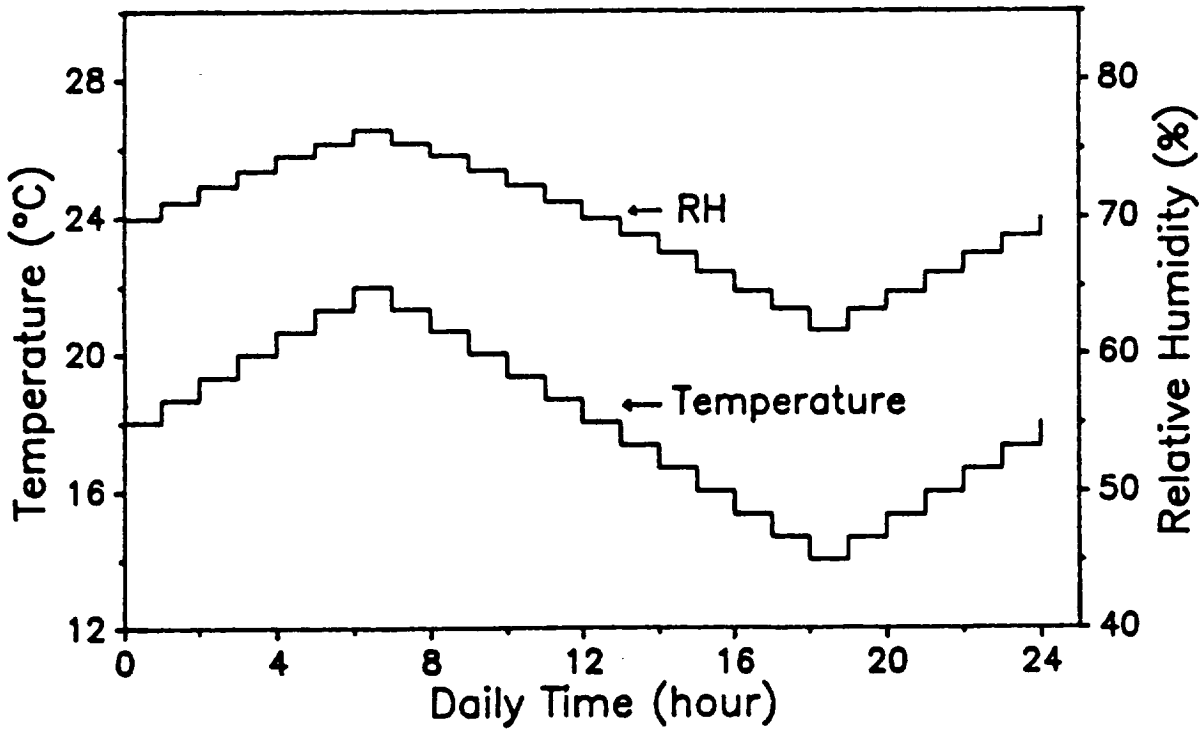


Figure 4.5. Diagram of the gradual changes of temperature (22/14°C) and relative humidity (62% to 76%) over a 24 h period.

Table 4.9. Dry weights of three potato cultivars grown for 42 days at different temperature regimes under continuous irradiation.

Temperatures	Cultivar	Dry weight			
		Shoots	Roots	Tubers	Total
°C		g			
18/18	Denali	47.8±19.4[z]	5.2±1.6	5.5±5.6	58.5±26.2
	Superior	1.3±0.5	0.1±0.1	<0.05	1.4±0.5
	Kennebec	1.4±0.8	0.1±0.1	0.1±0.1	1.5±0.8
20/16	Denali	60.1±4.8	4.7±0.7	15.7±8.1	80.6±11.4
	Superior	11.2±3.0	0.4±0.1	0.2±0.1	11.7±3.2
	Kennebec	5.0±2.3	0.2±0.1	0.1±0.1	5.3±2.4
22/14	Denali	53.3±10.9	5.4±1.5	3.8±1.6	62.5±13.0
	Superior	10.0±5.0	0.6±0.3	0.2±0.1	10.8±5.4
	Kennebec	3.3±0.7	0.2±0.1	0.1±0.1	3.5±0.8
24/12	Denali	59.0±9.4	8.6±2.3	11.2±6.9	78.8±10.7
	Superior	41.8±14.9	2.7±0.9	7.0±4.8	51.5±20.3
	Kennebec	46.5±19.8	2.7±1.6	0.2±0.2	49.3±21.4

[z]Means±SD of four replicate plants.

18, 20/16, and 22/14°C, but healthy growth under 24/12°C. Under 18, 20/16, 22/14°C, the total dry weight of Kennebec was only 10% of that under 24/12°C and total dry weight of Superior was 20% of that under 24/12°C. These results suggest that a temperature fluctuation with gradual change pattern could allow normal potato growth under continuous irradiation,

provided the change was large enough. Potato plants in a previous study under 22/14°C temperature fluctuation but with abrupt temperature change pattern on 12 hour basis were not injured, indicating that prevention from continuous light injury is a result of the total daily degree-hours below or above the average temperature.

VARIABLE LIGHTING

Studies were also undertaken to determine if short term fluctuations (of less than an hour) in light would increase CO_2 assimilation and growth of potatoes as compared with constant lighting with the same average PPF as detailed in Cao & Tibbitts (1993a). Two experiments with different light fluctuations were conducted. In the first experiment, PPF was continuously cycled with 30 minutes of 300 μmol m^{-2} s^{-1} and 30 minutes of 500 μmol m^{-2} s^{-1} in one room, and compared with a constant PPF of 400 μmol m^{-2} s^{-1} in a second room. In the second experiment, PPF was continuously cycled at 5 minute intervals a the same varying PPF levels, and again compared to a constant PPF in a second room. Plants of four potato cultivars, Norland, Russet Burbank, Denali, and Kennebec, were grown for 35 days after transplanting in both experiments.

Plant growth, measured as total dry weight, tuber dry weight and leaf area per plant was consistently, although only slightly, lower under variable PPF of 300 and 500 μmol m^{-2} s^{-1} than under constant PPF of 400 μmol m^{-2} s^{-1} in both experiments, whether the PPF was alternated every 30 minutes or every 5 minutes (Table 4.10). Averaged over the two experiments, variable PPF reduced total dry weight and tuber dry weight by 6%, and reduced leaf area by 5% as compared to the constant PPF. The probability levels for significance of these differences, however, were greater than 0.05 (0.08, 0.09, and 0.14 respectively) on this harvest date of 35 days after transplanting.

The decrease in plant growth under variable PPF was confirmed by CO_2 assimilation results. The CO_2 assimilation rates in leaves were increased at 500 μmol m^{-2} s^{-1} PPF and decreased at 300 μmol m^{-2} s^{-1} compared to 400 μmol m^{-2} s^{-1} (Fig. 4.6), a typical response of photosynthesis to unsaturated PPF. The leaf CO_2 assimilation rates under the variable PPF averaged about 2% lower than under the constant PPF in both experiments. The 2% decrease in average carbon assimilation rate under variable PPF was not significant at the 0.05 probability level, and this decrease was less than the decrease of 6% in carbon accumulation per plant under variable PPF. However, the continued decrease in leaf carbon assimilation rate at about 2% and

Table 4.10. Total dry weight, tuber dry weight, and leaf area per plant pooled for four cultivars of potatoes grown under variable and constant PPF in two separate experiments. The PPF of 300 and 500 μmol m^{-2} s^{-1} was alternated every 30 minutes in Experiment 1, and every 5 minutes in Experiment 2.

	PPF treatment (μmol m^{-2} s^{-1})	Total dry wt (g)	Tuber dry wt (g)	Leaf area (cm^2)
Exp. 1	300 and 500	16.1±1.6[z]	4.7±1.1	3008±194
	400	17.2±1.6	5.0±0.8	3146±238
Exp. 2	300 and 500	18.8±2.0	6.1±1.0	3608±370
	400	20.2±1.7	6.5±0.8	3827±310
Average	300 and 500	17.5	5.4	3308
	400	18.7	5.8	3487
	P level	0.08[y]	0.09	0.14

[z]Mean and SD pooled from four cultivars.

[y]No significant difference between variable and constant PPF, at $P = 0.05$.

the decrease in leaf area of 5% could account for the 6% reduction in plant carbon accumulation.

Stomatal conductance was essentially similar for PPF levels in variable and constant light conditions (Figure 4.6). This result suggests a lack of stomatal response to PPF fluctuations under the well-watered conditions of this study (increased CO_2 assimilation rates at higher PPF but similar stomatal conductance). The data suggest that under well-watered conditions, stomatal opening is not a limiting factor for photosynthesis, and is not responsive to this amount of PPF fluctuation.

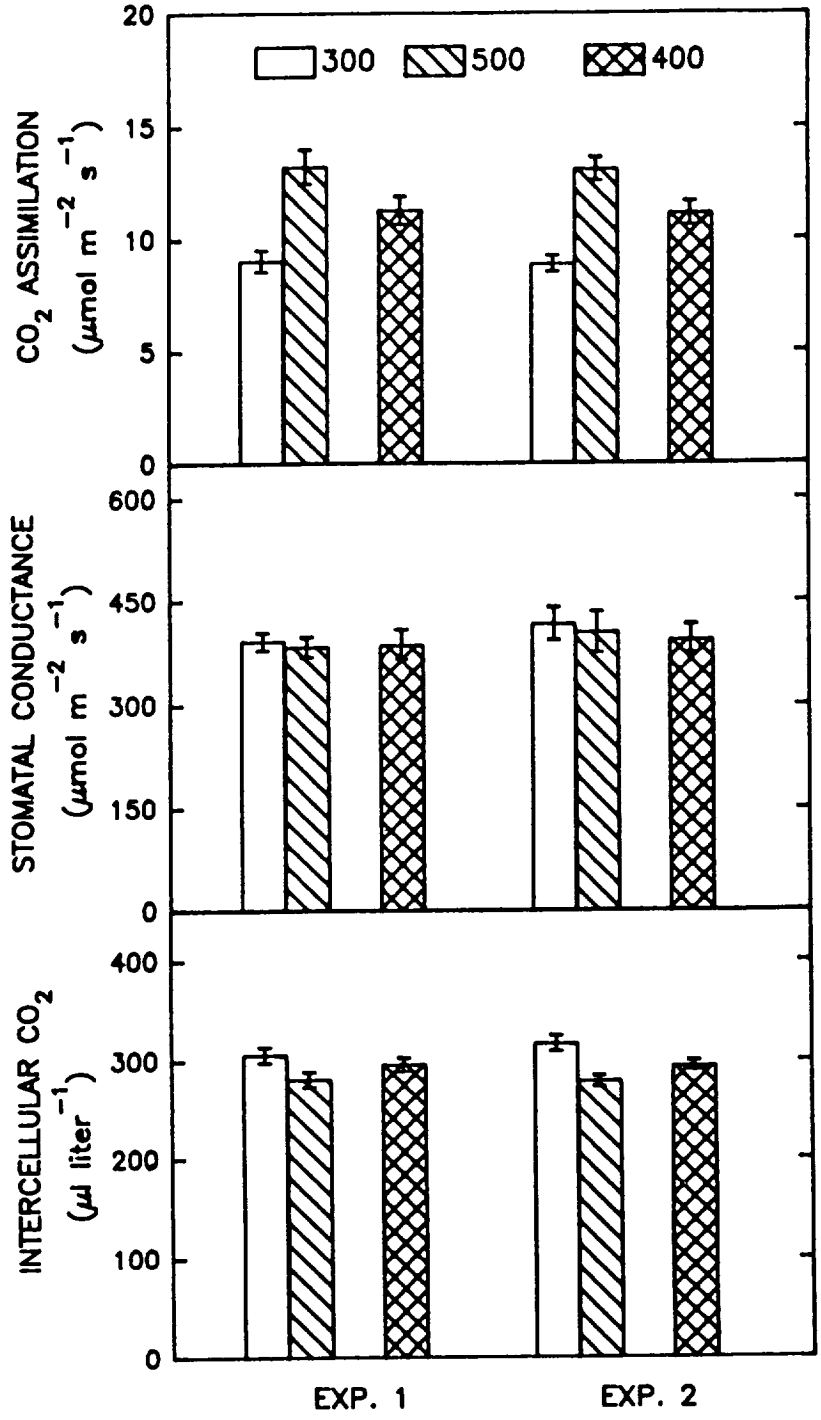


Figure. 4.6. Net CO_2 assimilation rates and stomatal conductance of potato leaves under variable and constant PPF in two separate experiments. The PPF of 300 and 500 μmol m^{-2} s^{-1} was alternated every 30 minutes in Experiment 1, and every 5 minutes in Experiment 2.

These results indicate that variable PPF is of no advantage over a constant PPF for plant growth in controlled environments. The present study suggests that the PPF outside, or in greenhouses, averaged over a certain time period (often one hour interval) will slightly overestimate dry matter production in these environments. These results are also of significance in modeling crop photosynthesis in field and greenhouse environments that commonly have varying light conditions.

WITHIN-CANOPY LIGHTING

Efforts were made to determine if lamps mounted at plant level among plants would provide greater light efficiency and have beneficial effects in reducing stem elongation. Studies were undertaken first with fluorescent lamps and then with 8" (20 cm) diameter light pipes.

Fluorescent Lamps. Cool white fluorescent lamps, 1500 mA rating and 72" (183 cm) length were mounted in vertical rows on each side of three rows of four potato plants. Lamps were mounted at 8 cm and 38 cm above the top of the plant containers. Four sets of lamps were mounted 45 cm apart. The lamps were located in one half of a Biotron room and an equal number of containers located in the other half of the room (Figure 4.7 & 4.8). An aluminum foil reflective barrier was hung between plants in the center of the room to prevent side lighting from the mounted fluorescent lamps reaching the plants in the other half of the room. Plants of the Norland cultivar were grown for 2 weeks in a reach-in chamber in 4" (10 cm) pots with peat-vermiculite and then a single plant transplanted into the twenty-four 19-liter containers for the experiment.

The photon flux (PPF) from the overhead cool white fluorescent lamps on both groups of plants was 390 μmol m^{-1} s^{-1}. The lamps mounted at 8 cm above the containers provided no significant additional PPF to horizontally directed measurements, however lamps mounted at 38 cm provided an additional 50 μmol m^{-1} s^{-1} at the center of each container. During the entire study, continuous lighting was provided.

The temperature maintained at the top of the plant canopy was initially set for 20°C, but was reduced to 16°C at 11 days after transplanting. The average air temperature near the plants over the course of the study was 0.8°C higher for plants with side-lighting than for plants without side-lighting. The RH was maintained at 70% and CO_2 at ambient.

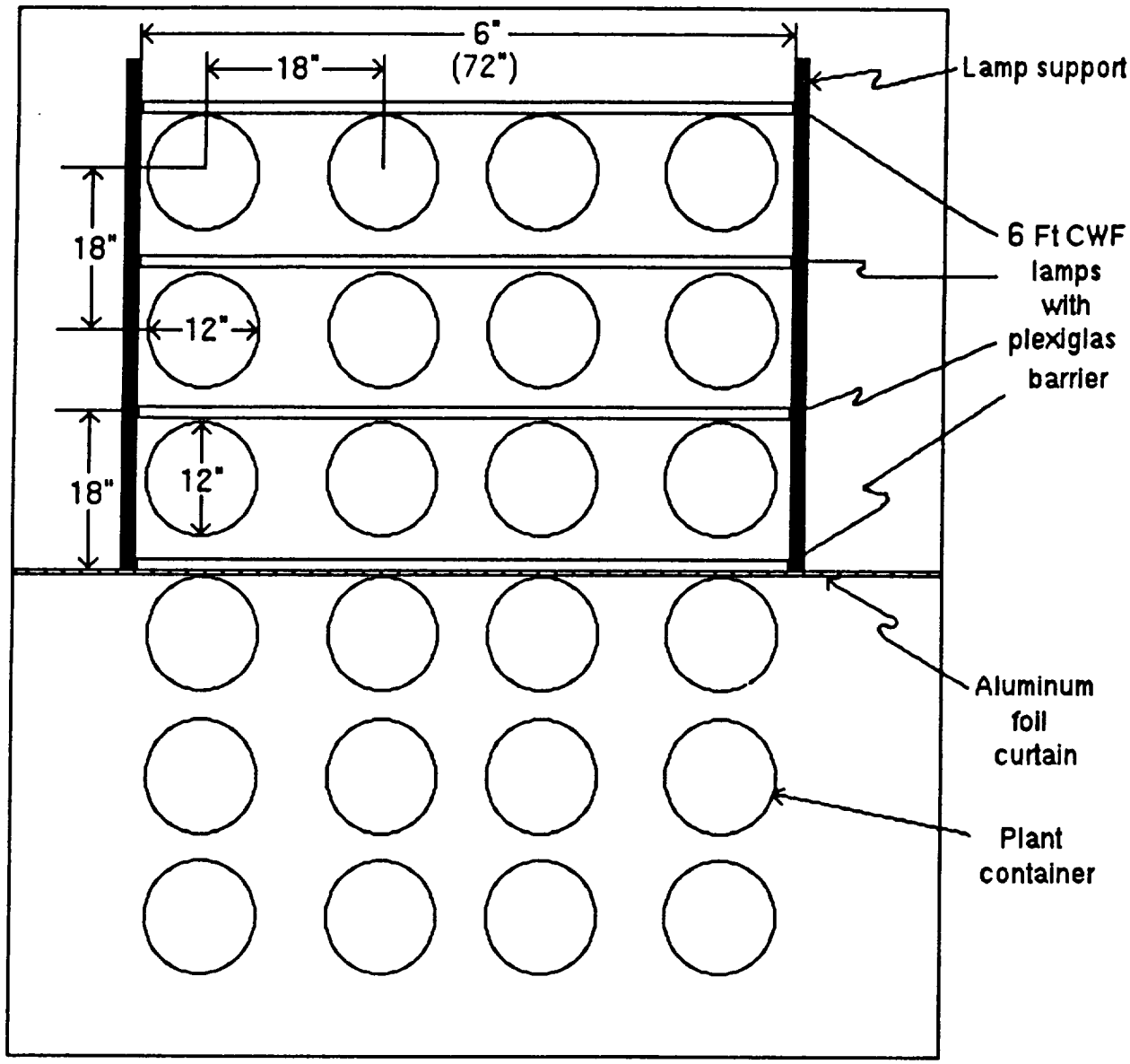


Figure 4.7. Diagram of fluorescent lamps used for within-canopy lighting. Dimensions were given in inches.

As the plants grew and enlarged, leaves contacted the fluorescent tubes and became necrotic. Therefore at 20 days after planting, transparent plexiglas barriers, 60 cm high, were installed to each side of the fluorescent tubes (8 cm apart) to keep leaves from contacting the

Figure 4.8. Photograph of the experiment layout using fluorescent lamps for within-canopy lighting.

warm tubes. A small squirrel-type blower was mounted on one side of each pair of barriers to provide ventilation and minimize heating of the plexiglass.

During growth, the plants with side-lighting were more chlorotic and did not have the vigor and healthy-look of the control plants. These side-lighted plants were shorter and did not have as much side branching. Plants were harvested 46 days after transplanting. Only data from the center four plants for both the side-lighted area and control area were averaged for comparison of growth.

The harvest data demonstrated that plants grown with side-lighting produced shorter plants of 24 cm stem length compared to plants with 32 cm stem length without side-lighting (Table 4.11). This was the hoped for response from the side-lighting. The yield of tubers was also nearly 27% greater with the side-lighting, but shoot growth was similar. However, it was theorized that if plants had been grown for a longer period of time, greater tuber weight m^{-1} day^{-1}

would have been obtained without side-lighting than with side-lighting because the non-lighted plants were more vigorous and leaves had less necrosis. It is felt that the increased light and slightly higher temperatures contributed significantly to the differences found and additional investigations are needed to confirm that there were definite advantages to the side-lighting. Further studies were undertaken with light pipes, which provided lighting that avoided the excess temperatures at, and around, fluorescent tubes.

Table 11. Growth data for Norland plants maintained with side lighting from cool white fluorescent lamps.

	Side lighting	No side lighting
Plant height (cm)	24.0±0.5	32.3±2.1
Shoot dry weight (g)	65.7±4.7	65.9±4.8
Tuber dry weight (g)	104.1±12.9	93.1±9.3
Total dry weight (g)	169.8±10.3	159.0±15.4
Harvest index (%)	61.9	58.6

Light Pipes. Light pipes were obtained from TIR Ltd in Burnaby, British Columbia, Canada. They were 20 cm in diameter and 250 cm in length. A 250 watt Venture metal halide lamp was mounted in a pear shaped reflector on each end with the radiation directed into the tube (Figure 4.9). In the first study, the tubes were constructed with a 90 degree reflector mounted within the tube on each side so that light was emitted from only 90 degrees on each side of the tubes. In the second study, tubes were reconfigured to have a reflection on only 120° of the lower part of the tube. Measurements were made on an individual tube before the first study to determine the uniformity in output over the length of the tube. This is shown in Figure 4.10.

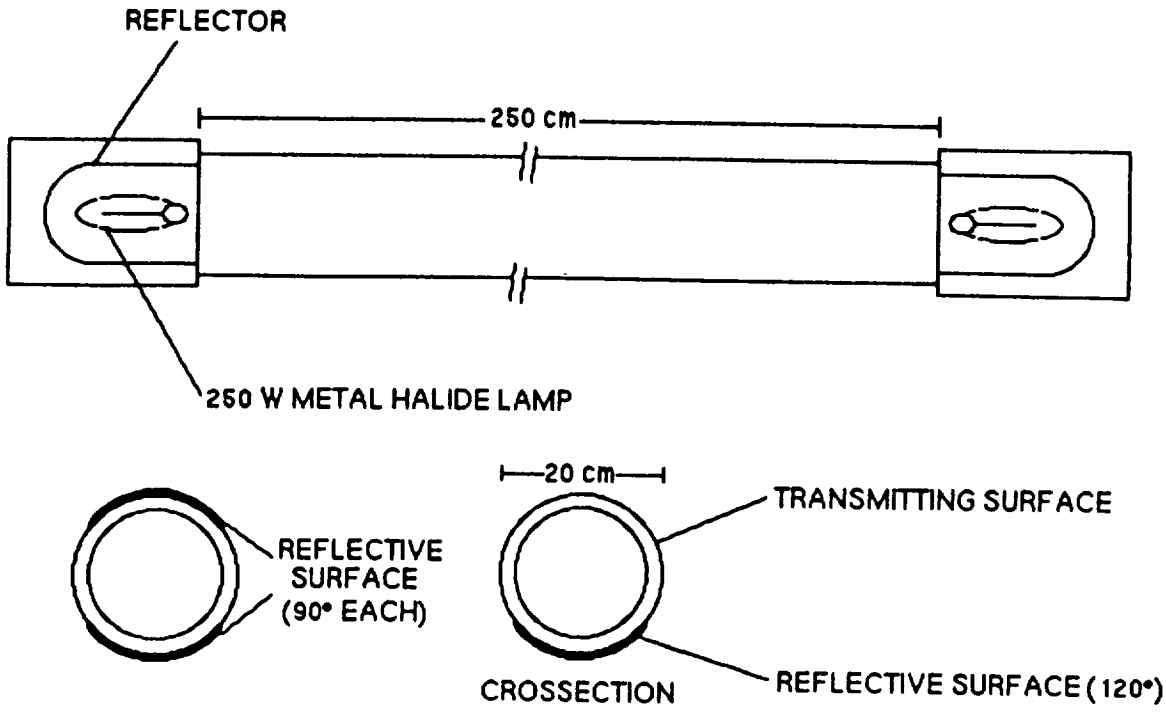


Figure 4.9. Diagram of the light pipe obtained from TIR Systems Ltd, Burnaby, British Columbia, Canada. The configuration with reflective surfaces on both the top and bottom was used in a first study and with reflective surface only on the bottom in a second study.

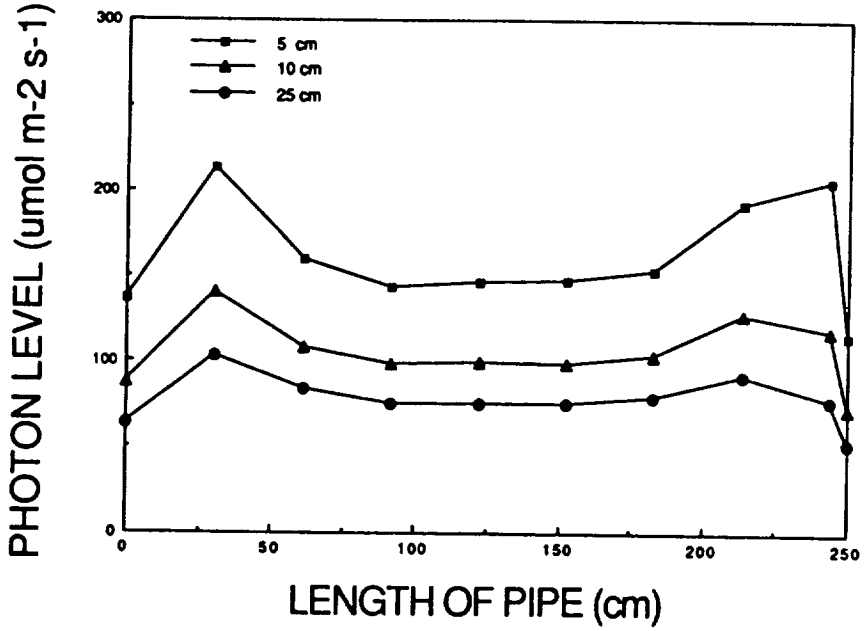


Figure 4.10. Photon flux along the length of the light pipe. Measurements were made with a sensor positioned perpendicular to the pipe at 5, 10, and 25 cm from the pipe.

Four light pipes were mounted in a Biotron controlled environment room. The pipes were spaced 38 cm apart on centers leaving 27 cm of space between pipes. Six 19 liter containers, each containing one potato plant, were spaced 38 cm apart on centers between each pair of pipes. Thus 24 plants were grown in each room in the arrangement as shown in the photograph (Figure 4.11). A second Biotron room was utilized with no light pipes but an equal number of containers with single plants placed at similar spacing as in the light pipe room.

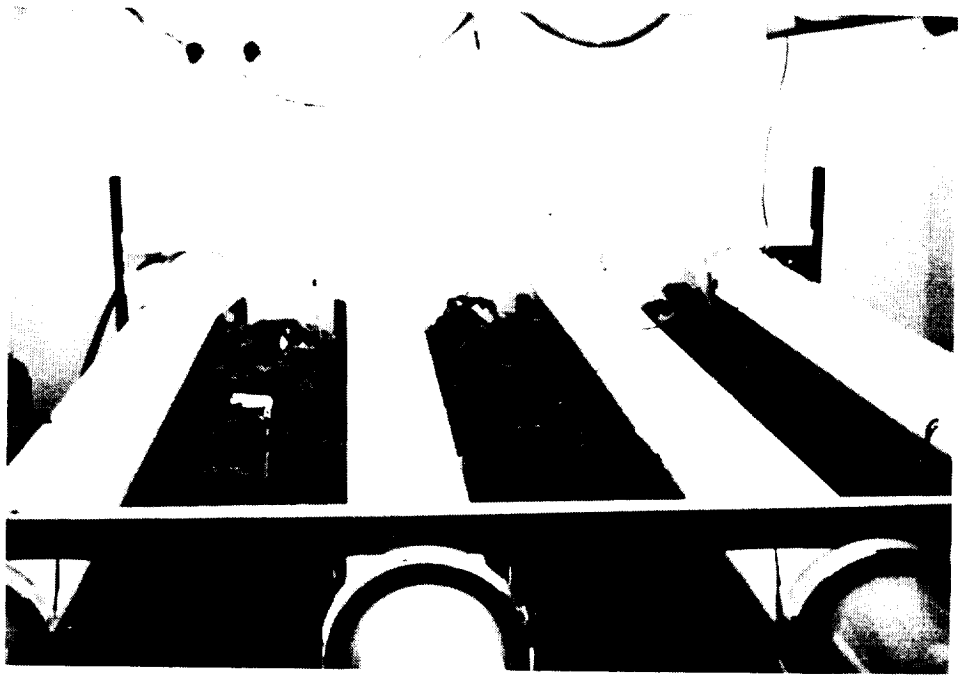


Figure 4.11. Photograph of 20 cm diameter light pipes positioned to the side of rows of potato plants in a growth room.

At the start of the experiment the PPF was balanced to have equal flux measured 10 cm above and at the center of each plant container using a quantum spherical sensor (LiCor, Inc). A number of the overhead lamps in the light pipe room were turned off to balance the lighting. As plants grew and extended upward, the height of the light pipes was adjusted upward. The pipes were moved up 15 cm on the 35th day after planting and another 15 cm on the 46th day. Weekly measurements were made at the top of the canopy and adjustments were made in the

number of overhead lamps to maintain equal PPF at the top of the canopy. The average PPF of weekly readings in the light pipe room with the spherical sensor at the top of the canopy was 566 μmol m^{-2} s^{-1} and in the control room 561 μmol m^{-2} s^{-1}. The PPF flux measurements with the standard cosine corrected (flat) sensor indicated significantly less PPF in the light pipe room than in the control room. The average PPF of weekly readings with the cosine corrected sensor was 319 μmol m^{-2} s^{-1} in the light pipe room and 383 μmol m^{-2} s^{-1} in the control room. An additional group of measurements made in each room with a cosine corrected sensor positioned near the overhead lamps (15 cm below the barrier) documented that the adjustments of overhead lighting to balance lighting, reduced overhead PPF 37% in the light pipe room compared to the control room.

Measurements of surface temperatures on the light pipes indicated that over most of the length, temperatures were between 22 and 23°C, 4-5°C above air temperatures. The leaf temperatures on plants were found to average between 20 and 22°C and were similar on plants within light pipes and control room.

The plants were harvested at 58 days after planting with data collected from the 12 center plants. Harvest data indicated that plants growing between the light pipes had less growth and tuber development than plants in the control room with only overhead lighting (Table 4.12).

It is apparent that the lighting from the light pipes did not provide as effective photosynthesis as overhead lighting. This apparently resulted from the fact that less PPF was

Table 4.12. Plant growth and harvest index of potatoes grown for 58 days under different lighting treatments.

Treatment	Total dry weight	Tuber dry weight	Harvest index
	g plant^{-1}		%
Light pipes & overhead lamps	228.1±20.3	68.0±16.8	29.6
Overhead lamps only	360.8±49.3	132.7±20.1	36.8

provided to the plants. Balancing light with spherical sensors located only at the center of the plants did not accurately measure the effective lighting for the entire plant. Particularly as plants enlarged and leaves extended over or below the light pipes, they obtained less PPF than plants in the control room. This was demonstrated in the measurement with the cosine corrected sensor. Also, the light pipes took significant amount of space within the plant canopy and reduced the area over which leaves could spread and receive PPF. Some growth reductions may also have occurred from plant injury with movement of the lamps at 35 and 46 days, for plants were large and there was some leaf breakage as pipes were elevated.

A second study was undertaken with the light pipes and procedures modified to compensate for some of the limitations recognized in the first study. First, the lamps were modified to place only a single internal 120° reflector down the length of each tube. The tubes were positioned in the room so that the reflection area was located on the lower portion of the tube and thus light was emitted from 240° out of the sides and top of each tube. The tubes were mounted with the lower surface at the height of the top of the containers and tubes remained in this position during the entire period of the study. In this study, the overhead lighting was balanced to maintain the same PPF at the top of the canopy as measured with a cosine-corrected (flat) sensor. The average PPF maintained in the light pipe room was 418 μmol m^{-2} s^{-1} and in the control room was 417 μmol m^{-2} s^{-1}. When measured with a spherical sensor, significantly more PPF was present in the light pipe room, averaging 808 μmol m^{-2} s^{-1} compared to 670 μmol m^{-2} s^{-1} in the control room. Temperatures were maintained at 21.0°C during the light and 16.5°C during the dark and RH was 70% in both rooms. A 12 h photoperiod was maintained with the potato cultivar, Denali (late maturing). The plants were harvested at 56 days.

In this study, the plants growing with the light pipes produced considerably more total dry weight and tuber dry weight than plants without light pipes (Table 4.13). Although harvest indices was slightly lower in the light pipe room, this is not felt to have much significance because the plants were not mature at harvest time of 56 days. This data helps document that within-canopy lighting does not significantly interfere with potato growth and can provide useful photons. In both experiments, there was no evidence of leaf epinasty or of leaves predominately growing toward or away from the lighted pipe. However, there was not found to be any reductions in stem length by use of within-canopy lighting with light pipes as seen in the previous study with fluorescent tubes. Thus, the reduced stem length with fluorescent tubes apparently

Table 4.13. Plant growth and harvest index of potatoes grown for 56 days under different lighting treatments.

Treatment	Total dry weight	Tuber dry weight	Harvest index
	g plant^{-1}		%
Light pipes & overhead lamps	161.9±26.9	63.4±12.1	39
Overhead lamps only	125.0±21.3	54.8±15.3	44

resulted from heat and water stress on the plants.

In summary of these studies, within-canopy lighting can be utilized for growth of potatoes. However, the light pipes utilized in these studies had some rather severe limitations. They were bulky, and occupied excessive plant canopy space, the leaves at some distance from the pipe were shaded from the light emitted by the light pipe, and the pipes were not fitted with heat filters to remove longwave radiation before it entered the light pipes. Therefore, it can be concluded that a useful and effective within-canopy light distribution system has to meet these three major requirements. 1) involve only small volume within plant canopy. 2) provide minimal longwave radiation releases within the canopy. 3) provide uniform PPF distribution within the canopy.

FAR-RED

An effort was made to study the use of supplemental far-red radiation to control branching of potatoes. There was evidence that branching and tillering of crop plants, including tomatoes a plant species in the same family as potatoes, is reduced with the additions of far-red radiation at the end of light period (Casal et al., 1987; Kasperbauer and Karlen, 1986; Tucker, 1975). It was theorized that far-red radiation could be used to stop or slow branching and thus increase assimilate partitioning into tubers.

In the first study far-red radiation was provided for 5 minutes at the end of the light

period in one room and no far-red radiation in the other control room. Four lamps, Sylvania F20T12/232, 61 cm length and 500 mAmp loading were suspended 100 cm above the plant containers in a Biotron growth room. The lamps were encased in a medium Roscolene #823 cellophane filter (Musson Theatrical, Santa Clara, CA) to absorb radiation below 650 nm. Thus the principal emission of the lamps was between 650 and 900 nm with a peak emission of 750 nm (Figure 4.12). A second Biotron room was maintained as control with no far-red lighting.

