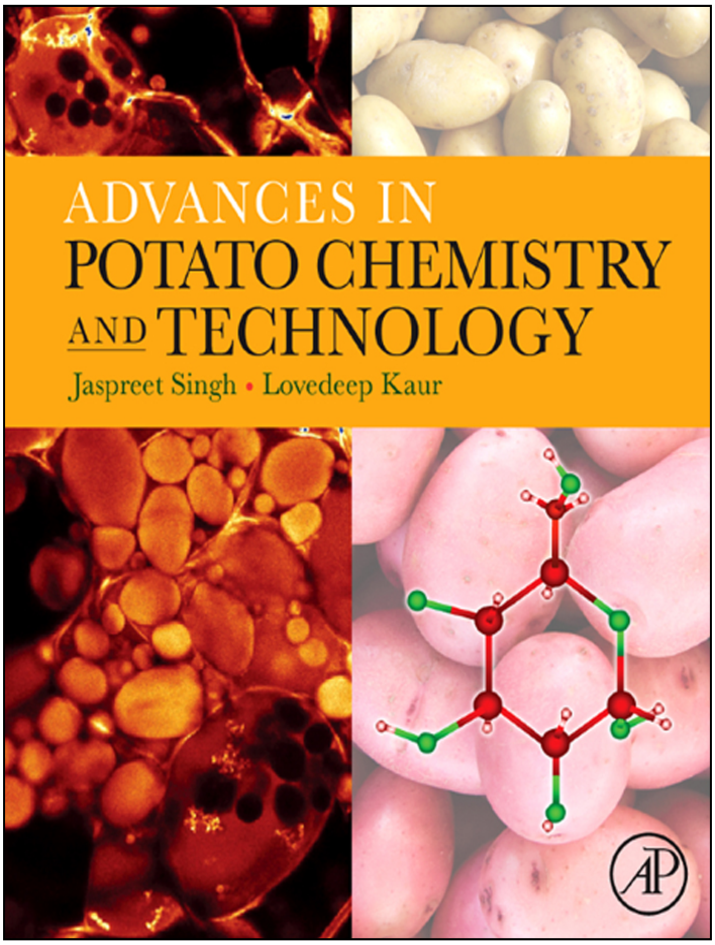

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CHAPTER 17

Potatoes for Human Life Support in Space

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17.1 Plants for Life Support in Space

Can this be serious – plants, no less the versatile potato, in space? When one thinks about the future of human kind, eventually we will travel on to other planets and establish long duration outposts. The 'when' and 'why' are largely political, but the 'how' is technological, and achievable. To do this will require innovative approaches for even the most fundamental requirements, such as meeting human life support requirements for breathable air, clean water, and food. Space missions to date have stowed life support provisions because the supply line has been relatively short. But as missions venture farther and stay longer, stowage and resupply become more costly and methods for regenerating life support consumables will be needed. There have been modest attempts to use regenerative physico-chemical systems on the Russian Mir and the International Space Stations, where, for example, oxygen (O_2) was produced using electrolysis and condensed humidity was collected and purified for reuse. These approaches can be expanded for future space missions, but such physico-chemical technologies become more massive and costly for long-duration missions and provide no means for producing food. An alternative would be to use biological technologies, such as plant photosynthesis to scrub the CO_2 from the air and generate O_2 (Galston, 1992; Myers, 1954). Photosynthesis produces the O_2 on Earth that humans now breathe and removes the CO_2 that we exhale, and it could be used in a similar fashion in space. In addition, if crops are used, the photosynthetic process could also produce food. Moreover, plant production systems in space could be used to assist in water purification, where, for example, gray water or pre-treated wastewater could be recycled to the plants; the plants would take up the water and generate humidity through transpiration, which could be condensed to provide clean water (Wolverton et al., 1983). Microbial communities associated with the plant root systems could breakdown the organic compounds in the wastewater and the plants could recycle the nutrients (Loader et al., 1999). Thus plants could provide four separate life support functions in one combined system: (1) removal of CO_2; (2) a source of O_2; (3) a source of food; and (4) a means for purifying and recycling wastewater (Figure 17.1). A key factor for driving this entire process is light, which could

