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# Potato and Human Exploration of Space: Some Observations from NASA-Sponsored Controlled Environment Studies

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**Abstract** Future space exploration by humans will require reliable supplies of food, oxygen and clean water to sustain the expeditions. Potato is one of several crops being studied for such a "life support" role. Tests sponsored by the US National Aeronautics and Space Administration (NASA) confirmed the well-known short day tendencies for tuberisation, but also revealed that some cultivars (e.g., Norland, Denali and Russet Burbank) could tuberise well under continuous high light. Horticultural tests showed that plants grew well and tuberised readily using a nutrient film technique (NFT). $CO_2$ enrichment studies with potato showed typical $C_3$ responses in photosynthesis and yield, with maximum rates occurring near 1000 $\mu mol\ mol^{-1}$. The highest tuber yields from these controlled environment studies reached 19.7 kg FM $m^{-2}$ or equivalent to nearly 200 t $ha^{-1}$. This equated to a productivity of 38 g DM $day^{-1}$. Stand evapotranspiration (ET) rates ranged from 3.4 to 5.2 l $m^{-2}$ $day^{-1}$ throughout growth, while maximum ET rates for canopies could approach 10 l $m^{-2}$ $day^{-1}$. Harvest indices (tuber DM/total DM) typically ranged from 0.7 to 0.8, indicating that waste (inedible) biomass from potato would be less than that from many other crops. An experiment was conducted in 1995 on NASA's Space Shuttle using excised potato leaves to study tuber formation at axillary buds during spaceflight. The results showed that tubers formed equally well in space as in the ground controls, indicating that reduced gravity should not be an impediment to tuberisation.

**Keywords** Tuber · Yield · Carbon Dioxide · $CO_2$ · Photoperiod · Hydroponics · Photosynthesis · Transpiration

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## Introduction

The use of plants to provide life support for humans during space travel was first suggested by Tsiolkovksy (1926), long before access to space was even possible. This concept came to be called bioregenerative life support, where plants would be grown under controlled environments to regenerate oxygen and food, while removing carbon dioxide and purifying waste water (Wheeler et al., 2001). The concept gained momentum in the 1950s with the works of Jack Myers (1954) and colleagues, with most early testing focused on algae (e.g., *Chlorella*) rather than higher plants (Miller and Ward, 1966). With improvements in controlled environment agriculture, such as the use of hydroponic cultivation to reduce water and nutrient stress (Cooper, 1979), the availability of high-intensity discharge lamps (Cathey and Campbell, 1977), and the routine use of $CO_2$ enrichment (Hicklenton, 1988), testing with higher plants for life support increased in the 1980s (MacElroy and Bredt, 1985). Much of this testing was sponsored by the Russian and US Space Agencies, but groups in France, Germany, Japan and Canada also conducted research in bioregenerative life support (Du Cloux et al., 1987; Daunicht and Brinkjans, 1992; Nitta et al., 1985; Gitelson et al., 1989; Waters et al., 2002).

Several panels were convened in the 1980s and 1990s to suggest crops for use in space life support systems. Criteria for selecting these crops included yield potential, nutritional value, horticultural and environmental requirements, harvest index, processing requirements and others (Hoff et al., 1982; Tibbitts and Alford, 1982; Salisbury and Clark, 1996; Waters et al., 2002). Potato (*Solanum tuberosum* L.) was present on all of these lists. Field studies and commercial agriculture showed potato to be highly productive, an excellent source of carbohydrate and protein, and versatile for different food preparations (Smith, 1977; Tibbitts and Alford, 1982). Yet experience with potato production was largely limited to field settings, with little information available from controlled environments. With this in mind, the US National Aeronautics and Space Administration (NASA) initiated a series of grants (1982–1994) to Ted Tibbitts at the University of Wisconsin, US, to study potato growth and development in controlled environment chambers at the University of Wisconsin Biotron. Following this, additional growth chamber testing and larger scale production studies with potato and several other crops were initiated at NASA's Kennedy Space Center beginning ca. 1988 (Wheeler et al., 2001). The following reviews some findings from this NASA sponsored research with potato.

## Cultivars for Controlled Environments

The initial NASA testing focused on cultivar comparisons under controlled environment conditions. A comparison of four North America cultivars, including cv. Norland (early season), Superior (early season), Norchip (mid season) and cv. Kennebec (late season) showed the greatest tuber yields from cv. Norland using 12, 16 and 20 h of light, with cv. Kennebec showing the lowest yields under the longer photoperiods (Wheeler and Tibbitts, 1986a) (Fig. 1). Subsequent testing with these cultivars along with cvs Russet Burbank (late season) and Denali (late season) showed that cvs Norland and Denali produced tubers most consistently under many different environmental conditions (Wheeler and Tibbitts, 1986b; Yandell et al.,

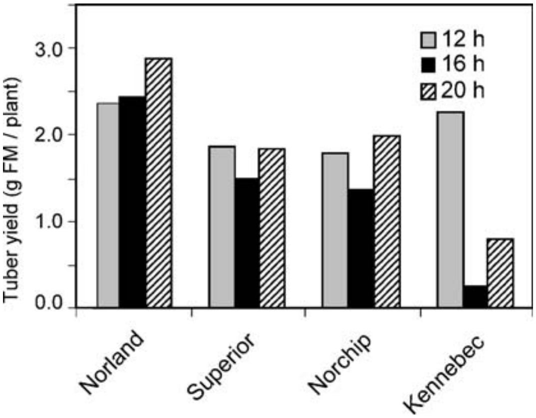

**Figure 1** Tuber yields from four North American cultivars grown for 105 days in controlled environments under three different photoperiods with 400 μmol $m^{-2}$ $s^{-1}$ PAR.

1988; Wheeler et al., 1991). Additional tests with 23 cultivars for tolerance to continuous light were conducted, and several cultivars from Alaska, Norway and Netherlands grew well in these studies (Tibbitts et al., 1994). Total glycoalkaloids (TGA) were also measured in tubers from several cultivars, and TGA levels in Denali > Russet Burbank > Norland, but all were within acceptable limits for human consumption (Nitithamyon et al., 1999). To maintain consistency with prior studies, subsequent testing at the University of Wisconsin and Kennedy Space Center continued to use cvs. Norland and Denali, but clearly other cultivars could be studied or developed for use in space life support systems.

## Horticultural Considerations

Horticultural strategies for growing any crops in space must consider the effects of reduced gravity (Wheeler et al., 2001). For example, in low-Earth orbit, as on the International Space Station, or on transit missions to Mars, one must deal with a near weightless environment (μ-gravity) unless centrifugation is used to generate artificial gravity. On the surface of the moon and Mars, approximate 1/3 and 3/8 gravity would exist. Clearly this would affect watering strategies for potato or any other plants, especially in weightlessness (Wright et al., 1988); but because simulating weightlessness or fractional g situations is so difficult on Earth, the decision was made to proceed with conventional watering techniques, which should work under the reduced gravities of the moon or Mars. Most studies at the University of Wisconsin used pots containing peat-vermiculite (50:50 vol.) medium with drip irrigation using a complete nutrient solution with nitrate (~7.5 mM) as the sole source of nitrogen (Wheeler and Tibbitts, 1986a; Tibbitts et al., 1994). Although this may have been a bit “rich” in nitrogen for later stages of growth, it proved to be a simple and reliable approach for getting good growth (Tibbitts et al., 1994; Goins et al., 2004). Other studies used “arcillite,” i.e., particles of calcined, montmorillinite clay (McCown and Kass, 1977; Tibbitts et al., 1994). Growth in arcillite was not as good as on peat-vermiculite, but the arcillite could be washed cleanly from the roots allowing easy reuse. Some comparisons of pot sizes were also conducted and in general, for long duration studies (c. 100 days or more), larger pots sustained better growth (Tibbitts et al., 1994). Hence much of the baseline testing used ~18- and ~36-l pots with a peat-vermiculite medium.