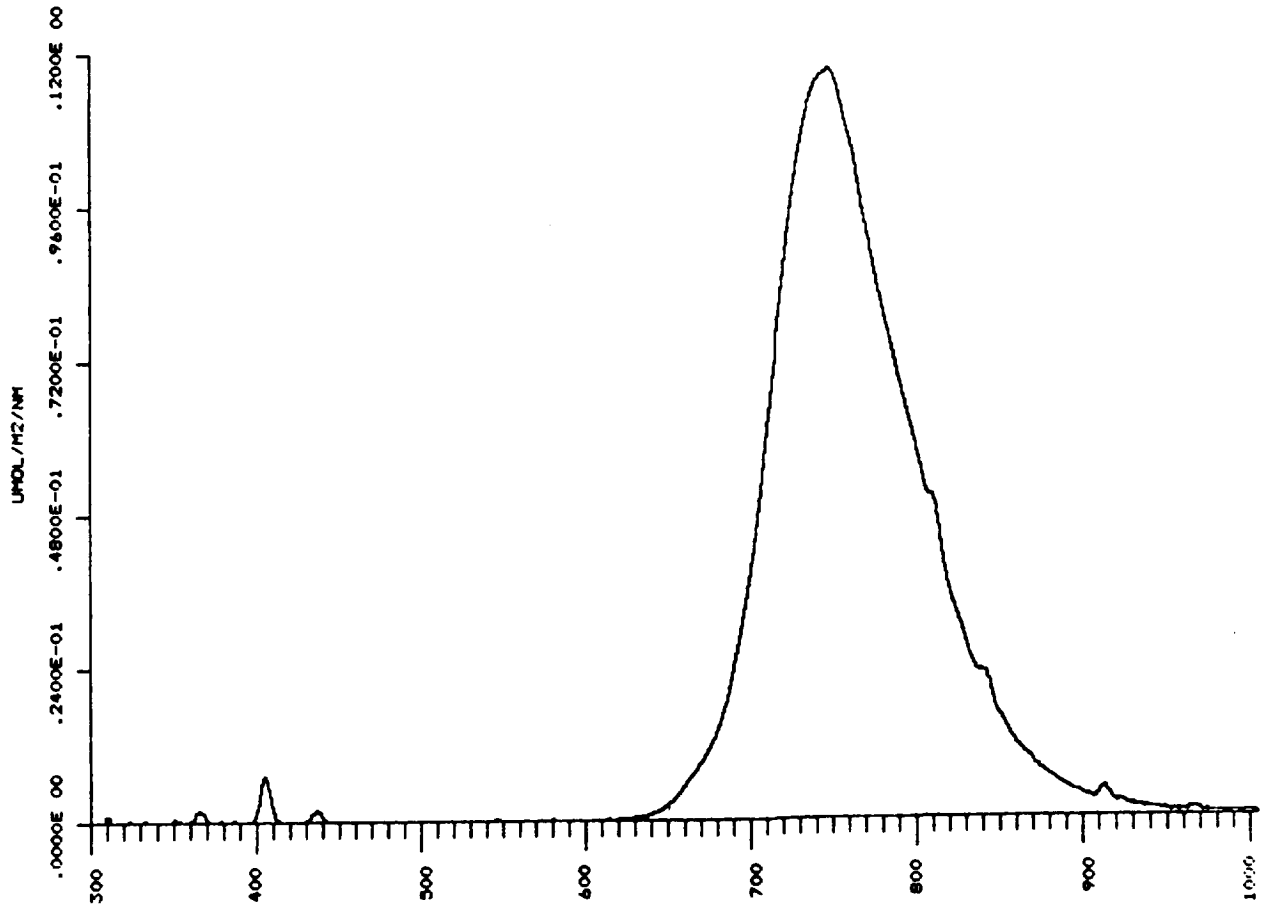


Figure 4.12. Spectral emission of Sylvania F20T12/232 far-red lamps with Roscolene #823 cellophane filters.

The average far-red photon flux measured at the plant container top was 2.7 μmol m^{-2} s^{-1} (700-800 nm) monitored with a spectroradiometer. The photon flux during the light period using cool white fluorescent lamps averaged over the separate plants was 408 μmol m^{-2} s^{-1} in the room with far-red lamps and 414 μmol m^{-2} s^{-1} in the control room. A photoperiod of 16 L:8 D was established. The temperature was 21 C during the light and 15 C during the dark in both rooms. RH was 71$\pm$3% in both rooms during the light and dark periods.

Two potato cultivars, Norland (early maturing) and Denali (late-maturing) were used. Sterile plantlets were transplanted into 8-liter containers of peat-vermiculite media and watered with nutrient solution 4 times daily. Four plants of each cultivar were placed in the far-red room and twelve plants of each in the control room at the start of the experiment. At 2 and 4 weeks, four plants of each cultivar were moved to the far-red room to obtain the most effective period of far-red treatment for optimum plant morphology for CELSS. Thus plants were obtained at harvest with 0, 2, 4, and 6 weeks of far-red treatment.

Plants were harvested 6 weeks after transplanting. There were no major differences in plant morphology or total dry matter accumulation with any of the far-red treatments for either cultivar (Table 4.14). There was an indication that the number of branches (>2 cm) was decreased with amount of time under far-red exposure, but the variation among plants was quite large and the data for the two different cultivars was not consistent, so no real significance can be attached to this response. Also, there are some differences in the far-red effect on plant height (stem length), weight of tubers, and total dry weight but again the differences were not consistent for the different cultivars.

Table 4.14. Plant growth data for two potato cultivars grown with far-red exposures for different periods following transplanting.

Cultivar	Measurement	Weeks of far-red exposure			
		0	2	4	6
Norland	Plant Height (cm)	20.0±0.1	23.3±1.5	22.0±1.2	22.5±2.3
	Branch number	16.8±1.1	16.8±2.7	16.0±1.2	15.8±1.6
	Tuber number	36.8±3.8	22.3±6.6	29.0±3.4	22.8±7.2
	Tuber dry wt (g)	15.0±2.7	6.8±2.9	7.5±3.7	8.3±3.8
	Total dry wt (g)	65.2±1.6	54.4±4.4	51.4±2.9	52.6±3.4
	Harvest index (%)	23.0	12.3	14.9	15.8
Denali	Plant height (cm)	21.0±1.2	22.0±1.9	21.5±2.1	22.8±3.3
	Branch number	22.0±3.7	17.5±1.1	17.0±1.6	17.3±1.1
	Tuber number	13.3±5.1	11.8±7.9	14.3±4.9	14.8±5.3
	Tuber dry wt (g)	8.7±3.6	6.6±1.9	6.8±3.4	9.2±3.0
	Total dry wt (g)	51.0±1.9	46.9±3.8	45.2±1.9	47.2±5.0
	Harvest index (%)	17.1	14.1	15.2	19.1

Because there was some indication of effects from far-red irradiation, a second study was undertaken to provide higher levels of far-red and also to determine if far-red levels during the main light period would influence plant morphology.

In the second study, similar far-red lamps, F72T12/232, 183 cm in length were used. A double fixture with two lamps was suspended 100 cm above the top of the plant containers at one end of the room. The lamps were also encased in # 823 medium red Roscolene cellophane to remove the visible and ultraviolet emissions. The spectrum of these lamps was as shown in Figure 4.12.

In both rooms, six rows of four plants were arranged across the room perpendicular to the lamps, providing a gradient of far-red photon flux on the different rows of plants. The far-red photon flux was monitored with the sensor oriented in the direction toward the far-red lamps to obtain maximum readings. In the room exposed to far-red radiation at the end of the light period, the average far-red levels were 16.0, 9.0, 6.5, 4.6, 3.3, and 2.6 μmol m^{-2} s^{-1} respectively for the 6 rows of plants at increasing distances from the far-red lamps, and in the room exposed to far-red radiation during the light period, they were 12.2, 7.0, 5.1, 3.2, 2.6, and 1.9 μmol m^{-2} s^{-1} respectively for the 6 rows of plants.

The Norland (early maturing) cultivar was utilized in this study and cultural conditions were the same as in the first study. The light period was shortened to 12L:12D. The light was carefully balanced with extra shading within the rooms to insure that each row of plants was provided a similar PPF of 400 μmol m^{-2} s^{-1} during the light period. Temperature was maintained at 21 C during the light and 15 C during the dark and RH held at 70% during both the light and dark.

Plants were harvested after a 42-day period of growth. Again, there were no obvious indications of any significant differences in plant morphology in either room under the different levels of far-red radiation (Tables 4.15 & 4.16). However, the number of branches and the number of tubers was considerably lower than those of the control plants in the first study (Table 4.13). This suggests that reduced branching in the present study with far-red exposures at the end of light period or during the light may be a true far-red effect. It is possible that no significant differences were seen in plant responses to the different far-red levels because the far-red photon flux was provided at saturation levels for the different rows of plants in both growth rooms so that maximum response was obtained at all far-red levels. Also, the branch number and tuber number were less with far-red after the main light period than with far-red during the main light period, indicating that far-red exposure following the light was more effective for inhibiting branching than the exposure during the light.

However it should be recognized that there could have been some uncontrolled factors associated with the two rooms within which these experiments were conducted, that produced the different responses instead of the far-red radiation.

Table 4.15. Plant growth with far-red exposures at different photon flux following the light period.

	Far-red intensity (μmol m^{-2} s^{-1})					
Measurement	16	9	6.5	4.6	3.3	2.6
Plant height (cm)	25.8±3.5	27.5±3.7	25.8±3.8	28.0±4.9	28.0±4.5	26.5±2.6
Branch number	2.5±2.1	2.0±2.2	1.5±1.4	2.3±1.5	3.0±2.1	1.5±1.5
Tuber number	6.5±2.7	6.5±1.7	5.8±1.5	9.8±2.5	9.0±3.1	6.8±2.8
Tuber dry wt (g)	17.8±2.1	18.1±1.0	18.9±3.3	19.0±4.6	18.3±2.8	15.0±2.9
Shoot dry wt (g)	13.9±2.9	14.0±1.5	13.9±3.9	14.6±4.5	14.6±3.6	12.2±3.2
Total dry wt (g)	32.1±4.9	32.0±1.4	33.1±6.8	34.1±9.2	33.5±6.2	27.7±6.2

Table 4.16. Plant growth with far-red exposures at different photon flux during light period.

	Far-red intensity (μmol m^{-2} s^{-1})					
Measurement	12.2	7	5.1	3.2	2.6	1.9
Plant height (cm)	23.0±2.2	22.5±2.5	24.1±2.8	23.3±4.5	27.0±3.9	27.1±3.9
Branch number	5.0±1.8	4.8±1.5	5.5±2.2	5.8±2.1	6.0±1.7	5.3±1.7
Tuber number	13.0±4.6	9.3±2.1	13.5±1.9	13.5±4.4	20.0±5.1	16.3±6.5
Tuber dry wt (g)	16.5±2.7	13.3±2.9	15.7±2.2	16.3±2.2	18.3±2.4	14.8±3.9
Shoot dry wt (g)	15.8±4.2	13.9±4.3	16.1±2.5	16.2±4.4	18.6±4.5	16.6±6.6
Total dry wt (g)	33.1±7.2	27.9±6.8	32.6±4.4	33.3±6.6	37.8±7.1	32.3±10.7

In related study, dim light extension with incandescent light (5 μmol m^{-2} s^{-1}) produced significantly longer stem growth than daylength extension with fluorescent light (5 μmol m^{-2} s^{-1}) (Wheeler and Tibbitts, 1986a).

In summary of these far-red studies, it appears that far-red radiation following the light period may have an inhibitory effect on branching and thus effect the morphology of potato plants. Additional work is needed to investigate the use of far-red radiation during the middle of the dark period, when stimulation is known to be maximum, and to grow the experimental plants for a minimum of 12 weeks to determine if branch growth is permanently slowed and if tuber production is affected.

SECTION 5. TEMPERATURE

The controlling effects of temperature on the growth and tuberization of potatoes have been known for many years (Bushnell, 1925). Bushnell showed that the optimal temperature for tuber development centered near 17 C and Benoit et al. (1983) documented that shoot growth was maximized at 25 C. Other reports have documented the effects of different cultivars and diurnal temperature alternations (Gregory, 1965, Ewing and Struik, 1992; Steward et al., 1981).

LEVELS

Studies were undertaken to determine the growth and development of potatoes maintained at five different temperatures under 12 h and 24 h (continuous light) photoperiods. It was conducted in controlled environment rooms at the Biotron where temperatures, PPF level, and humidity could be closely monitored and controlled. A detailed report of this study is provided in Wheeler et al. (1986).

Potato plants, cv. Norland, were transplanted to 6-liter plastic containers of peat-vermiculite mix. For the first 14 days after transplanting, all plants were maintained in a common growth room under constant 20 C and 70% RH. After 14 days, plants were transferred to individual chambers for constant temperature treatments of 12, 16, 20, 24, and 28 C. Final average temperatures as determined from daily treatments were: 12.1 ± 0.2, 15.9 ± 0.4, 20.0 ± 0.1, 24.4 ± 0.1, and 28.1 ± 0.1 C. The first experiment was undertaken with continuous lighting (no dark period), and the second experiment with 12 h light/12 h dark. Lighting was provided with cool white fluorescent lamps throughout the experiment, including the first 14 days at 20 C. The PPF at the top of the canopy averaged 395 (± 15) μmol m^{-2} s^{-1} in the separate chambers for all treatments. The PPF levels were adjusted either by turning out lamps as the plants grew in height or by adding pieces of neutral muslin shading just below the lamp barrier. Relative humidities were constant at 70% ($\pm 7\%$) in the separate chambers for all treatments.

All plants were watered to excess four times daily using a complete nutrient solution. Three plants were harvested from each treatment at 8 weeks after transplanting. Statistical differences among treatments were shown as standard deviations since individual plants were subsamples and not true replicates.

Differences in shoot growth between treatments became obvious as early as 1 week after initiation of temperature treatments. This difference was most apparent in stem lengths, with warmer temperatures promoting greater stem elongation. By 8-weeks-age, stems on plants under 24 h photoperiod had exceeded 90 cm in length for the 28 C, but less than 20 cm at the 12 C (Table 5.1). A similar promotion of stem elongation by warmer temperatures could be seen under the 12 h photoperiod, but to a lesser extent than under 24 h (Table 5.1). The greater stem elongation in response to warmer temperatures under both photoperiods was caused by both increased numbers of nodes and increased internodal lengths. In contrast to stem length, leaf size was seen to be inversely related to temperature where cooler temperatures promoted greater leaf expansion, particularly under the 12 h photoperiod.

Warm temperatures significantly decreased both number of tubers (Table 5.2) and total tuber fresh weight yields (Figure 5.1). Essentially no tuberization occurred under the 28 C temperatures under either photoperiod, and very little tuberization occurred at 24 C under the 24 h photoperiod. The highest tuber yield under the 24 h photoperiod occurred at 16 C (755 g per plant), while the highest yield under the 12 h photoperiod occurred at 20 C (460 g per plant), with 16 C only slightly less (Figure 5.1). Lower temperatures reduced the normal red periderm

Table 5.1. Stem length of 8-week-old Norland potatoes in response to temperature and photoperiod.

	Temperature (C)				
Photoperiod[z]	12	16	20	24	28
h			cm		
12	10.3±1.5[y]	30.3±0.6	56.7±7.4	62.3±7.2	79.7±5.9
24	17.7±0.6	36.7±4.0	48.0±2.8	74.0±7.1	94.3±2.1

[z]400 μmol m^{-2} s^{-1} photosynthetic photon flux.

[y]Data represent means±SD of three plants.

Table 5.2. Number of tubers (>2.5 cm) on 8-week-old Norland potatoes in response to temperature and photoperiod.

	Temperature (C)				
Photoperiod[z]	12	16	20	24	28
h			number/plant		
12	10.7±2.1[y]	12.7±2.5	12.3±1.2	7.7±0.6	0.0
24	12.7±0.6	17.0±3.0	9.7±2.5	0.3±0.6	0.0

[z]400 μmol m^{-2} s^{-1} photosynthetic photon flux.

[y]Data represent means±SD of three plants.

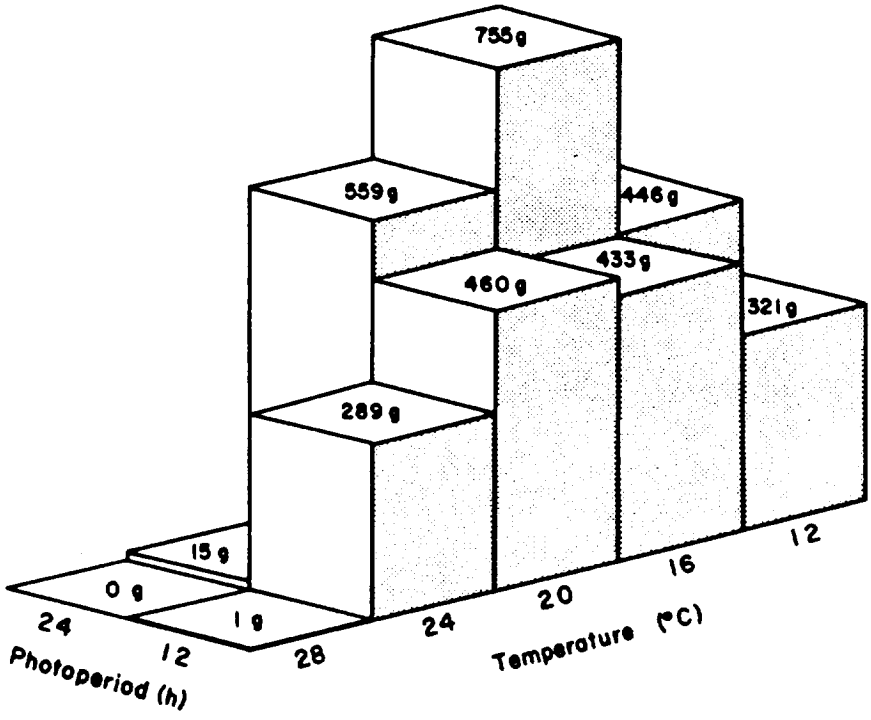


Figure 5.1. Tuber production (g fresh weight per plant) of 8-week-old Norland potato in response to temperature and photoperiod.

coloration of the tubers regardless of the photoperiod, so that tubers under the 12 C treatment barely showed any red coloration and tubers under 20 and 24 C treatments showed the deepest red color. In addition, the "strength" of the stolon-tuber connection increased with increasing temperature. This resulted in tubers remaining well-attached to stolons from the 20 and 24 C plants and tubers breaking free of the stolons very easily from 12 C plants.

The total plant dry weight production under the different temperature and photoperiod treatments closely followed trends in tuber yield (Figure 5.2). Under 24 h photoperiod, the maximum dry weight was produced at 16 C, while the lowest total plant dry' weight occurred at 12 and 28 C. Under the 12 h photoperiod, the greatest production occurred at 20 C with the least about equal at 12 and 28 C.

The biomass in leaves, stems, and tubers varied as a function of both temperature and photoperiod (Figure 5.3). As temperature increased, tubers contributed proportionately less to

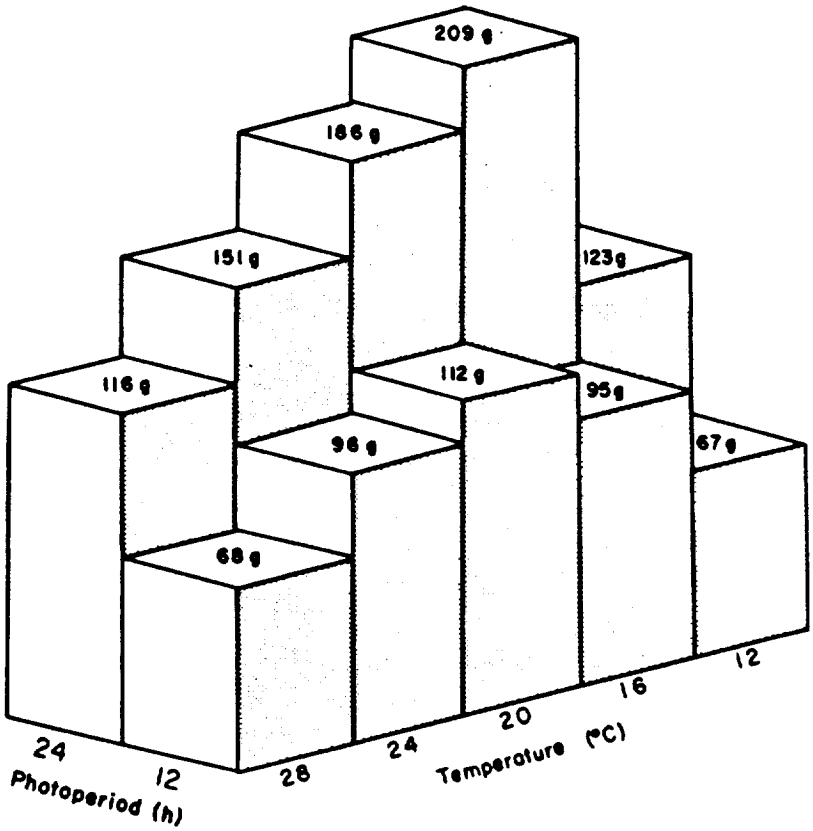


Figure 5.2. Total plant dry weight (g) of 8-week-old Norland potato in response to temperature and photoperiod.

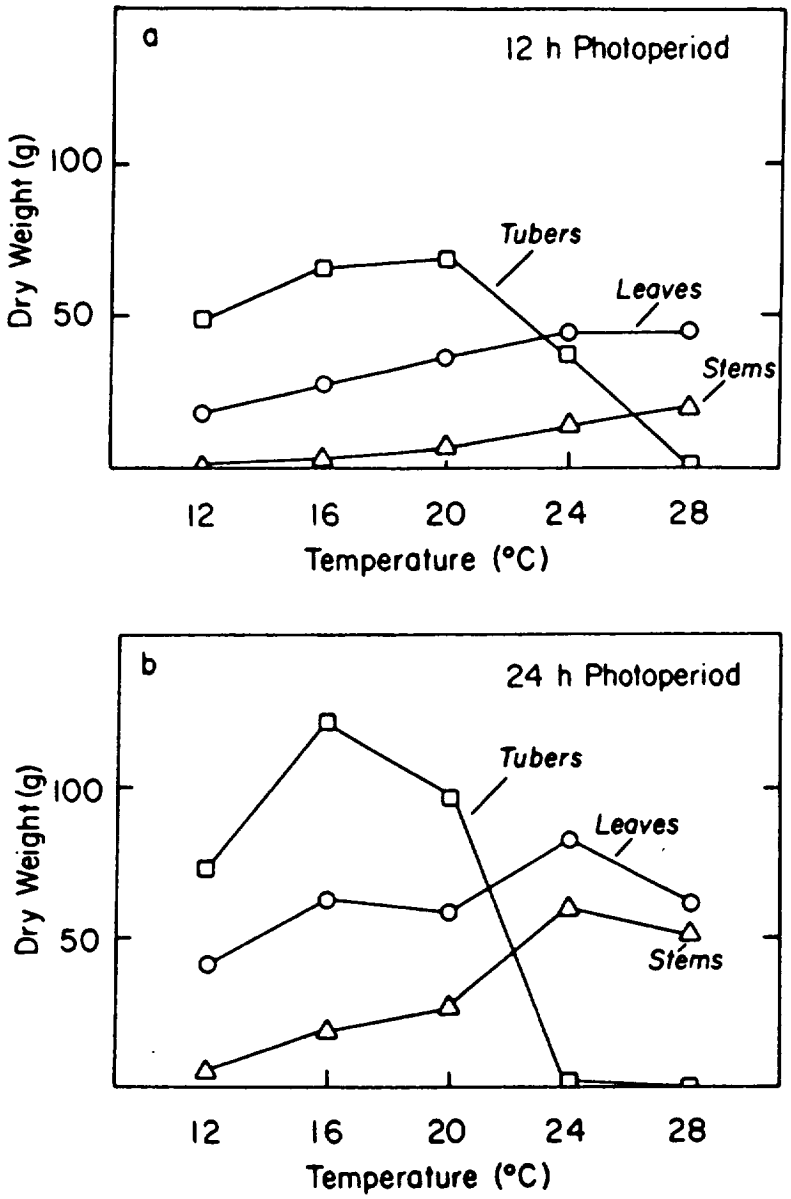


Figure 5.3. The biomass in leaves, stems, and tubers in response to temperatures under 12 h (a) and 24 h (b) photoperiod.

the total biomass of plants under each photoperiod while stems and leaves contributed more to the total biomass. In addition, the proportion of stems to leaves increased with increasing temperature.

A comparison of the ratios of tuber dry weight to total plant dry weight, i.e. harvest index, is shown in Table 5.3. Two trends are apparent in these data: First, under a given photoperiod, reducing the temperature increased the proportion of dry weight allocated to tubers; second, under a given temperature, reducing the photoperiod also increased the proportion of dry weight allocated to tubers. Thus, both short photoperiod (12 h) and cool temperatures (<20 C) favor tuberization. This supports previous findings (Gregory, 1965; Bodlaender, 1963; Ewing and Struik, 1992).

Table 5.3. Ratio of tuber dry weight to total plant dry weight (harvest index) of 8-week-old Norland potatoes in response to temperature and photoperiod.

	Temperature (C)				
Photoperiod[z]	12	16	20	24	28
h			g/g		
12	0.73±.01[y]	0.68±.01	0.60±.06	0.38±.02	<0.01±.01
24	0.59±.02	0.59±.02	0.51±.03	0.01±.02	0.0

[z]400 μmol m^{-2} s^{-1} photosynthetic photon flux.

[y]Data represent means±SD of three plants.

With the cv. Norland, the optimal temperature for tuber development appeared to shift downward to 16 C under continuous light in comparison to the optimal temperature near 20 C under the shorter 12 h photoperiod. It is possible that this apparent difference in temperature requirement may be a result of small differences in plant temperatures because of the increased radiant warming of the plants under the 24 h photoperiod. It is noteworthy, however, that no tuberization occurred under constant 28 C temperatures regardless of the photoperiod. This demonstrates the profound nature of temperature's controlling effects in tuber induction of the

potato.

Plants under increasing temperatures would have been subjected to increasing atmosphere water stress because humidity was maintained at constant 70% at all temperatures. This does not appear to be a significant factor in the conclusions drawn in this study, for water stress would be expected to encourage tuberization and also decrease growth of stems in relation of the amount of tubers.

The results show that the tuberization of the Norland potato can progress well under continuous light, i.e., without any dark period, provided temperatures are maintained sufficiently low, e.g., less than 20 C. Thus the need for an inductive dark period in cv. Norland is essentially supplanted by cooler temperatures. Also, the temperature environment apparently need not have a diurnal cycle or change to provide this induction. Whether diurnal cycling of temperatures would enhance tuberization under continuous light was studied in the following experiments.

DIURNAL TEMPERATURE ALTERNATIONS

There is a general assumption that temperature cycling is desirable and in some cases necessary for good growth of plants. Previous studies with potatoes in growth cabinets under diurnal temperature changes by Steward et al. (1981) have shown that lowered night temperature (24 C light/12 C dark) under 10 and 14 h photoperiods increased growth and tuberization in potatoes as compared to lowered day temperature (12 C light/24 C dark). However, there was no comparison of these alternating temperature treatments to a constant temperature treatment in this study by Steward et al. Also, these treatments did not have the same average daily temperatures because they did not have equal periods of light and dark. Thus, we investigated potato responses to temperature cycling on a 12 hour basis both under a 12 h photoperiod and under continuous light.

Temperature Cycling under 12 h Photoperiod. In the study with 12 h photoperiod as detailed in Bennett et al. (1991), uniform single plantlets of cvs Norland (early maturity) and Denali (late maturity) were transplanted into 38 liter (30 cm diameter) plastic containers with one plant per container. Eight containers of each cultivar were grown from planting in each walk-in growth room under the treatment conditions listed below. The potting material was peat and

vermiculite. Five weeks after transplanting, 1 meter high cylindrical cages of 10 cm mesh fencing were placed around the plants in order to support the plant canopy and avoid unequal shading competition between adjacent plants of the two cultivars. Plants were watered to excess four times daily with nutrient solution.

Two growth rooms were utilized for two treatments. One room was maintained with temperature at 22 C during the light and 14 C during the dark, with a similar 0.62 kPa vapor pressure deficit (VPD) during both the light and dark periods. The relative humidity (RH) was 77% at 22 C and 61% at 14 C. Another room was maintained at a constant 18 C temperature with 0.62 kPa VPD (70% RH) during both light and dark periods. Lighting was provided by cool white fluorescent lamps with 12 h photoperiod and 440 μmol m^{-2} s^{-1} PPF, maintained at plant canopy level. This experiment was repeated with the two temperature treatments switched between rooms to negate any possible chamber effects.

The six containers of each cultivar in each growth room were harvested 90 days after transplanting. Tuber dry weights (Table 5.4) under diurnal temperatures were increased by 54% in Denali and 8% in Norland. Total dry weight values were 30% higher for Denali grown in fluctuating temperatures and 10% higher for Norland.

The alternating temperatures affected stem growth of the potato plants (Table 5.4). For both cultivars in the two replications, alternating temperatures appeared to produce taller plants

Table 5.4. Effect of diurnal temperature fluctuations on growth and tuberization of potatoes.

Cultivar	Light/dark temperature	Tuber dry dry weight	Total dry dry weight	Plant height	Harvest index
	C	g $plant^{-1}$	g $plant^{-1}$	cm	%
Norland	22/14	332	492	107	67
	18/18	309	449	94	69
Denali	22/14	405	649	120	62
	18/18	263	499	106	53

than the constant temperatures. Denali was taller than Norland in both treatments. The increased stem lengths under alternating temperatures is consistent with the reports by Steward et at. (1981) in potatoes. The node numbers per stem did not change much on plants grown at 22/14 C (35 ± 2) and 18/18 C (38 ± 4), therefore the increase in plant height under alternating temperatures was primarily a result of greater internode elongation (3.2 cm per node for 22/14 C, and 2.6 cm, per node for 18/18 C) than of node numbers.

The harvest index of the plants (tuber weight/total weight) demonstrated no particular response to alternating temperatures (Table 5.4). The harvest index in this study was quite low because the plants were not taken to maturity. The harvest index of the Norland plants was higher than that of Denali because this is an earlier maturing cultivar and thus closer to maturity at the 90-day harvest date. Plants of both cultivars would obtain an index of 80% if grown to full maturity (Wheeler and Tibbitts, 1987).

The determination of tuber size distribution did not indicate an obvious shift for the Norland cultivar with alternating temperatures (Table 5.5). For Denali, the number of tubers >5 cm was slightly increased due to diurnal temperature fluctuations although the total number of tubers did not change consistently in either experiment. Thus it appears that with Denali the alternating temperature treatment may have promoted tuber enlargement but not tuber initiation. However, this conclusion is questionable because the plants were not taken to maturity.

The early maturing Norland cultivar that obtained only a small benefit from alternating temperatures commonly tuberizes in field plantings under warmer conditions and under less light/dark temperature fluctuation than late maturing cultivars. The late maturing Denali cultivar thus might be expected to produce a greater growth gain with alternating temperatures. Additional early and late maturing cultivars should be compared to determine if this is a consistent response to alternating temperatures.

Table 5.5. Effect of diurnal temperature changes on tuber size distribution of two potato cultivars in two separate experiments.

Cultivar	Experiment	Light/dark temperature (C)	Tuber size distribution			
			<2.5	2.5-5 (cm)	>5	Total
Norland	A	18/18	17±4	11±4	11±5	39±4
		22/14	17±5	10±3	10±2	37±5
	B	18/18	21±9	4±2	16±9	41±8
		22/14	22±4	4±1	12±2	38±4
Denali	A	18/18	31±15	18±3	6±2	55±16
		22/14	24±5	14±3	9±2	47±5
	B	18/18	31±10	14±3	7±2	52±12
		22/14	28±15	15±3	12±1	55±17

The information from this study is consistent with the reports by Stewart et al. (1981) about promotive effects of lower night temperature on plant growth and tuberization although the results indicate benefits of providing an alternating temperature environment to only one of the two potato cultivars studied. In previous studies of alternating temperatures (Steward et al., 1981), the vapor pressure deficit (VPD) of the air varied with changing temperature and thus it could not be determined whether effects from alternating temperatures were a result of temperature or VPD effects on the plants. Thus, the use of a constant VPD in this study helps document that temperature, and not water stress, is the controlling factor in increased growth under alternating temperature cycles.

Included in the first experiment was a treatment having a light/dark cycle of 14/22 C, thus the temperatures were reversed so that the cooler temperature occurred during the light and

warmer temperature during the dark. This was studied to determine if this temperature reversal could be used to reduce the length of stems of potatoes as seen by Berghage and Heins (1991) and Karlsson et al. (1989) for chrysanthemum and poinsettia. However, plants under the 14/22 C were significantly stunted and had a significant amount of chlorosis. As compared with the constant 18 C, the tuber yield with 14/22 C was reduced 49% for Norland and 22% for Denali, total plant biomass was reduced 64% for Norland and 29% for Denali, and plant height was reduced 53% for Norland and 38% for Denali. However, the number of tubers increased 50% for Norland and 100% for Denali with 14/22 C compared to the constant 18 C. This indicates that low day and high night temperature stimulated tuber initiation but inhibited tuber enlargement. Thus temperature reversal does not appear to be a useful procedure for producing potatoes for it reduced whole plant growth, including plant height and tuber weight.

Temperature Cycling under Continuous Light. A single experiment was undertaken to study alternating temperatures under continuous light. Denali and Norland cultivars were grown for 91 days in 38-liter containers under similar procedures and environmental conditions as with the previous 12 h photoperiod studies. Again, an equal VPD was maintained in both treatments.

The benefits of diurnal temperature changes were less under continuous light than under 12 h photoperiod and of questionable significance because of the large variation among plants in each treatment. Tuber dry weights (Table 5.6) under diurnal temperatures were increased by

Table 5.6. Effect of temperature alternations on growth of potatoes under continuous light.

Cultivar	Temperature	Plant height	Tuber dry wt	Total dry wt	Harvest index
	°C	g plant^{-1}	g plant^{-1}	cm	%
Norland	18/18	108±6	282±19	725±35	39±2
	22/14	122±4	288±114	797±124	35±9
Denali	18/18	109±6	351±51	854±39	41±5
	22/14	116±5	378±74	799±73	42±9

only 8% in Denali and 2% in Norland. Total dry weight was increased only 16% in Denali and 10% in Norland. Similar harvest indices were found with the two treatments. Plant height was also increased about 10% with alternating temperatures for both cultivars.

The results in the different studies document that alternating temperatures are of some benefit depending upon the light duration and the cultivars being grown.

TEMPERATURE CYCLING PERIODS

A study was undertaken to determine if the periods of temperature cycling could be varied to obtain greater growth and better tuberization. The temperature cycling periods were changed under continuous light conditions.

The experiment was conducted in the Biotron with four cultivars, Denali, Norland, Haig, and Kennebec. Kennebec is injured under continuous light when temperature is kept constant, while the other three cultivars are not sensitive to continuous light (Cao and Tibbitts, 1991a; Wheeler et al., 1986). Uniform single plantlets of these cultivars were transplanted into the centers of 8-liter plastic pots containing commercial peat:vermiculite mix.