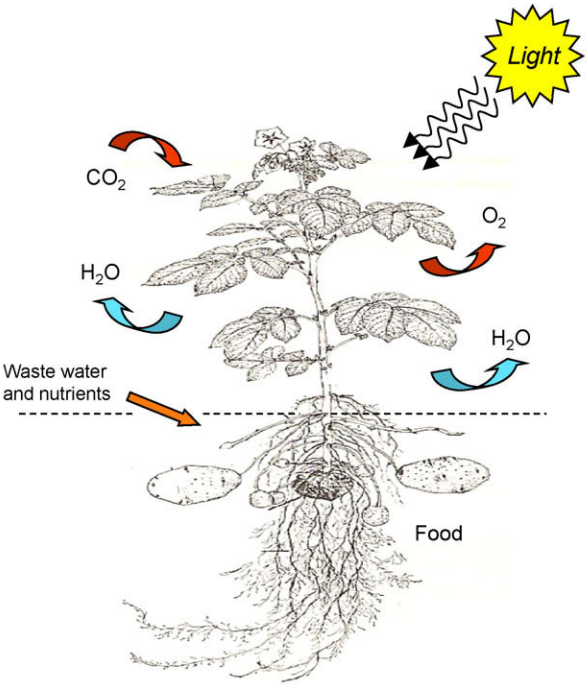

Figure 17.1: Plants as life support machines for space travel. Plant photosynthesis could provide oxygen and food, while removing carbon dioxide. Plant growing systems could also help waste water processing where the plant transpiration serves as a final distillation step after which the humidity is condensed as clean water.

be provided either from the Sun or with the use of electric lamps, and I will return to this later.

17.2 Why the Potato?

One of the first meetings to discuss crops for space travelers was the Biologistics Symposium held at Wright Patterson Air Force Base, US in 1962 (Boeing Comp., 1962). The recommendations focused largely on vegetables and perishable crops that could supplement the diet of stowed foods. Related conferences held about 15 years later generated more comprehensive lists to meet the broader needs of human diets (e.g., a more complete supply of carbohydrate, protein, and fat), and considered yield potential, harvest index (ratio of edible to total biomass), food processing, and horticultural requirements, such as planting, pollination, and harvesting (Hoff et al., 1982; Masuda et al., 2005; Mitchell et al., 1996; Salisbury and Clark, 1996; Tibbitts and Alford, 1982; Waters et al., 2002). Most of these lists contained a mix of staple crops that provide carbohydrate, protein, and fat, along with a balance of vegetables and small fruits. But it was recognized that meeting 100% of the dietary needs including all the micronutrients

Figure 17.2: Dr. Ted Tibbitts of the University of Wisconsin, Madison, WI, USA, working with potato plants in a growth chamber. Ted Tibbitts was the principal investigator for NASA-sponsored studies with potatoes from 1982 through 1994, and work from his laboratory has provided baseline information on controlled environment production techniques bioregenerative life support systems in space.

would require large plantings with numerous species, and that using some dietary supplements to supply micronutrients would be more cost effective for near-term missions.

A crop common to most of these lists was the potato, *Solanum tuberosum* L. Potatoes are highly productive, rich in digestible carbohydrate, a significant source of protein, and are easily propagated (Tibbitts and Alford, 1982). In addition, potatoes do not require extensive processing steps for consumption, as do crops like soybean and some grains, and when potatoes are strongly induced to tuberize, their harvest index can exceed 80%, which is nearly double that of grain crops (Wheeler and Tibbitts, 1987). This high harvest index increases the intrinsic yield potential per unit area and reduces the amount of inedible biomass for recycling. Reducing the amount of inedible biomass in turn minimizes the amount of O_2 required (and CO_2 produced) during waste processing in closed systems (Wheeler, 2003).

Despite these virtues, experience with potatoes was largely limited to field settings with little information available on controlled environment production. With this in mind, the US National Aeronautics and Space Administration (NASA) initiated a series of grants (1982–1994) to Ted Tibbitts (Figure 17.2) at the University Wisconsin, US to study potato growth and development in environmental chambers at the University of Wisconsin Biotron. Following this, additional growth chamber testing and larger-scale production studies with potatoes and 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 potatoes and is largely excerpted from Wheeler (2006) and Wheeler et al. (2008a).