## Hydroponics

Exploratory tests were conducted with solution and aeroponic cultures, where roots and stolons were either submerged in a recirculating nutrient solution or suspended in dark chambers and continuously sprayed with nutrient solutions. Related techniques had been used previously for growth and development (Chapman, 1958; Greiss, 1979) and mineral nutrition studies (Fong and Ulrich, 1969; Krauss, 1978; Sattelmacher and Marschner, 1978). Plants grown in the standing solution cultures or under continuous misting showed good shoot growth but tuberisation was inconsistent, and stolons often showed pigmentation (cv. Norland) and callus development (Fong and Ulrich, 1969; Tibbitts et al., 1994); but a recirculating nutrient film technique (Cooper, 1979) where stolons and tubers were not submerged worked well and became the standard approach for testing at Kennedy Space Center (Wheeler et al., 1990, 1997) (Fig. 2). The results suggested that stolons and tubers require good aeration (gas exchange), which is consistent with observations from field settings (Smith, 1977). The poor tuberisation from the aeroponic (mist) culture was somewhat surprising, yet the misting in these studies was maintained constantly, keeping the developing tubers continuously wet. An interesting comparison would have been to test an aeroponic approach with intermittent misting, which might have allowed better aeration (Ritter et al., 2001).

For most of the NFT studies, the electrical conductivity (EC) was maintained near 0.12 $S\ m^{-1}$ with daily additions of a stock solution, and pH was maintained near 5.8 with the addition of dilute (0.4 M) nitric acid. The approach worked well but resulted in high nitrogen levels both in the shoot biomass and tubers (Wheeler et al., 1994; McKeehen et al., 1996). In some cases, more than 30% of the nitrogen came from the nitric acid in this hydroponic approach (Wheeler et al., 1990). Much

**Figure 2** Potato tubers from cv. Norland plants grown for 105 days using a recirculating nutrient film technique (NFT) in NASA's Biomass Production Chamber at Kennedy Space Center, Florida.

of the nitrogen in the shoot tissues was in the form of nitrate, but there was little nitrate in the tubers (McKeehen et al., 1996). Nitrogen in the tubers was a combination of protein and other non-protein nitrogen, possibly including nucleic acids, amino acids, amides and peptides (McKeehen et al., 1996). Related studies showed that potatoes grew well on nutrients that were reclaimed from shoot biomass from previous plantings; the shoot materials were treated in aerobic, stirred-tank reactors and the effluent was then used to reconstitute nutrient solution (Mackowiak et al., 1997). This demonstrated that nutrient recycling can reduce fertiliser costs for space missions (Mackowiak et al., 1997).

## Mineral Nutrition

Several tests were conducted to study the effects of varying levels of essential nutrients on potato growth and development. For example, potato growth in NFT was reduced at 0.1 mM and 9.8 mM K concentrations compared to 0.5, 1.6, 3.2 and 6.4 mM K, but no differences in leaf photosynthetic rates or stomatal conductance were noted among treatments (Cao and Tibbitts, 1991a). Similar studies with Mg at 0.05, 0.12, 0.25, 1.0, 2.0 and 4.0 mM showed total plant and tuber growth increased with increased Mg up to 1.0 mM and then decreased with further increases in Mg. Single leaf photosynthetic rates were lowest and respiration rates were highest at 0.05 and 4.0 mM Mg (Cao and Tibbitts, 1992a). A comparison of different combination of $NH_4/NO_3$ in a flow through NFT system showed better growth with mixed N forms compared to only $NH_4$ or only $NO_3$ (Cao and Tibbitts, 1993), and that $NH_4$ in solutions increased P and Cl, and decreased Ca and Mg in shoot tissue (Cao and Tibbitts, 1993). Subsequent studies lasting 84 days showed no advantage to using $NO_3/NH_4$ mixes vs. $NO_3$ only on final tuber yield, but that $NO_3$ levels could be reduced from 7.5 to 1.0 mM for the last half of growth with no significant loss in tuber yield (Goins et al., 2004). Moreover, any reductions in nitrogen generally increased harvest index (Goins et al., 2004). When $NO_3$ was used alone, maximum growth occurred at 2, 4 and 8 mM levels with reduced growth at 0.5 and 12 mM (Cao and Tibbitts, 1998). When ammonium was used alone, maximum growth occurred at 2 mM with decreased growth at 0.5 and at 4, 8 and 12 mM (Cao and Tibbitts, 1998).

## Propagation

For all of the testing at Wisconsin and Kennedy Space Center, in vitro nodal cuttings were used to start the plants (Hussey and Stacey, 1981; Wheeler et al., 1986). This assured uniform, disease-free planting stock for the experiments. Plantlets about 10-cm long were transplanted ex vitro into solid media by burying about 2/3 of the plantlet length. Transplants were then covered with a glass beaker for the first 3 days to allow acclimation. Most plantlets were grown on an MS-type medium with 6% sucrose (Hussey and Stacey, 1981; Tibbitts et al., 1994), but related NASA testing confirmed that sucrose levels could be reduced if some air exchange and $CO_2$ could reach the plants (Yorio et al., 1995a; see also Kozai et al., 1988). Other testing showed that light spectral quality could be used to control stem and internodal elongation, where for example, blue-deficient light sources such as red fluorescent or low-pressure sodium lamps produced leggy plants with long internodes, while blue fluorescent lamps produced short plants with short internodes (Wilson et al., 1993). Although these in vitro propagated cuttings were useful for research purposes, it might impose unneeded costs for actual production systems in space, and further testing is needed to study the use of micro- and minitubers harvested from plants as propagules.

## Environmental Response Testing

Many responses of potato to environmental factors were well documented and provided the baseline for initial controlled environment testing in the 1980s. For example, tuberisation was known to be a short-day response (Garner and Allard, 1923; Gregory, 1956, 1965; Ewing and Wareing, 1978) and even showed the classic red/far-red reversal for phytochrome control (Batutis and Ewing, 1982). Yet some studies showed that potato grew well and tuberised even under continuous light (Arthur et al., 1930). The strong effects of light intensity (Bodlaender, 1963), temperature (Werner, 1942; Bodlaender, 1963; Menzel, 1983), and nitrogen nutrition (Krauss, 1978, 1985; Sattelmacher and Marschner, 1978) were also well established and suggested that these factors could all be manipulated to control whole plant growth and tuberisation.