Three temperature cycling periods were established at 6/6 h, 12/12 h and 24/24 h with a temperature regime of 22/14C. Relative humidity levels of 76% at 22C and 62% at 14C were provided to maintain a constant vapor pressure deficit (VPD) of 0.60 kPa at both temperatures. The three thermoperiod treatments were maintained in three separate growth rooms. In each growth room, the four cultivars were arranged in six randomized blocks. Continuous irradiation was provided by metal halide lamps at a photosynthetic photon flux (PPF) of 385 μmol m^{-2} s^{-1}. Carbon dioxide levels were ambient at 350 μmol mol^{-1}.

Following the first study, the experiment was repeated, but treatments were switched among growth rooms. The precise conditions maintained in each experiment are provided in Cao and Tibbitts (1992a).

The plants were harvested 42 days after transplanting. Number of tubers was counted for each cultivar. Analysis of variance was performed for each cultivar separately in a randomized block design with three thermoperiod treatments and two replications between growth rooms.

The number of tubers increased with increasing thermoperiods in all four cultivars, although the difference between 6/6 h and 12/12 h was significant only for 'Denali' (Table 5.7). The promotive effect of 24/24 h thermoperiod on tuber initiation was especially marked in

Table 5.7. Number of tubers of four potato cultivars grown for 42 days under three thermoperiods at alternating temperatures of 22/14 C.

	Thermoperiod (h)		
Cultivar	6/6	12/12	24/24
		no./plant	
Denali	16.1c[z]	20.1b	24.3a
Norland	24.2b	28.8b	44.2a
Haig	30.1ab	25.6b	38.7a
Kennebec	7.3b	8.3ab	11.4a

[z]Means of 12 plants. Mean separation in each row by Duncan's multiple range test, P=0.05.

'Denali' and 'Norland'. Number of tubers for all cultivars averaged 48% higher with 24/24 h thermoperiod than with other thermoperiods. These results indicate that thermoperiods can significantly affect tuber formation in potatoes.

The effects of thermoperiod on tuber dry weights varied with cultivar (Table 5.8). Tuber dry weights of 'Norland' and 'Haig' were similar under the three thermoperiods. However, tuber dry weight in 'Denali' was significantly higher under the 6/6 h thermoperiod than under 12/12 h or 24/24 h thermoperiods. Tuber dry weight in Kennebec under the 12/12 h thermoperiod was higher than under 24/24 h and not significantly different from that under 6/6 h. The Kennebec cv. has been shown to be injured by constant temperature when light is continuous (Tibbitts et al., 1990), and thus had a different response to the thermoperiods as compared to the other cultivars. It appears that the short and long thermoperiods reduced tuber growth in this cultivar sensitive to continuous light but plants were healthy at all three thermoperiods.

With different cultivars, the 24/24 h thermoperiod increased number of tubers (Table 5.7) but did not increase tuber dry weight (Table 5.8) relative to the 6/6 h or 12/12 h thermoperiods. Thus, the average dry weight per tuber was lowest under the 24/24 h thermoperiod, suggesting

Table 5.8. Tuber dry weights of four potato cultivars grown under three thermoperiods at alternating temperatures of 22/14 C.

	Thermoperiod (h)		
Cultivar	6/6	12/12	24/24
		g/plant	
Denali	32.1a[z]	25.5b	24.4a
Norland	9.0b	7.3a	7.3a
Haig	12.8a	13.2a	12.6a
Kennebec	3.3b	5.3a	2.1b

[z]Means of 12 plants. Mean separation in each row by Duncan's multiple range test, P=0.05.

that this thermoperiod slows tuber enlargement in potatoes.

Total plant dry weights (Table 5.9) for each cultivar were similar under the three thermoperiods, except that 'Denali' produced significantly higher total dry weight under 6/6 h thermoperiod than under 12/12 h (73.0 vs. 64.4 g). The difference for 'Denali' was apparently related to the significantly higher tuber dry weight under the 6/6 h thermoperiod (Table 5.8). Shoot and root dry weights of each cultivar were similar under the various thermoperiods.

This study demonstrates that the major effect of thermoperiods under continuous irradiation was on the tuber development of potatoes. A 24/24 h thermoperiod promoted tuber initiation but slowed tuber enlargement in some cultivars as compared with 6/6 h and 12/12 h thermoperiods. The results suggest that it may be possible to use long thermoperiods during early growth to promote tuber initiation, and then use short thermoperiods during late development to promote tuber enlargement. Thus, it seems likely that a careful control of thermoperiods at particular growth stages would increase yields of potatoes in controlled growing facilities.

Table 5.9. Total plant dry weights of four potato cultivars grown under three thermoperiods at alternating temperatures of 22/14 C.

	Thermoperiod (h)		
Cultivar	6/6	12/12	24/24
		g/plant	
Denali	73.0a[z]	64.4b	66.6ab
Norland	57.6a	56.6a	57.2a
Haig	47.0a	45.3a	48.2a
Kennebec	49.6a	48.5a	44.8a

[z]Means of 12 plants. Mean separation in each row by Duncan's multiple range test, P=0.05.

CULTIVAR SCREENING

Effort was made to screen a large number of potato cultivars for tolerance to elevated temperatures to find those that could tolerate a wider range of temperature conditions in a CELSS. Tolerance to a wide range of temperatures would permit potatoes to be included in the same growing compartment with many other crop species most of which would have useful growing temperatures above that of potatoes. The same procedures were utilized as in the screening of cultivars for continuous light tolerance and the same 23 cultivars were evaluated (Table 4.6) as detailed in Tibbitts et al. (1992).

Of the cultivars evaluated (Table 5.10), Atlantic, Desiree, LaRouge, Spunta, Pontiac and Kennebec were known or suspected to have the capacity for good production under warm conditions. Four plants of each cultivar were grown in 2-liter containers of peat-vermiculite media at 30 C with 600 μmol m^{-2} s^{-1} PPF and 12 h photoperiod, 1000 μmol mol^{-1} CO_2, and 70% RH. The plants were grown for 35 days and then a first evaluation was made. At this time plants were evaluated in terms of plant morphology and growth status, and one medium size plant of each cultivar was harvested to evaluate tuber initiation. The twelve cultivars that showed best

growth and tuberization were selected and saved for extended growth in larger containers that were widely spaced. The remaining three plants of these selected cultivars were carefully transplanted into 16-liter containers and grown for an additional 21 days.

Most cultivars evaluated under the 30 C growing temperature generally grew and developed well. The twelve cultivars with most vigorous growth and best tuberization were selected for extended growth. The cultivars selected for additional growth are shown in Table 5.10. Several of these selected cultivars exhibited an upright orientation of leaves, such as Bake King, Haig, Kennebec, Norland, Rutt, and Troll, indicating some response to the high

Table 5.10. Plant height, dry weight, tuber dry weight, and tuber number in 12 potato cultivars grown for 56 days under high temperature.

Cultivar	Plant height	Total dry weight	Tuber dry weight	Tuber number
	cm	g	g	
Alpha	90.3cd[z]	116.9bc	2.4cd	5.0cd
Atlantic	71.7e	122.2bc	1.5d	2.0d
Bake King	91.0cd	93.5cd	10.4bcd	17.7bc
Denali	101.7abc	155.0a	2.7cd	16.7bcd
Desiree	108.3abc	119.6bc	1.2d	24.0b
Haig	93.7bcd	94.2cd	17.4bc	41.3a
Kennebec	77.3de	125.2b	5.7cd	6.0cd
Norland	94.3bcd	105.5bcd	3.8cd	19.3bc
R. Burbank	111.7ab	127.8ab	3.5cd	6.7cd
Rutt	117.7a	134.7ab	22.2b	29.0ab
Superior	68.5e	80.5d	38.9a	15.0bcd
Troll	113.0a	117.5bc	17.1bc	19.0bc

[z]Means of three replicate plants. Mean separation in each column by Duncan's multiple range test, P=0.05.

temperature. The cultivars discarded were Alaska 114, Binge, Galuge, La Rouge, ND 86, NY 72, NY 81, Ottar, Snogg, Snowchip, Spunta, and Stately. La Rouge and ND 86 also exhibited upright orientation of the leaves, and New York 72 showed severe stunting and necrosis (the only cultivar severely stunted). The source of each of these cultivars is shown in Table 4.6.

In the final evaluation, plant height was greatest in Rutt, Troll, Russet Burbank, Desiree, and Denali, and least in Superior, Atlantic and Kennebec (Table 5.10). Total dry weight was highest in Denali, Rutt, and Russet Burbank, and lowest in Superior, Bake King, and Haig.

Tuber dry weight was highest in Superior, intermediate in Rutt, Haig, Troll and Bake King, and lowest in Desiree and Atlantic of the 12 selected cultivars (Table 5.10). Tuber number was highest in Haig, intermediate in Rutt and Desiree, and lowest in Atlantic, Alpha, Kennebec, and Russet Burbank. Tuber quality was poor in Superior with some knobby tubers developing. Knobby tubers were also present in Russet Burbank. Thus, of the 12 cultivars harvested, Rutt, Haig, Troll and Bake King showed the highest production potential whereas Atlantic, Alpha, Kennebec and Russet Burbank had the least potential of the selected cultivars for growing under high temperature conditions. The genotypical differences in response to high temperature in this study generally agree with previous reports (Ewing and Struik, 1992, Bodlaender,1963). The four best cultivars under high temperature in this study (Table 5.10) are all late maturity types. This suggests that the late maturity cultivars have greater potential for adaptation to high temperature conditions. In contrast, Marinas and Bodlaender (1975) found that cultivar response to high temperature was independent of maturity types when evaluated in greenhouse conditions. Thus, it appears that cultivar evaluation in controlled environments can provide different information for establishing plant response to environment.

Among the 24 cultivars evaluated for performance under both continuous light and high temperature, Desiree, Ottar, Haig, Rutt, Denali, and Alaska 114 were potentially best for growing under continuous irradiation while Rutt, Haig, Troll, and Bake King were the best cultivars under high temperature. Thus, Haig and Rutt were the only cultivars well adapted to continuous irradiation and high temperature conditions, and may have the best potential for adaptation to stress conditions. These two cultivars would be potentially best for future use in space farming in which extreme environments may exist and broad adaptability is needed. However, it should be emphasized that these evaluations were made after only 56 days of growth and additional evaluation should be made in long term productivity studies.

TEMPERATURE CHANGES DURING GROWTH

With the evidence that elevated temperatures favor vegetative growth and lowered temperatures favor tuber growth, efforts were undertaken to study the effect of temperature changes during different growth periods. It was hypothesized from the work of McCown and Kass (1977) that elevated temperatures during early growth would provide a large plant and that then reduced temperatures during later growth would insure a high production of tubers.

Eight combinations of 17 and 22 C air temperatures were maintained during three successive growth periods (Table 5.11). These two temperatures were selected for their differential promotion of tuber growth (17 C) and shoot growth (22 C). A daily constant temperature, instead of a diurnal fluctuation, was maintained to simplify the experiment conditions, for it was found that the Norland cultivar did not significantly benefit from diurnal

Table 5.11. Temperature change treatments during three growth periods, and total growing degree days accumulated over the 63-day growth duration. Day 21 and day 42 were nearly at the beginning of tuber initiation and tuber enlargement, respectively.

Growth period			Total growing
Day 1-21	Day 22-42	Day 43-63	degree-days
C			
17	17	17	693
17	17	22	798
17	22	17	798
22	17	17	798
17	22	22	903
22	17	22	903
22	22	17	903
22	22	22	1008

temperature fluctuations (Bennett et al., 1991). The 63-day duration of this study from transplanting to harvest was divided into three 21-day periods: day 1 to 21, day 22 to 42, and day 43 to 63 for reasons as discussed in Cao and Tibbitts (1994b).

The experiment was repeated, and the two growth rooms were switched for the temperature treatments in order to minimize possible room variation.

PPF of 430 μmol m^{-2} s^{-1} at the top of the canopy was provided by cool white fluorescent lamps for a 14 hour period. Relative humidity (RH) was maintained at 68% and 76% for the 17 and 22 C air temperatures respectively, providing a constant vapor pressure deficit of 0.60 kPa for both temperature levels. Carbon dioxide levels were ambient at about 350 μmol mol^{-1}.

Total growing degree-days accumulated over the 63-day experiment period were calculated for the different temperature change treatments using a base temperature of 6 C (Bodlaender, 1963; Moorby and Milthorpe, 1975).

Growth and Tuberization. Total plant growth was significantly different for the eight patterns of temperature changes over the three growth periods. The total dry weight per plant was highest with the 22-17-17 and 22-22-17 C treatments (Table 5.12). All treatments with 22 C during the first period had higher total plant dry weights than those beginning with 17 C. Thus, relatively high temperatures during early vegetative period promoted growth of the whole potato plant.

The dry weights of shoots and tubers responded to temperature change treatments differently. Shoot dry weight increased with the increasing amount of time at 22 C compared to constant 17 C (Table 5.12). With the same amount of time at 22 C, shoot growth tended to increase with the 22 C during later growth period, as seen with 17-17-22 C. This effect was accompanied by reduced tuber growth in these plants.

Tuber dry weight varied among the eight treatments more than shoot dry weight (Table 5.12). Tuber dry weight was highest with 22-17-17 C, and lowest with 17-22-22 and 17-17-22 C. Tuber dry weight with 22-17-17 C was at least 20% higher than that of any other treatment and 60% higher than with constant 17 or 22 C. The high to low temperature pattern significantly favored tuber growth.

Dry weights of stolons and roots were small compared to those for shoots and tubers (Table 5.12). Stolon dry weight was highest with 17-22-17 and 17-17-22 C, whereas root dry

weight was highest with 22-22-22 and 22-22-17 C. There were no consistent relationships between stolon and root mass or between stolon/root mass and tuber production, yet the treatment with the greatest tuber mass (22-17-17C) had the lowest dry weights of stolons and roots.

The results confirm that tuber growth was greater with air temperature of 17 C than with 22 C, whereas shoot growth was greater at 22 C than at 17 C (Table 5.12). This study also demonstrates that changes in temperature patterns during growth can significantly increase or decrease tuber production of potatoes. Highest tuber dry weights were obtained with early high

Table 5.12. Dry weights of the different parts of potato plants grown with various temperature change patterns.

		Plant parts			
Treatment	Total plant	Shoot	Tuber	Stolon	Root
C	g plant^{-1}				
17-17-17	196.7d[y]	116.6f	74.9c	2.87d	2.33d
17-17-22	190.6d	147.2cd	36.6f	4.04ab	2.71d
17-22-17	202.6d	140.9de	53.8e	4.25a	3.62bc
22-17-17	258.5ab	132.7e	120.5a	2.85d	2.46d
17-22-22	205.3d	164.2b	33.9f	3.60bc	3.57bc
22-17-22	234.2c	157.2bc	70.5cd	3.37c	3.18c
22-22-17	261.6a	154.3bc	99.5b	3.77abc	4.03ab
22-22-22	243.5bc	176.3a	59.1de	3.99ab	4.22a
P value[z]	0.0001	0.0001	0.0001	0.0019	0.0002
CV[z]	0.03	0.03	0.09	0.06	0.06

[z]Probability of a significant F value for treatments, and coefficient of variation (CV).

[y]Mean separation in each column by the Duncan's multiple range test at P=0.05.

temperature followed by low temperature as in the 22-17-17 and 22-22-17 C treatments, whereas the lowest tuber dry weight was produced with early low temperature followed by high temperature, viz. 17-22-22 and 17-17-22 C. Apparently, the 22 C temperature during initial vegetative period produced a rapid establishment of foliar canopy and thus promoted plant growth, whereas the 17 C during later stages maximized tuber growth with sufficient support of leaf assimilates. Thus, potatoes can tolerate, or even benefit from, warm temperatures during early growth. However, cool temperatures will be of particular importance during tuber growth.

The highest tuber dry weight obtained with 22-17-17 C was 60% greater than that obtained at constant 17 C and 100% higher than at constant 22 C (Table 5.12). According to a previous study (Wheeler et al., 1986), it might be argued that an optimum temperature of 20C constant could have provided significantly higher tuber yields than the 22-17-17 C in this study. However, in that study maximum tuber mass obtained at constant 20 C was only 6% higher than at constant 16 C (Wheeler et al., 1986). These data suggest that tuber productivity with a high-low temperature pattern will be potentially greater than at any constant temperature. This information will be particularly useful for optimizing temperature conditions for maximum tuber productivity in controlled growing facilities.

Shoot dry weight (Table 5.12) was closely correlated to the growing degree-days accumulated for each treatment (Table 5.11) with a R^2 of 0.93. However, tuber dry weight was not related to the growing degree-days (R^2=0.02), and instead was regulated by temperature change patterns during growth periods. Tuber dry weight varied three fold with different temperature patterns for the same number of growing degree-days. Thus, total plant dry weight also was not closely correlated to the growing degree-days. This suggests that temperature change patterns during the growing season under various production environments may affect tuber development more than the growing degree-days accumulated.

Total tuber number varied substantially with the different patterns of temperature changes. Tuber number was highest with 17-17-17 and 17-17-22 C, and lowest with 17-22-22 and 22-22-22 C (Table 5.13). Thus, tuber initiation was depressed most when the temperature was 22C from the beginning of tuber initiation, but was not affected by a temperature increase delayed until the beginning of tuber enlargement. It has been shown that tuber dry weights were lowest with both 17-17-22 and 17-22-22 C treatments (Table 5.12), yet tuber number was highest (70 tubers) with 17-17-22 C and lowest (33 tubers) with 17-22-22 C. Apparently, tuber initiation

Table 5.13. Total number of tubers per plant and separation into different size categories for potatoes grown with various temperature change patterns.

Treatment	Total tubers	Size category (cm)		
		<2.5	2.5-5.0	>5.0
C	no.			
17-17-17	75.2a[y]	48.8a	23.7b	2.7c
17-17-22	70.0ab	51.0a	19.0c	0.0d
17-22-17	53.0c	31.8b	20.7bc	0.5d
22-17-17	59.7bc	30.3b	20.8bc	8.5a
17-22-22	33.3e	19.3c	13.8d	0.2d
22-17-22	61.5bc	30.5b	29.5a	1.5cd
22-22-17	50.8cd	33.2b	10.8d	6.8b
22-22-22	40.0de	25.2bc	12.7d	2.2c
P value[z]	0.0001	0.0001	0.0001	0.0002
CV[z]	0.09	0.10	0.10	0.23

[z]Probability of a significance F value for treatments, and coefficient of variation (CV).
[y]Mean separation in each column by the Duncan's multiple range test at P=0.05.

and tuber enlargement responded differently to temperature change treatments.

The data indicated that to obtain a maximum number of tubers, relatively low temperatures are required even from the beginning of the plant growth cycle. In contrast, the number of large tubers was highest with 22-17-17 and 22-22-17 C. This high-low temperature pattern was even more important for tuber enlargement than a constant temperature level during the growth cycle such as 17-17-17 C.

Leaf Emergence. In the course of this study, data were collected on the rate of emergence of leaves to provide needed information for modelling leaf development of potatoes (Ingram and McCloud, 1984). Data were collected on four treatments, the two constant temperatures of 17 and 22 C, and two changed temperatures of 17-22-17 and 22-17-22 C as detailed in Cao and Tibbitts (1994c).

Leaf numbers on main stems and uppermost apical branches were recorded every 2-3 days during the course of the experiments. The leaf number increased linearly with accumulated growing degree-days (GDD) over the whole experiment duration for each of the four treatments, whether the temperature was constant or changed (Table 5.14). The phyllochron in GDD per leaf (6 C base temperature) was lowest at constant 17 C (19.2 GDD), highest at constant 22 C (22.8 GDD), and intermediate at the changed temperatures (about 21.3 GDD). Detailed analysis of the leaf emergence rates during each of the three 21-day periods indicates that the phyllochron at either 17 or 22 C was also slightly lower during the second 21-day period than during the first and third 21-day periods (data not shown).

The total leaf number increased with increasing total GDD among the treatments, primarily from increasing leaf number on apical branches (Table 5.15).

Table 5.14. Coefficient of determination (R^2) for the linear regression of leaf number against growing degree-days (GDD), and leaf emergence rate and phyllochron on potato stems with different temperature treatments. Data are averages from two experiments.

Treatment	R^2	Leaf emergence rate	Phyllochron
C		leaves GDD^{-1}	GDD $leaf^{-1}$
17-17-17	0.997	0.0520a[z]	19.2c
17-22-17	0.998	0.0468b	21.4b
22-17-22	0.997	0.0469b	21.3b
22-22-22	0.998	0.0439c	22.8a

[z]Mean separation in each column by the Duncan's multiple range test, P=0.05.

Table 5.15. Leaf number on main stem and uppermost apical branches in potato plants grown under different temperature treatments. Data are averages from two experiments.

Treatment				Branch order		
	Total	Main stem	Branches	First	Second	Third
C			no. plant^{-1}			
17-17-17	35.2d[z]	21.0a	14.2d	6.2a	8.0b	0.0c
17-22-17	37.2c	21.0a	16.2c	7.0a	5.7c	3.5b
22-17-22	40.7b	22.5a	18.2b	6.3a	6.2c	5.7a
22-22-22	43.1a	22.4a	20.7a	6.4a	14.3a	0.0c

[z]Mean separation in each column by the Duncan's multiple range test, P=0.05.

The data in this study suggest that a constant phyllochron for a particular growing area may provide sufficient accuracy for predicting leaf emergence on potato stems in the field environment.

SECTION 6. HUMIDITY

Studies on the effects of relative humidity on plants are uncommon in comparison to other atmospheric factors, such as air temperature or CO_2 level. Yet, the effects of humidity on plant growth can be profound (Tibbitts, 1979). We are not aware of any studies to determine the relationship of relative humidity to tuber production of potato. Goknur (1987) reported a slightly decreased stomatal conductance in potatoes when grown under 35% RH as compared to 70% RH, but no measurements were taken on tuber development and overall plant growth.

We conducted three separate studies to investigate growth responses of potatoes to relative humidity. Two of the studies were conducted under continuous light with growth periods of different lengths. The plants were grown for 56 days in the first study to obtain data on initial tuberization, and grown for 140 days in the second study to obtain data on tuber yield. The third study was undertaken under a 12 h photoperiod for 91 days.

HUMIDITY EFFECTS UNDER CONTINUOUS LIGHT

In the first study, potato cultivars Norland, Russet Burbank, and Denali were used. 'Norland' is early maturing and 'Russet Burbank' and 'Denali' are late maturing. Six plantlets of each cultivar were transplanted into a peat:vermiculite medium in 19-liter black plastic containers. At 33 days, individual plants were enclosed in cylindrical wire fence cages (34 cm in diameter) to contain shoot growth.

The plants were grown in two separate walk-in rooms of the Biotron. Relative humidity measurements were taken daily near the center of each growth room. One room averaged 83% RH and the second room 51%. The respective vapor pressure deficits were 0.40 kPa and 1.15 kPa. Continuous irradiation (24 h photoperiod) was provided by cool white fluorescent lamps. A 24 h photoperiod was chosen to maximize the rate of growth and, we assumed, to emphasize any difference between relative humidity treatments. Temperature and PPF were 20 C and 400 μmol m^{-2} s^{-1}. Precise conditions of each room are provided in Wheeler et al. (1989).

All plants were harvested at 56 days, and the area of 20 randomly selected leaves from each cultivar was measured. These leaves then were dried separately and the area:dry weight ratio was used to estimate the total plant leaf area from the total leaf dry weight.

For each of the cultivars, leaf dry weight and leaf area were higher at 50% than at 85% RH, but tuber dry weight was higher at 85%, which resulted in similar total plant dry weights for plants grown at the two humidity levels (Table 6.1).

Exposed leaves in the 50% RH atmosphere were the same or no more than 0.1 C warmer than the air 1 cm above the leaf. In contrast, leaves under 85% RH were 0.7 to 0.9 C warmer than the surrounding air. Despite the differences in leaf temperature, no consistent differences in leaf stomatal conductance were detected between relative humidity levels. However, Denali consistently showed higher stomatal conductance than either Russet Burbank or Norland and showed indications of greater conductance at 85% RH than at 50% RH. Carbon dioxide assimilation rates, measured with a LI-6000 portable photosynthesis system, also showed no

Table 6.1. Effects of relative humidity on potato growth characteristics under continuous light.

Growth measurement	Humidity (%)	Cultivar		
		Russet Burbank	Norland	Denali
Leaf dry wt (g)	50	122±18[z]	119±21	106±16
	85	110±9	98±10	89±10
Stem dry wt (g)	50	65±13	51±14	50±14
	85	69±6	40±7	44±7
Tuber dry wt (g)	50	28±25	27±26	66±21
	85	42±21	67±11	105±16
Total dry wt (g)	50	223±16	204±15	232±18
	85	229±9	210±14	249±14
Leaf area (m^2)	50	3.57±0.35	3.22±0.64	3.41±0.99
	85	3.13±0.40	2.57±0.38	2.60±0.46

[z]Means ± SD of six plants harvested after 56 days.

significant differences, ranging from 6.6 to 9.3 μmol m^{-2} s^{-1} for the three cultivars at both relative humidity levels. However, CO_2 assimilation rates measured on certain exposed leaves may not have represented whole-plant photosynthesis accurately. Water potential measurements on excised leaflets varied between 0.3 and 0.4 MPa for the separate cultivars at the two RH levels.

This study was undertaken at 20 C and it is important to note that the tuber yields of plants at both relative humidity levels were low in comparison to what has been reported for 56-day-old plants grown at cooler temperatures (e.g., 16 C) (Wheeler et al., 1986). We used 20 C and continuous light to provide a large VPD difference between treatments.

An ancillary objective of this study was to determine whether increased relative humidity would reduce apparent injury from continuous light (Wheeler and Tibbitts, 1986). Two cultivars that were sensitive to continuous light, Kennebec and Superior, also were grown in this study. Data were not shown for these cultivars because plants were severely stunted and exhibited leaf chlorosis under both humidity levels. Thus, there was no evidence for any reduction in injury with increased relative humidity, and instead there was evidence of slightly increased injury with increased relative humidity.

In the second study, only Denali plants were grown under 50% and 85% RH. In each of the two rooms, twelve Denali plants were grown in 38-liter pots for 140 days. Temperature was 18 C constant, 2 C lower than in the first study. PPF was 420 μmol m^{-2} s^{-1} with continuous lighting. At harvest, plant and tuber dry weights were determined and tubers from each humidity level were sampled for proximate analysis. No standard deviations for plants in each room are provided because the plants were grown in a solid canopy which caused very large plant-to-plant variability as some plants were shaded severely.

As shown in Table 6.2, dry weights of shoots and tubers under different humidity levels essentially followed a similar pattern as those in the first study. At 85% RH, the shoot dry weight was slightly lower while tuber dry weight higher than at 50% RH, suggesting a more favorable partitioning between shoots and tubers at 85% RH. The total dry weight was also somewhat higher at 50% RH than at 85% RH due to the larger difference in the shoot dry weight than in the tuber dry weight.

Proximate analysis of tubers indicated no substantial differences in the contents of protein, moisture, fat, ash, carbohydrates, and calories between 50% and 85% humidity levels (Table 6.3). Only slight increases in carbohydrates and calories were found at 85% RH as compared to

Table 6.2. Growth and yield of Denali cv. in response to relative humidity under continuous light.

Measurement	Humidity (%)	
	50	85
Shoot dry wt (g/plant)	1088[z]	913
Tuber dry wt (g/plant)	421	502
Total dry wt (g/plant)	1530	1436

[z]Means of twelve plants harvested at 140 days after transplanting.

Table 6.3. Proximate analysis of potato tubers produced at different humidity levels under continuous light.

Measurement (g/100g)	Humidity (%)	
	50	85
Protein	1.75[z]	1.60
Moisture	83.0	82.1
Fat	0.15	0.25
Ash	1.5	1.4
Carbohydrates	13.70	14.65
Calories	62.7	67.3

[z]Means of two samples each from four tubers under each humidity level.

the 50% RH. Thus, nutritional quality of potato tubers was not significantly affected by the relative humidity levels.

The results in these two studies suggest a possible benefit of raising humidity levels for increasing the yield of potato tubers. Increases in tuber yields will occur without any apparent increase in total plant dry weight. Thus, the elevated humidity appeared to shift the allocation pattern of photosynthates to favor allocation to the tubers over allocation to leaves and stems. Since continuous light tends to stimulate shoot growth (Wheeler et al., 1986), one would expect an enhanced partitioning of photosynthates to tubers under a 12 h (short) photoperiod.

HUMIDITY EFFECTS UNDER 12 H PHOTOPERIOD

Two cultivars, Norland and Denali, were used for this study. Five plants of each cultivar were grown in 38-liter pots under 50% and 90% RH. Light period was 12 hours at a PPF of 420 μmol m^{-2} s^{-1} and temperature was 18 C constant. Plants were harvested at 91 days after transplanting. Other growing procedures and environmental conditions were similar to those in the first two studies.

With both cultivars, dry weights of shoots, tubers, and whole plant were higher under the 90% RH than under the 50% RH (Table 6.4). The growth promotions were greater with Denali than with Norland cv. These responses are in contrast with the data under continuous light where shoot growth was increased under 50% RH.

Separate studies have shown that under continuous light, biomass partitioning into shoots was increased (Wheeler et al., 1986) and stomatal conductance was reduced (Cao et al., 1993) as compared to 12 h photoperiod. Low stomatal opening under continuous light may make transpiration and photosynthesis less responsive to different humidity levels. Thus, the possible effects of high humidity on transpiration and CO_2 assimilation, and on shoot growth were diminished under continuous light as compared to 12 h photoperiod. This may explain the different responses of shoot growth to relative humidity under different photoperiods.

Table 6.4. Potato growth and yield in response to relative humidity under 12 h photoperiod.

Measurement	Humidity (%)	Cultivar	
		Norland	Denali
Shoot dry wt (g)	50	179±10[z]	209±21
	90	195±12	257±33
Tuber dry wt (g)	50	209±33	94±13
	90	227±29	156±36
Total dry wt (g)	50	391±24	308±20
	90	425±29	419±36

[z]Means ± SD of five plants harvested at 91 days after transplanting.

In conclusion, tuber production of potatoes was greater at high relative humidity than at low humidity, particularly under short photoperiods. Partitioning patterns between shoots and tubers were shifted with different photoperiods. Under continuous light, shoot growth was greater at low humidity than at high humidity whereas under 12 h photoperiod, shoot growth was less at low humidity than at high humidity. These responses to humidity were more significant with Denali cultivar than with Norland cultivar.

SECTION 7. CARBON DIOXIDE

RESPONSE TO CARBON DIOXIDE ENRICHMENT

Constant CO_2 Enrichment. Long-term experiments have generally indicated that crop plants under elevated CO_2 concentrations have higher photosynthetic rates, faster dry matter accumulation, and greater yield as compared to the plants under ambient CO_2 levels, especially with C_3 plants (Farrar and Williams, 1991; Mortenson, 1987).

The potato is a C_3 crop and has shown a positive response to CO_2 enrichment in two previous reports (Arthur et al, 1930; Collins, 1976) and a slight negative effect in the study by Goudriaan and de Ruiter (1983). This study was conducted to determine growth and tuber productivity of two potato cultivars in response to constant CO_2 enrichment during long term growth periods.

The two cultivars, Norland (early maturing) and Russet Burbank (late maturing), were grown in solid stands in separate controlled environmental rooms at the Biotron. Two CO_2 levels, 370 μmol mol^{-1} and 1000 μmol mol^{-1}, were maintained separately so that a total of four single room experiments were undertaken. Rooms were maintained under continuous cool white fluorescent lamps at a PPF of 450 μmol m^{-2} s^{-1} at 16 C and 70% RH. Specific details of the control in each room can be obtained in Wheeler and Tibbitts (1989). Each room (2.6 m x 3.6 m) was planted with 24 plants maintained in 38-liter containers spaced on 45 cm centers across the room leaving a walkway around the perimeter. At 42 days, the stands in each of the rooms were fenced around the perimeter with 76 cm high hardware cloth screening to contain the plants within the specified area.

Beginning at 21 days after transplanting for Norland and 28 days for Russet Burbank, carbon dioxide assimilation rates (net photosynthetic rates) of exposed mature leaves were measured at weekly intervals for 11 weeks using a portable photosynthesis system (LI-6000). A minimum of seven, but typically 12 measurements, were taken at each sampling in each room.

Norland plants were harvested at 110 days after planting and Russet Burbank at 126 days. Data are reported as the average plant yields for the 24 plants in each treatment.

Final harvest data for both cultivars under both CO_2 levels are shown in Table 7.1. The highest tuber yields were obtained under the high CO_2 level (1000 μmol mol^{-1}) for both Norland

Table 7.1. Growth of three potato cultivars under two levels of carbon dioxide.

Cultivar[z]	Carbon dioxide	Dry weight				Harvest index
		Shoots	Roots[y]	Tubers	Total	
	μmol mol^{-1}	g plant^{-1}				%
Norland	365	181	7	416	604	68.9
	1000	209	8	423	641	66.0
Russet	370	356	7	440	803	54.8
Burbank	1000	334	5	495	834	59.4

[z]Norland plants harvested at 110 days, and R. Burbank plants at 126 days.

[y]Including stolons.

and Russet Burbank, 423 g dry weight/plant and 495 dry weight/plant, respectively. However, with both cultivars, increases resulting from CO_2 enrichment were small, 2% for Norland and 12% for Russet Burbank. Total plant dry weights were also increased by high CO_2 for both cultivars, but only 6% and 4% for Norland and Russet Burbank, respectively. Shoot dry weight of Norland plants was high at high CO_2, while Russet Burbank shoot weight was higher at low (ambient) CO_2. The highest harvest index for Norland (69%) occurred under the low CO_2 level while the highest harvest index for Russet Burbank (59%) occurred under the high CO_2 level.

The harvest index values (55-69%) obtained from the solid stands in these studies are substantially less than the 80-82% values obtained with 'caged' plants of similar age in previous studies as shown in Table 3.2. Since temperature and humidity were the same in both studies, the difference is likely attributable to the additional side lighting available to the 'caged' plants. Thus, high PPF on each plant appears crucial for promoting tuber bulking instead of shoot growth. This idea is supported further by the fact that guard row plants from both cultivars under both CO_2 levels yielded more than the center plants.

Throughout most of their growth, leaves of both cultivars under the CO_2-enriched

atmosphere were noticeably chlorotic in comparison to plants under low CO_2. In addition, leaves on the original main stem of Norland plants under high CO_2 were purple colored (anthocyanin) in comparison to the low-CO_2 plants. The upper canopy leaves of the high CO_2 plants of Norland showed senescence after 90 days, while low CO_2 plant leaves showed some senescence only at the final harvest (110 days). High CO_2 Russet Burbank leaves were often inclined upward and folded along the midvein, exhibiting reddish-purple coloration on the adaxial surfaces, but neither upright orientation nor purple coloration were apparent at low CO_2. No distinct leaf senescence was noted at 126 days on the Russet Burbank plants at either CO_2 level.