17.3 Cultivars for Space

Obviously plants cannot withstand the harsh vacuum, extreme temperatures, and high UV radiation of space; hence controlled environments will be required for plant production, perhaps not unlike growth chambers we use on Earth. Initial NASA testing focused on identifying lines that would perform well in controlled environments. A comparison of four North America cultivars, Norland (early season), Superior (early season), Norchip (mid season), and Kennebec (late season), showed the greatest tuber yields from Norland under 12, 16, and 20 h of light, while Kennebec showed the lowest yields under the longer photoperiods (Wheeler and Tibbitts, 1986a) (Figures 17.3 and 17.4). Subsequent testing with these cultivars along with Russet Burbank (late season) and Denali (late season) showed that cvs. Norland and Denali produced tubers consistently under many different environments (Wheeler and Tibbitts, 1986b; Yandell et al., 1988; Wheeler et al., 1991). Additional tests with 23 cultivars for tolerance to continuous light were conducted later and several cultivars from Alaska, Norway and Netherlands performed well (Tibbitts et al., 1994). Total glycoalkaloids (TGA) were measured in tubers from some of these studies, 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, University of Wisconsin and Kennedy Space Center continued to use cvs. Norland and Denali, but further testing with different cultivars and/or targeted development of genetically engineered cultivars will be needed to maximize yields for space life support systems.

Figure 17.3: Potato tubers harvested from (left to right) cvs. Norchip, Kennebec, Norland, and Superior after 105 days growth at 20°C and a 12-h photoperiod with 400 μmol m^{-2} s^{-1} of PAR. A meter stick was place in the photo for reference.

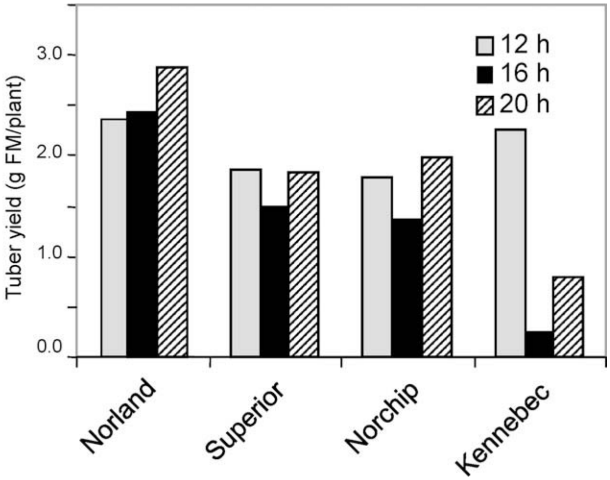

Figure 17.4: Tuber yields from four North American cultivars grown under 12, 16, and 20 h of 400 μmol m^{-2} s^{-1} PAR. Kennebec, a late-season cultivar did not produce well under the longer photoperiods, while Norland, and early season cultivar produced well under all the photoperiods (Wheeler and Tibbitts, 1986a).

17.4 Horticultural Considerations

17.4.1 Cultivation techniques

Horticultural strategies for growing crops in space must consider the effects of reduced gravity (Wheeler et al., 2001). In low-Earth orbit, such as on the Space Shuttle or the International Space Station, or during transit missions to the Moon and Mars, one must deal with weightlessness (μ-gravity). On the surface of the Moon and Mars, approximately 1/6 and 3/8 gravity exist (Salisbury, 1991). All of these reduced gravities will affect watering strategies for plants, but especially in weightlessness where water can only move by capillary forces (Wright et al., 1988; Porterfield, 2002). On the Moon and Mars, water should drain through solid media, although it will be slower than under 1 g, but recirculating hydroponics systems should be adequate for plant cultivation (Bugbee and Salisbury, 1989). It is interesting to note that a NASA-sponsored workshop in 1987 focused entirely on issues facing lunar base agriculture and the potential for using lunar regolith as a growing medium for plants (Ming and Henninger, 1989).