### Light-photoperiod, PAR and Spectrum

Some of the earliest NASA testing focused on the photoperiod responses of potato cultivars, and in particular which cultivars might be tolerant of continuous light. The rationale for this was simple: If plant growth and tuber yield could be increased with longer photoperiods, the total crop area required to sustain humans in a life support system could be reduced. The good performance of the early cultivar Norland and the poor performance of the late cv. Kennebec under 20 h of light (Fig. 1) indicated genotypic differences in response to photoperiod. The low yields of Kennebec under the long photoperiods suggested a stronger requirement for short days in this late season cv., but leaves of these plants folded upward and became chlorotic under the 20-h photoperiod, suggesting the plants were physiologically intolerant of this environment (Wheeler and Tibbitts, 1986a). This prompted a more focused look at cultivar tolerance to long photoperiods, where five cultivars were grown under a 12/12 light/dark cycle using 400 μmol $m^{-2}$ $s^{-1}$ PAR (controls), a 24-h photoperiod with 200 μmol $m^{-2}$ $s^{-1}$ PAR, a 24-h photoperiod with 400 μmol $m^{-2}$ $s^{-1}$ PAR, and 12 h of 400 + 12 h of 5 μmol $m^{-2}$ $s^{-1}$ PAR. All cultivars tuberised well and showed the highest harvest index under 12 h light/12 h dark treatment, while cvs Norland and Russet Burbank also grew well and tuberised under continuous 400 μmol $m^{-2}$ $s^{-1}$. Cv. Norchip showed moderate tuberisation under continuous 400 μmol $m^{-2}$ $s^{-1}$, but cvs Superior and Kennebec showed little tuber development and chlorotic leaves with rustic flecks (Wheeler and Tibbitts, 1986b; Cao and Tibbitts, 1991b; Cushman et al., 1995). Plants grown under continuous 200 μmol $m^{-2}$ $s^{-1}$ showed a similar trend but with less total growth and tuber development. In contrast, plants grown with the dim day length extension showed little tuberisation but no injury to the leaves (Wheeler and Tibbitts, 1986b). These results suggested that all the cultivars were intrinsically “short day” with regard to tuber initiation but that this tendency could be overridden with greater total light levels in some cultivars (viz. Norland and Russet Burbank). In contrast, cvs Superior, Norchip and Kennebec were physiologically intolerant to continuous light at 200 and 400 μmol $m^{-2}$ $s^{-1}$ PAR (Wheeler and Tibbitts, 1986b). Subsequent studies showed elevated starch levels in leaves of tolerant cultivars grown under continuous light (Cao and Tibbitts, 1994; Tibbitts et al., 1994; Stutte et al., 1996), and that the injuries to intolerant cultivars could be mitigated by providing a thermoperiod (Tibbitts et al., 1990; Cao and Tibbitts, 1991a, 1992a). Continuous light injury resulted in loss of chloroplast membrane integrity and photosynthetic competence in intolerant cultivars (Cushman et al., 1995). Ethylene also played a role in the injuries observed under continuous light (Cushman and Tibbitts, 1998). Additional studies showed that Denali and several other Alaskan cultivars, along with several cultivars from Norway and Netherlands also grew well under continuous light (Wheeler et al., 1991; Tibbitts et al., 1994). Not surprisingly, this suggested that cultivars selected for high latitudes were more tolerant to long photoperiods.

Despite the ability of some cultivars to grow and tuberise under long photoperiods, short-day tendencies were still apparent: For example, harvest index, which is an indicator of the partitioning to tubers, was nearly always greatest under short photoperiods, and hence efficiencies for converting light into edible biomass were greatest under short photoperiods (Wheeler and Tibbitts, 1986a; Wheeler et al., 1988, 1991). These observations suggested that yields might be optimised if strong induction could be combined with high total light. This idea was tested by moving plants between a 12 h light/12 h dark and a 24-h light environment at different stages of growth. The results with cv. Denali showed that at equal total irradiance, plants given short days early in growth followed by long days later in growth produced greater tuber yields than plants given long days followed by short days (Wheeler and Tibbitts, 1997). This suggests that it is best to first establish strong tuber initiation and then follow with high total light to sustain bulking (Wheeler and Tibbitts, 1997).

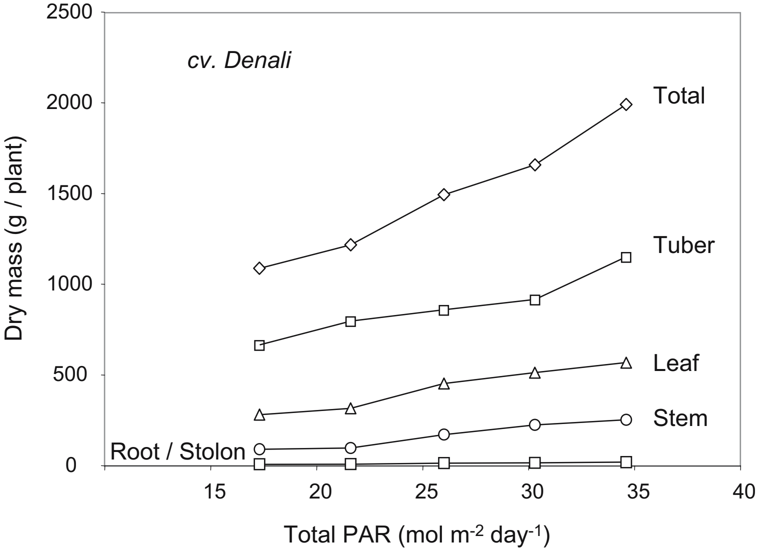

**Figure 3** Growth of cv. Denali plants at different levels of total photosynthetically active radiation.

Except for when injury occurred with continuous light-intolerant cultivars, total growth and tuber yield generally increased with total irradiance, regardless of photoperiods or other environmental treatments (Yandell et al., 1988; Wheeler et al., 1991; Wheeler and Tibbitts, 1997) (Fig. 3). This demonstrated the strong influence of light on overall yield and performance of potato in controlled environments, and its importance in planning of bioregenerative life support systems for space. Similar findings have been reported for other crops under study for life support (Bugbee and Salisbury, 1988; Wheeler et al., 2001).

It is still unknown whether electric lamps or direct solar lighting will be ultimately used for crops in space. The use of solar lighting will ultimately depend on the setting: For example, on the moon there are roughly 14 days of dark and 14 days of light (Salisbury, 1992). On Mars, the photoperiod is 24.6 h, similar to the Earth's, but the solar intensity at Mars' orbit is only 43% that of Earth's, and extensive dust storms can occur at some latitudes on Mars (Salisbury, 1992; Wheeler, 2004). In addition, techniques for capturing the light and delivering it to a protected environment will be needed (Wheeler and Martin-Brennan, 2000). On the other hand, electric lighting can be used in any setting, provided sufficient electrical power is available; but the effects of lamp spectra must be considered. For example, high-pressure sodium lamps are electrically efficient, but are relatively deficient in blue wavelengths, which can cause elongated stems (Yorio et al., 1995b). Novel approaches such as light-emitting diodes (LEDs) have the advantage of a long operating life and low thermal radiation, but their spectra are narrow and selecting the optimal colour combination of LEDs needs further study (Bula et al., 1991; Goins et al., 1997).

## Temperature

The strong influence of temperature on potato growth and tuberisation was well known (Bodlaender, 1963; Slater, 1968; Burton, 1972; Marinus and Bodlaender, 1975; Gregory, 1965; Menzel, 1983; Cao and Tibbitts, 1995). Nonetheless, several temperature studies were undertaken to study its effects on the cultivars used in NASA-sponsored tests. Tests with Russet Burbank and Norland grown under continuous light showed that 17.5 and 18.7 °C were the optimum for tuber yield, respectively (Yandell et al., 1988). Prior studies with Norland showed that tuber yields were greatest at 20 °C when a 12-h photoperiod was used, and at 16 °C when continuous light was used (Fig. 4). In addition, stem lengths increased with temperature, regardless of the photoperiod. These studies showed that cooler temperatures could be used to offset the less inductive influence of a long photoperiod, and that warmer temperatures were tolerable if short photoperiods were used (Wheeler et al., 1986). Other studies showed that providing a thermoperiod improved tuberisation under both short and long photoperiods, and that thermoperiods reduced injury from continuous light (Tibbitts et al., 1990; Bennet et al., 1991; Cao and Tibbitts, 1992b). Related studies showed that warm temperatures early in growth followed by cool temperatures later in growth promoted greater tuberisation than the reverse treatment (Cao and Tibbitts, 1994).