Net carbon dioxide assimilation rates of Norland leaves were increased by CO_2 enrichment, averaging 9.3 and 7.5 μmol m^{-2} s^{-1} at the high and low CO_2 levels, respectively (Figure 7.1). Most of the increase in response to CO_2 enrichment occurred prior to 70 days. In contrast, CO_2 assimilation rates of Russet Burbank leaves were decreased by CO_2 enrichment over much of the growing period, averaging 7.5 and 8.6 μmol m^{-2} s^{-1} at the high and low CO_2 levels, respectively (Figure 7.1). The CO_2 assimilation rates of Russet Burbank leaves under high CO_2 showed little change over time in comparison to Norland leaves at high CO_2. The differences in response of the two cultivars can be seen as a plot of percent change in CO_2 assimilation rate in Figure 7.2.

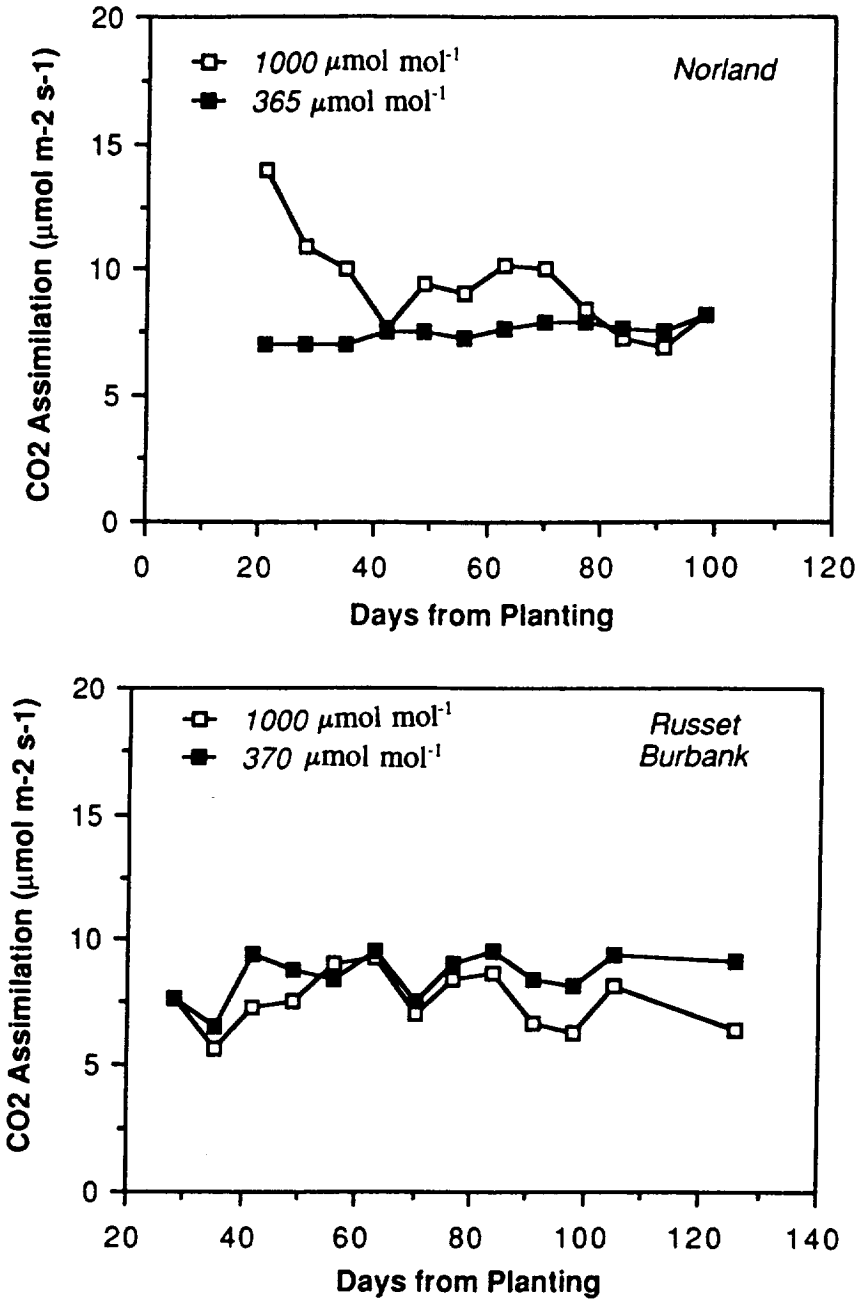


Figure 7.1. Carbon dioxide assimilation rate of Norland and Russet Burbank potato leaves under ambient and enriched CO_2 levels.

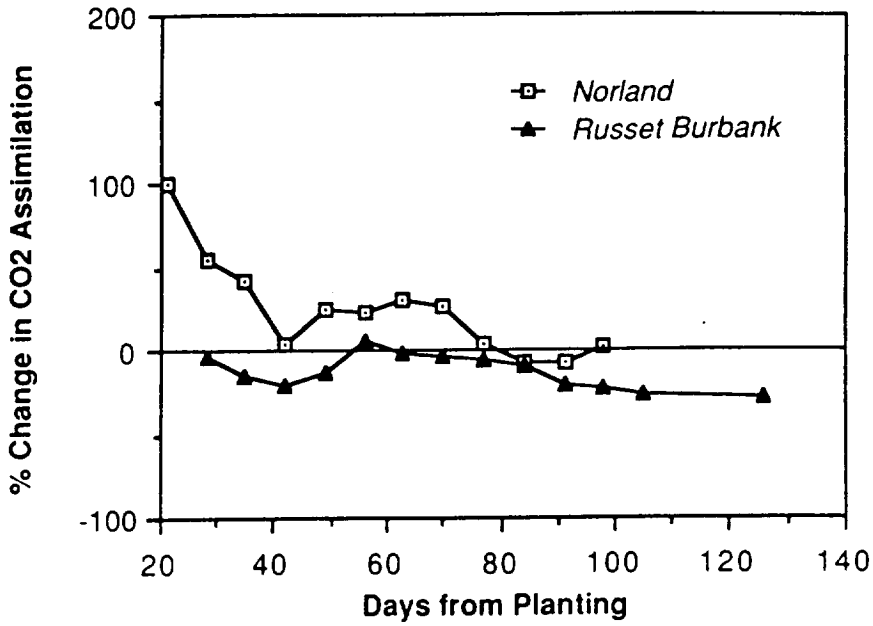


Figure 7.2. Percent change in carbon dioxide assimilation rates of leaves resulting from enriching CO_2 levels to 1000 μmol mol^{-1}.

The slight negative effect of elevated CO_2 on assimilation rates of exposed Russet Burbank leaves was rather surprising. Chapman and Loomis (1953) and Ku et al. (1977) in studies with other cultivars reported significant increases in photosynthetic rates when potato leaves were exposed to higher CO_2 levels, but these exposures lasted less than 1 hour and the plants were not grown at elevated CO_2 throughout their life cycles.

The results in the present study indicate that potatoes show only marginal growth gains from elevated CO_2 concentrations when grown under the conditions used in this study. However, additional experiments are needed to determine if the CO_2 effects would vary with PPF and temperature.

Dark CO_2 Enrichment. This experiment was conducted to establish if growth of potato plants would be affected by elevated CO_2 concentrations only during the dark period in controlled environments. CO_2 concentrations were maintained at a constant 350 μmol mol^{-1} in one room

and at alternating 350/1000 μmol mol^{-1} day/night in another room. PPF was 450 μmol m^{-2} s^{-1} for a 12 h photoperiod, temperature constant 19 C, and humidity 70%. Tissue culture plantlets of 'Norland' and 'Russet Burbank' cultivars were transplanted into 8 liter plastic pots containing commercial peat-vermiculite media, and were grown for 35 days.

Plant growth measured as total dry weight, and separate dry weights of leaves, stems, tubers, and roots was similar between the two CO_2 treatments (Table 7.2). The tuber dry weight and thus total dry weight were only slightly increased with elevated CO_2 during the dark period. Although it is not known if this potential effect might become significant after long term growth, this small promotion, if any, may not justify the use of CO_2 during the dark period for enhancing plant production under greenhouse conditions or within other controlled growing facilities.

Table 7.2. Dry weights of potato plants grown for 35 days under ambient CO_2 and elevated CO_2 at night. Values are means ± SD of 12 plants.

CO_2	Dry weight				
Day/night	Total plant	Leaves	Stems	Tubers	Roots
μmol mol^{-1}	g				
350/350	21.6±1.4[z]	10.4±0.5	2.9±0.3	7.4±0.9	0.89±0.1
350/1000	22.4±1.8	10.4±0.7	2.7±0.3	8.5±1.0	0.84±0.1

The similar growth responses in the two CO_2 treatments were supported with gas exchange parameters measured on major leaflets during the light period (Table 7.3). The average net CO_2 assimilation rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate of leaves did not change markedly with the treatments, although there was a small increase in all parameters with CO_2 enrichment during night.

Table 7.3. Leaf gas exchange parameters of potato plants maintained under ambient CO_2 and elevated CO_2 at night.

CO_2 Day/night	Net CO_2 assimilation	Stomatal conductance	Internal CO_2 concentration	Transpiration
μmol mol^{-1}	μmol m^{-2} s^{-1}	mmol m^{-2} s^{-1}	μl liter^{-1}	mmol m^{-2} s^{-1}
350/350	12.0±0.4[z]	394.4±15.2	291.4±7.0	4.33±0.1
350/1000	12.3±0.5	417.7±19.2	294.9±8.7	4.50±0.2

[z]Values are means ± SD of 24 measurements taken during light period.

The specific leaf weight and leaf water content were also similar between the two CO_2 treatments, and this pattern was consistent at different times during the light period (Table 7.4). The data indicate that the specific leaf weight increased and water content decreased with increasing time under the light. These changes appear to result from increasing accumulation of photosynthates in the leaves during the light period. Also, the similar specific leaf weight at the beginning of the light period implies that dark respiration and/or carbohydrate translocation from the leaves were not affected by the high CO_2 during the night period.

The results in this study help document that CO_2 elevations during the night period do not significantly promote carbon accumulation and plant growth in potatoes. This suggests that under continuously elevated CO_2 levels during both dark and light periods, growth promotion primarily results from enhanced photosynthate production during the light period. Also, it should be noted that leaf stomatal gas exchange in this study did not show any acclimation response to elevated night CO_2 concentrations even after a 30-day growth period. This is in contrast to the reported photosynthetic adjustment in soybean plants to short term CO_2 increases during the dark (Bunce, 1992).

Table 7.4. Specific leaf weight and leaf water content of potato leaves at different times during light period under ambient CO_2 and elevated CO_2 at night. Values are means ± SD of 6 plants.

CO_2 Day/night	Times after light start	Specific leaf weight	Water content
μl liter^{-1}	h	g m^{-2}	%
350/350	0.5	25.5±1.0	91.8±0.2
	6.0	28.7±0.7	90.7±0.4
	11.5	31.8±0.4	89.8±0.2
350/1000	0.5	25.5±1.1	91.8±0.2
	6.0	29.7±0.7	90.6±0.2
	11.5	31.5±10.6	89.9±0.2

CARBON DIOXIDE AND LIGHT INTERACTIONS

The purpose of this study was to compare effects of CO_2 enrichment under different lighting levels on the growth and development of potatoes. This study is reported in detail by Wheeler et al. (1991). Lighting treatments were provided by different combinations of photoperiod and PPF. Three cultivars were included to assess genetic differences in CO_2 response.

Potato plants, cvs Norland (early maturing), Russet Burbank (late), and Denali (late) were transplanted to 8-liter plastic pots containing peat-vermiculite (1:1 v:v). For the first 12 days after planting, all plants were maintained under 400 μmol m^{-2} s^{-1} PPF provided by high-pressure sodium and metal halide lamps. Twelve days after planting, individual plants were transplanted to 19-L plastic containers filled with peat-vermiculite. Three containers of a single cultivar were placed on a movable cart with adjustable platform height. Two carts (six plants) were used for

each treatment combination. As plants grew, leaves and branches were confined to the 72-cm by 72-cm cross-sectional area of the carts using twine supports between the upright corner posts of the carts. This allotted 0.52 m^2 per cart, or ≈ 0.17 m^2 of area per plant.

All experiments were conducted in 5.2 m by 3.8 m walk-in growth rooms at the Biotron. Environmental combinations included two CO_2 levels, ambient (nominally 350 μmol mol^{-1}) and 1000 μmol mol^{-1}; two photoperiods, 12 h light/12 h dark and 24 h light (continuous light); and two PPF levels, 400 and 800 μmol m^{-2} s^{-1}. This provided on daily basis 17 and 34 mol m^{-2} per day under the 12 h light treatments, and 34 and 68 mol m^{-2} per day under 24 h continuous light. The interactions created a 2 x 2 x 2 factorial, or eight different environmental combinations. Each combination of CO_2 and photoperiod required separate experimental rooms (four total). The two PPF levels were provided simultaneously within a room by arranging lamps to attain zones of 400 and 800 μmol m^{-2} s^{-1} (Figure 7.3). Radiation was provided by a 60:40 mixture of 400 W high-pressure Na and 400 W metal halide lamps, respectively. Air temperature for all experiments was maintained at 16 C and relative humidity at 70% (1.27 kPa). Initial measurements of leaf temperatures indicated that leaves in 800 μmol m^{-2} s^{-1} PPF zone were 3 C warmer than leaves at 400 μmol m^{-2} s^{-1}. To reduce this difference, clear acrylic barriers

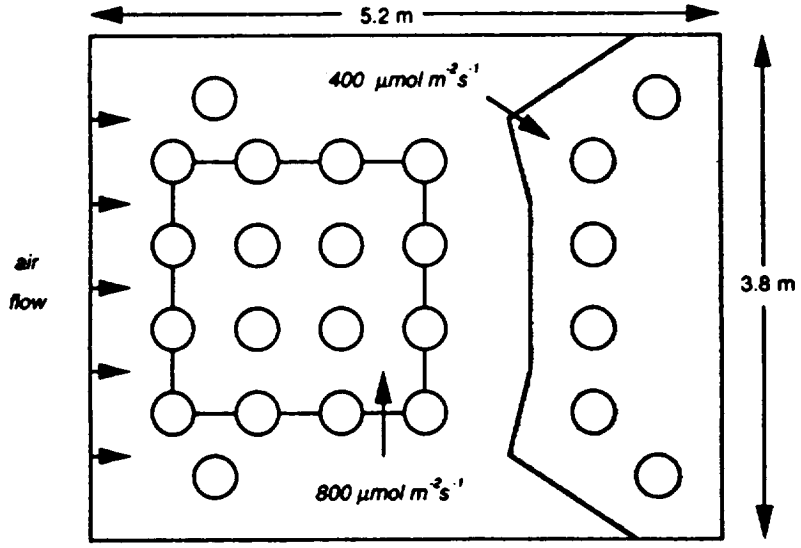


Figure 7.3. PPF set up for the different light intensity treatments in a single growth room.

(UV-transmitting) were suspended below the lamps in the 800 μmol m^{-2} s^{-1} zone. This reduced total radiation (primarily longwave) reaching the leaves by 32% and consequently reduced the leaf temperature difference between PPF treatments to 0.5 C.

Net CO_2 assimilation rates and stomatal conductance of leaves were measured at 4, 6, 8, and 10 weeks after transplanting using a portable photosynthesis system (LI-6000, Li-Cor Inc). At each stage, a total of 12 measurements for each cultivar were made on exposed and fully-expanded leaflets in each environmental treatment. Each measurement was taken with 13 cm^2 of leaf surface enclosed in a 330 ml leaf chamber for 20 to 40 s. Plants were harvested at 90 days after transplanting.

The response of the three cultivars to increasing CO_2 was similar, therefore data for the three cultivars has been combined in the data reports here. Data on individual cultivars is provided in Wheeler et al (1991).

The effects of increasing CO_2 levels on growth of potatoes differed with PPF and photoperiod. Most significant interactions between CO_2 and irradiance were found in tuber dry weight (Table 7.5). Tuber dry weight was greater with 1000 μmol mol^{-1} CO_2 than with 350 μmol mol^{-1} CO_2 at low PPF (17 and 34 mol m^{-2} d^{-1}), but less with the CO_2 enrichment at high PPF (68 mol m^{-2} d^{-1}).

The interactions between CO_2 and irradiance were much less on shoot dry weight than on tuber dry weight (Table 7.5). The CO_2 effects on shoot dry weight were of such small magnitude that they are likely of no real significance. In contrast, photoperiod had a much more dramatic effect on shoot growth than on tuber growth. At similar PPF levels, shoot growth was twice as much at 24 h photoperiod as under 12 h photoperiod. This resulted with both 350 and 1000 μmol mol^{-1} CO_2 levels.

Table 7.5. Dry weights of shoots and tubers of potatoes in response to CO_2 enrichment at different PPF and photoperiods.

PPF (mol m^{-2} d^{-1})	Photoperiod (h)	CO_2 (μmol mol^{-1}) 350	1000	Change with added CO_2
		Shoot (g $plant^{-1}$)		
17	12	90[z]	111	21
34	12	105	98	-7
34	24	205	222	17
68	24	172	161	-11
		Tuber (g $plant^{-1}$)		
17	12	242	335	93
34	12	301	383	82
34	24	326	355	29
68	24	372	341	-31

[z]Averages of 18 plants from three cultivars.

The interactions of CO_2 and irradiance on total plant dry weight (Table 7.6) followed the pattern of tuber dry weight because of the larger interaction associated with tuber weights than with shoot weights. Also, the long photoperiod stimulation of stem growth produced greater total dry weight with the 24 h treatments than with the 12 h treatments.

Partitioning of plant dry weight into tubers (harvest index) was not significantly altered with CO_2 enrichment (Table 7.6). The harvest index was significantly higher with 12 h than with 24 h photoperiods as a result of decreased shoot growth with short photoperiods. These data suggest that dry matter partitioning into tubers was affected primarily by irradiance and little by CO_2 concentrations.

Table 7.6. Total dry weight and partitioning into tubers of potatoes in response to CO_2 enrichment at different PPF and photoperiods.

PPF (mol m^{-2} d^{-1})	Photoperiod (h)	CO_2 (μmol mol^{-1}) 350	1000	Change with added CO_2
		Total (g $plant^{-1}$)		
17	12	334	448	114
34	12	408	486	78
34	24	535	582	47
68	24	548	505	-43
		Harvest Index (%)		
17	12	72	75	3
34	12	74	79	5
34	24	61	61	0
68	24	68	68	0

It should be noted that this data was collected from plants harvested at 90 days after transplanting and plants had not reached full maturity. In a previous study (Table 3.2), it was found that even under 24 h photoperiods with 26 mol m^{-2} d^{-1} PPF the harvest index of plants reached 80% after 105-day growth. The similar harvest index was obtained in this study for plants grown for only 90 days under 12 h photoperiod with 34 mol m^{-2} d^{-1} PPF.

When averaged across all irradiance treatments, Denali showed the greatest gain in tuber and total weight (21 and 18%, respectively) in response to increased CO_2 for the three cultivars tested. Norland showed the least (9% and 9%), while Russet Burbank showed an intermediate response, with gains nearly as great as for Denali under a 12-h photoperiod (18%) but less than Denali under a 24-h photoperiod (12%). This range in genotypic responsiveness may, in part, explain the differing results from previous CO_2 studies with potatoes (Collins, 1976; Wheeler and

Tibbitts, 1989).

CO_2 assimilation rates and stomatal conductance in leaves showed greater responses to elevated CO_2 concentration with 12 h than with 24 h photoperiod (Table 7.7). With the CO_2 enrichment, CO_2 assimilation rates were significantly increased under 12 h photoperiod, but slightly reduced under 24 h photoperiod. Stomatal conductance of leaves decreased with CO_2 enrichment under 12 h photoperiod, but had no real change under 24 h photoperiod. Both photosynthesis and stomatal conductance were slightly reduced with 24 h photoperiod compared to 12 h photoperiod, but increased with increasing PPF under each photoperiod.

Table 7.7. Net CO_2 assimilation rate and stomatal conductance of potato leaves in response to CO_2 enrichment at different PPF and photoperiods.

PPF (mol m^{-2} d^{-1})	Photoperiod (h)	CO_2 (μmol mol^{-1}) 350	1000	Change with added CO_2
		CO_2 Assimilation (μmol m^{-2} s^{-1})		
17	12	12.0[z]	16.8	4.8
34	12	18.2	23.2	5.0
34	24	9.5	8.6	-0.9
68	24	12.3	10.2	-2.1
		Stomatal Conductance (mmol m^{-2} s^{-1})		
17	12	522	384	-138
34	12	660	415	-245
34	24	223	259	36
68	24	299	290	-9

[z]Averages of 144 measurements taken on three cultivars at 4, 6, 8, and 10 weeks.

Previous studies have indicated that potato leaves under CO_2 enrichment have high photosynthetic rates and lower stomatal conductance (Ku et al., 1977). The results in this present study (Table 7.7) for plants maintained under 12h light period are consistent with the findings of Ku et al, however with 24 h photoperiod, leaf photosynthesis exhibited a negative response to CO_2 enrichment. This provides explanation for the lack of significant CO_2 stimulation on plant growth under continuous irradiation in this study and as reported previously by Wheeler and Tibbitts (1989). It has been found that even normally-growing plants accumulate large amounts of starch in leaves under continuous irradiation (Figure 4.3). This carbohydrate build-up may cause feedback inhibition to photosynthetic systems, especially under the relatively low temperature of 16°C that was used in this study.

The results from this study demonstrate that CO_2 enrichment produces the greatest proportionate increases in growth of potatoes at relatively low daily irradiance levels and indicate that elevated CO_2 may be a detriment if daily PPF is above 50 mol m^{-2} d^{-1}.

CARBON DIOXIDE AND TEMPERATURE INTERACTIONS

A study was undertaken to determine if there was any important interaction of increased carbon dioxide with temperature that would help regulate growth of potatoes in a CELSS. Concentrations of 500, 1000, 1500, and 2000 μmol mol^{-1} CO_2 were studied at two temperatures, 16 and 20 C, both within the optimum range for potato growth and tuberization (Wheeler et al., 1986).

Studies were conducted in the Biotron, with the four CO_2 concentrations maintained in separate sections of a large room, first operated at 16 C and then at 20 C. Three cultivars, Norland (early maturing), Denali and Russet Burbank (both late maturing) were grown. Five plants of each cultivar were grown in 8-liter containers of peat-vermiculite for 35 days.

During the experiment periods, RH was maintained at 66% under 16°C and 73% under 20°C to provide a constant VPD of 0.60 kPa at both temperatures (Table 7.8). The light period was maintained at 12 hours with a PPF of 19 mol m^{-2} d^{-1} (440 μmol m^{-2} s^{-1}).

Table 7.8. Average levels and ranges of environmental conditions for two separate experiment runs under various CO_2 concentrations at two temperatures.

Experiment	CO_2 (μmol mol^{-1})	Temperature (°C)	RH[z] (%)	PPF (μmol m^{-2} s^{-1})	Photoperiod (h)
1	501±13	16.2±0.4	65±2	433±14	12
	999±19	16.1±0.3	67±3	436±26	12
	1497±32	16.3±0.2	65±2	438±20	12
	1995±54	16.0±0.4	65±3	430±13	12
2	500±4	20.1±0.3	74±1	436±10	12
	999±17	20.0±0.4	73±2	439±11	12
	1499±28	20.0±0.4	74±3	437±15	12
	1995±52	20.1±0.2	74±3	439±18	12

[z]RH 66.1% at 16 C and RH 73.4% at 20 C for a common vapor pressure deficit of 0.60 kPa.

Tuber and shoot dry weights on day 35 after transplanting were greater under elevated CO_2 concentrations of 1000, 1500 and 2000 μmol mol^{-1} than under the lowest CO_2 level of 500 μmol mol^{-1} at both 16 and 20 C (Table 7.9). There were large CO_2 and temperature interactions on tuber dry weight. With increasing CO_2 from 1000 to 2000 μmol mol^{-1}, tuber dry weight decreased at 16 C, but increased at 20 C. However, shoot dry weight exhibited similar responses to CO_2 concentrations at 16 and 20 C. It appears that the combination of 2000 μmol mol^{-1} CO_2 and 20 C temperature can potentially produce highest tuber yield, but this needs to be confirmed with an extended growth period to full maturity of the plants.

Table 7.9. Dry weights of shoots and tubers of potatoes in response to CO_2 concentration and temperature.

	CO_2 (μmol mol^{-1})			
Temperature (C)	500	1000	1500	2000
	Shoot (g plant^{-1})			
16	7.2±0.8[z]	11.4±1.3	11.6±1.5	10.5±1.1
20	13.6±1.0	17.2±1.4	18.6±0.8	17.9±1.5
Change with 20 C	5.6	5.8	7.0	7.4
	Tuber (g plant^{-1})			
16	3.2±0.9	6.6±1.8	6.1±2.1	5.3±1.5
20	5.6±0.9	9.3±0.8	9.7±1.6	12.4±1.6
Change with 20 C	1.6	2.7	3.6	7.1

[z] Means ± SD of 15 plants from three cultivars.

Total plant dry weight followed the pattern of tuber dry weight in response to CO_2 concentrations and temperatures, with maximum growth under 1000 μmol mol^{-1} CO_2 at 16 C and under 2000 μmol mol^{-1} CO_2 at 20 C (Table 7.10). High CO_2 concentrations of 1000, 1500 and 2000 μmol mol^{-1} enhanced partitioning of total dry weight into tubers as compared to 500 μmol mol^{-1} CO_2 at both temperatures. High temperature of 20 C significantly increased partitioning into tubers under 2000 μmol mol^{-1} CO_2, but slightly reduced partitioning into tubers under the lower CO_2 concentrations. Decreased partitioning into tubers with increasing temperatures at ambient CO_2 was shown in a previous report to the point that temperature of 28 C produced essentially no tubers (Wheeler et al, 1986).

Table 7.10. Total dry weight and partitioning into tubers of potatoes in response to CO_2 concentration and temperature.

	CO_2 (μmol mol^{-1})			
Temperature (C)	500	1000	1500	2000
	Total (g plant^{-1})			
16	11.0±1.6	18.8±2.7	18.5±2.9	16.4±2.3
20	20.3±1.4	27.6±1.6	29.5±2.3	31.6±2.3
Change with 20 C	9.3	8.8	11.0	15.2
	Harvest Index (%)			
16	29.1±5.4	35.1±5.6	33.0±7.1	32.3±5.2
20	27.6±4.3	33.7±2.5	32.9±3.6	39.2±4.8
Change with 20 C	-1.5	-1.4	-0.1	6.9

Leaf area per plant showed a similar pattern to shoot dry weight, yet specific leaf weight (SLW) had a different response to CO_2 concentrations at different temperatures (Table 7.11). As compared to 500 μmol mol^{-1} CO_2, the SLW under 1000, 1500, and 2000 μmol mol^{-1} CO_2 increased substantially at 16 C, but only slightly at 20 C. The high SLW in CO_2 enriched plants at 16 C may reflect a slow transport and utilization of photosynthetic assimilates as suggested by Farrar and Williams (1991).

The concentrations of starch were determined in the green leaves of the plants. These concentrations, averaged over the three cultivars, increased with increasing CO_2 concentrations at both 16 and 20 C (Table 7.11). The largest increase occurred between 500 and 1000 μmol mol^{-1} of CO_2 although there were distinct increases with all concentrations to 2000

Table 7.11. Leaf area, specific leaf weight (SLW), and leaf starch concentration of potato plants grown under four CO_2 concentrations and two temperatures.

Measurement	Temperature (C)	CO_2 (μmol mol^{-1}) 500	1000	1500	2000
Leaf area (cm^2)	16	1531±79[z]	2069±139	2159±126	1912±196
	20	3111±190	3721±92	3972±195	3814±59
SLW ($g\ m^{-2}$)	16	37.4±0.1	44.8±1.3	44.9±0.6	46.9±1.2
	20	33.0±0.8	35.5±0.6	35.3±0.2	37.1±1.2
Starch (% d.w.)	16	10.0±0.6	16.1±0.3	17.4±0.3	18.5±0.9
	20	4.37±0.2	6.96±0.3	7.81±0.2	8.50±0.3

[z]Mean ± SD of nine plants pooled for three cultivars.

μmol mol^{-1}, where leaves had nearly twice as much starch as at 500 μmol mol^{-1}. There was significantly more starch in leaves of plants grown at 16 C than at 20 C, this increase at 16 C was more than 100% of the starch at 20 C for all CO_2 concentrations. The starch concentrations led to significant increases in the specific leaf weight as seen in the close correlation of these two factors (Figure 7.4).

Previous studies under continuous light also showed that specific leaf weight was associated with starch accumulation in leaves (Cao and Tibbitts, 1991a). The high carbohydrate accumulation in leaves under low temperature and/or continuous light may depress plant responses to increased CO_2 concentrations. It appears that the plants can take greater advantage of elevated CO_2 and irradiance under higher temperatures.

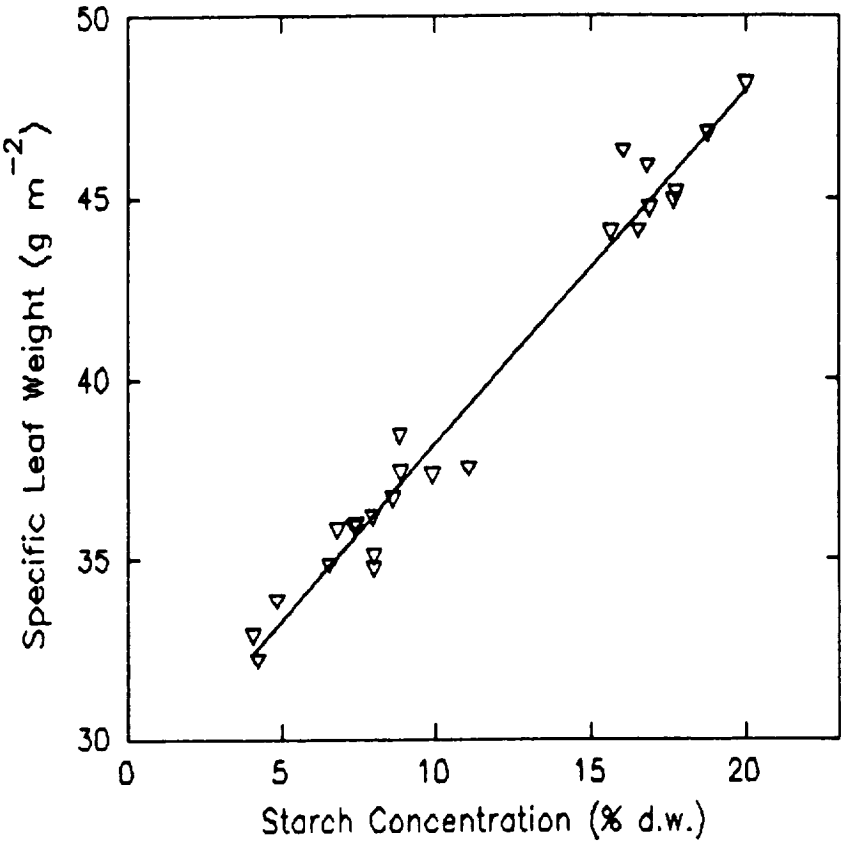


Figure 7.4. Linear relationship of specific leaf weight to starch concentrations in potato leaves under different CO_2 and temperature levels, $Y=28.350+0.983X$, $R^2=0.970^{**}$.

The concentrations on a dry weight basis of N, P, Ca, and Mg nutrients in the leaf tissues decreased with increasing CO_2 concentrations (Table 7.12) whereas K had no significant change. The major decrease in nutrient levels occurred in leaves from 500 to 1000 μmol mol^{-1} CO_2. Also, the nutrient concentrations were higher at 20 C than at 16 C whereas this was reversed for K. The changed concentrations of N, P, Ca, and Mg in response to CO_2 levels and temperatures might be assumed to result from the increased starch concentrations. However, after correcting for starch amounts, the nutrient concentrations (data not shown) exhibited similar patterns as those shown in Table 7.12, although the nutrient concentrations were slightly lower on the starch-free basis than on a total dry weight basis. Thus, the results document that there are nutrient concentration changes in plant tissues both with temperature level and carbon dioxide level.

Table 7.12. The concentrations of major minerals in potato leaves under four CO_2 concentrations and two temperatures.

Element	Temperature (C)	CO_2 (μmol mol^{-1})			
		500	1000	1500	2000
		% dry weight			
N	16	5.11±0.2[z]	4.00±0.1	4.07±0.1	4.06±0.1
	20	5.68±0.1	5.05±0.1	4.97±0.1	4.62±0.1
P	16	0.66±0.07	0.52±0.02	0.53±0.01	0.53±0.01
	20	1.14±0.03	0.91±0.01	0.95±0.02	0.81±0.01
K	16	5.76±0.2	5.18±0.2	5.35±0.2	5.45±0.1
	20	4.79±0.1	4.67±0.1	4.63±0.1	4.77±0.1
Ca	16	2.36±0.1	2.06±0.1	2.00±0.1	1.95±0.1
	20	3.12±0.1	2.99±0.1	3.00±0.1	2.92±0.1
Mg	16	0.69±0.06	0.59±0.02	0.56±0.03	0.54±0.02
	20	0.96±0.02	0.90±0.02	0.93±0.01	0.84±0.02

[z]Means ± SD of nine plants pooled for three cultivars.

CARBON DIOXIDE AND HUMIDITY INTERACTIONS

The objective of this study was to compare the effects of CO_2 enrichment on potato growth at different humidity levels and to determine if there were genotypical differences in response to CO_2 and humidity.

Two successive experiments were conducted in two reach-in growth chambers at the

Biotron, the first at 85% RH and the second at 55% RH. In each of the experiments, CO_2 concentrations of 400 ($\pm$10) and 950 ($\pm$50) μmol mol^{-1} were maintained in separate chambers. Temperature was constant at 18 C ($\pm$0.5), light period was 16 hours provided with cool white fluorescent lamps, and PPF was 340 μmol m^{-2} s^{-1}. Three potato cultivars, Denali, Norland, and Haig, were used in both experiments. For each experiment, 5 plants of each cultivar were grown in each chamber. Uniform single plantlets were transplanted into the centers of 4 liter plastic containers containing peat:vermiculite. Plants were harvested at 28 days after transplanting.

High CO_2 increased total plant dry weight and shoot dry matter content in all three cultivars at each RH level, increased leaf area except for Norland and Haig at 85% RH, and increased specific leaf weight except for Haig at 55% RH (Table 7.13). For all three cultivars, relative CO_2 effects at 55% RH on plant dry weight and leaf area (averaging 38% and 23% respectively over cultivars) were greater than those at 85% RH (averaging 25% and 5% respectively). Yet, CO_2 effects on specific leaf weight and shoot dry weight to fresh weight ratio were smaller at 55% RH (11% and 13% respectively) than those at 85% RH (22% and 18%).

The data indicate that CO_2 enrichment can increase plant growth more at low RH than at high RH, however it should be recognized that plant growth was slightly less at low RH even with elevated CO_2 than at high RH with no elevation of CO_2.

Table 7.13. Growth of three potato cultivars in response to CO_2 enrichment at two relative humidity levels.