Most studies at the University of Wisconsin used pots containing peat–vermiculite (50:50 vol.) medium and drip irrigation with a complete nutrient solution with 7.5 mM nitrate (Figure 17.5; Wheeler and Tibbitts, 1986a; Tibbitts et al., 1994). Other studies used arcillite (turface), which consists of calcined, clay particles (McCown and Kass, 1977; Tibbitts et al., 1994). Growth in arcillite was not as good as on peat-vermiculite, but the arcillite had excellent drainage and could be washed cleanly from the roots allowing easy reuse, and it has since been used in several

Figure 17.5: A typical experiment with potatoes conducted at the University of Wisconsin Biotron in the 1980s and 1990s. Plants were propagated with in vitro grown nodal cuttings and planted into a peat–vermiculite (50:50) and watered to excess with a nutrient solution four times daily. The watering tubes for the pots are shown hanging from an overhead delivery line (Wheeler and Tibbitts, 1987).

space flight experiments with plants (Croxdale et al., 1997; Levinskikh et al., 2000; Morrow et al., 1995; Stutte et al., 2005). Some comparisons of pot sizes were also conducted and in general, for long-duration studies (ca. 100 days or more), larger pots sustained better growth (Tibbitts et al., 1994).

Exploratory tests were conducted at Wisconsin with hydroponic 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 (Tibbitts et al., 1994). Hydroponic techniques had been used previously for potato research (Chapman, 1958; Fong and Ulrich, 1969; Krauss, 1978; Sattelmacher and Marschner, 1978) and seemed to hold a lot of potential. Unfortunately, the plants grown in the standing solution cultures, under continuous misting, or even in wet arcillite with continuous flowing nutrient solution showed good shoot growth but tuberization was inconsistent and stolons and tubers often developed callus and became pigmented (Figure 17.6) (Fong and Ulrich, 1969; Tibbitts et al., 1994). Later testing with nutrient film technique–NFT (Resh, 1989) at Kennedy Space Center proved more successful: the stolons and tubers were not submerged and the solution could be recirculated allowing control of pH and electrical conductivity (Wheeler et al., 1990, 1997) (Figure 17.7). The combined results with hydroponic testing suggested that stolons and tubers require good aeration (gas exchange), which is consistent with observations poor yields from wet or poorly drained fields (Smith, 1977) and recent advances in the use of hydroponic techniques with potato (Muro et al., 1997; Ritter et al., 2001).

Figure 17.6: Callus development around the lenticels of a tuber (cv. Norland) grown in media that was too wet. Similar responses were noted with submerged tubers grown in solution cultures or aeroponic cultures with continuous misting (source: Tibbitts et al., 1994).

Figure 17.7: Tubers from cv Norland plants grown in nutrient film technique (NFT) for 105 days at NASA's Kennedy Space Center, FL, USA (source: Wheeler et al., 1990). Nutrient solution was pumped continuously to the back end of the trays and flowed to a drain at the front for return to the reservoir. NFT proved more successful for producing good tuber yields and allowed easy harvesting.

For recirculating NFT studies, the electrical conductivity (EC) was maintained near $0.12\ \mathrm{S\ m^{-1}}$ with daily additions of a stock solution, and pH was maintained automatically near 5.8 with additions 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., 1994a; McKeehen et al., 1996). In some cases, greater than 30% of the nitrogen came from the nitric acid in this hydroponic approach (Wheeler et al., 1990). Much of the nitrogen in the shoot was in the form of nitrate, but fortunately there was little nitrate in the tubers, which would raise food safety concerns (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).

17.4.2 Mineral nutrition

Numerous tests were conducted at the Wisconsin to study different concentrations of essential nutrients on potato growth and development. Total plant 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 (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. A comparison of different combinations of NH_4/NO_3 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, and 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, reductions in nitrogen later in growth increased harvest index (Goins et al., 2004). When NO_3 was used alone, maximum growth occurred at 2, 4, and 8 mM levels but growth was reduced 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).

17.4.3 Propagation

For all of the NASA sponsored testing, in vitro nodal cuttings were used to start the plants (Tibbitts et al., 1994). 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. Transplants were then covered with glass beakers for 3 days to allow acclimation. Most plantlets were grown on an MS type medium with 6% sucrose, but related testing showed that sucrose levels could be reduced if some air exchange and CO_2 could reach the plants (Kozai et al., 1988; Yorio et al., 1995a). Other tests showed that light spectral quality could be used to control stem and internodal elongation (Wilson et al., 1993). Although the in vitro propagation was useful for research, it might be cumbersome and costly for space and further testing is needed to study the use of micro and mini-tubers harvested from plants as propagules.