Temperatures also showed a significant effect on the level of glycoalkaloids (-α-chaconine and α-solanine) in tuber tissues (Nitithamyon et al., 1999). Total

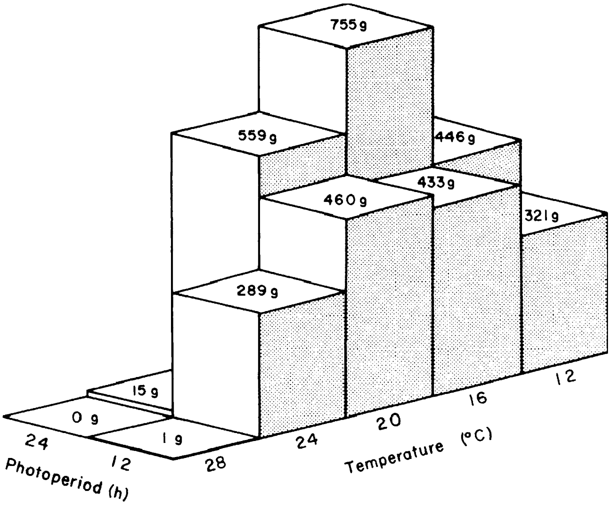

**Figure 4** Tuber yields (g FM/plant) from 56-day-old cv. Norland plants grown at different temperatures with either a 12-h photoperiod or continuous (24 h) light (from Wheeler et al., 1986).

glycoalkaloids were lowest at 16 °C and increased when temperature increased to 24 °C or when temperature decreased to 12 °C (Nitithamyon et al., 1999).

## Carbon Dioxide

The closed environments of space will require continuous control of the atmospheric composition and pressure, including the partial pressure of carbon dioxide ($CO_2$). At the beginning of NASA-sponsored testing, little research had occurred on $CO_2$ effects on potato. Single leaf studies showed the classic $C_3$ responses with increased photosynthetic rates at elevated $CO_2$ levels (Ku et al., 1977), while whole-plant studies showed both positive (Collins, 1976) and negative effects (Goudriaan and de Ruiter, 1983). Initial studies at the University of Wisconsin showed that increasing the $CO_2$ from ~360 to 1000 μmol $mol^{-1}$ (0.036 to 0.10 kPa) increased single leaf photosynthetic rates slightly for cultivars Norland but decreased rates slightly for cv. Russet Burbank, while tuber yields for both cvs. increased only slightly (Wheeler and Tibbitts, 1988). These results were somewhat surprising, but the plants in those studies were grown under a 24-h photoperiod (i.e., continuous light) and it was not clear whether the continuous light was suppressing $CO_2$ benefits. This led to a series of studies with cvs Norland, Russet Burbank, and Denali where plants were grown under 12- or 24-h photoperiods, 400 and 800 μmol $m^{-2}$ $s^{-1}$ PAR, and ambient (~360 μmol $mol^{-1}$) and 1000 μmol $mol^{-1}$ $CO_2$. Results showed that upper canopy, single leaf photosynthetic rates under a 12-h photoperiod were higher than under continuous light, and the rates increased with both increased $CO_2$ and increased PAR (Cao et al., 1994). In contrast, photosynthetic rates under continuous light increased only slightly for cv. Norland, and decreased for cvs Russet Burbank and Denali at elevated $CO_2$ (Wheeler and Tibbitts, 1988). Total plant biomass and tuber yields after 90 days showed similar trends, where elevated

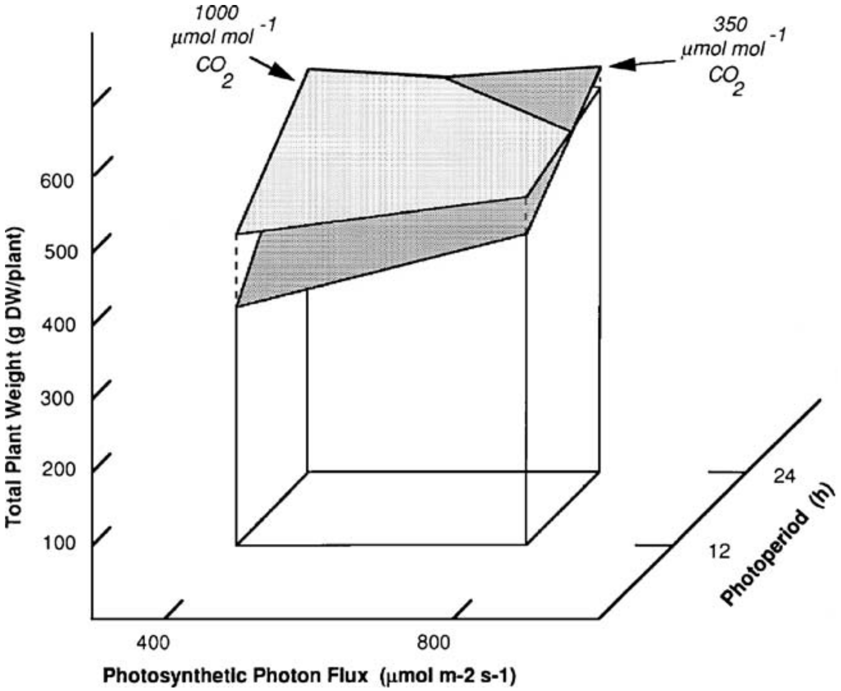

**Figure 5** Total biomass of 90-day-old cv. Norland plants grown at two different photoperiods, two different $CO_2$ concentrations, and two different PAR levels.

$CO_2$ and increased PAR increased yields under a 12-h photoperiod, but had only a slight or even negative effect under continuous light (R. Wheeler et al., 1991) (Fig. 5).

These findings were pursued further by studying the effect of $CO_2$ on cv. Denali plants moved between short (12 h) and long (24 h) photoperiods at different stages

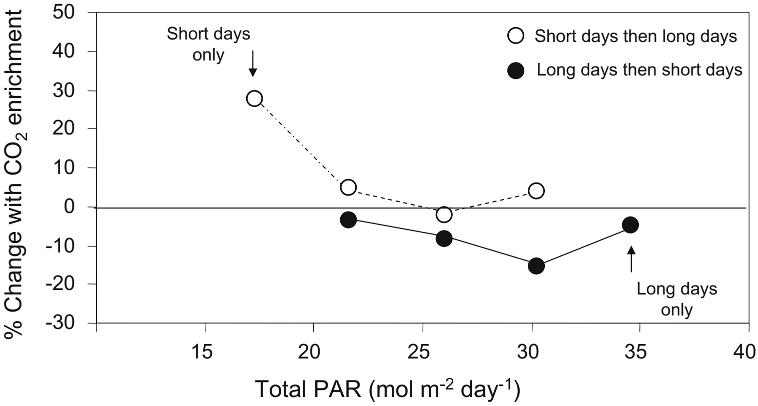

**Figure 6** Percentage changes in growth of different parts of potato cv. Denali in response to $CO_2$ enrichment from ~350 to 1000 µmol $mol^{-1}$ versus total PAR. *Open symbols* indicate plants given short days only (17.4 mol $m^{-2}$ $day^{-1}$) or short days followed by long days. *Filled symbols* indicate plants given long days followed by short days or long days only (35 mol $m^{-2}$ $day^{-1}$).

of development. The results showed a positive effect of $CO_2$ enrichment (from ~360 to 1000 mmol $mol^{-1}$) on tuber yield under short days but a decreased effect with a greater number of long days (Wheeler and Tibbitts, 1997) (Fig. 6). Collectively, the findings suggest the greatest benefits from $CO_2$ enrichment occur at lower light levels, and that the plants are most efficient at partitioning to tubers under high $CO_2$ and a short photoperiod. The findings from the 12-h photoperiod tests with $CO_2$ enrichment match more closely the recent findings reported from $CO_2$ enrichment in field settings (Miglietta et al., 1998).