Cultivar	RH	CO_2	Plant dry wt	Leaf area	Specific leaf wt	Shoot dry wt/fresh wt
	%	μmol mol^{-1}	g	dm^2	mg cm^{-2}	%
Denali	55	400	3.8±0.2[z]	6.7±0.6	3.8±0.4	8.3±0.6
	55	950	5.4±0.6	8.1±0.3	4.5±0.5	9.9±0.9
	85	400	6.3±0.5	9.7±0.6	4.1±0.3	8.7±0.5
	85	950	8.7±0.7	11.4±0.8	5.0±0.6	10.9±1.0
Norland	55	400	5.6±0.5	9.6±0.9	3.8±0.4	8.0±0.5
	55	950	7.3±0.6	11.0±0.4	4.4±0.5	9.2±0.6
	85	400	8.1±0.7	12.4±0.1	4.1±0.3	8.4±0.7
	85	950	10.4±0.6	12.4±0.9	5.3±0.2	9.9±0.4
Haig	55	400	3.2±0.2	5.8±0.3	3.7±0.3	8.2±0.5
	55	950	4.5±0.3	7.7±0.5	3.7±0.4	8.6±0.7
	85	400	4.6±0.5	7.0±0.5	4.2±0.4	8.5±0.5
	85	950	5.0±0.5	6.8±0.5	4.8±0.3	9.3±0.7

[z]Means±SD of five replicate plants.

SECTION 8. MINERAL NUTRITION

A series of experiments have been conducted to establish potato responses to nutrient concentrations, nitrogen forms, and pH levels in solution. Measurements have been taken on plant growth and mineral composition in all studies, along with measurements on water and nutrient uptake, and leaf gas exchange in certain studies. These experiments have been undertaken to provide a basis for regulating mineral nutrition for effective and/or optimum potato growth in CELSS.

A non-recirculating nutrient film system with trays was used for all nutrient experiments. White polystyrene plastic trays, 51 cm long, 26 cm wide and 3 cm deep, were provided with a 1 cm layer of quartz gravel (2-3 mm diameter). A group of 18 trays were arranged in a large Biotron room to permit study of 6 randomized treatments with three replications. The trays were inclined at a 4 degree slope and covered with an opaque polyethylene plastic sheet, white upper surface and black lower surface.

Nutrient solution was pumped from a large reservoir tank into a small light-tight plastic jar (4 liters) from which it flowed by gravity through a small tube into each tray. The solution inside of each jar was maintained at a constant level with an automatic float switch that controlled the operation of the pump. The flow rate was controlled by the length of the tubing and the height of the plastic jar above the trays. Fresh nutrient solution was continuously supplied to the elevated end of the trays at a flow rate of 4 ml min^{-1}. This drained from the lower end and was discarded. Preliminary experiments showed that this flow rate was sufficient to provide maximum plant growth for at least a 6-week period, and the effluent from the trays equalled more than 70% of incoming flow by the end of experiment. During most experiments, the effluent from each tray was collected weekly to monitor water uptake and nutrient concentrations in the effluent.

Plants were grown under a 12 hour light period provided by metal halide lamps and a PPF of 450-500 μmol m^{-2} s^{-1} at the top of the canopy. Temperature and relative humidity were 21/15°C light/dark and 70% respectively. CO_2 levels were ambient at about 350 μmol mol^{-1}.

A single plantlet of Norland cv. was transplanted into each tray and grown in different experiments for 4 to 6 weeks. At harvest, leaf area, tuber number, and dry weights of different

plant parts were determined. Leaf tissue was ground and analyzed for mineral composition by inductively-coupled plasma emission spectrophotometry.

In certain experiments, as with potassium and magnesium, leaf gas exchange measurements were made during the middle of the light period using a Li-Cor photosynthesis system (LI-6000 and LI-6200). The measurements were taken on the fourth and fifth terminal leaflets (terminal leaflets over 1 cm long from the tip) of separate plants. In the magnesium experiment, photosynthetic assimilation and CO_2 response curves, and dark respiration rates were also determined.

In one experiment, the uptake of various nutrients at different times during both the light and dark periods was determined by measuring the volume and nutrient concentrations of the incoming and outgoing solution from the trays.

SOLUTION CONCENTRATIONS

Two studies were undertaken to determine the effect of nutrient solution concentration on potato growth with plants maintained in the tray culture system described above. Also, in these studies the influence of flow rates was investigated to establish a minimal flow rate for succeeding experiments, which would reduce maintenance problems and limit the amount of nutrient solution discarded into the sewer.

Three concentrations of nutrient solutions, 0.6, 1.2 and 2.4 dS m^{-1} (mmhos cm^{-1}) were used, which were approximately equivalent to 1/4, 1/2 and full strength Hoagland's solutions. Three flow rates, 120, 240, and 480 ml h^{-1}, were combined with the three concentrations. The total 9 treatment combinations were carried out in two separate experiments as shown in Table 8.1. Each study included three treatments with same solution concentrations and flow rates.

The outgoing solution was collected weekly from 14 days after transplanting to harvest from each tray during the middle of the light period. The solution volume, pH, and conductivity of these samples were determined. It was found that the flow rates to the trays were 16% less during the dark period than during the light period. Apparently, the cooler temperatures during the dark (15 C) had an influence on the liquid and small polyethylene tubing to reduce flow over the dark period when temperatures were 6 C lower. Plants were harvested 42 days after transplanting in both studies. The shoot and tuber tissue in the first study were analyzed for mineral composition.

Table 8.1. Growth of potato plants grown for 42 days at different flow rates and concentrations of nutrient solution. The data shown without underlining were from the treatment combinations in the first study whereas the data shown with underlining were from the treatment combinations in the second study.

	Flow rate ($ml\ h^{-1}$)	Concentration ($dS\ m^{-1}$) 0.6	1.2	2.4
Shoot dry weight (g)	120	21.5c[z]	27.2bc	23.0bc 10.7
	240	31.4b	44.5a 21.9	11.1
	480	40.8a 30.5	16.6	15.3
Root dry weight (g)	120	3.6b	3.4b	3.3b 0.5
	240	4.6ab	6.3a 1.9	0.9
	480	5.8a 3.2	1.5	1.3
Tuber dry weight (g)	120	26.0a	28.3a	23.6a 11.0
	240	22.2a	26.9a 36.7	22.9
	480	24.2a 38.7	33.8	28.8
Total dry weight (g)	120	51.0c	58.9bc	49.9c 22.2
	240	58.1bc	77.8a 60.4	34.9
	480	70.8ab 72.4	51.7	45.4
Leaf area (dm^2)	120	51.7c	60.4bc	49.5c 11.0
	240	74.4b	99.7a 47.0	20.1
	480	95.8a 71.3	36.5	35.0

[z]Mean separation for data in the first experiment by Duncan's multiple range test, P=0.05.

Plant Growth. The growth responses of plants in the first study are shown in Table 8.1. The shoot dry weights increased with increasing flow rates from 120 to 480 ml h^{-1} at the 0. 6 dS m^{-1} concentration and from 120 to 240 ml h^{-1} at the 1.2 dS m^{-1} concentration. The shoot dry weights also increased with increasing concentrations from 0.6 to 1.2 dS m^{-1} at the flow rates of 120 and 240 ml h^{-1}. However the 2.4 dS m^{-1} concentration at the flow rate of 120 ml h^{-1}, did not produce less dry matter than the 0.6 and 1.2 dS m^{-1} concentrations at the same flow rate. The shoot dry weights were closely related to stolon plus root dry weights ($R = 0.79^{**}$), but not to tuber dry weights. The tuber dry weights did not vary significantly among treatments. Total plant dry matter increased with increasing flow rates at a given concentration, and increased with increasing concentrations at a constant flow rate except that the high concentration at 120 ml h^{-1} had the similar total dry weight as the low concentration at 120 ml h^{-1}. The variations in shoot and total dry matter production were closely related to leaf area produced (Table 8.1). The leaf area was greatest with 1.2 dS m^{-1} concentration at 240 ml h^{-1} and 0.6 dS m^{-1} concentration at 480 ml h^{-1} flow rate and almost twice as great as with the high nutrient concentration at 120 ml h^{-1}.

The growth responses of plants in the second study also are shown in the Table 8.1. The shoot and stolon/root dry weights were closely correlated and decreased with increasing concentrations and decreasing flow rates. Tuber dry weights followed a similar pattern but exhibited less differences among treatments than the shoot and stolon/root differences. It was noted that most of the plants in treatments with the highest nutrient concentrations and low flow rates had stopped terminal shoot growth at the time of harvest and thus were directing a greater portion of the assimilates to tubers than to the shoots. The total dry weights and leaf area followed similar pattern as the shoot dry weights among treatments. The leaf area of plants at 0.6 dS m^{-1} concentration and 480 ml h^{-1} flow rate was considerably larger than other treatments and proportionately greater than the difference in dry weight. This was apparently due to the fact that these plants were continuing to produce terminal shoot growth and thus continuing to produce large amounts of leaf and stem tissues.

Comparisons of growth in the second study with growth in the first study provide some interesting similarities but also some contrasts. Total weight of plants was similar but a greater proportion of the dry weight was directed to tubers in the second study. There was evidence that plants had slowed or stopped shoot growth sooner in the second study than in the first study, providing evidence that tuberization had been promoted more strongly in the second study. No obvious reason for this different response between the two studies was found. In both experiments there was some swelling on the main stem nodes, indicating a lack of sufficient sinks for plant assimilates in either the shoots or in enlarging tubers. This swelling was more pronounced in the second study than in the first study. One plant in the first study at 1.2 dS m^{-1} concentration and 240 ml h^{-1} flow rate developed enlarged nodes soon after transplanting, apparently due to transplanting damage to the lower part of the stem, and thus was omitted from the data summary.

Water Use, Conductivity and pH Changes. Water use by plants was closely proportional to shoot weight and leaf area in both studies (Table 8.2). Water use never exceeded 50% of the liquid flowing through any of the treatments until within a week of harvest. At harvest, the largest plants at 120 and 240 ml h^{-1} flow rate removed up to 70% of the water. However, even though there was a significant amount of the liquid utilized, the conductivity of the solutions did not change dramatically in any treatments. The significant changes in conductivity were only with plants at the lowest concentration, 0.6 dS m^{-1}, and were greatest with plants growing most rapidly. The lowest concentrations reached for any one plant was 0.3 dS m^{-1} in the low concentration treatments and 1.1 dS m^{-1} in the medium concentration treatments.

Interestingly, time-course measurements indicated that the lowest conductivity measurements were not usually at the end of the study, but instead occurred at about 27 and 34 days, coinciding apparently with the most rapid plant growth and nutrient accumulation as tuber growth began accelerating (Tables 8.3, 8.4).

Table 8.2. The solution volume consumed, conductivity, and pH of the nutrient solution after flowing through the trays during the 6th week of plant growth. The data shown without underlining were from the treatment combinations in the first study whereas the data shown with underlining were from the treatment combinations in the second study.

	Flow rate	Concentration (dS m^{-1})		
	(ml h^{-1})	0.6	1.2	2.4
Volume consumed (ml h^{-1})	120	81	86	58 <u>21</u>
	240	140	162 <u>73</u>	<u>42</u>
	480	172 <u>100</u>	<u>47</u>	<u>43</u>
Conductivity (dS m^{-1})	120	0.54	1.43	2.82 <u>2.36</u>
	240	0.48	1.23 <u>1.22</u>	<u>2.35</u>
	480	0.46 <u>0.55</u>	<u>1.19</u>	<u>2.29</u>
pH[z]	120	7.67	7.65	7.18 <u>6.50</u>
	240	7.35	7.48 <u>7.17</u>	<u>6.45</u>
	480	7.02 <u>7.22</u>	<u>6.62</u>	<u>6.37</u>

[z]The pH for all incoming nutrient solutions was 5.6-5.7.

Table 8.3. The conductivity of the nutrient solution after flowing through the trays over the growth period of 6 weeks in the first study.

Treatment		Days after transplanting				
Conductivity ($dS\ m^{-1}$)	Flow rate ($ml\ h^{-1}$)	13	21	27	34	41
0.6	120	0.55	0.52	0.37	0.36	0.54
0.6	240	0.62	0.58	0.50	0.39	0.48
0.6	480	0.64	0.65	0.59	0.53	0.46
1.2	120	1.20	1.17	1.06	1.15	1.43
1.2	240	1.15	1.17	1.12	1.12	1.23
2.4	120	2.26	2.30	2.29	2.51	2.82

Table 8.4. The conductivity of the nutrient solution after flowing through the trays over the growth period of 6 weeks in the second study.

Treatment		Days after transplanting				
Conductivity ($dS\ m^{-1}$)	Flow rate ($ml\ h^{-1}$)	13	21	27	34	41
0.6	480	0.63	0.62	0.56	0.55	0.55
1.2	240	1.12	1.27	1.17	1.22	1.29
1.2	480	1.22	1.23	1.16	1.19	1.23
2.4	120	2.33	2.36	2.39	2.36	2.41
2.4	240	2.29	2.46	2.33	2.35	2.39
2.4	480	2.29	2.35	2.25	2.29	2.39

The pH of solutions entering the trays was 5.6 to 5.7 and was increased as moved down the trays and left the trays. The pH in both studies continued to increase over the growth of all treatments, with highest levels at the end of each experiment. The increase was essentially proportional to the amount of dry matter in plants. In low flow rate (120 ml h^{-1}) treatments, a pH level of 7.0 was exceeded after 21 days whereas with 240 ml h^{-1}, this was not reached until 34 days (Table 8.5, 8.6). With 480 ml this was only seen to exceed 7.0 at the final harvest date. A maximum pH level of 7.65 was found with the low flow rate (120 ml h^{-1}) for both 0.6 and 1.2 dS m^{-1} concentrations at harvest time.

Table 8.5. The pH of the nutrient solution after flowing through the trays over the growth period of 6 weeks in the first study.

Treatment		Days after transplanting				
Conductivity (dS m^{-1})	Flow rate (ml h^{-1})	13	21	27	34	41
0.6	120	6.45	7.00	7.23	7.57	7.67
0.6	240	6.27	6.73	6.98	6.98	7.35
0.6	480	6.15	6.43	6.68	6.68	7.02
1.2	120	6.33	6.97	7.18	7.30	7.65
1.2	240	6.08	6.48	6.82	7.02	7.48
2.4	120	5.98	6.48	6.95	7.08	7.18

Table 8.6. The pH of the nutrient solution after flowing through the trays over the growth period of 6 weeks in the second study.

Treatment		Days after transplanting				
Conductivity ($dS\ m^{-1}$)	Flow rate ($ml\ h^{-1}$)	13	21	27	34	41
0.6	480	6.08	6.70	6.87	6.95	7.22
1.2	240	6.10	6.85	6.98	7.05	7.17
1.2	480	5.97	6.50	6.52	6.68	6.62
2.4	120	6.05	6.65	6.22	6.37	6.50
2.4	240	5.92	6.32	6.23	6.38	6.45
2.4	480	5.78	6.13	6.20	6.28	6.37

Tissue Mineral Composition. Tissue analysis was only undertaken with the samples harvested in the first study. Elemental concentrations in shoots are shown in Tables 8.7 and 8.8, and in tubers in Tables 8.9 and 8.10. In shoots (Table 8.7), the N level increased with increasing flow rates and concentrations except at the high nutrient concentration of 2.4 $dS\ m^{-1}$ and flow rate of 120 $ml\ h^{-1}$. The P level consistently increased with solution concentration, with almost two times higher level at 2.4 $dS\ m^{-1}$ concentration than at other concentrations. The levels of K and S had no consistent patterns with nutrient concentrations or flow rate and were not statistically different. The levels of Ca and Mg increased slightly with increasing nutrient concentrations and but decreased with increasing flow rates. This is in contrast to the pattern of N and P levels.

Most of the micro-nutrients varied less than macro-nutrients (Table 8.8). Fe and Mn levels increased with higher concentrations and flow rates. The Fe level at 2.4 $dS\ m^{-1}$ concentration increased 50-100% compared to other treatments. Zn levels decreased with higher nutrient concentrations. B and Cu had no large variations over the different treatments.

Table 8.7. The concentrations of macro-nutrients in the shoots of potatoes grown at different flow rates and concentrations of nutrient solution.

Element	Flow rate (ml h^{-1})	Concentration (dS m^{-1})		
		0.6	1.2	2.4
			mg g^{-1}	
N	120	52.7c[z]	57.4b	53.5c
	240	57.7b	60.5ab	
	480	62.0a		
P	120	5.4d	9.8b	18.6a
	240	6.5cd	8.6bc	
	480	7.5bcd		
K	120	62.8a	69.3a	58.7a
	240	60.7a	64.3a	
	480	73.2a		
Ca	120	28.2b	29.0b	32.1a
	240	26.1c	25.7c	
	480	23.5d		
Mg	120	8.0b	8.1b	9.7a
	240	7.0cd	7.4c	
	480	6.6d		
S	120	3.4a	3.5a	3.4a
	240	3.5a	3.5a	
	480	3.5a		

[z]Mean separation by Duncan's multiple range test, P=0.05.

Table 8.8. The concentrations of micro-nutrients in the shoots of potatoes grown at different flow rates and concentrations of nutrient solution.

Element	Flow rate (ml h^{-1})	Concentration (dS m^{-1}) 0.6	1.2	2.4
			mg g^{-1}	
	120	153.5d[z]	264.2b	380.2a
Fe	240	183.5cd	217.0bc	
	480	227.5bc		
	120	37.5a	40.3a	32.1b
B	240	40.2a	39.8a	
	480	39.4a		
	120	22.2c	25.0bc	28.8a
Mn	240	25.3abc	24.3c	
	480	28.3ab		
	120	22.3a	14.0c	14.2c
Zn	240	20.6a	17.3b	
	480	20.4a		
	120	7.3bc	8.8a	6.5c
Cu	240	7.4bc	7.7b	
	480	6.7c		

[z]Mean separation by Duncan's multiple range test, P=0.05.

As a whole, the composition of most of the nutrients in the tubers was less variable than in the shoots and their concentrations as the percentage of the dry weight was also lower than in the shoots (Tables 8.9, 8.10). Particularly the levels of Ca and Mg were greatly reduced in the tubers. For particular treatments, it is of note that Ca and Mg increased slightly with nutrient concentration and flow rates rather than decreasing with flow rates as in the shoot tissue. Also tissue Zn concentration had much greater proportional reductions in tubers with increasing nutrient concentrations than in shoots.

The results indicate that leaf area development, dry matter production, and nutrient composition in potato plants is significantly changed at different concentrations and flow rates of external nutrient solutions. It appeared that a suitable selection of concentration and flow of solution is necessary to provide water and nutrition for effective potato growth.

Table 8.9. The concentrations of macro-nutrients in the tubers of potatoes grown at different flow rates and concentrations of nutrient solution.

Element	Flow rate (ml h^{-1})	Concentration (dS m^{-1})		
		0.6	1.2	2.4
			mg g^{-1}	
	120	19.3b	20.9ab	20.0ab
N	240	19.7ab	20.9ab	
	480	21.4a		
	120	3.9d	4.8b	5.8a
P	240	4.3c	4.9b	
	480	4.9b		
	120	23.3e	28.8bc	28.3c
K	240	27.0d	29.8ab	
	480	30.8a		
	120	0.7a	0.7a	0.9a
Ca	240	0.8a	0.9a	
	480	0.9a		
	120	1.1b	1.2b	1.1b
Mg	240	1.1b	1.2b	
	480	1.3a		
	120	1.4a	1.5a	1.4a
S	240	1.4a	1.4a	
	480	1.5a		

[z]Mean separation by Duncan's multiple range test, P=0.05.

Table 8.10. The concentrations of micro-nutrients in the tubers of potatoes grown at different flow rates and concentrations of nutrient solution.

Element	Flow rate ($ml\ h^{-1}$)	Concentration ($dS\ m^{-1}$) 0.6	1.2	2.4
			$mg\ g^{-1}$	
Fe	120	65.4a	81.2a	85.9a
	240	65.9a	88.7a	
	480	76.3a		
B	120	7.2a	6.9a	7.4a
	240	6.9a	7.3a	
	480	7.6a		
Mn	120	5.6b	5.9ab	6.1ab
	240	5.7ab	5.7ab	
	480	6.4a		
Zn	120	13.3a	7.0b	5.8b
	240	12.6a	8.7b	
	480	14.0a		
Cu	120	3.1ab	3.0b	2.7b
	240	3.3ab	3.8a	
	480	3.2ab		

[z]Mean separation by Duncan's multiple range test, P=0.05.

CONCENTRATIONS OF INDIVIDUAL NUTRIENTS

A series of studies were undertaken to establish concentrations of different nutrients for effective potato growth and tuberization. This involved separate studies with NO_3-N, NH_4-N, P, K, Ca, Mg, Fe and Mn. In each study, six concentrations of each nutrient (Table 8.11) were selected that ranged from assumed deficient concentrations to excess concentrations of each particular nutrient. In each experiment certain other nutrients had to be altered as co-ions in order to provide the desired concentrations of the experimental nutrient. These are also shown in Table 8.11. However, for all treatments the concentrations of co-ions were elevated to sufficient levels in order to minimize plant responses to the different co-ions.

Table 8.11. Nutrient concentrations studied and co-ions associated with varied concentrations in each experiment.

Nutrient	Concentration studied	Co-ions (mM)	
NO_3	0.5-16 mM	Ca^{2+}:1.7-4.8	K^+:2.2-6.4
NH_4	0.5-12 mM	HCO_3^-:0.3-7.2	SO_4^{2-}:3.1-5.4
P	0.1-2 mM	K^+:3.1-5.0	
K	0.1-9 mM	SO_4^{2-}:1.1-5.5	
Ca	0.05-7.5 mM	Cl_2^{2-}:0.5-6.0	SO_4^{2-}:1.0-2.5
Mg	0.5-4 mM	SO_4^{2-}:0.6-4.5	
Fe	0.01-10 ppm	SO_4^{2-}:1.0-1.2	
Mn	0.01-10 ppm	SO_4^{2-}:1.0-1.2	

Plant Growth. The plant response to each different nutrient is shown in the series of tables, 8.12 through 8.19. These tables provide data on leaf area, tuber and total dry weight, and concentrations in leaves of the nutrient being studied. Details of specific nutrient experiments can be found for K (Cao & Tibbitts, 1991b), and Mg (Cao & Tibbitts, 1992b).

Table 8.12. Nitrogen concentration in leaves and growth responses of 6-week old potatoes with varied solution concentrations of nitrate nitrogen.

	Nitrate in solution (mM)					
	0.5	2	4	8	12	16
Leaf N (mg g^{-1})	39.9c[z]	54.3b	53.9b	60.1a	59.9a	56.5ab
Total DW (g)	33.2b	43.2ab	47.7a	46.3a	38.9ab	40.0ab
Tuber DW (g)	23.3b	28.2ab	31.7a	29.0ab	24.1b	25.4b
Leaf area (dm^2)	18.5b	30.3ab	34.1a	38.3a	33.4a	29.7ab

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

Table 8.13. Nitrogen concentration in shoots and growth responses of 5-week old potatoes with varied solution concentrations of ammonium nitrogen.

	Ammonia in solution (mM)					
	0.5	1	2	4	8	12
Shoot N[y] (mg g^{-1})	43.7c[z]	45.8c	47.3c	54.5b	59.6ab	62.0a
Total DW (g)	15.2c	16.8bc	20.3a	18.0b	10.6d	6.2e
Tuber DW (g)	8.9c	10.2b	11.9a	10.1b	4.0d	1.5e
Leaf area (dm^2)	12.8cd	13.7c	18.5a	17.8ab	14.0bc	9.4d

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

[y]Shoots rather than leaves analyzed for leaf tissue was not sufficient with all treatments.

Table 8.14. Phosphorus concentration in leaves and growth responses of 6-week old potatoes with varied solution concentrations of phosphorus.

	Phosphorus in solution (mM)					
	0.1	0.25	0.5	0.9	1.4	2
Leaf P (mg g^{-1})	5.0c[z]	6.0b	7.5a	7.5a	7.9a	7.8a
Total DW (g)	49.0[y]	49.3	53.6	58.2	54.6	48.3
Tuber DW (g)	29.2[y]	30.1	32.2	33.7	31.8	28.0
Leaf area (dm^2)	41.6[y]	42.2	44.4	51.7	48.3	43.7

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

[y]No significant difference for each of the three measurement at P=0.05.

Table 8.15. Potassium concentration in leaves and growth responses of 6-week old potatoes with varied solution concentrations of potassium.

	Potassium in solution (mM)					
	0.1	0.5	1.5	3	6	9
Leaf K (mg g^{-1})	20.3b[z]	52.9a	53.5a	50.9a	54.5a	61.6a
Total DW (g)	35.7b	51.0a	46.9a	52.2a	51.0a	41.2ab
Tuber DW (g)	22.5b	30.9a	28.7a	30.8a	29.9a	25.0ab
Leaf area (dm^2)	26.2b	42.5a	37.3ab	45.2a	43.5a	29.6b

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

Table 8.16. Calcium concentration in leaves and growth responses of 6-week old potatoes with varied solution concentrations of calcium.

	Calcium in solution (mM)					
	0.05	0.25	1	2.5	5	7.5
Leaf Ca (mg g^{-1})	3.9e[z]	11.6d	24.0c	35.2b	43.2a	46.7a
Total DW (g)	22.6c	40.5ab	46.3a	42.0ab	37.5ab	33.1bc
Tuber DW (g)	7.4c	25.2ab	30.4a	27.8ab	24.5ab	21.9b
Leaf area (dm^2)	12.4c	23.3ab	30.7a	28.1ab	23.1ab	21.2b

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

Table 8.17. Magnesium concentration in leaves and growth responses of 6-week old potatoes with varied solution concentrations of magnesium.

	Magnesium in solution (mM)					
	0.05	0.125	0.25	1	2	4
Leaf Mg (mg g^{-1})	1.1f[z]	2.5e	4.1d	6.7c	8.7b	11.2a
Total DW (g)	42.6c	49.7b	53.3b	59.7a	52.6b	38.6c
Tuber DW (g)	22.7c	29.4b	32.3ab	35.6a	30.4b	22.7c
Leaf area (dm^2)	40.3b	41.1b	42.7ab	50.2a	46.7ab	32.4c

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

Table 8.18. Iron concentration in leaves and growth responses of 5-week old potatoes with varied solution concentrations of iron.

	Iron in solution (ppm)					
	0.01	0.1	0.5	2	5	10
Leaf Fe ($\mu g\ g^{-1}$)	98d[z]	119d	168c	271b	298b	428a
Total DW (g)	22.7b	30.4a	31.8a	31.7a	30.5a	24.8b
Tuber DW (g)	7.5ab	5.2b	8.1a	8.2a	7.5ab	7.2ab
Leaf area (dm^2)	32.7b	50.6a	50.8a	50.3a	52.0a	38.3b

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

Table 8.19. Manganese concentration in leaves and growth responses of 5-week old potatoes with varied solution concentrations of manganese.

	Manganese in solution (ppm)					
	0.01	0.1	0.5	2	5	10
Leaf Mn ($\mu g\ g^{-1}$)	15.0e[z]	32.0e	73.2d	164.1c	700b	1179a
Total DW (g)	24.3b	32.4ab	36.3a	32.7ab	34.1a	31.7ab
Tuber DW (g)	6.3c	10.3a	10.3a	9.1ab	7.6bc	7.5bc
Leaf area (dm^2)	40.9	--	53.5	--	--	50.4

[z]Mean separate in row with the Duncan's multiple range test, P=0.05.

The concentrations of each particular nutrient in tissues changed significantly with solution concentrations (Tables 8.12-8.19). The responses in tissue concentrations showed two different patterns with various nutrients that were studied. With NO_3, NH_4, P, and K, tissue concentrations of the specific nutrients were reduced at low solution levels, and then increased to a constant or nearly constant level from the middle to high range of solution concentrations. With Ca, Mg, Fe, and Mn, tissue concentrations increased substantially with increasing concentrations in solution. This increasing response was particularly significant with Mn nutrient.

Plant growth as total dry weight, tuber dry weight, and leaf area were depressed at both deficient and excess concentrations of each nutrient, although the differences were not statistically significant with P concentrations (Tables 8.12-8.19). For most nutrients studied, plant growth was adequate only over a range of the concentrations, and optimum at a particular concentration level (Table 8.20). The optimum concentrations for most nutrients studied were similar to those in the nutrient solution utilized for potato research (Table 2.2) except for N and Ca. The

Table 8.20. Useful range and optimum concentration for each of the nutrients in solution.

	Useful range	Optimum concentration
	mM	
NO_3	2-8	5
NH_4	2-4	3
P	0.5-1.4	1
K	0.5-6	3
Ca	0.25-5	1
Mg	0.25-2	1
	ppm	
Fe	0.5-5	2
Mn	0.1-10	0.5

optimum concentrations of N and Ca were found to be lower than in the commonly utilized solution. The data also show that the most favorable concentration range for nitrogen supplied as NH_4^+ was lower than for nitrogen supplied as NO_{3-}.

It should be recognized that the results from these studies may vary from conclusions drawn in other research because of the procedures used for supplying nutrients. Many researchers have utilized systems in which the nutrient concentration decreases over time and is replenished to the reported concentrations only at intervals. For instance, in this study Mg concentrations of 2 mM or higher inhibited potato growth whereas in a previously reported solution culture study with potatoes (Fong and Ulrich, 1974) growth was not inhibited even at 8 mM Mg. However in that research the Mg concentrations were permitted to decrease from the reported concentrations over the 30 day period of the study.

Leaf Gas Exchange. Measurements of CO_2 exchange and transpiration of leaflets demonstrated significant leaf stomatal responses to the varied nutrient concentrations in some experiments, as with Mg, but not in others, as with K. At the lowest and highest Mg concentrations in solution, CO_2 assimilation rates were significant reduced whereas CO_2 dark respiration rates were increased as compared to those at intermediate concentrations (Fig. 8.1). The assimilation vs. CO_2 concentration curves also showed that the photosynthetic rates were consistently lower across varied intercellular CO_2 concentrations at the 0.05 mM and 4 mM of Mg than at 1 mM of Mg (Fig. 8.2). These data indicate that the depressed photosynthesis with deficient and excess Mg concentrations resulted largely from reduced leaf mesophyll activities. In contrast, with different K concentrations between 0.1 and 9 mM in solution, CO_2 assimilation rates, stomatal conductance, intercellular CO_2 concentrations, and transpiration rates were all similar (Table 8.21). The data suggest that photosynthesis in plants is altered less by varied K concentrations than by varied Mg concentrations.

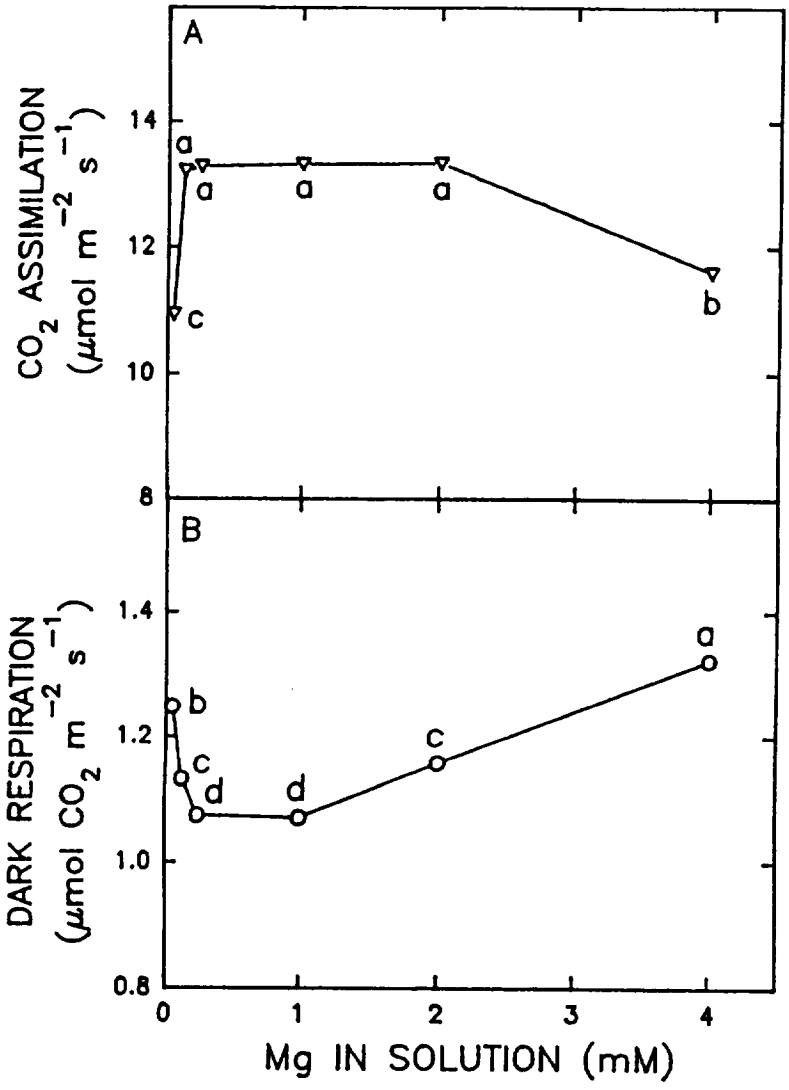


Figure 8.1. Leaf CO_2 assimilation and dark respiration of potato plants grown at different Mg concentrations.

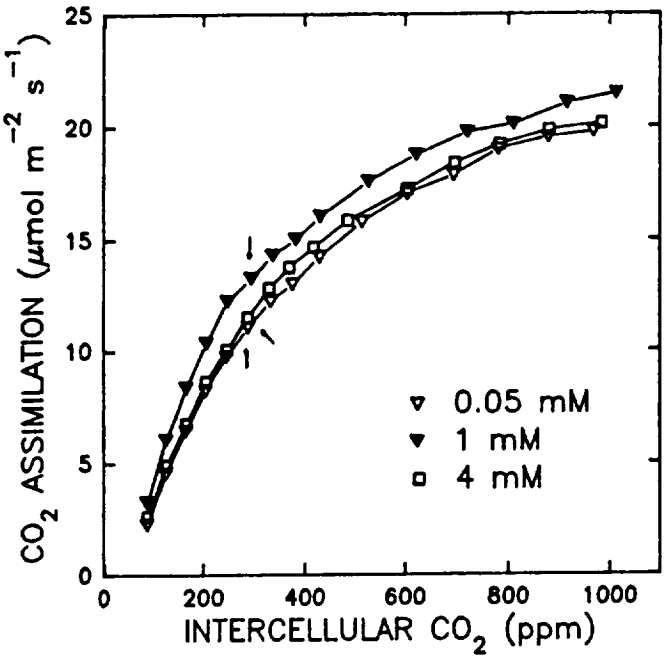


Figure 8.2. Responses of CO_2 assimilation to intercellular CO_2 concentrations in potato leaves at three Mg concentrations.

Table 8.21. Leaf gas exchange measurements with different potassium concentrations.