17.5 Physiological Responses in Controlled Environments

17.5.1 Light

Tuberization is known to be a short-day response (Garner and Allard, 1923; Gregory, 1965) and even shows the classic red / far-red reversal for phytochrome control (Batutis and Ewing, 1982). Yet studies showed that some potato cultivars tuberized even under continuous light (Arthur et al., 1930; Harvey, 1922). Because of this, early NASA testing focused on the photoperiod responses of potato cultivars, and in particular which cultivars might tolerate continuous light. The rationale for this was simple: If total growth and tuber yield could be increased per unit area with longer photoperiods, the crop area required to sustain humans in a life support system could be reduced (Salisbury, 1991). The good performance of the early cultivar Norland and the poor performance of the late cv. Kennebec under 20 h of light indicated genotypic differences in response to photoperiod (Figure 17.4). In addition, leaves of the Kennebec plants folded upward and became chlorotic under the 20 h photoperiod, suggesting a physiologically intolerance to the long photoperiod (Wheeler and Tibbitts, 1986a). To explore this further, cvs. Norland, Norchip, Russet Burbank, Superior, and Kennebec were grown under a 12/12 h light/dark cycle using 400 μmol m^{-2} s^{-1} PAR (controls), 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 tuberized well under 12 h light / 12 h dark treatment, while cvs. Norland and Russet Burbank also grew well and tuberized under continuous 400 μmol m^{-2} s^{-1}, which had twice the total light as the 12 h treatment. Cv. Norchip showed moderate tuberization under continuous 400 μmol m^{-2} s^{-1}, but cvs. Superior and Kennebec had poor tuber development and chlorotic leaves with rustic flecks (Wheeler and Tibbitts, 1986b; Cao and Tibbitts, 1991b). In contrast, plants grown with the dim day length extension showed little tuberization but healthy, dark green leaves and stems (Wheeler and Tibbitts, 1986b). This suggested that all the cvs. responded well and tuberized under short days but that requirements for a dark period could be overcome with greater amounts of total light in cvs. Norland and Russet Burbank. In contrast, cvs. Superior, Norchip, and Kennebec were physiologically intolerant to continuous light at 400 μmol m^{-2} s^{-1} PAR (Wheeler and Tibbitts, 1986b). Subsequent studies showed injuries to intolerant cultivars could be mitigated by providing a thermoperiod (Tibbitts et al., 1990; Cao and Tibbitts, 1991a, 1992b). Closer examinations showed that continuous light injury resulted in loss of chloroplast membrane integrity and photosynthetic competence in intolerant cultivars (Cushman et al., 1995), with ethylene also playing a role (Cushman and Tibbitts, 1998).

Despite the ability of some cultivars to grow and tuberize under long photoperiods, short-day tendencies were still apparent: Harvest index, which indicates the partitioning of growth to tubers, was nearly always greater under short photoperiods (Wheeler and Tibbitts, 1986a; Wheeler et al., 1988, 1991). This indicated that yields might be optimized if strong induction could be combined with high total light. This idea was tested by moving plants between 12 h light / 12 h dark and a 24 h light chambers at different stages of growth. The results with cv.

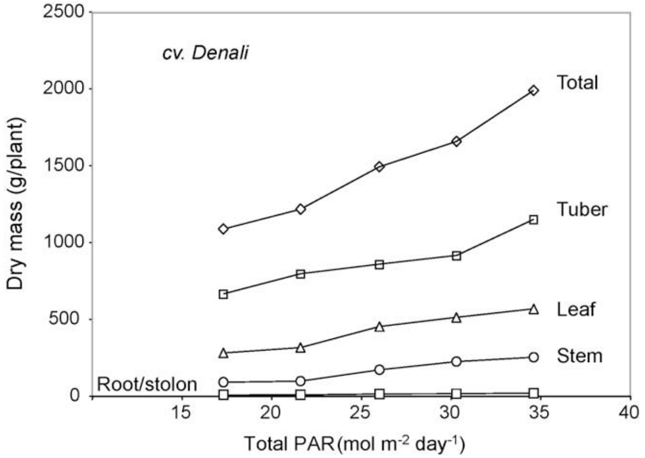

Figure 17.8: For most of the NASA-sponsored studies with potatoes, increased light (PAR) resulted in increased biomass. The relative partitioning of biomass among plant parts is shown for a range of PAR from studies by Wheeler and Tibbitts (1997).