A $CO_2$ concentration of 1000 μmol $mol^{-1}$ is elevated in comparison to Earth ambient levels and probably close to where maximum photosynthetic rates and minimum stomatal conductance occur in many species (Drake et al., 1997). Yet $CO_2$ concentrations in spaceflight environments are typically higher than 1000 μmol $mol^{-1}$ due to the relative inefficiency of the molecular sieves and lithium hydroxide scrubbing systems. For example, $CO_2$ on the International Space Station typically ranges from ~2000 to 6000 μmol $mol^{-1}$. Consequently, NASA was interested in plant responses to "super-elevated" $CO_2$ levels, i.e., $CO_2 > 2000$ μmol $mol^{-1}$. When cvs Norland and Denali plants were grown under 400, 1000 and 10,000 μmol $mol^{-1}$ $CO_2$, some bleaching was noted on leaves after 90 days growth at 10,000, but there was no significant difference in total biomass when compared to 1000 μmol $mol^{-1}$-grown plants (Mackowiak and Wheeler, 1996); but interestingly, water use rates and mid-day stomatal conductance were greatest at 10,000 μmol $mol^{-1}$ (Mackowiak and Wheeler, 1996).

In a subsequent study, potato plants (cv. Denali) were grown at 400, 1000 and 10,000 μmol $mol^{-1}$ $CO_2$ and stomatal conductance measured through the light and dark period (Wheeler et al., 1999). Measurements showed: (1) distinct circadian rhythms in stomatal conductance, (2) conductance at 10,000 > 400 > 1000 μmol

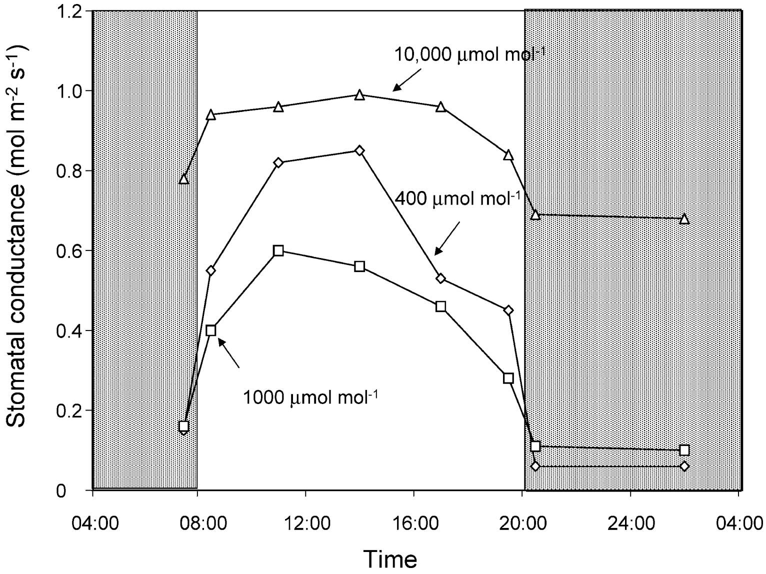

**Figure 7** Diurnal patterns of stomatal conductance of cv. Denali leaves at different $CO_2$ concentrations (*lines*). Stomata at 10,000 μmol $mol^{-1}$ remained relatively open at night.

mol$^{-1}$, and (3) that stomatal closure at night was reduced at the super-elevated 10,000 μmol mol$^{-1}$ treatment (Fig. 7). The decreased conductance as $CO_2$ was raised from 400 to 1000 μmol mol$^{-1}$ was expected, but the increased conductance as $CO_2$ was raised further to 10,000 μmol mol$^{-1}$ was not. Similar stomatal responses to super-elevated $CO_2$ have been seen in other dicots such as soybean, sweetpotato, bean and radish, but the mechanisms behind it are not known (Wheeler et al., 1999).

As with increased lighting, increased $CO_2$ concentrations up to 2000 μmol mol$^{-1}$ resulted in increased foliar starch levels and specific leaf weights (Cao and Tibbitts, 1997). Foliar starch increased 60% as $CO_2$ was increased from 500 to 1000 μmol mol$^{-1}$, and another 15–20% as $CO_2$ was increased further to 2000 μmol mol$^{-1}$ (Cao and Tibbitts, 1997).

## Canopy Gas Exchange and Ethylene Production

When cv. Norland plants were grown in the atmospherically closed Biomass Production Chamber at Kennedy Space Center, canopy gas exchange rates could be tracked throughout growth and development for an entire 20 m$^2$ stand (Wheeler et al., 2003). These traces throughout growth showed several distinctive features: First, stand (canopy) net photosynthetic rates increased rapidly as stand ground cover increased and approached 100% at c. 35 days-age (Wheeler et al., 2003) (Fig. 8). Secondly, stand net photosynthesis continued to rise as the canopy height grew closer to the lamps (c. days 35–50). Third, overall stand photosynthetic rates were a strong function of incident light (PAR). Short duration tests during which the light intensity was changed for 1-h intervals showed that photosynthetic rates

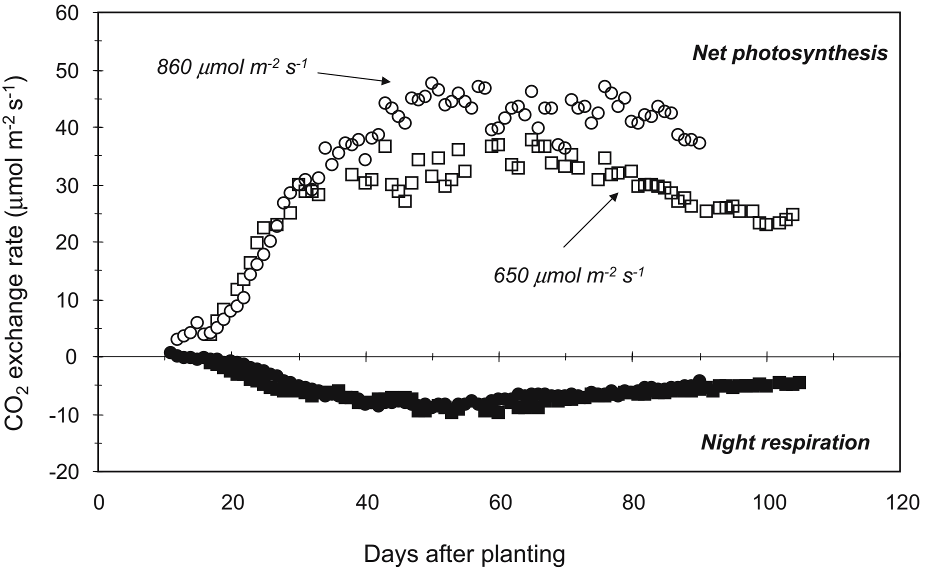

**Figure 8** Net photosynthesis and dark period respiration for 20 m$^2$ stands of potato grown at 860 and 650 μmol m$^{-2}$ s$^{-1}$ PAR in NASA's Biomass Production Chamber at Kennedy Space Center, Florida.