	Potassium in solution (mM)					
	0.1	0.5	1.5	3	6	9
CO_2 assimilation (μmol m^{-2} s^{-1})	11.9	11.7	11.5	11.5	11.6	11.4
Stomatal conductance (mmol m^{-2} s^{-1})	458	467	443	434	438	429
Intercellular CO_2 concentration (ppm)	311	310	314	303	311	307
Transpiration (mmol m^{-2} s^{-1})	5.2	5.3	5.1	5.2	5.1	5.0

Nutrient Depletion in Solution. Nutrient concentrations in the effluent after passage through the trays usually did not change during the first two weeks of the experiments as compared to the concentrations in the incoming solutions. However, from week three until harvest the nutrient concentrations in the effluent decreased for low concentration treatments, and slightly increased for high concentration treatments. These different patterns in nutrient changes across the trays during plant growth were shown for the K experiment in the following table (Table 8.22). Thus the depletion in concentrations at the lowest concentrations occurred early in the growth of the plants and undoubtedly produced the severe stunting of the plants at the lowest concentration with most of the nutrients. If a significantly greater amount of solution had been provided to the plants, enhanced plant growth may have resulted at the low nutrient concentrations as shown by Asher and Ozanne (1967) in K experiments using several other crop species. The flow rate was maintained at only 4 ml min^{-1} for it was too difficult to provide a higher flow rate for this study. It is interesting to note that with K at 0.5 mM concentration (Table 8.22), nutrient concentrations were essentially depleted by day 34 as they exited the trays, although there was no significant growth reductions at this concentration (Table 8.15). The K

Table 8.22. The changes of potassium concentrations in the effluent for different treatments after passage through the trays.

	Potassium in solution (mM)					
Days	0.1	0.5	1.5	3	6	9
6	0.12	0.54	1.59	3.36	6.52	9.74
13	0.08	0.49	1.58	3.32	6.63	9.94
20	0.02	0.31	1.49	3.21	6.68	10.40
27	<0.02	0.05	1.09	2.61	6.06	9.81
34	<0.02	0.02	0.83	2.53	6.21	9.81
41	<0.02	<0.02	0.90	2.73	6.68	10.54

concentrations in the effluent for treatments at 1.5, 3, 6, and 9 mM varied over the experiment period apparently due to the changing balance between nutrient uptake and water uptake by plants as they enlarged. The data suggest that potato plants can be grown at a wide range of concentrations of nutrients during early growth. It may be more efficient to start with low concentrations during early growth, and then increase concentrations as plants enlarge and require more nutrients.

Nutrient Uptake Efficiency. Uptake rates and uptake efficiencies for each of the major nutrients at varied solution concentrations were determined on day 41 after transplanting. With increasing solution concentrations of N (NO_3), P, K, and Mg, the rates of nutrient uptake by plants markedly increased and uptake efficiencies decreased. Figure 8.3 shows the data on K uptake in response to solution concentrations that represents the patterns for N, P, and Mg

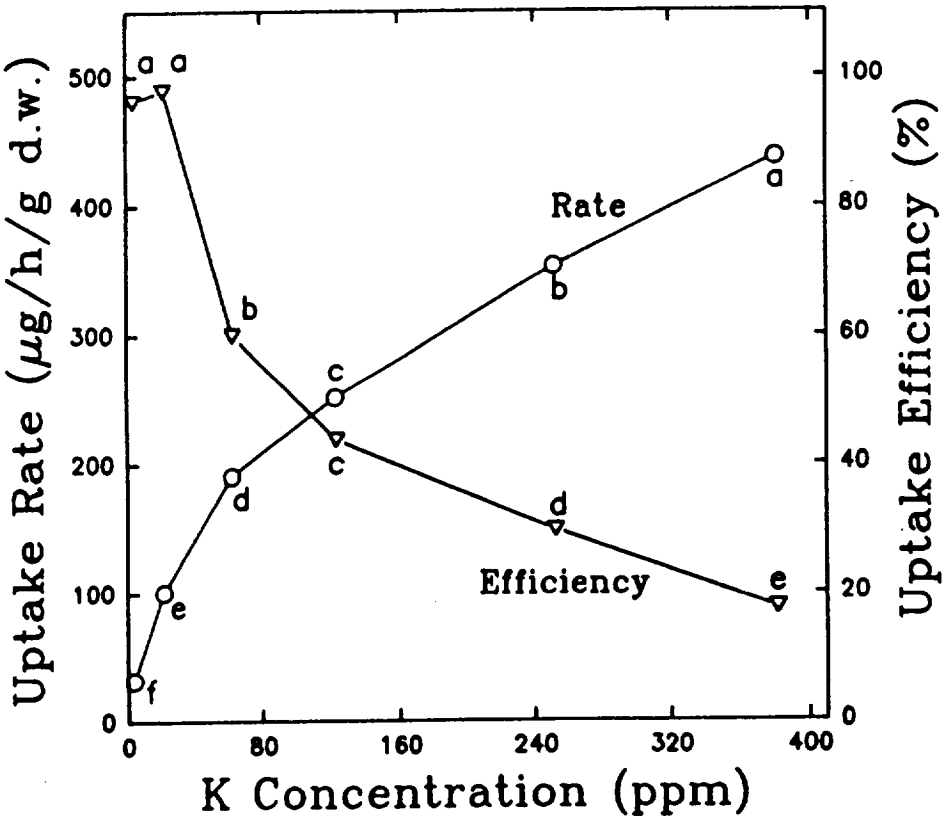


Figure 8.3. Uptake rate and uptake efficiency of K at varied concentrations in solution.

uptake. With increasing solution concentrations, uptake efficiency for N, P and K changed from about 95% to 20%, and for Mg changed from 70% to 10%. With varied solution concentrations of Ca, however, uptake efficiency exhibited only small changes from 30% to 10% (Figure 8.4), and at the lowest Ca concentration the uptake efficiency was even lower than at the intermediate concentrations of Ca.

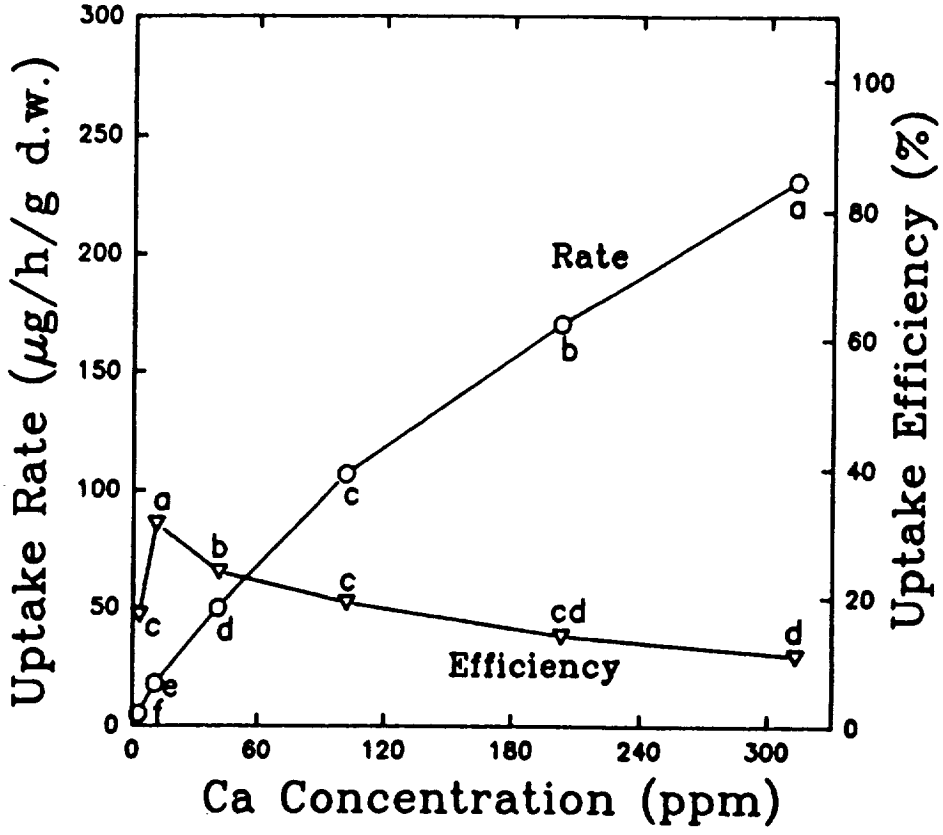


Figure 8.4. Uptake rate and uptake efficiency of Ca at varied concentrations in solution.

The data indicate that maximum uptake efficiency was highest for N, P, and K, lowest for Ca, and intermediate for Mg. These results suggest that with N, P, and K, high uptake efficiency would partly compensate for low amount of nutrients present in solution, but with Ca, the low uptake efficiency would require that an adequate amount of Ca has to be present in solution for effective plant growth. This low uptake efficiency likely can not be effectively offset

by higher flow rates as seen in data of Table 8.7, for Ca concentrations in shoots decreased with increasing flow rate. The different patterns of uptake efficiency for different nutrients may change ion proportion and nutrient balance in a recirculating solution. Thus measurements of solution conductivity may not accurately reflect the availability of the individual nutrients as the solution is depleted by plants.

Mineral Interactions in Tissues. Varied concentrations of a particular nutrient in solution controlled not only the concentration of that nutrient in tissues, but also altered the concentration of certain other minerals in the tissues. In response to the varied concentrations of a given nutrient, some other nutrients in tissues were reduced, some were enhanced, and others were not changed (Table 8.23).

Tissue concentrations of N, P, and K varied less with changed concentrations of other nutrients in the solution than tissue Ca, Mg, Mn, and Fe. Tissue N was not altered by any other

Table 8.23. Variations in tissue mineral composition in response to increasing concentrations of individual nutrients in solution.

Nutrient in tissue	Nutrient in solution						
	N	P	K	Ca	Mg	Mn	Fe
N		o	o	o	o	o	o
P	+[z]		o	o	o	o	o
K	o	o		o	-	o	o
Ca	-	o	-		-	-	o
Mg	-	o	-	-		-	o
Mn	-	o	-	-	-		-
Fe	+	+	-	o	+	o	

[z]+: increase, -: decrease, o: no change.

nutrients studied. Tissue P increased only with increased N in solution whereas tissue K decreased only with increased Mg. Tissue Ca, Mg, or Mn reduced respectively with increased N, K, Ca, Mg, or Mn in solution. The inhibitory effect of certain cations on the accumulation of Ca and Mg in plants is consistent with the previous reports for potatoes (Fageria et al., 1991;Fong and Ulrich, 1974). Tissue Fe increased with increased N, P, or Mg, but decreased with increased K in solution. These interactive effects of certain nutrients with other minerals in tissues may not be sufficient to affect normal growth responses of plants, but could be significant for amount of mineral recovery from plant tissues under different nutrient conditions.

DIURNAL UPTAKE OF NUTRIENTS

Diurnal uptake patterns for various nutrients were determined from influx and effluent of the solution on day 41 of the experiment with potassium. Only the treatment having 3 mM K was utilized, because this K concentration is present in the nutrient solution used for all other potato research as detailed in Table 2.2. This treatment had mM concentrations of 7.5 for N, 3.0 for K, 0.5 of P, 2.5 of Ca, 1.0 of Mg, 1.0 of S, 0.5 of Cl and μM concentrations of 90 of Fe, 23 of B, 9 of Mn, 0.38 of Zn, 0.16 of Cu, and 0.06 of Mo. The nutrient uptake rates were obtained at ten equally spaced times 2.4 hours apart during a 12 L:12 D cycle using a 30 minute period for each sampling. Samplings were started at 1.0, 3.25, 5.45, 8.25, and 10.5 hours both after the start of light period and after the start of dark period. Data are plotted in the following figures with uptake rates against the mid-point of each 30-minute sampling period.

Uptake of K and B, along with water, peaked at 6 h after the start of light period, and then decreased with additional marked decreases during the dark (Fig. 8.5, 8.6, 8.8). The uptake of P, S, Ca, Mg, Fe, and Mn did not show significant peaks during the light or dark, but did exhibit a marked decreased over the dark period (Fig. 8.7-8.10). N uptake (Figure 8.7) had a sharp drop about 3 hours after the start of the light period, and a second sharp drop at the beginning of the dark period, but then increased steadily over the dark period. For all measured nutrients, along with water, the cumulative uptake during light period was substantially higher than during the dark period (Table 8.24). The dark period reduction was proportionately greater for Ca, Mg, Fe, Mn, and B than for N, P, S, and K. The data suggest that a reduced flow rate of nutrient solution during the dark could be provided if this would increase efficiency in plant growing.

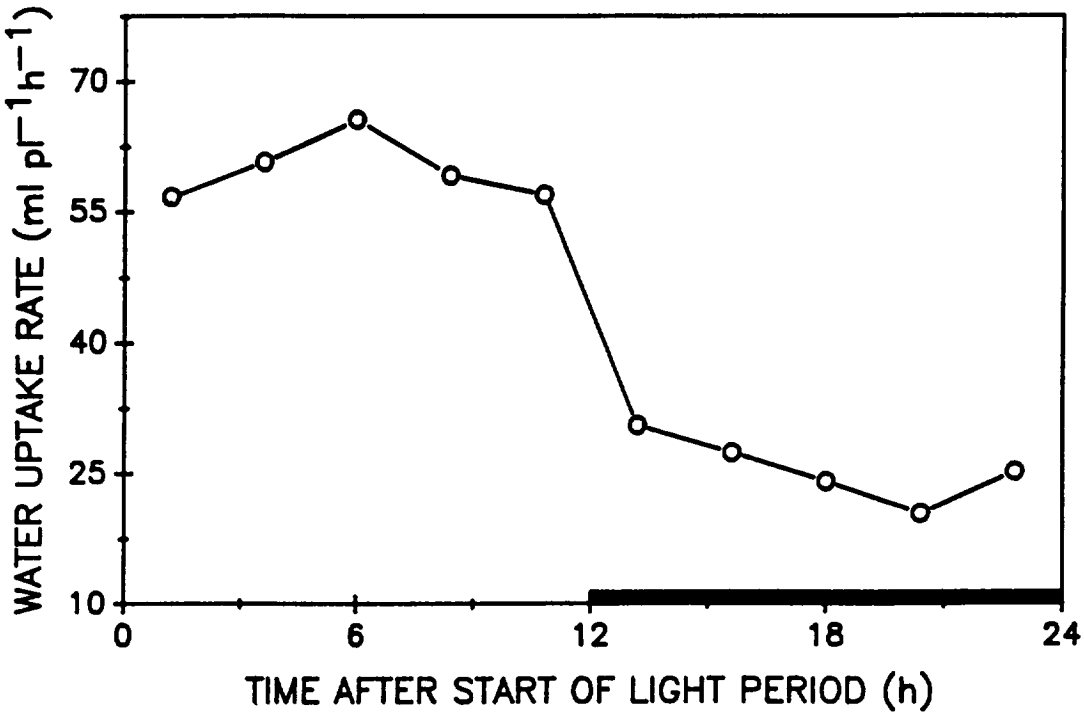


Figure 8.5. Diurnal changes of water uptake by 41-day old potato plants.

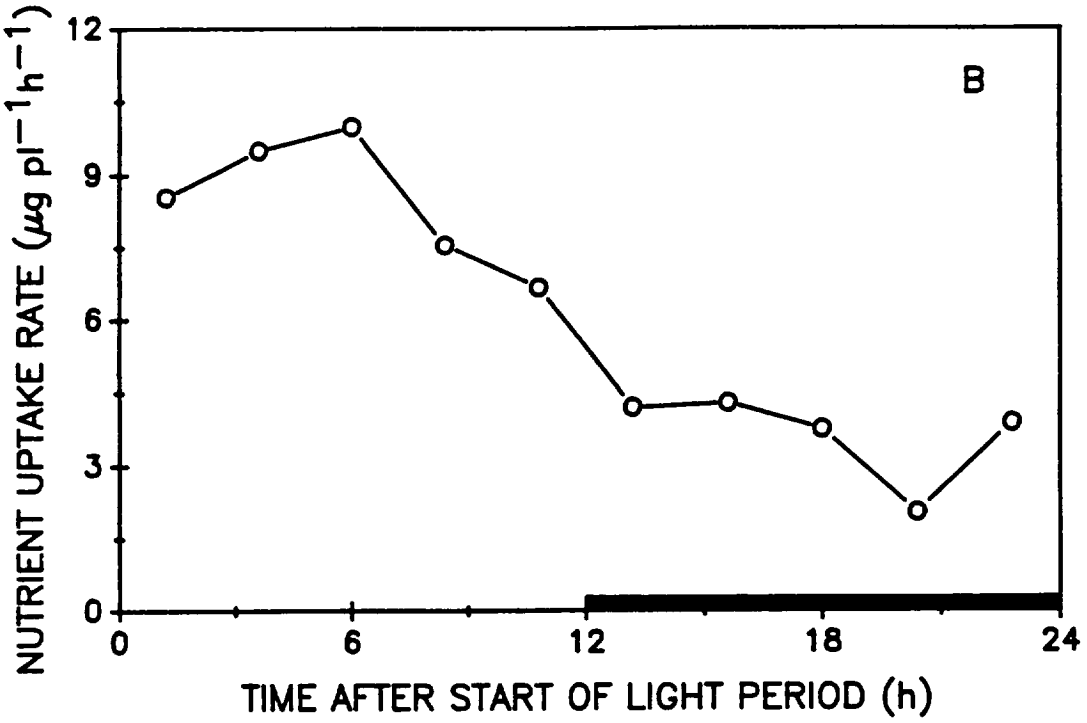


Figure 8.6. Diurnal uptake pattern of B by 41-day old potato plants.

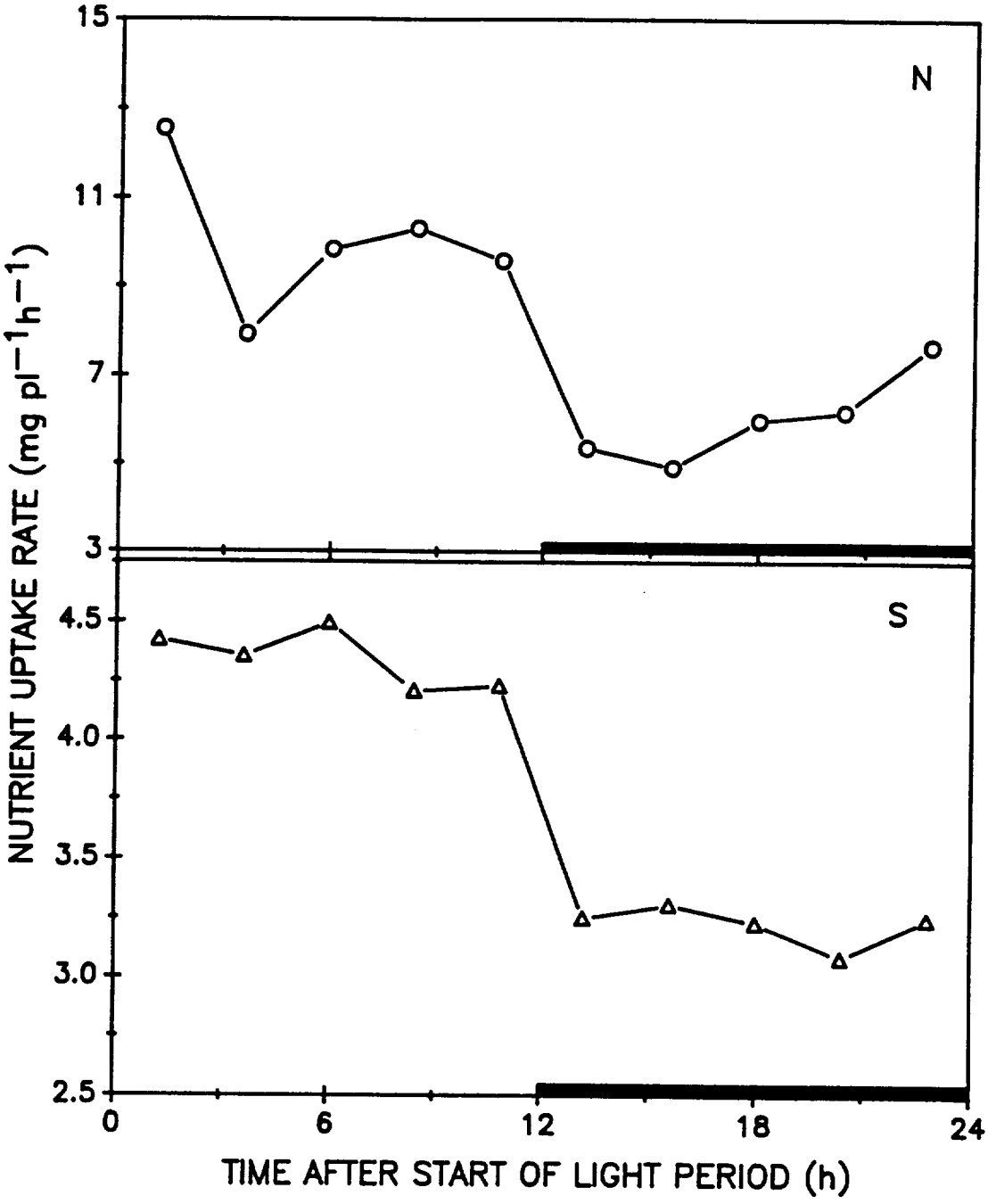


Figure 8.7. Diurnal uptake patterns of N and S by 41-day old potato plants.

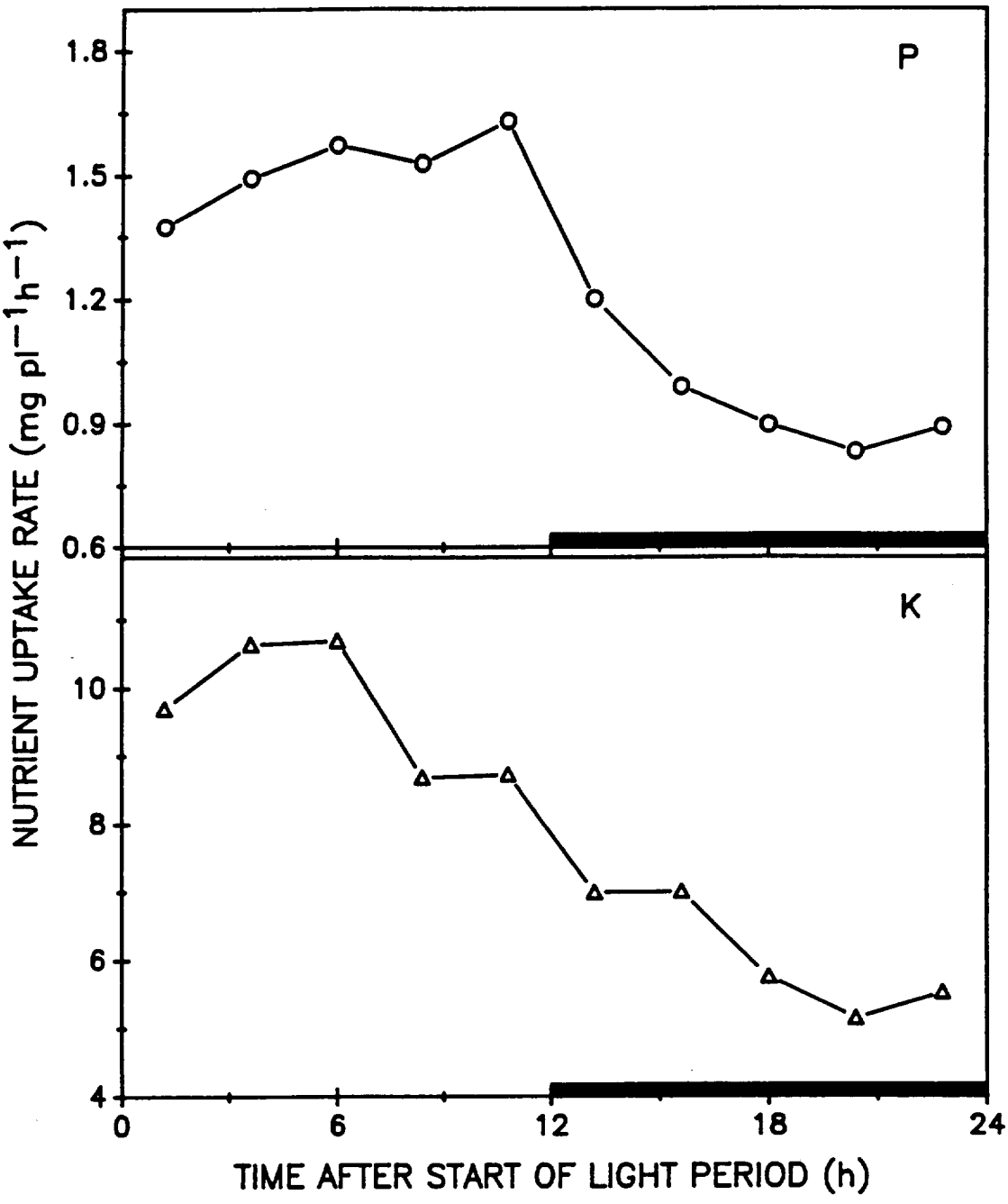


Figure 8.8. Diurnal uptake patterns of P and K by 41-day old potato plants.

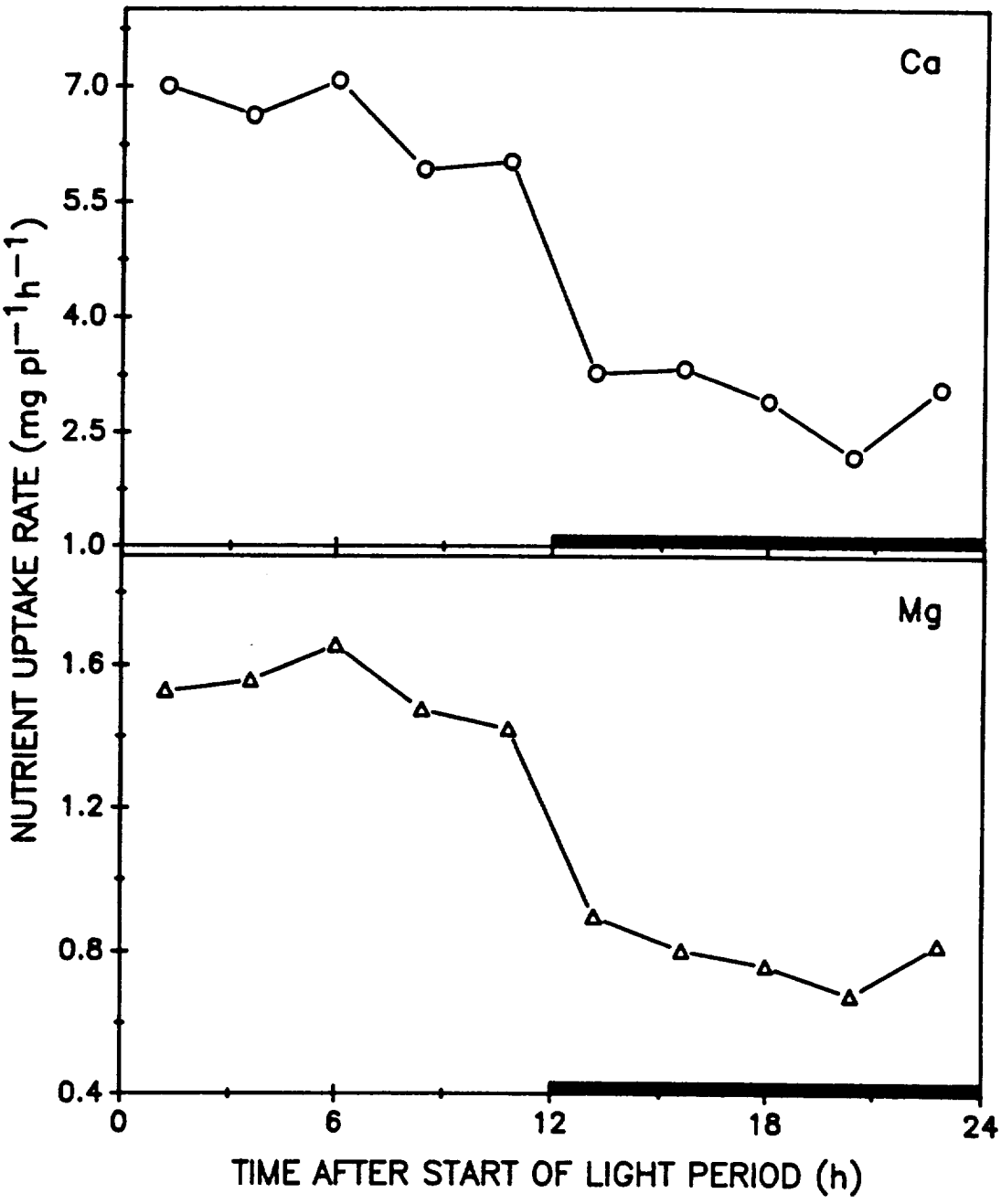


Figure 8.9. Diurnal uptake patterns of Ca and Mg by 41-day old potato plants.

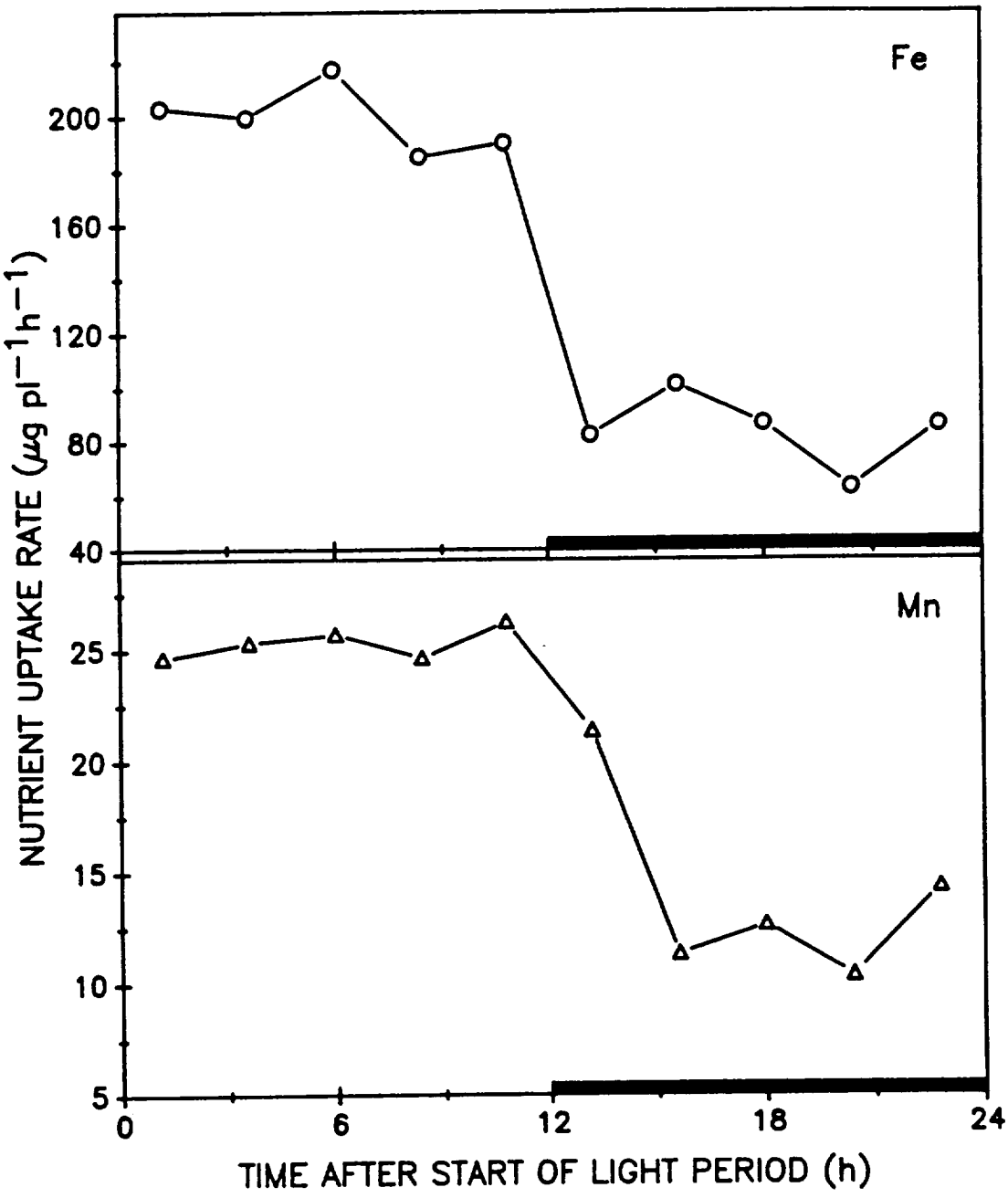


Figure 8.10. Diurnal uptake patterns of Fe and Mn by 41-day old potato plants.

The data on total uptake of the nutrients over a 24 h period (Table 8.24) indicate that the ratios of daily nutrient uptake for N:S:P:K:Ca:Mg were approximately 100:47:15:98:59:14. In comparison, the ratios of major nutrients in the commonly used solution were 100:31:15:112:96:24. The data suggest that the Ca and Mg uptake from the solution is proportionately less than other major nutrients. These data provide a basis for replenishing nutrients in the solution during plant growth. However the uptake data should be used in conjunction with tissue composition data to arrive at the optimal replenishment. Additional data need to be obtained on nutrient uptake at different stages of plant development for requirements may change markedly during maturation of plants.

Table 8.24. Cumulative uptake of different nutrients during light and dark periods.

Element	Uptake in light	Uptake in dark	Dark over light	Uptake per day
	mg/plant/12 h		%	mg/plant/24 h
N	120.44	72.28	60	192.72
P	18.33	11.54	63	29.77
S	52.08	38.64	74	90.73
K	116.17	72.88	63	189.05
Ca	78.31	35.48	45	113.79
Mg	18.31	9.48	52	27.79
Fe	2.39	1.00	42	3.39
Mn	0.30	0.17	55	0.47
B	0.10	0.04	43	0.14

NITROGEN FORMS

Ammonium (NH_4^+) and nitrate (NO_3^-) are the two forms of nitrogen available for plant growth. It has been well documented that most plant species grow better with NO_3^- than with NH_4^+ nutrition (Pilbeam and Kirkby, 1992; Salsac et al., 1987). There is also evidence that crop plants supplied with both NH_4^+ and NO_3^- forms can be more productive than those supplied with NO_3^- alone (Pilbeam and Kirkby, 1992). Thus fertilization with combined NH_4^+ and NO_3^- forms has become a common practice in many crop production systems.

However, mixed nitrogen forms have not consistently produced growth promotion with potatoes in controlled culture systems. In one hydroponic study (Davis et al., 1986), dry weights of shoots and roots were lower although tuber dry weight was higher with mixed nitrogen than with NO_3^- alone. In another hydroponic study (Polizotto et al, 1975), dry weights of shoots, roots, and tubers were all significantly lower with mixed nitrogen than with NO_3^- alone.