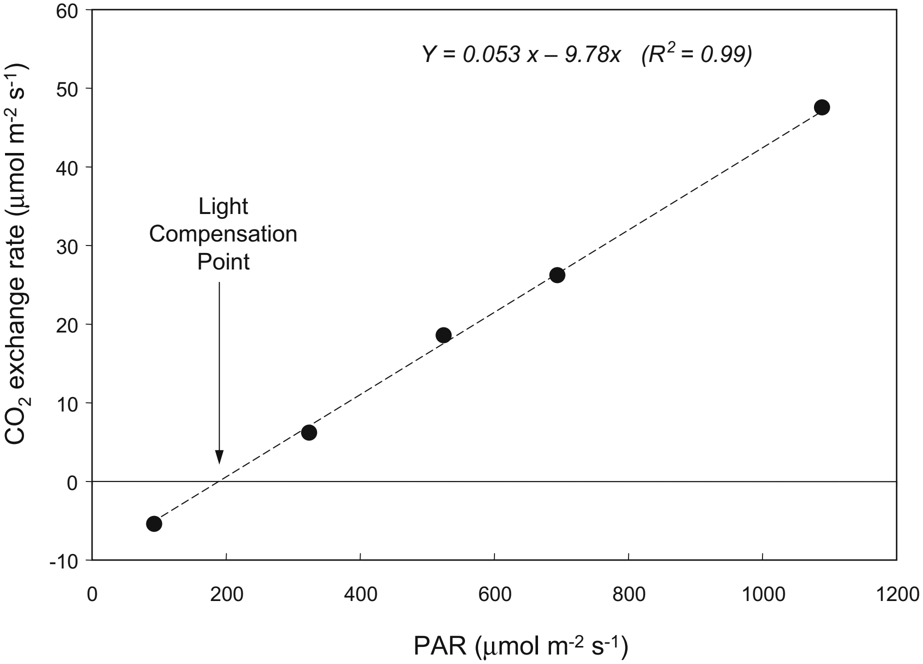

**Figure 9** Effect of photosynthetic photon flux (PAR) on $CO_2$ exchange rates of a 20- $m^2$ stand of potato (cv. Norland). Data were gathered by temporarily changing the incident PAR and then tracking photosynthetic rates for ~1 h intervals. All measurements taken at ~1000 µmol $mol^{-1}$ $CO_2$. Light compensation point (x-intercept) for the stand was near 200 µmol $m^{-2}$ $s^{-1}$. The dark respiration rate can be estimated by extending the light curve to zero (y-intercept) and approximately equaled −10 µmol $m^{-2}$ $s^{-1}$ $CO_2$.

increased linearly up to ~1000 µmol $m^{-2}$ $s^{-1}$ PAR at 50 days after planting (Fig. 9). Stand light compensation points in these studies were nearly 200 µmol $m^{-2}$ $s^{-1}$ PAR, indicating the point where photosynthesis equaled background respiration of the stand. Extending the light response curve to zero light (y-intercept) indicated that stand respiration rates were approximately 10 µmol $m^{-2}$ $s^{-1}$ under these conditions (Fig. 9). Fourth, net photosynthetic rates decreased with age depending on the extent of leaf senescence (Fig. 8). This latter effect was especially apparent in one test in which the photoperiod was changed from 12 h to continuous light (24 h). Immediately following the change to continuous light, photosynthetic rates dropped as a result of some "scorching" of the upper canopy leaves (not shown). Fifth, net photosynthetic rates for potato stands showed a classic $C_3$ response to $CO_2$, where rates increased rapidly as $CO_2$ was increased up to ~400–500 µmol $mol^{-1}$, and saturated near ~1000 µmol $mol^{-1}$ (see also, Ku et al., 1977; Drake et al., 1997) (Fig. 10).

During these same studies with 20-$m^2$ stands of potato, chamber concentrations of ethylene gas could be monitored throughout growth and development. Ethylene accumulation during potato growth was generally low in comparison to wheat, soybean and lettuce (Wheeler et al., 2004), but even at the relatively low concentration of ~40 ppb, chronic exposure caused epinasty in young expanding

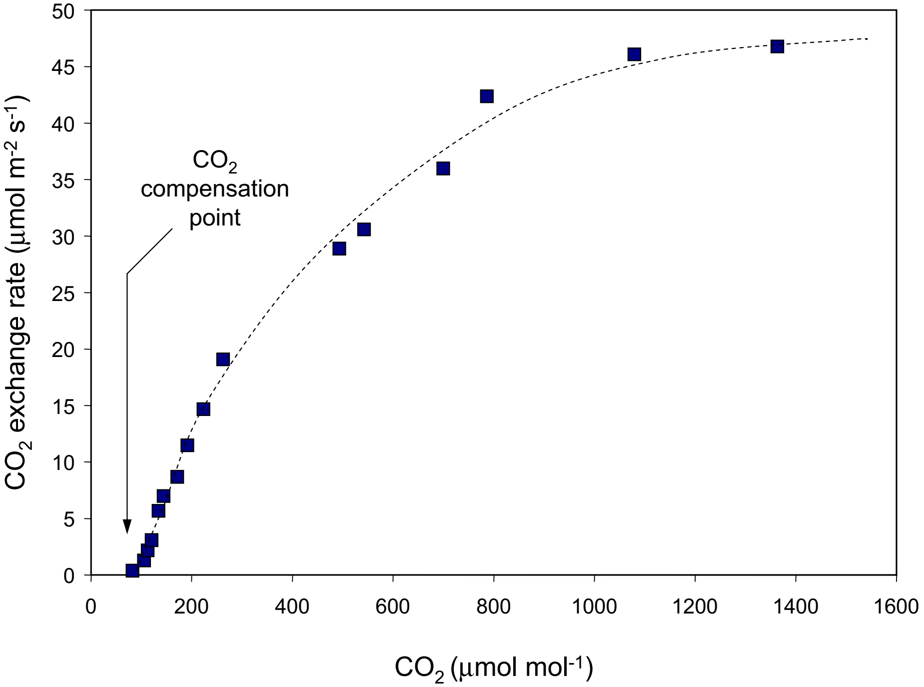

**Figure 10** Effect of $CO_2$ concentration on $CO_2$ exchange (net photosynthesis) rates for 20 $m^2$ stand of potato (cv. Norland). Note that potato shows a classic $C_3$ response, with photosynthetic rates saturating near 1000 µmol $mol^{-1}$. $CO_2$ compensation point for the stand was near 80 µmol $mol^{-1}$.

**Figure 11** Epinastic potato leaves from cv. Denali plants growing at ~40 ppb ethylene inside an atmospherically closed chamber (from Wheeler et al., 2004).

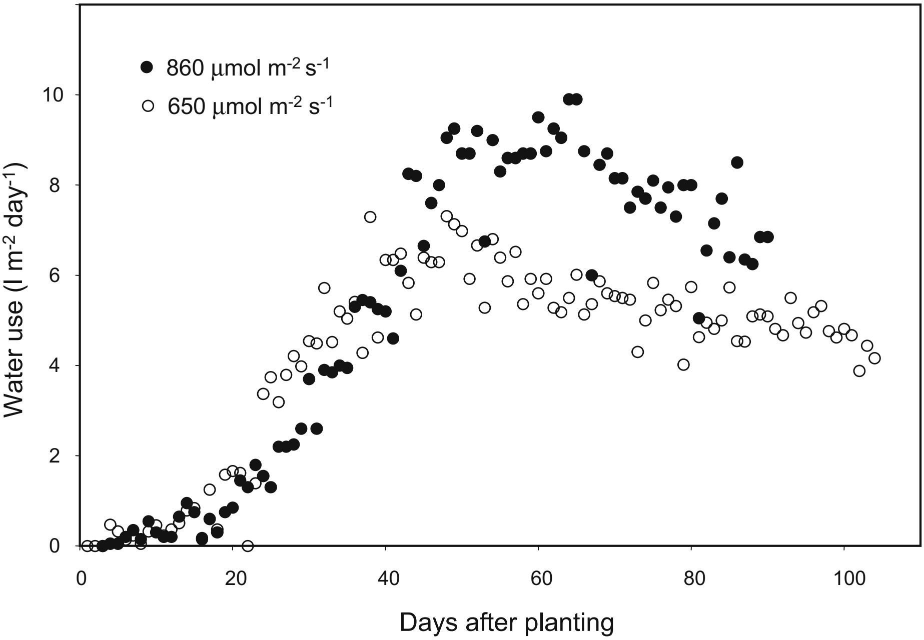

**Figure 12** Evapotranspiration rates throughout growth and development of 20 m$^2$ stands of potato (cv. Norland) grown in recirculating nutrient film technique. Plants were grown at 860 and 650 µmol m$^{-2}$ s$^{-1}$ PAR in NASA's Biomass Production Chamber at Kennedy Space Center, Florida.

leaves (Wheeler et al., 2004) (Fig. 11). In the study in which the photoperiod was changed from 12 to 24 h, ethylene levels rose rapidly following this change from a basal rate of 0.4 nmol m$^{-2}$ day$^{-1}$ to 6.2 nmol m$^{-2}$ day$^{-1}$, presumably from stress to the plants (Wheeler et al., 2004). When the photoperiod was reduced from 24 to 12 h, ethylene levels decreased.