In this study, two experiments were conducted to determine the effects of various ratios of NH_4^+ and NO_3^- forms of nitrogen on growth and mineral concentrations in potato plants as detailed in Cao and Tibbitts (1993b). The first experiment included six NH_4^+-N/NO_3^--N percentages at 0/100, 20/80, 40/60, 60/40, 80/20, and 100/0 with the same total N concentration of 4 mM. The mineral salts used to make up these separate nitrogen treatments are shown in Table 8.25. The second experiment included six NH_4^+-N/NO_3^--N percentages at 0/100, 4/96, 8/92, 12/88, 16/84, and 20/80 again with the same total N of 4 mM. The mineral salts used for each treatment in the second experiment are not shown, but changed proportionally between the 0/100% and 20/80% NH_4^+-N/NO_3^--N as seen for the first experiment. In each experiment, plants were harvested 35 days after transplanting when tubers had been initiated and begun to enlarge.

Table 8.25. Composition of six nutrient solutions with varied percentages of NH_4^+-N/NO_3^--N.

Salt[z]	NH_4^+-N/NO_3^--N percentage					
	0/100	20/80	40/60	60/40	80/20	100/0
	(mM)					
$Ca(NO_3)_2$	1.0	0.8	0.6	0.4	0.2	0
KNO_3	2.0	1.6	1.2	0.8	0.4	0
$(NH_4)_2SO_4$	0	0.4	0.8	1.2	1.6	2.0
K_2SO_4	0	0.2	0.4	0.6	0.8	1.0
$CaSO_4$	0	0.1	0.2	0.3	0.4	0.5
$CaCl_2$	0	0.1	0.2	0.3	0.4	0.5
KH_2PO_4	1.0	1.0	1.0	1.0	1.0	1.0
$MgSO_4$	1.0	1.0	1.0	1.0	1.0	1.0
NaCl	0.5	0.5	0.5	0.5	0.5	0.5

[z]Minor nutrients were supplied as shown in Table 2.2.

Dry weights of shoots, tubers, and whole plant at harvest were greater with mixed nitrogen treatments as compared with single NH_4^+ or NO_3^- form (Table 8.26, 8.27). The enhanced growth with mixed nitrogen was greatest at 8% to 20% NH_4^+-N. Thus, additions of NH_4^+-N to the nutrient solution even as a small proportion, promote growth and tuber development in potatoes as compared to only NO_3^- nutrition.

Table 8.26. Dry weights of 5-week old potatoes grown with varied NH_4^+-N/NO_3^--N percentages at 20% intervals.

	NH_4^+-N/NO_3^--N percentage					
	0/100	20/80	40/60	60/40	80/20	100/0
	(g plant^{-1})					
Total	23.3c[z]	36.4a	31.1b	31.3b	29.1b	7.0d
Shoots	12.3c	21.4a	16.6b	16.4b	14.5b	3.4d
Roots	1.3b	2.5a	2.1a	2.0a	1.9ab	0.4c
Tubers	9.6b	12.6a	12.4a	12.8a	12.7a	3.1c

[z]Mean separation in each row by the Duncan's multiple range test, P=0.05.

Table 8.27. Dry weights of 5-week old potatoes grown with varied NH_4^+-N/NO_3^--N percentages at 4% intervals.

	NH_4^+-N/NO_3^--N percentage					
	0/100	4/96	8/92	12/88	16/84	20/80
	(g plant^{-1})					
Total	25.6b[z]	32.9a	36.9a	34.0a	36.4a	35.9a
Shoots	17.1b	21.0a	23.8a	22.5a	23.7a	23.6a
Roots	2.4a	3.0a	2.8a	2.8a	3.2a	3.1a
Tubers	6.0b	8.9a	10.3a	8.7a	9.6a	9.2a

[z]Mean separation in each row by the Duncan's multiple range test, P=0.05.

The concentrations, as well as accumulation, of total N in the shoots and roots were greater with mixed nitrogen than with separate NH_4^+ or NO_3^- nutrition (Table 8.28), suggesting that potato plants can more effectively utilize mixed NH_4^+/NO_3^- nutrition than single nitrogen forms. There was an indication that partitioning of total N between shoots and roots changed with nitrogen forms. With the NO_3^- alone, the total N in shoots was 51% higher than in roots, whereas with the NH_4^+ alone, total N in shoots was only 25% higher than in roots. Also, the reduced N concentrations in tissues, determined as differences between total N and nitrate N, tended to be higher with increasing percentages of NH_4^+-N in the solutions (Table 8.28).

Table 8.28. Concentrations of nitrogenous components in the shoots and roots of potatoes grown with varied percentages of NH_4^+-N/NO_3^--N.

	NH_4^+-N/NO_3^--N percentages					
	0/100	20/80	40/60	60/40	80/20	100/0
	Shoots (mg g^{-1})					
NO_3^--N	15.3ab[z]	16.7a	15.6ab	14.2b	8.1c	1.0d
Reduced N	35.7b	45.6ab	47.9a	48.8a	49.5a	44.8ab
Total N	51.0bc	62.3a	63.5a	63.0a	57.6ab	45.8c
	Roots (mg g^{-1})					
NO_3^--N	8.3a	6.5b	6.3b	4.2c	2.3d	0.6e
Reduced N	25.5d	30.5c	32.8bc	33.7ab	34.9ab	36.0a
Total N	33.8b	37.0a	39.2a	38.0a	37.2a	36.7ab

[z]Mean separation in each row by the Duncan's multiple range test, P=0.05.

With NH_4^+ present in the solutions, the concentrations of P and Cl in the shoots were increased compared to NO_3^- alone, whereas the tissue concentrations of Ca and Mg were decreased (Table 8.29). The changes in tissue concentrations were particularly substantial with Ca and Cl. With NH_4^+ additions an increased Ca supply may be required to prevent possible Ca deficiency in plants. Increases in Cl, along with S, would be expected because both anions were co-ions that increased with increasing NH_4^+ in the solution (Table 8.25). However, the increases in tissue Cl were substantially greater than the proportional increases in the solution with increasing NH_4^+. This suggests a possible promotion of Cl uptake by the NH_4^+ ion. The data indicate that there is less risk using SO_4 than using Cl as co-ion for balancing concentrations of nutrients. The changed mineral composition and plant growth with different forms of nitrogen also have been demonstrated in other crop species (Pilbeam and Kirkby, 1992; Salsac et al., 1987).

Table 8.29. Mineral composition in the shoots of potatoes grown with varied percentages of NH_4^+-N/NO_3^--N.

	NH_4^+-N/NO_3^--N percentage					
	0/100	20/80	40/60	60/40	80/20	100/0
	(mg g^{-1})					
P	6.0b[z]	7.5a	8.0a	8.4a	8.0a	7.3a
K	50.0a	53.2a	45.9a	61.7a	57.7a	51.1a
Ca	16.2a	7.5b	5.6b	5.5b	5.8b	5.7b
Mg	7.1a	5.3b	4.8b	4.8b	4.8b	4.6b
S	3.5b	4.2ab	4.4ab	4.4ab	4.5a	4.4ab
Cl	2.5c	7.0bc	9.1b	11.2b	22.7a	26.5a

[z]Mean separation in each row by the Duncan's multiple range test, P=0.05.

SOLUTION pH LEVELS

The pH levels in rooting media affect mineral availability and growth of crop plants. Most plant species achieve maximum or near-maximum growth within the pH range of 4.0 to 6.5, although certain species as corn, soybean, and alfalfa prefer pH levels slightly above this range whereas species, as cranberries and blueberries, prefer pH levels at the bottom end of this range (Findenegg, 1987; Islam et al., 1980; Jariel et al., 1991). It has also been found that the increases in pH promote NH_4^+ uptake whereas the decreases in pH promote NO_3^- uptake in several crop species (Findenegg, 1987; Pilbeam and Kirkby, 1992). These differential effects of pH changes on uptake of NO_3^- and NH_4^+ imply that, when both NH_4^+ and NO_3^- forms are present in a nutrient solution, the uptake of total nitrogen by plants would be less affected by the changes in ambient pH levels. As a result, an optimum pH range for plant growth might be wider with mixed NO_3^-/NH_4^+ than with either NO_3^- or NH_4^+ alone.

Studies have indicated that potato plants can utilize both NO_3^- and NH_4^+ nitrogen forms although the amount of growth is usually greater with NO_3^- than with NH_4^+ (Cao and Tibbitts, 1994a; Davis et al., 1986; Polizotto et al., 1975). For effective potato production, solution pH range is desired at pH 5 to 6.5 (McLean and Brown, 1984).

The main objective of the following nutrient culture experiments was to compare the responses of potato plants to various solution pH levels with nitrogen supplied as NO_3^-, NH_4^+, and mixed NO_3^-/NH_4^+ at the same total N concentration (4 mM). Initially, three separate experiments were conducted over a wide range of pH levels with NO_3^-, NH_4^+, or mixed NO_3^-/NH_4^+ in a particular experiment. Then one experiment was conducted with pH 5 and 6 combined with NO_3^-, NH_4^+, and mixed NO_3^-/NH_4^+.

pH Effects with Separate Nitrogen Forms. In the first and second experiments, pH levels were maintained at 3.5, 4, 5, 6, 7, and 7.5 with separate NO_3^- and NH_4^+. In the third experiment, pH levels were provided at 4, 4.5, 5, 6, 6.5, 7 with mixed NO_3^-/NH_4^+. The plants were grown for 28 days after transplanting of tissue culture plantlets. Complete details of these experiments are provided in a separate report (Cao & Tibbitts, 1994a).

With mixed nitrogen, plant growth as total dry weight, leaf area and tuber number per plants were essentially similar for pH 4.5 to 7, and only decreased at pH 4 (Fig. 8.11). With

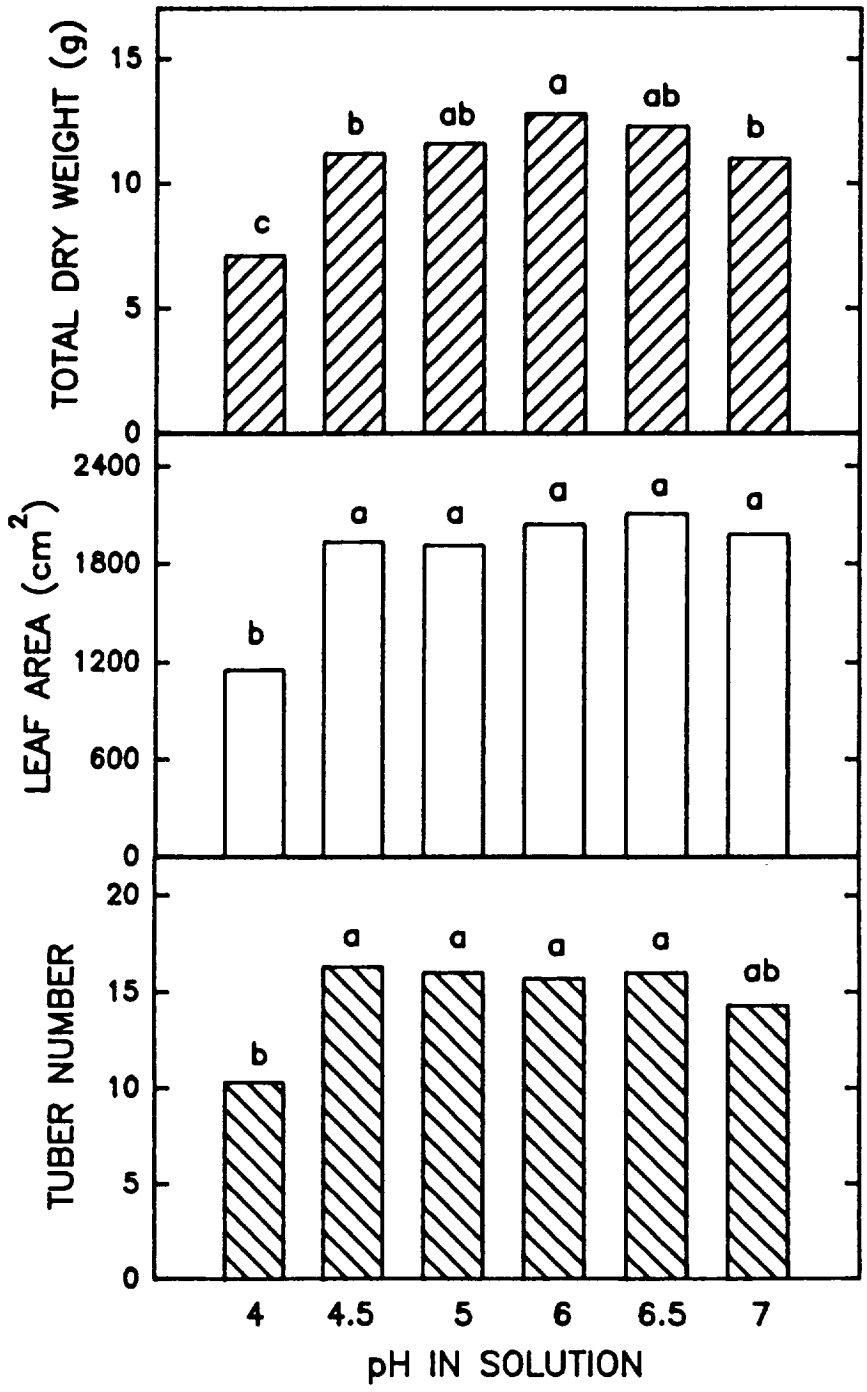


Figure 8.11. Total dry weight, leaf area, and tuber number per plant in potatoes grown at various solution pH levels with mixed NO_3^--N/NH_4^+-N. Mean separation by Duncan's multiple range test, p=0.05.

either nitrogen form alone, however, plant growth peaked at a particular pH level, pH 5 with NO_3^- and pH 6 with NH_4^+, and decreased at other pH levels (Fig. 8.12, 8.13). These results indicate that the effective pH range for potato growth is broader with mixed nitrogen nutrition than with single nitrogen form nutrition. The data also show that the pH range with NH_4^+ was narrower than with NO_3^- for growth of potatoes. Thus a more careful control of pH is needed to obtain desirable growth using a nutrient solution with only NO_3^- or NH_4^+, and particularly with only NH_4^+.

The shoot concentrations of N, K, Ca, Mg, and P varied little from pH 4 to 7 with mixed nitrogen whereas they varied considerably between pH 4 and 7 with either NO_3^- or NH_4^+ (Tables 8.30-8.32). It is possible that a uniform accumulation of the major nutrients at different pH levels with mixed nitrogen forms may have minimized the adverse effects from low and high pH levels. Particularly, a constancy in tissue N concentrations across varied pH levels with mixed nitrogen may have made plants less sensitive to the ambient pH changes.

Table 8.30. Concentrations of major nutrients in the shoots of potatoes grown at various solution pH levels with mixed NO_3^--N/NH_4^+-N.

Nutrient element	pH treatment					
	4	4.5	5	6	6.5	7
	mg g^{-1} shoot					
N	65.2a[z]	65.3a	65.4a	63.4a	63.8a	64.8a
K	71.3a	63.7a	60.7a	61.1a	63.7a	67.8a
Ca	6.4a	5.5ab	5.5ab	5.3b	5.1b	6.4a
Mg	5.2ab	4.7c	4.9bc	4.7bc	4.9bc	5.5a
P	8.8a	8.1a	8.1a	7.8a	7.9a	8.4a
S	4.5a	4.2a	4.1a	4.1a	4.1a	4.0a

[z]Mean separation in each row by Duncan's multiple range test, p=0.05.

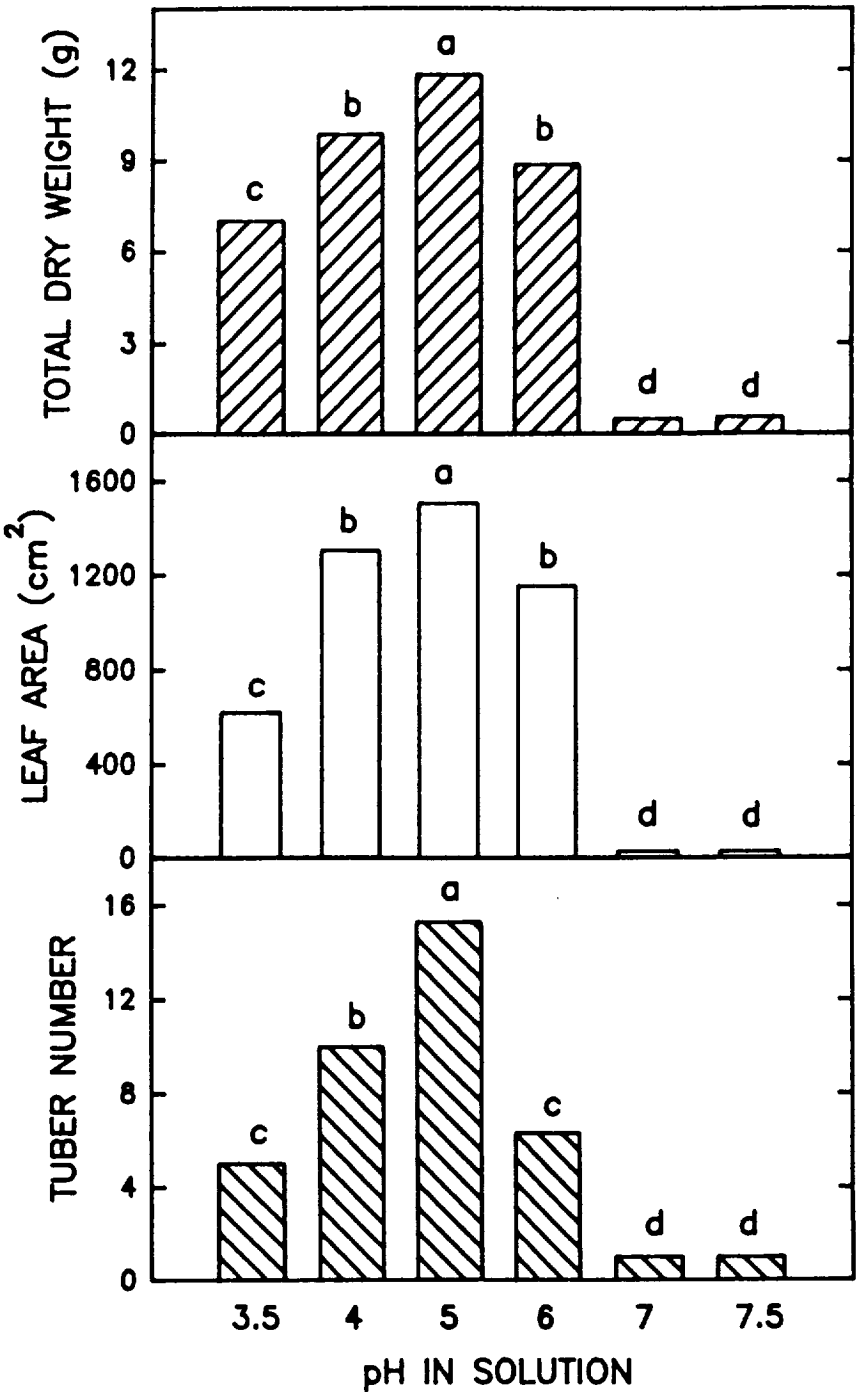


Figure 8.12. Total dry weight, leaf area, and tuber number per plant in potatoes grown at various solution pH levels with NO_3^--N alone. Mean separation by Duncan's multiple range test, p=0.05.

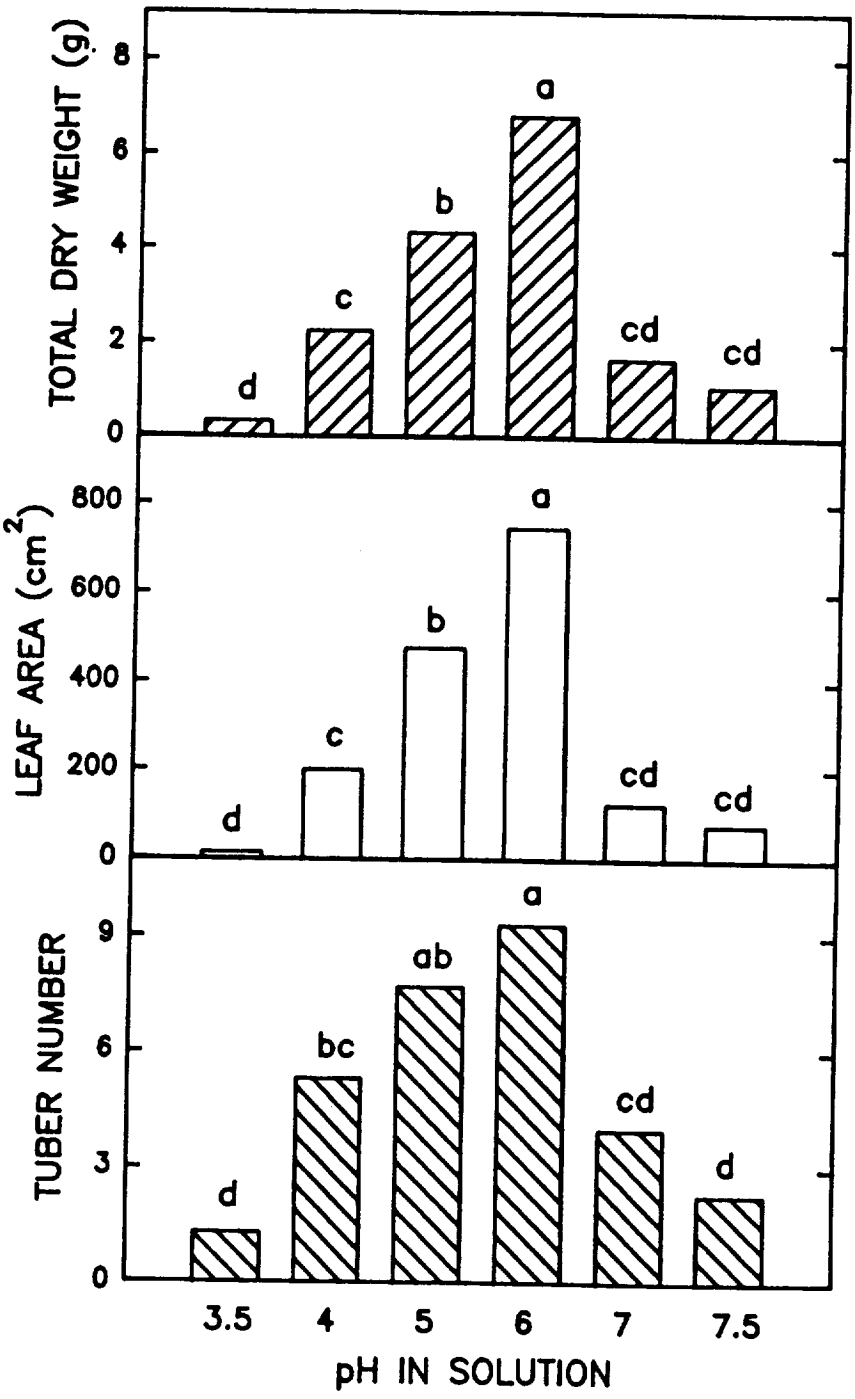


Figure 8.13. Total dry weight, leaf area, and tuber number per plant in potatoes grown at various solution pH levels with NH_4^+-N alone. Mean separation by Duncan's multiple range test, p=0.05.

Table 8.31. Concentrations of major nutrients in the shoots of potatoes grown at different solution pH levels with NO_3^--N alone.

Nutrient element	pH treatment 3.5	4	5	6	7	7.5
	mg g^{-1} shoot					
N	51.9abc[z]	57.1a	53.5ab	50.7bc	46.9cd	43.8d
K	47.9ab	53.8a	54.0a	56.2a	39.8b	39.2b
Ca	18.9c	16.9c	20.4bc	22.6b	33.6a	33.6a
Mg	6.0c	5.3c	5.5c	7.4b	10.8a	11.2a
P	4.8b	5.8b	5.6b	6.7b	35.4a	36.5a
S	3.2b	3.3b	3.2b	3.5b	5.5a	5.2a

[z]Mean separation in each row by Duncan's multiple range test, p=0.05.

The P concentrations of shoots in this study were unusually high at pH 7 and 7.5 with either nitrogen form alone. However these plants were severely stunted and thus it appears that the P might have been concentrated by transpiration in the stunted shoots.

Table 8.32. Concentrations of major nutrients in the shoots of potatoes grown at different solution pH levels with NH_4^+-N alone.

Nutrient element	pH treatment					
	3.5	4	5	6	7	7.5
	mg g^{-1} shoot					
N	30.9c[z]	46.4b	54.4ab	55.3ab	61.4a	59.0a
K	41.1c	58.4ab	64.1a	62.9ab	48.1bc	38.0c
Ca	2.8c	3.8bc	4.9b	5.0b	8.6a	7.6a
Mg	3.0b	3.6b	4.1b	3.7b	5.7a	5.3a
P	8.1b	7.8b	8.5b	8.0b	36.2a	26.3a
S	6.8a	4.8a	4.9a	5.4a	5.4a	5.0a

[z]Mean separation in each row by Duncan's multiple range test, p=0.05.

pH and Nitrogen Form Interactions. In this experiment, pH levels of 5 and 6 were maintained in combination with NO_3^-, NH_4^+, and mixed NO_3^-/NH_4^+ to carefully evaluate within a single experiment the nitrogen form and pH interactions observed in the previous three experiments. The nitrogen in all treatments was at a 4 mM concentration. Plants were grown for 28 days after transplanting.

The total dry weight, leaf area, and tuber number per plant were greater at pH 5 than at pH 6 with NO_3^-, but greater at pH 6 than at pH 5 with NH_4^+, and were similar at pH 5 and 6 with mixed NO_3^-/NH_4^+ (Table 8.33). This essentially duplicates the interacting effects of pH levels and nitrogen forms on plant growth found in the separate experiments. The data also document that plant growth was greater with mixed nitrogen than with NO_3^- or NH_4^+ alone although the number of tubers with NO_3^- alone at pH 5 was as high as with mixed nitrogen.

Table 8.33. Leaf area, total dry weight, and tuber number per plant in potatoes grown with combined pH and nitrogen form treatments.

Treatment		Total dry weight	Leaf area	Tuber number
Nitrogen	pH	(g)	(cm^2)	
NO_3^-:NH_4^+	5	12.2a	1982a	17.7a
	6	12.4a	1975a	19.3a
NO_3^-	5	10.6b[z]	1539b	18.0a
	6	7.0d	857c	7.3b
NH_4^+	5	5.4e	477d	3.7b
	6	9.4c	955c	6.7b
Nitrogen		**	**	**
pH		NS	NS	NS
Nitrogen X pH		**	**	**

[z]Mean separation among treatments by Protected LSD test, $P = 0.05$.

NS, **Nonsignificant or significant at $P = 0.01$.

The concentrations of N, K, Ca, Mg, P, and S in shoots with changed pH and nitrogen forms (Table 8.34) also showed similar patterns as in the previous separate experiments documenting that, with either N form alone, nutrient concentrations vary more than with mixed N. The data provides additional confirmation that the tissue concentrations of N, Ca, Mg, P, and S change significantly with nitrogen forms. The total N in tissues was higher with mixed NO_3^- /NH_4^+ than with either nitrogen form alone. With NH_4^+ and mixed nitrogen forms, tissue Ca and Mg were significantly reduced whereas P and S were increased as compared to NO_3^- alone.

In addition, the data indicate that the tissue Cl concentration was increased substantially with increasing amount of NH_4^+ in solution (Table 8.34), as seen in the previous experiments. It can be also seen that the Cl accumulation was influenced by pH. The tissue Cl was higher at pH

Table 8.34. Concentrations of major nutrients in the shoots of potatoes grown with combined pH and nitrogen form treatments.

Treatment		Concentration in shoots (mg g^{-1})						
Nitrogen	pH	N	K	Ca	Mg	P	S	Cl
NO_3^-:NH_4^+	5	64.2a	60.9	6.6b	5.0cd	8.1abc	3.6c	19.6c
	6	65.1a	58.4	6.2bc	5.2c	8.4ab	3.5cd	15.7d
NO_3^-	5	58.6b[z]	54.3	15.7a	7.1b	7.2c	3.3de	2.6e
	6	51.9c	59.1	14.7a	8.4a	7.7bc	3.1e	1.7e
NH_4^+	5	54.3c	57.9	4.3d	3.6e	8.9a	5.1a	30.6b
	6	55.7bc	54.5	5.4cd	4.3de	8.1abc	4.3b	50.1a
Nitrogen		**	NS	**	**	*	**	**
pH		NS	NS	NS	**	NS	**	**
Nitrogen X pH		**	NS	NS	NS	NS	**	**

[z]Mean separation among treatments by Protected LSD test, $P = 0.05$.

NS, *, **Nonsignificant or significant at $P = 0.05$ or 0.01, respectively.

6 than at pH 5 with NH_4^+ alone, but slightly higher at pH 5 than at pH 6 with mixed nitrogen forms.

The results with these different studies indicate that, as compared to either nitrogen form alone, mixed nitrogen nutrition can provide two major benefits for potato plants: broadening pH range and enhancing growth. This information provides a basis for effective management of solution pH and nitrogen fertilization for crop production in controlled environment and greenhouse conditions.

SECTION 9. GLYCOALKALOIDS

Glycoalkaloids occur naturally in all potato tissues (Kozukue, 1987). They are present in small amounts and are believed to impart some of the characteristic flavors to potato tubers (Baerug, 1962). In high quantities, however, glycoalkaloids will give tubers a bitter taste and lower the cooking quality. Although there is no established upper limit for glycoalkaloid content of potatoes for food safety, it is generally accepted that a value of 20 mg/100 g fresh weight be used (Sinden and Webb, 1974).

Many factors influence the level of glycoalkaloids in potatoes (Maga, 1980). Varietal difference is one of the most important factors. The total glycoalkaloid (TGA) levels of potatoes are primarily determined by genetic factors and, secondarily, by the environment (Sinden et al., 1984). TGA contents of tubers of 32 American cultivars have been reported to range from 1.8 to 13 mg/100 g fresh weight (Wolf and Duggar, 1946). Immature tubers have been found to have higher amount of TGA than mature tubers (Wolf and Duggar, 1946). Therefore, any environmental factor that retards maturation has been assumed to contribute to an increased level of glycoalkaloids (Ramaswamy et al., 1976).

The purpose of this study was to determine if any particular environmental factors during growth (temperature, light level, length of light period, carbon dioxide (CO_2) concentration and relative humidity) would significantly alter glycoalkaloid levels and thus should be carefully regulated in a CELSS when growing potatoes. The study was conducted in cooperation and directed by Dr. Joseph von Eble of the Food Science Department. The chemical analysis and data summarization were undertaken by Anadi Chungcharoen (Chungcharoen, 1988).

TISSUE SOURCES

Potato tissue for glycoalkaloid analysis was obtained from several of the environmental studies conducted under this grant and reported in preceding sections of this report.

The effect of temperature and length of light period during growth on TGA content of potato tubers was determined only on plants from the cultivar Norland. Plants were maintained in separate growing chambers at 12, 16, 20 and 24°C under 12 or 24 hr light period. Tubers were harvested at 8 weeks after planting (Wheeler et al. 1986).

The relationship between maturity and TGA level of potato tubers was determined only in potatoes from the cultivar Norland. The tubers were harvested at 9, 12, 15, 18 and 21 weeks after planting (Wheeler and Tibbitts, 1987).

The effect of CO_2 concentration during growth on the TGA content was determined on plants from the cultivars Norland and Russet Burbank. The plants were grown under 24 hr light duration and CO_2 concentrations of 350 and 1000 μmol mol^{-1} (Wheeler and Tibbitts, 1989).

The effect of light level and relative humidity on the TGA content was determined with cultivars Norland, Russet Burbank and Denali. The light level was maintained at 400 and 800 μmol m^{-2} s^{-1}. The relative humidity was held at 50 and 80% while the temperature was constant at 20°C. Tubers were harvested at 17 weeks after planting (Wheeler et al., 1989).

ANALYSIS PROCEDURE

Moisture content of potato tubers was determined immediately after harvest. Medium size tubers over 1" ($\approx$2.5 cm) in diameter were sampled from three separate replicate plants in each treatment. Six tubers were longitudinally quartered and one quarter of each tuber was chopped and combined to give a homogeneous sample per lot. Three grams of this material were used for moisture determination, the remaining sample was freeze dried for later analysis of glycoalkaloids. The 3-gram sample was placed in an aluminum dish and dried in a vacuum oven for 18 hr at 70°C. The sample was then transferred to a desiccator and allowed to cool. The dry weight was determined and moisture content calculated.

The amount of α-solanine, α-chaconine and total glycoalkaloids (TGA) was determined. Only α-solanine and α-chaconine were found in the tubers and were consistently in a ratio of 60:40 respectively in the different treatments. Eight grams of each freeze-dried sample were mixed with 40 ml distilled water and blended in an Eberbach blender. This slurry was extracted with a mixture of methanol and chloroform (2:1, v/v) using the method by Bushway et al. (1980) followed by vacuum filtration using a Buchner funnel with Whatman filter paper no. 1. The filtrate was concentrated to 10-20 ml in a vacuum rotary evaporator. Fifteen milliliters of 0.2N HCL were added to the concentrate. The mixture was sonicated for 5 min and centrifuged for 10 min. The supernatant liquid was transferred to a 250 ml Erlenmeyer flask followed by the addition of 30 ml concentrated NH_4OH (14.8 N). The solution was placed in a controlled temperature water bath at 70°C for 30 min after which it was removed from the water bath and

allowed to stand overnight at 5°C. The precipitate was collected by centrifugation and dissolved in the HPLC solvent. Individual glycoalkaloids in the samples were separated by HPLC. An isocratic solvent system consisting of tetrahydrofuran:water:acetonitrile (56:14:30, v/v/v) was employed with a carbohydrate analysis column (Waters Associates) as the stationary support. The glycoalkaloids were monitored at 215 nm using a Varian Vari-chrom variable wavelength detector. The chromatogram was recorded on a Houston Instrument Omniscribe recorder equipped with a disk integrator. For each sample, duplicate 20 μl injections were made and the concentrations were calculated from a previously determined standard calibration curve using pure α-solanine and α-chaconine (Sigma Chemical Company, St. Louis, MO). The total glycoalkaloids (TGA) were calculated as the sum of the 2 major glycoalkaloids; α-solanine and α-chaconine. Statistical analysis with Student's t test and Duncan's Multiple Range test was undertaken only with the total glycoalkaloids values because these total values were a summation of the two other individual glycoalkaloids and not a separate analysis.

The methods used for the determination with HPLC was verified by conducting a recovery study on a freeze-dried Norland potato sample. The results are illustrated in Table 9.1, indicating a recovery between 96 and 99%.