Stand evapotranspiration (ET) rates for 20-m$^2$ stands using the NFT approach at Kennedy Space Center ranged from 3.4 to 5.2 l m$^{-2}$ day$^{-1}$ (3.4–5.2 mm day$^{-1}$) throughout growth, while maximum ET rates for canopies approached 10 l m$^{-2}$ day$^{-1}$ (10 mm day$^{-1}$) (Fig. 12). Higher ET rates occurred at higher PAR but it is not clear whether this was due to increased leaf temperatures, increased stomatal conductance, or both (Fig. 12). Time course measurements of ET typically showed a rapid rise early in growth as the canopy cover filled in, followed by a relatively constant rate during mature growth and tuber bulking (Fig. 12).

## Production Studies

For application to life support systems, estimating the yield rate or productivity (g m$^{-2}$ day$^{-1}$) is more meaningful than traditional yield per unit area (g m$^{-2}$, t ha$^{-1}$, etc.). This is because there are no seasons in controlled environments and crop cultivation can be continuous. These productivities can then be used to conduct trade studies of what area of crops would be needed to meet the food and oxygen needs for a given number of people (Wheeler et al., 2001). An additional

**Figure 13** Individual plant tuber yields from 21-week-old cv. Norland plants grown under 12-h photoperiod (3.6 kg) and 24-h continuous light (4.9 kg) at the University of Wisconsin Biotron.

consideration is when to harvest. Sequential harvest studies showed that tuber yields continued to increase up to 148 days in controlled environments, even with an early season cultivar like Norland. Yet the optimum harvest date for productivity occurred as early as 105 days with continuous light (Wheeler and Tibbitts, 1987). At that point, it was more efficient to harvest and replant rather than going on until 148 days. Plants in these studies were grown in large pots and confined to a cross-sectional area of 0.2 $m^2$, and their tuber yields reached 3.4 and 4.3 kg fresh mass per plant under 12-h photoperiod and continuous light, respectively (Fig. 13). This equaled 0.57 kg per plant and 0.79 kg per plant dry mass (DM) and a harvest index of 81% (Wheeler and Tibbitts, 1987). Dividing these yields by the cross-sectional area and number of growing days showed tuber productivity of 29.4 g DM $m^{-2}$ $day^{-1}$ at 126 days for continuous light and 19.5 g DM $m^{-2}$ $day^{-1}$ at 148 days for a 12-h photoperiod. Although these plants were confined to an area of 0.2 $m^2$ using screen cages, plants received some side lighting through the cages, which means that the total light reaching the plants was underestimated. As a consequence, yields per unit area were inflated, although in theory the extra light might be provided within the canopy using imbedded lamps or light pipes (Tibbitts et al., 1994). A less equivocal approach would be to grow the plants in a contiguous stand where side lighting is eliminated. When this was done with cv. Norland, productivities were 21.9 g DM $m^{-2}$ $day^{-1}$ at 110 days (Wheeler and Tibbitts, 1988), which is 23% less than the 28.5 g DM $m^{-2}$ $day^{-1}$ observed with individually caged plants harvested at a similar age (Wheeler and Tibbitts, 1987).

Follow-up production studies were conducted with cv. Denali, which has a higher tuber dry matter content, using a contiguous stand approach where only the centre plants were harvested. The first study provided short days for the first 40 days to initiate strong tuber sinks followed by continuous light for 92 days to promote tuber bulking. For the first 18 days, plants were grown in smaller pots and spaced closely (0.02 $m^2$ per plant) to reduce overall area requirement, after which they were transplanted to larger pots spaced at 0.25 $m^2$ per plant for the final growout. Final tuber yields from this test reached 19.7 kg FM $m^{-2}$ (197 t $ha^{-1}$) or 4.35 kg DM $m^{-2}$

**Table 1** Some high yields from potato grown in controlled environments.

| | Study duration (days) | Tuber FM (kg m$^{-2}$) | Tuber DM (kg m$^{-2}$) | Total DM productivity (g m$^{-2}$ day$^{-1}$) | Tuber DM productivity (g m$^{-2}$ day$^{-1}$) | PAR (mol m$^{-2}$ day$^{-1}$) | Radiation use efficiency (total) (g mol$^{-1}$) | Radiation use efficiency (tuber) (g mol$^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Univ. Wisconsin (12-h photoperiod) | 132 | 18.0 | 3.61 | 38.3 | 27.3 | 37.8 | 1.01 | 0.72 |
| Values adjusted for transplanting | | | | 43.6 | 31.1 | 37.8 | 1.15 | 0.82 |
| Univ. Wisconsin (12 then 24-h photoperiod) | 132 | 19.7 | 4.35 | 44.8 | 33.0 | 52.4 | 0.85 | 0.63 |
| Values adjusted for transplanting | | | | 51.0 | 37.5 | 52.4 | 0.97 | 0.71 |
| Ken. Space Cen. (12-h then 16-h photoperiod) | 105 | 10.5 | 1.88 | 27.2 | 18.4 | 42.2 | 0.64 | 0.44 |
| Estimated values with transplanting | | | | 32.1 | 21.7 | 42.2 | 0.76 | 0.51 |

(Table 1). These yields are roughly twice that for record field yields (Knowles and Thornton, 2000), suggesting there is still potential for increasing yields in field settings. Accounting for the reduced area requirement prior to transplanting, the tuber productivity in this study was 37.5 g DM $m^{-2}$ $day^{-1}$ (Table 1). Radiation use efficiencies from this study were approximately 0.71 g DM $mol^{-1}$ PAR for tuber biomass and 0.97 g DM $mol^{-1}$ PAR for total biomass (Table 1). When a second study was conducted but with a 12-h photoperiod for the entire 132 days, tuber productivity was slightly less (31.1 g $m^{-2}$ $day^{-1}$) but radiation use efficiencies increased to 0.82 g DM $mol^{-1}$ PAR for tuber biomass and 1.15 g DM $mol^{-1}$ PAR for total biomass. In all cases, these radiation use efficiencies included the reduced area required prior to transplanting. Related studies with 20-$m^2$ stands at Kennedy Space Center but using NFT, cv. Norland, and no transplant step produced up to 27.2 g $m^{-2}$ $day^{-1}$ total biomass and 18.4 g $m^{-2}$ $day^{-1}$ tuber biomass for single production cycles (Wheeler et al., 2003), with radiation use efficiencies of 0.64 g DM $mol^{-1}$ PAR for total biomass and 0.44 g DM $mol^{-1}$ PAR for tuber biomass (Table 1). If a similar transplanting scheme had been used to eliminate ~16 days use of the final growing area, productivities and radiation use efficiencies could have been increased (Table 1). When the NFT systems were run continuously for 418 days to produce four plantings, the productivities were even higher: 32.6 g $m^{-2}$ $day^{-1}$ total dry biomass and 20.0 g $m^{-2}$ $day^{-1}$ tuber biomass (Stutte et al., 1999; Wheeler et al., 2003). This was likely a result of the staggered harvesting of groups of trays, which created gaps in the canopy and allowed additional side-lighting to the remaining trays (Stutte et al., 1999).

Assuming one human requires about 2500 kcal $day^{-1}$ and there are ~3.7 kcal $g^{-1}$ DW for potato (Wheeler et al., 1994), then 38 g $m^{-2}$ $day^{-1}$ × 3.7 kcal $g^{-1}$ = 141 kcal $m^{-2}$ $day^{-1}$. Then dividing 2500 kcal $day^{-1}$ per person by 141 kcal $m^{-2}$ $day^{-1}$ $\approx$ 17.8 $m^2$ of potato would be required to continuously provide the food (dietary energy) for one person. The total area required to remove the $CO_2$ (~1000 g $day^{-1}$) and supply the $O_2$ (~800 g $day^{-1}$) for one person would be somewhat less, since the gas exchange is a function of the total biomass produced and not just tuber yields. The total biomass productivity from this test was 43.6 g $m^{-2}$ $day^{-1}$ (Table 1); assuming this biomass was mostly carbohydrate ($CH_2O$) and that all of the C came from $CO_2$ fixed during photosynthesis, an equivalent amount of $CO_2$ needed to produce this could be estimated by dividing 0.68, which is the ratio of 30 (g $mol^{-1}$ of $CH_2O$)/44 (g $mol^{-1}$ of $CO_2$) (Wheeler, 1996). Then (43.6 g $m^{-2}$ $day^{-1}$)/0.68 = 63.9 g $CO_2$ $m^{-2}$ $day^{-1}$. Then (1000 g $CO_2$ $day^{-1}$ per person)/63.9 g $CO_2$ $m^{-2}$ $day^{-1}$ $\approx$ 15.6 $m^2$ of potato to remove the $CO_2$ and supply the $O_2$ for one person in this study. This assumes a 1:1 molar ratio of $CO_2$ produced to $O_2$ consumed by the human, which is reasonably close for a high carbohydrate diet (Wheeler, 1996).

## Physiological Disorders

During these controlled environment tests, some interesting physiological disorders often appeared. These included leaf tipburn, which appeared as a constriction of full expansion and marginal necrosis at the tips of young leaves, especially cv. Russet Burbank. This was not common but occurred occasionally when young leaves initially developed under the canopy pushed through the upper canopy. This is relatively common with some other crops in controlled environments, such as lettuce (Collier and Tibbitts, 1982), and was likely related to Ca deficiency that occurred while the leaves expanded in the humid lower canopy environment. Another disorder was oedema or intumescence (Lang and Tibbitts, 1983). This appeared as small galls or callus like growth on the upper and lower sides of leaves, especially in cv. Denali. It was mild in most studies and was likely caused by a lack of UV light reaching the leaves due to the clear acrylic barriers used to separate the lamp banks from the plant growing area in the studies (Lang and Tibbitts, 1983). Oedema seemed to be more prevalent under HPS lighting, which has very little UV in its spectrum. Leaf epinasty occurred in a tightly closed chamber where ethylene could accumulate (Fig. 11), and some mild bleaching of leaves occurred at super-elevated $CO_2$ concentrations later in growth (Mackowiak and Wheeler, 1996). And as noted earlier, sudden changes in photoperiod (e.g., 12 h to continuous light) caused a scorching of leaves in one study at Kennedy Space Center. A small percentage of tubers (cv. Norland) grown in NFT showed growth or expansion cracks, and occasionally small areas of periderm showed damage, which appeared as darkened areas surrounded by white encrustation. This latter injury may have been related to salt accumulation and burn as nutrient solution evaporated from the surface of some tubers. Clearly these are not issues of concern for field settings but must be considered for controlled environment plantings with potato.

## Spaceflight Testing

With the relatively short supply line to spacecraft in low-Earth orbit, food can be replenished with regular deliveries from Earth. Hence, no space studies have occurred to date where plants were grown specifically for life support; but exploratory studies have been conducted with a range of crops (Nechitailo and Mashinsky, 1993; Levinskikh et al., 2000; Musgrave, 2002). Among these tests were several with potato. The first study involved flying potato tubers cv. Priekulsky packed in moist moss for 18 days on a Russian Soyuz flight in 1970 (Nechitailo and Mashinsky, 1993). All three tubers flown in space sprouted and formed small roots but development was slightly delayed when compared to ground controls. When these tubers from space and ground were grown out as whole plants, little difference was noted between the plants (Nechitailo and Mashinsky, 1993). A second study used in vitro potato plantlets that were grown in the laboratory for 4 weeks on Earth and then launched to the Mir Space Station in May of 1991 (Kordyum et al., 1997). Plantlets were maintained in dark containers for 8 days on board Mir, during which they formed small spherical tubers containing starch, similar to plantlets kept on Earth. The starch grain size in the space tubers was smaller than those on Earth and the lamellae within the amyloplasts were locally enlarged (Kordyum et al., 1997). The third experiment used excised leaves to determine whether photosynthetically driven tuber formation could occur under space flight conditions (Ewing, 1985; Wheeler et al., 1988). Five leaves from induced cv. Norland plants were placed in the University of Wisconsin's Astroculture plant chamber (Morrow et al., 1995) and flown on the Space Shuttle mission STS-73 in November of 1995. The cut ends of the cuttings were buried in arcillite particles kept moist by a porous tube watering system (Morrow et al., 1995). Light was provided to the leaves using a combination of red and blue light emitting diodes (LEDs) to provide a 12-h photoperiod of 150

**Figure 14** Potato tubers formed at the axillary buds of leaf cuttings (cv. Norland) flown on the Space Shuttle STS-73 mission for 15 days. Tubers developed equally well in the μ-gravity of space as on the ground (from Croxdale et al., 1997).

mol $m^{-2}$ $s^{-1}$ PAR (Croxdale et al., 1997). In-flight data showed that $CO_2$ concentrations in the chamber rose in the dark, and then quickly drew down to a set-point of 500 μmol $mol^{-1}$ during the light, indicating the leaves were respiring and photosynthetically active (Brown et al., 1997). The leaves were retrieved from the Space Shuttle after 16 days and analysed. Leaves had senesced significantly but had tubers developed at all five leaf axils after 16 days in space (Fig. 14) (Croxdale et al., 1997; Cook et al., 1998). The size and shape of tubers from space were similar to those grown in a ground control chamber, as were the distributions of starch grains and proteinaceous crystals in the tubers. There were more small starch grains in the space-grown tubers (Croxdale et al., 1997; Cook et al., 1998), similar to results reported by Kordyum et al. (1997). Collectively, the results indicate that gravity is not required for tuber formation.

## Concluding Comments

Findings from controlled environment studies for NASA were consistent with many previous observations with potato, but also revealed some interesting phenomena, including physiological intolerance of some cultivars to continuous light, increased stomatal conductance at super-elevated $CO_2$ concentrations, ethylene production by whole canopies, successful growth in NFT culture, and yields approaching 200 t $ha^{-1}$ under high light and $CO_2$ enrichment. Small-scale space flight experiments showed that tubers can form and sprout in weightlessness. Clearly these are just modest steps toward the ultimate use of plants for human life support in space, but I am convinced that potato will one day supply food and oxygen to humans living on other planets, just as it has for hundreds of years on Earth.

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