Table 9.1. Glycoalkaloids recovered from freeze-dried potato samples with added α-chaconine and α-solanine

Potato samples		Added	Added	Theoretical	Recovery
α-chaconine	α-solanine	α-chaconine	α-solanine	total	total
mg					
0.32	0.24	0.5	0.5	1.56	1.55
0.32	0.24	1.0	1.0	2.56	2.52
0.64	0.48	0.5	0.5	2.12	2.04
0.64	0.48	1.0	1.0	3.12	3.07

GLYCOALKALOID LEVELS

The accumulation of glycoalkaloids in potato tubers of Norland cultivar as a function of maturity and length of light period is shown in Table 9.2. The TGA content did not vary significantly with maturity. Over the period from 9 weeks to 21 weeks after planting there was no consistent increase or decrease in TGA. However, in all samples tested the amount of TGA increased with increasing length of light period. The average TGA level over all maturities when tubers were grown under 12 hr light period was 5.6 mg/100 g fresh weight (0.32 mg/g dry weight) and increased ($P < 0.05$) to 6.6 mg/100 g (0.37 mg/g dry weight) when grown under 24 hr light period. The ratio of the individual glycoalkaloids remained constant for both light period and time of harvest, and was determined to be 60:40±2 for α-chaconine:α-solanine.

Table 9.2. Glycoalkaloid content of potatoes as influenced by maturity and light period.[1,2]

Glycoalkaloid	Light Period (hr)	Maturity (weeks after planting)				
		9	12	15	18	21
		(mg/100g fresh weight)				
α-chaconine	12	3.6	3.5	3.6	3.4	3.5
	24	4.2	4.0	4.0	4.0	3.9
α-solanine	12	2.2	2.0	2.0	2.2	2.2
	24	2.7	2.7	2.5	2.6	2.7
Total glycoalkaloids	12	5.8[3]	5.5	5.6	5.6	5.7
	24	6.9[3]	6.7	6.5	6.6	6.6

[1]Norland variety.
[2]Light level of 400 μmol $m^{-2}s^{-1}$ and temperature of 16°C.
[3]Average of 3 determinations. Values in rows did not differ significantly using Duncan's Multiple Range Test at P=0.05.

Difference in growing temperature resulted in a variation in the TGA content of Norland tubers at both 12 and 24 hr light periods (Table 9.3). Minimum TGA levels were found in tubers grown at 16°C. The TGA content increased significantly ($P < 0.05$) at lower and higher temperatures. Norland potatoes at 8 weeks after planting and 12 hr light period had a TGA level of 5.0 ± 0.3 mg/100 g fresh weight when grown at 16°C as compared to 6.6 and 11.4 ± 0.3 mg/100 g fresh weight at 12 and 24°C, respectively. The TGA level, as in the previous experiment, increased by approximately 20% with the longer light duration. The concentration of α-chaconine was about the same as that of α-solanine at 12C whereas the α-chaconine and α-solanine concentrations were in the concentration ratio of 60:40 at other temperatures.

Table 9.3. Glycoalkaloid content of potatoes as influenced by temperature and light period.[1,2]

Glycoalkaloid	Light Period (hr)	Temperature (C)			
		12	16	20	24
		(mg/100g fresh weight)			
α-chaconine	12	3.4	2.8	6.0	7.0
	24	4.2	3.5	6.8	no tubers
α-solanine	12	3.2	2.2	3.3	4.4
	24	4.0	2.8	4.6	no tubers
Total glycoalkaloids	12	6.6b[3]	5.0a	9.3c	11.4d
	24	8.2c	6.3b	11.4d	no tubers

[1]Norland variety (8 weeks after planting).
[2]Light level of 400 μmol $m^{-2}s^{-1}$.
[3]Average of 3 determinations. Values in rows followed by the same letter do not differ significantly using Duncan's Multiple Range Test at P=0.05.

The effect of light level on TGA content is shown in Table 9.4. For all cultivars (Norland, Russet Burbank and Denali), there was an increase in TGA level when light level was increased from 400 to 800 μmol m^{-2} s^{-1}. The highest concentration of TGA (12.2 $\pm$ 0.4 mg/100 g fresh weight or 0.5 $\pm$ 0.02 mg/g dry weight) was found in Denali tubers. However, Denali tubers had the lowest increase in TGA (8%) when light level was increased. Increase in light level on Norland and Russet Burbank caused a 13 and 20% increase in TGA content, respectively. In all samples tested the ratio of α-chaconine to α-solanine remained 60:40.

Table 9.4. Glycoalkaloid content of potatoes as influenced by light level.[1]

Cultivar[2]	Light level (μmol $m^{-2}s^{-1}$)	α-chaconine	α-solanine	Total glycoalkaloids
		(mg/100g fresh weight)		
Norland	400	3.5	2.8	6.3a[3]
	800	4.4	3.4	7.8b
Russet Burbank	400	4.8	3.1	7.9b
	800	5.9	3.9	9.8d
Denali	400	6.2	4.0	10.2c
	800	7.1	5.1	12.2d

[1]At 16°C and 24 hr light period.
[2]At 12 weeks after planting.
[3]Average of 3 determinations. Values in columns followed by the same letter do not differ significantly using Duncan's Multiple Range Test at P=0.05.

Table 9.5 lists the accumulation of glycoalkaloids as influenced by relative humidity during growth for all three cultivars. Though a slight difference among cultivars is apparent, the level of relative humidity did not affect the TGA level in tubers.

Table 9.5. Glycoalkaloid content of potatoes as influenced by relative humidity.[1]

Cultivar[2]	Relative humidity (%)	α-chaconine	α-solanine	Total glycoalkaloids
		(mg/100g fresh weight)		
Norland	50	5.7	4.2	9.9[3]
	80	5.8	4.7	10.5
Russet Burbank	50	6.8	4.5	11.3
	80	6.3	4.4	10.7
Denali	50	7.4	5.0	12.4
	80	6.8	4.9	11.7

[1]At 20°C and 24 hr light period.
[2]At 8 weeks after planting.
[3]Average of 3 determinations. Values do not differ significantly within each cultivar using Student's t test at P=0.05.

The effect of CO_2 concentration during growth of Norland and Russet Burbank on TGA level of the tubers is shown in Table 9.6. A significant ($P < 0.05$) increase occurred when the CO_2 concentration was raised from 350 to 1000 μmol mol^{-1}. In Norland and Russet Burbank cultivars the TGA level increased from 6.1 to 7.4 mg/100 g fresh weight and from 6.3 to 8.7 mg/100 g, respectively when the CO_2 concentration was increased from 350 to 1000 μmol mol^{-1} in the atmosphere of the growing chamber.

Table 9.6. Glycoalkaloid content of potatoes as influenced by CO_2 content in the atmosphere.[1]

Cultivar[2]	CO_2 level (μmol mol^{-1})	α-chaconine	α-solanine	Total glycoalkaloids
		(mg/100g fresh weight)		
Norland	350	3.5	2.7	6.1a[3]
	1000	4.6	2.8	7.4b
Russet Burbank	350	3.8	2.5	6.3a
	1000	5.2	3.5	8.7b

[1]At 16°C and 24 hr light period.
[2]At 17 weeks after planting.
[3]Average of 3 determinations. Values for each cultivar followed by the same letter do not differ significantly using Student's t test at P=0.05.

The variation of glycoalkaloid content found among cultivars (Denali, Russet Burbank and Norland) produced in controlled environments in this study was consistent with previous investigations for field grown potatoes (Sinden et al., 1984; Wolf and Duggar, 1946) and the TGA values were within the range of commercially grown cultivars (Wolf and Duggar, 1946). The highest amount was found in Denali followed by Russet Burbank and Norland tubers. The TGA levels ranged from 6.1 to 12.4 mg/100 g fresh weight under different growing conditions and were well below the 20 mg/100 g level usually considered the upper range for food safety. Glycoalkaloid level of potato tubers did not decrease with maturity although it is commonly assumed on the basis of previously reported data that glycoalkaloid levels decrease with maturity

of the plants (Wolf and Duggar, 1946). A change in glycoalkaloid content has been considered as part of the normal maturation process.

The increase in glycoalkaloid accumulation with an increase in light level and length of light period is consistent with previous studies which showed that increasing light induced greater glycoalkaloid synthesis in potato leaves (Deahl et al., 1991). Some products of photosynthesis are required for the incorporation of solanidine, the aglycone of both α-solanine and α-chaconine (Ramaswamy et al., 1976). Therefore, a close relationship has been demonstrated between photosynthetic activity and glycoalkaloid synthesis.

Higher TGA content was observed at a higher CO_2 concentration when compared to a lower CO_2 level. Carbon dioxide is another factor which may cause an increase in glycoalkaloid production by means of its promotive effect on photosynthesis. Since some photosynthetic products are precursors for glycoalkaloid synthesis (Ramaswamy et al., 1976), increasing CO_2 concentration during growth could result in higher glycoalkaloid amounts, as found in this study.

The effect of temperature during growth on the accumulation of glycoalkaloids is not clear. Data from this study suggests an optimum temperature of growth (16°C) at which minimum levels of TGA accumulate in tubers. A deviation from this temperature (lower or higher) seemed to cause stress and trigger greater accumulation of glycoalkaloids. The same effect was also repeated in the humidity study where the temperature was maintained at 20°C instead of 16°C and increased levels of glycoalkaloids were observed. This supports other studies which suggested that both cold stress and heat stress increase glycoalkaloid content of potatoes (Hutchinson and Hilton, 1955).

It can be concluded that there should be no unacceptable glycoalkaloid accumulations in potatoes in CELSS.

SECTION 10. ALLELOPATHY

A study was directed toward determining if plant species recommended for growth in CELSS will have allelopathic interactions when grown with a common recirculating nutrient solution. That is, if one species will have a negative or deleterious effects on the other species. This study was conducted with potatoes, cv Norland, and wheat, cv Yeco Rojo.

The experiment was conducted in a walk-in room at the Biotron. The plants were raised in 30 cm X 23.5 X 5 cm trays. The trays were filled to a depth of 1.5 cm with medium-sized quartz gravel of a 2-4 mm diameter. The gravel was washed with distilled water and soaked in nutrient solution (Table 2.2) for 14 hours before placing in the trays. Three treatments were used, each on a separate recirculating nutrient system. One system supplied six trays, three replicate trays of potatoes and three of wheat. A second system supplied three replicate trays of potatoes and a third system supplied three replicate trays of wheat (Figure 9.1). Thus a total of 12 trays were utilized. The potato trays contained one plant each, The wheat trays contained four plants per tray. The trays containing the plants were covered with opaque white-on-black polyethylene plastic. The potato plants were positioned in the center of the plastic and tray. The wheat was seeded to grow from four slots cut into the plastic located 6 cm in for the sides of the tray and 7.5 cm down or up from the top and bottom edges of the trays. The wheat seeds were imbibed using deionized water before planting. To eliminate the factor that one or more of the wheat seedlings would not germinate and grow normally, two wheat seeds were planted beneath each slot. Weaker plants, and those that did not germinate properly, were removed on day 5.

Each cultural system consisted of a 10.5 liter tank, a pump, trays holding plants, and a reservoir of nutrient solution (Figure 9.1). The solution was pumped from the tank with a magnetic drive pump. The pump moved the solution to a polyethylene header of 7/8 cm diameter and 17 cm in length. The header had tubes that fed the nutrient solution to the trays. The length of the tubes was varied to balance the flow to the trays. A 1 inch diameter PVC pipe was glued to the bottom edge of the tray to collect the effluent from the trays. The PVC pipe was cut to a 3/4 circumference so that it could be glued to the trays corner edge. A 1 cm tubing connected the modified pipe into the nutrient supply tank to recycle the nutrient solution.

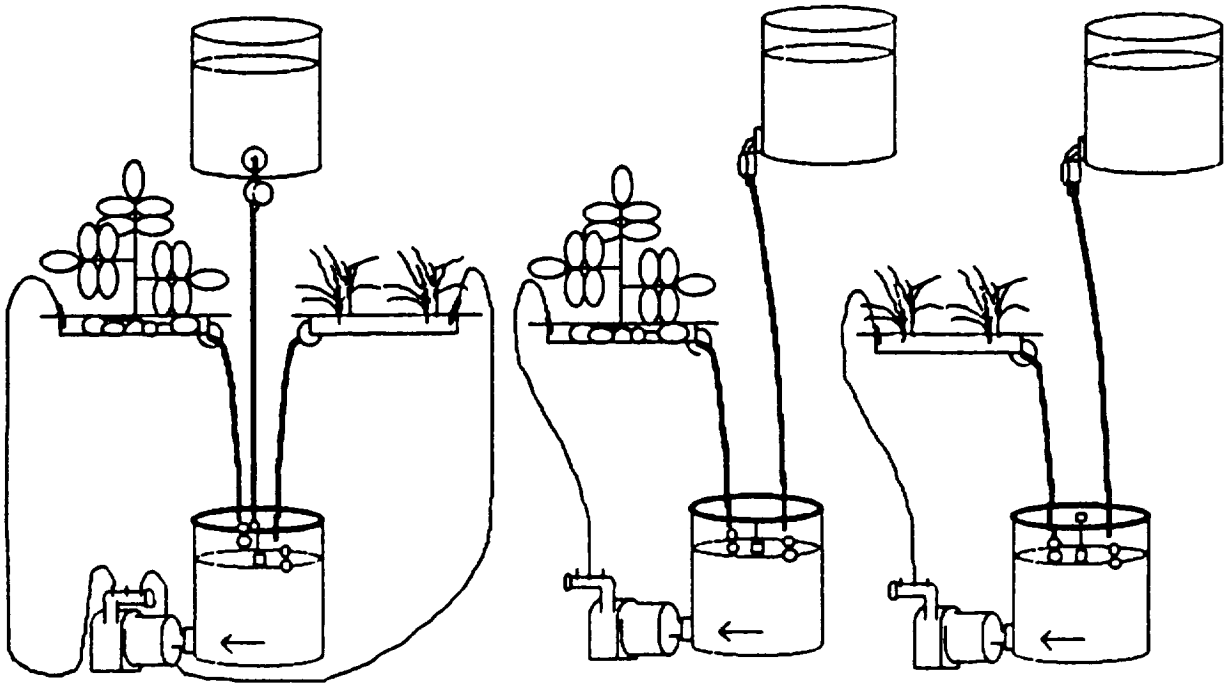


Figure 10.1. Diagram of the three recirculating nutrient systems set up in a Biotron. Each system supplied an additional two trays of each species shown.

Nutrient solution was supplied continuously to each tray at the rate of 40 ml min^{-1}. The tube providing the nutrient solution was located at the center top of each tray. Trays were at a slant allowing liquid movement to holes at the bottom of the containers.

The pH of each system was controlled automatically with a pH controller and pump. The pH was kept within a 5.5 to 6.5 range using H_2SO_4 except that the system with potatoes alone had increases to 7.0 on two occasions. Baseline conductivity was 1.10 dS m^{-1} and was monitored and maintained manually. Double strength nutrient solution was added to the solution when the conductivity fell below 0.87 dS m^{-1} and deionized water was added when the conductivity went above 1.30 dS m^{-1}. This kept the conductivity within a $\pm 10\%$ of the set-point.

The plants were maintained under a 12 h photoperiod at a PPF of 555 μmol m^{-2} s^{-1}, temperature of 20 C and RH of 70% with ambient CO_2. The plants were harvested 35 days after

transplanting at a time when tubers were enlarging in potatoes and spikes were heading in wheat.

The plants grew well in all three systems. There was no obvious differences in plant growth between the plants growing in separate systems and in the combined system (Table 10.1). The Haun stage (Haun, 1973) of the main stem of wheat in both systems was at 8.7 on the harvest date. However, although the harvest data indicated no significant differences between the systems, there was less dry weight for plants of both wheat and potato species that were grown in the combined system than in the separate systems. With potatoes, the difference resulted from a decrease in tuber production in combined systems for shoot weight was slightly greater in the combined system than in the separate system. Also leaf area for potatoes was less and the tiller number for wheat was less in the combined system.

Table 10.1. Growth of potato and wheat in combined and separate culture treatments.

Plant species	Leaf area	Tillers	Shoot/root dry wt	Tuber dry wt	Total dry wt
	dm^2	# $Plant^{-1}$		g $plant^{-1}$	
Potato with wheat	31.9±7.0		18.8±1.1	16.2±2.3	35.1±3.2
Potato alone	35.6±3.7		17.3±3.7	21.9±1.2	39.2±4.9
Wheat with potato		20.8±2.3			44.3±5.6
Wheat alone		22.8±1.9			48.6±3.1

In summary, it is concluded that there is no significant negative (allelopathic) effects of potatoes on wheat, or wheat on potatoes. However, the small growth differences found justify additional allelopathic study with these two species with growth maintained to maturity of both crops.

SECTION 11. REFERENCES

Arthur, J.M., J.D. Guthrie, and J.M. Newell. 1930. Some effects of artificial climates on the growth and chemical composition of plants. Amer. J. Bot. 17: 416-482.

Asher, C.J. and P.G. Ozanne. 1967. Growth and potassium content of plants in solution cultures maintained at constant potasium concentrations. Soil Science 103:155-161.

Baerug, R. 1962. Influence of different rates and intensities of light on solanine content and cooking quality of potato tubers. Eur. Potato J. 5:242-251.

Benoit, G.R., C.D. Stanley, W.J. Grant, and D.B. Torrey. 1983. Potato top growth as influenced by temperatures. Amer. Potato. J. 60:489-501.

Bennett, S.M., T.W. Tibbitts, and W. Cao. 1991. Diurnal temperature fluctuation effects on potatoes grown with 12 hr photoperiods. Amer. Potato J. 68:81-86.

Berghage, R.D. and R.D. Heins. 1991. Quantification of temperature effects on poinsettia stem elongation. J. Amer. Soc. Hort. Sci. 116:14-18.

Bodlaender, K.B.A. 1963. Influence of temperature, radiation and photoperiod on development and yield, p. 199-210. In: J.D. Ivins and F.L. Milthorpe (eds.). The growth of the potato. Butterworths, U.K.

Bunce, J.A. 1992. Light, temperature and nutrients as factors in photosynthetic adjustment to an elevated concentrations of carbon dioxide. Physiol. Plant. 86:173-179.

Bushnell, J. 1925. The relation of temperature to growth and respiration in the potato plant. Univ. Minnesota Agric. Exp. Stn. Tech. Bull. 34.

Bushway, R.J., E.S. Barden, A.M. Wilson and A.A. Bushway. 1980. Analysis of potato glycoalkaloids by high-performance liquid chromatography. J. Food Sci. 45:1088-1089.

Cao, W and T.W. Tibbitts. 1990. Effect of gradual temperature fluctuations on continuous irradiation injury in potatoes. Paper # 904529. International Winter Meeting of Amer. Soc. Agric. Enginr., Chicago, IL.

Cao, W. and T.W. Tibbitts. 1991a. Physiological response in potato plants under continuous irradiation. J. Amer. Soc. Hort. Sci. 116:525-527.

Cao, W. and T.W. Tibbitts. 1991b. Potassium concentration effect on growth, gas exchange and mineral accumulation in potatoes. J. Plant Nutr. 14:525-537.

Cao, W. and T.W. Tibbitts. 1992a. Temperature cycling periods affect growth and tuberization in potatoes under continuous irradiation. HortScience 27:344-345.

Cao, W. and T.W. Tibbitts. 1992b. Growth, carbon dioxide exchange and mineral accumulation in potatoes grown at different magnesium concentrations. J. Plant Nutr. 15:1359-1371.

Cao, W. and T.W. Tibbitts. 1993a. Growth and carbon assimilation in potato plants as affected by light fluctuations. HortScience 28:748.

Cao, W. and T.W. Tibbitts. 1993b. Study of various NH_4^-/NO_3^- mixtures for enhancing growth of potatoes. J. Plant Nutr. 16:1691-1704.

Cao, W., T.W. Tibbitts, and R.M. Wheeler. 1993. Carbon dioxide interactions with irradiance and temperature in potatoes. Adv. Space Res. 13: (In press)

Cao, W. and T.W. Tibbitts. 1994a. Responses of potatoes to solution pH levels with different forms of nitrogen. J. Plant Nutr 17(1): (In press)

Cao, W. and T.W. Tibbitts. 1994b. Phasic temperature change patterns affect growth and tuberization in potatoes. Accepted to J. Amer. Soc. Hort. Sci.

Cao, W. and T.W. Tibbitts. 1994c. Leaf emergence on potato stems in relation to thermal time. Submitted to Agron. J.

Cao, W. and T.W. Tibbitts. 1994d. Specific leaf weight, starch and mineral concentrations in potato leaves as affected by carbon dioxide and temperature. In review for J. Amer. Soc. Hort. Sci.

Casal, J., R. Sanchez, and V. Deregibus. 1987. Tillering responses of *Lolium multiflorum* plants to changes of red/far-red ratio typical of sparse canopies. J. Expt. Bot. 38:1432-1439.

Chapman, H.W. and W.E. Loomis. 1953. Photosynthesis in the potato under field conditions. Plant Physiol. 28:703-716

Chungcharoen, A. 1988. Glycoalkaloid content of potatoes grown under controlled environments and stability of glycoalkaloids during processing. Ph.D. Dissertation, University of Wisconsin, Madison.

Collins, W.B. 1976. Effect of carbon dioxide enrichment on growth of the potato plant. HortScience 11:467-469.

Davis, J.M., W.H. Loescher, M.W. Hammond, and R.E. Thornton. 1986. Response of potatoes to nitrogen form and to change in nitrogen form at tuber initiation. J. Amer. Soc. Hort. Sci. 111:70-72.

Deahl, K.L., W.W. Cantelo, S.L. Sinden and L.L. Sanford. 1991. The effect of light intensity

on Colorado potato beetle resistance and foliar glycoalkaloid concentration of four *Solanum chacoense* clones. Amer. Potato J. 68:659-666.

Desborough , S.L. 1985. Potato proteins, p.329-351. In: P.H.Li (ed.) POtato Physiology. Academic Press, Orlando, FL.

Ewing, E.E. and P.C. Struik. 1992. Tuber formation in potato: induction, initiation, and growth. Hort. Rev. 14:89-198.

Fageria, N.K., V.C. Baligar, and C.A. Jones. 1991. Growth and mineral nutrition of field crops. Marcel Dekker, Inc. New York.

Farrar, J.F. and M.L. Williams. 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. Plant Cell Envir. 14:819-830.

Findenegg, G.R. 1987. A comparative study of ammonium toxicity at different pH of the nutrient solution. Plant Soil. 103:239-243.

Fong, K.H. and A. Ulrich. 1974. Magnesioum nutrition of white rose potato in relation to vegetative growth and minerals of leaf and root tissues. J. Amer. Soc. Hort. 99:334-337.

Goknur, A.B. 1987. Dark opening of potato stomata and its relation to pollutant sensitivity. Ph.D. Dissertation, University of Wisconsin, Madison.

Goodwin, P.B. 1981. Rapid propgation of potato by single node cut. Field Crop Res. 4:165-173.

Goudriaan, J., and H.E. de Ruiter. 1983. Plant growth in response to CO_2 enrichment, at two levels of nitrogen and phosphorus supply: I. Dry matter, leafarea and development. Neth. J. Agric. Sci. 31: 157-169.

Gregory, L.E. 1965. Physiology of tuberization in plants. Ency. Plant Physiol. 15:1328-1354.

Hammer, P.A., T.W. Tibbitts, R.W. Langhans, and J.C. McFarlane. 1978. Baseline growth studies of 'Grand Rapids' lettuce in controlled environments. J. Amer. Soc. Hort. Sci. 103:649-655.

Haun, J.R. 1973. Visual quantification of wheat development. Agron. J. 65:116-119

Hillman, W.S. 1956. Injury of tomato plants by continuous light and unfavorable photoperiodic cycles. Amer. J. Bot. 43:89-96.

Hutchinson, A. and R.J. Hilton. 1955. Influence of certain cultural practices on the solanine content and tuber yields in netted gem potatoes. Can. J. Agric. Sci. 35:485-491.

Ingram, K.T. and D.E. McCloud. 1984. Simulation of potato crop growth and development. Crop Sci. 24:21-27.

Islam, A.K.M.S., D.G. Edwards, and C.J. Asher. 1980. pH optima for crop growth. Results of a flow solution culture experiment with six species. Plant Soil. 54:339-357.

Jariel, D.M., S.U. Wallace. U.S. Jones, and H.P. Samonte. 1991. Growth and nutrient composition of maize genotypes in acid nutrient solutions. Agron. J. 83:612-617.

Karlsson, M.G., R.D. Heins, J.E. Erwin, R.D. Berghage, W.H. Carlson, and J.A. Biernbaum. 1989. Temperature and photosynthetic photon flux influence chrysanthermum shoot development and flower initiation under short-day conditions. J. Amer. Soc. Hort. Sci.114:158-163.

Kasperbauer, M.J. and D.L. Karlen. 1986. Light-mediated bioregulation of tillering and photosynthate partitioning in wheat. Physiol. Plant. Suppl. 66:159-163.

Kozukue, N., E. Kozukue and S. Mizuno. 1987. Glycoalkaloids in potato plants and tubers. HortScience 22:294-296.

Krauss, A. 1985. Interaction of nitrogen nutrition, phytohormones, and tuberization, p. 209-230. In: P.H. Li (ed.) Potato Physiology. Academic Press, Orlando.

Ku, S.B., G.E. Edwards, and C.B. Tanner. 1977. Effects of light, carbon dioxide, and temperature on photosynthesis, oxygen inhibition of photosynthesis, and transpiration in *Solanum tuberosum*. Plant Physiol. 59:868-872.

Maga, J.A. 1980. Potato glycoalkaloids. CRC Crit. Rev. Food Sci. Nutr. 12:371-405.

Marinas, J. and K.B.A. Bodlaender. 1975. Response of some potato varieties to temperature. Potato Res. 18: 189-204.

McCown, B.H. and I. Kass. 1977. Effect of production temperature of seed potatoes on subsequent yielding potential. Amer. Potato J. 54:277-287.

McLean, E.O. and J.R. Brown. 1984. Crop response to lime in the midwestern United States. p. 267-303. In: F. Adams (ed.). Soil acidity and liming. American Society of Agronomy, Madison, WI.

Moorby, J. and F.L. Milthorpe. 1975. Potato, p. 225-257. In: L.T. Evans (ed.). Crop physiology. Cambridge Univ. Press, U.K.

Morrow, R.C., R.J. Bula, T.W. Tibbitts, and W.R. Dinauer. 1992. A matrix-based porous tube water and nutrient delivery system. Paper No. 921390, Proceedings of 22nd International Conference on Environmental Systems, Seattle, WA.

Mortensen, L.M. 1987. Review: CO_2 enrichment in greenhouse. Crop responses. Sci. Hort. 33:1-25.

Murashige, T. and F. Skoog. 1962. A revised medium for rapid growth and bioassays with tobacco tissue cultures. Physiol. Plant. 15:473-497.

Pilbeam, D.J. and E.A. Kirkby. 1992. Some aspects of the utilization of nitrate and ammonium by plants. In: K. Mengel and D.J. Pilbeam (eds.), Nitrogen metabolism of plants. Clarendon Press, Oxford.

Polizotto, K.R., G.E. Wilcox, and C.M. Jones. 1975. Response of growth and mineral composition of potato to nitrate and ammonium nitrogen. J. Amer. Soc. Hort. Sci. 100:165-168.

Ramaswamy, N.K., A.G. Behere and P.M. Nair. 1976. A novel pathway for the synthesis of solanidine in the isolated chloroplast from greening potatoes. Eur. J. Biochem. 67:275-282.

Salsac, L., S. Chaillou, J.F. Morot-Gaudry, C. Lesaint, and E. Jolivet. 1987. Nitrate and ammonium nutrition in plants. Plant Physiol. Biochem. 25:805-812.

Sinden, S.L., L.L. Sanford and R.E. Webb. 1984. Genetic and environmental control of potato glycoalkaloids. Amer. Potato J. 61:141-156.

Sinden, S.L. and R.E. Webb. 1974. Effect of environment on glycoalkaloid content of six potato varieties at 39 locations. USDA Tech. Bull. 1472. 30p.

Steward, F.C., U. Moreno, and W.M. Roca. 1981. Growth, form and composition of potato plants as affected by environment. Ann. Bot. 48: 1-45 (suppl. 2).

Tibbitts, T .W. 1979. Humidity and plants. BioSci. 29: 358-363.

Tibbitts, T.W. and D.K. Alford. 1982. Controlled ecological life support system: Use of higher plants. NASA Conf. Pub. 2231. Ames Research Center, MoffettField, CA.

Tibbitts, T.W., S.M. Bennett, and W. Cao. 1990. Control of continuous irradiation injury on potatoes with daily temperature cycling. Plant Physiol. 93:409-411.

Tibbitts, T.W., S.M. Bennett, R.C. Morrow and R.J. Bula. 1989. Utilization of white potatoes in CELSS. Adv. Space Res. 9:853-859.

Tibbitts, T.W. and W. Cao. 1992. Use of potatoes for bioregenerative life support systems. p. 285-294. In: Proceedings of International Conference on Life support and Biospherics. 1992, Huntsville, AL.

Tibbitts, T.W. and W. Cao. 1993. Solid matrix and liquid culture procedures for growth of potatoes. Adv. Space Res. 13: (In press)

Tibbitts, T.W., W. Cao, and S.M. Bennett. 1992. Utilization of potatoes for life support in space. V. Evaluation of cultivars in response to continuous light and high temperature. Amer. Potato. J. 69:229-237.

Tibbitts, T.W. and R.M. Wheeler. 1986a. Utilization of potatoes in bioregenerative life support systems. In R.D. MacElroy and D.T. Smernoff (eds.), Controlled Ecological Life Support System. Regenerative Life Support System in Space. NASA Conf. Publ. 2480:113-120.

Tibbitts, T.W. and R.M. Wheeler. 1986b. Utilization of plants for lunar life support. A case for the potato plant. Proceedings of the MAGLEV Lunar Symposium '86 Conf., Pitman, NJ, USA.

Tibbitts, T.W. and R.M. Wheeler. 1987. Utilization of potatoes in bioregenerative life support systems. Adv. Space Res. 7:4115-4122.

Tucker, D. 1975. Far-red light as a suppressor of side shoot growth in the tomato. Plant Sci. Let. 5:127-130.

Wan, W., W. Cao, and T.W. Tibbitts. 1994. Tuber initiation in hydroponically grown potatoes by alterations of nutrient solution pH. HortScience 29(3): (In press)

Wheeler, R.M., D.J. Hannapel, and T.W. Tibbitts. 1988. Comparison of axillary bud growth and patatin accumulation in potato leaf cuttings as assays for tuber induction. Ann. Bot. 62:25-30.

Wheeler, R.M., C.L. Mackowiak, J.C. Sager, W.M. Knott, and C.R. Hinkle. 1990. Potato growth and yield using nutrient film technique (NFT). Amer. Potato J. 67:177-187.

Wheeler, R.M., R.C. Morrow, R.J. Bula, and T.W. Tibbitts. 1988. Scenarios for optimizing potato productivity in a lunar CELSS. In W.W. Mendel (ed.), Lunar Bases and Space Activities of the 21st Century. Lunar and Planetary Institute, Houston, TX.

Wheeler, R.M., K.L. Steffen, T.W. Tibbitts, and J.P. Palta. 1986. Utilization of potatoes for life support systems. II. The effects of temperature under 24-h and 12-h photoperiods. Amer. Potato. J. 63. 639-647.

Wheeler, R.M. and T.W. Tibbitts. 1986a. Growth and tuberization of potato (*Solanum tuberosum* L.) under continuous light. Plant Physiol. 80:801-804.

Wheeler, R.M. and T.W. Tibbitts. 1986b. Utilization of potatoes for life support systems in space. I. Cultivar-photoperiod interactions. Amer. Potato J. 63:315-323.

Wheeler, R.M. and T.W. Tibbitts. 1987. Utilization of potatoes for life support systems in space. III. Productivity at successive harvest dates under 12-h and 24-h photoperiods. Amer. Potato J. 64:311-320.

Wheeler, R.M. and T.W. Tibbitts. 1989. Utilization of potatoes for life support systems in space. IV. effect of CO_2 enrichment. Amer. Potato J. 66:25-34.

Wheeler, R.M., T.W. Tibbitts, and A.H. Fitzpatrick. 1989. Potato growth in response to relative humidity. HortScience 24:482-484.

Wheeler, R.M., T.W. Tibbitts, and A.H. Fitzpatrick. 1991. Carbon dioxide effects on potato growth under different photoperiods and irradiance. Crop Sci. 31:1209-1213.

Wolf, M.J. and B.M. Duggar. 1946. Estimation and physiological role of solanine in potato. J. Agric. Res. 73:1-32.

Wolf, S., A. Marani, and J. Rudich. 1990. Effects of temperature and photoperiod on assimilate partitioning in potato plants. Ann. Bot. 66:513-520.

Yandell, B.S., A. Najar, R.M. Wheeler, and T.W. Tibbitts. 1988. Modeling the effects of light, carbon dioxide, and temperature on the growth of potato. Crop Sci. 28:811-818.

REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. AGENCY USE ONLY *(Leave blank)*	2. REPORT DATE	3. REPORT TYPE AND DATES COVERED
	December 1993	Contractor Report

4. TITLE AND SUBTITLE

Growth of Potatoes for CELSS

5. FUNDING NUMBERS

NCC2-301

6. AUTHOR(S)

T. W. Tibbitts, W. Cao, and R. M. Wheeler

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

University of Wisconsin–Madison
Department of Horticulture
Madison, WI 53706

8. PERFORMING ORGANIZATION REPORT NUMBER

A-94129

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

National Aeronautics and Space Administration
Washington, DC 20546-0001

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

NASA CR-177646

11. SUPPLEMENTARY NOTES

Point of Contact: R. D. MacElroy, Ames Research Center, MS 239-23, Moffett Field, CA 94035-1000; (415) 604-5573

12a. DISTRIBUTION/AVAILABILITY STATEMENT

Unclassified-Unlimited
Subject Category – 54

12b. DISTRIBUTION CODE

13. ABSTRACT ***(Maximum 200 words)***

This report summarizes research on the utilization of white potatoes (Solanum tuberosum L.) for space life support systems at the University of Wisconsin–Madison over the period of 1984 to 1993. At full maturity the tuber productivity was 37.5 g m^{-2} d^{-1}, equating to a growing area requirement for one human (2800 kcal d^{-1}) of 10.1 m^{-2}.

A recirculating nutrient system using slanted trays produced best potato growth and tuber yields when a 2–3 cm layer of gravel or arcillite media was utilized.

Potato production was close to maximum under lighting levels of 400 µmol m^{-2} s^{-1} of photosynthetic photon flux (PPF) for 24 hours or 800 µmol m^{-2} s^{-1} for 12 hours, alternating diurnal temperatures of 22°C and 14°C, relative humidity of 85%, and a carbon dioxide level of 1000 µmol m^{-1}. The range of effective concentrations of each separate nutrient is reported.

The extensive studies with potatoes in this project have demonstrated that this crop has high productivity of nutritious tubers with a high harvest index in controlled environments, and can fulfill a significant portion of the energy and protein requirements for humans in space.

14. SUBJECT TERMS	15. NUMBER OF PAGES
CELSS, White potatoes, Productivity, Growing conditions	200
	16. PRICE CODE: A09

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
Unclassified	Unclassified		