Denali showed that 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).

Depending on the system constraints in space, use of short photoperiods throughout growth still might be desirable. For example, if electrical power for lighting is limited but growing volume is not, larger areas might be planted and alternate halves illuminated at 12-h intervals. Lamps over each of the areas could be turned on for 12 h, or the lamps could be mounted on a track to move back and forth to provide alternate 12-h light cycles. Either of these approaches would be more efficient than continuous light for tuber yield per MJ of energy (Wheeler et al., 1992).

Except for when injury occurred with continuous light-intolerant cvs., total growth and tuber yield generally increased with total irradiance, regardless of photoperiods or other environmental treatments (Wheeler et al., 1991; Wheeler and Tibbitts, 1997; Yandell et al., 1988) (Figure 17.8). This emphasized the strong influence of light and its importance in designing bioregenerative life support systems for space. Similar findings have been reported for wheat, lettuce, and soybean in life support studies (Bugbee and Salisbury, 1988; Knight and Mitchell, 1988; Wheeler et al., 2001).

17.5.2 Temperature

The strong influence of temperature on potato growth and tuberization is well documented (Burton, 1972; Gregory, 1965; Cao and Tibbitts, 1995; Marinus and Bodlaender, 1975). Nonetheless several temperature studies were conducted for the NASA studies. Tests with

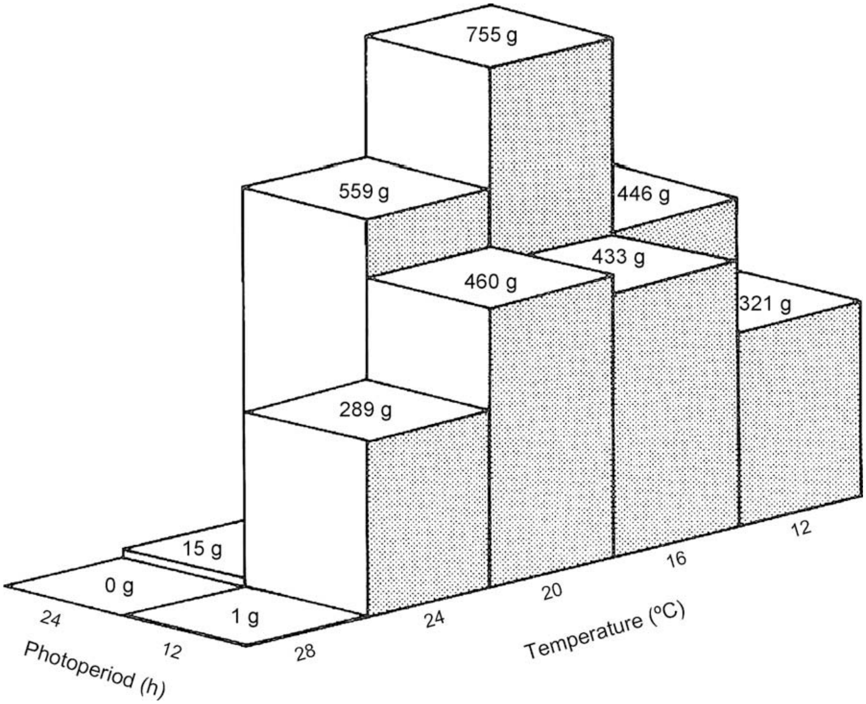

Figure 17.9: The effect of temperature on tuber yield from 56-day-old cv. Norland potato plants grown under 12 h or 24 h (continuous) 400 μmol m^{-2} s^{-1} PAR. Peak yields under 12 h occurred at 20°C, while peak yields under 24 h occurred at 16°C. Few or no tubers were produced at 28°C (Wheeler et al., 1986a).

Russet Burbank and Norland grown under continuous light showed that 17.5°C 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 (Figure 17.9). For all studies, stem lengths increased with temperature, regardless of the photoperiod. Thus cooler temperatures could be used to offset the less inductive influence of a long photoperiod, and warmer temperatures were tolerable if short photoperiods were used (Wheeler et al., 1986b). Other studies showed that a thermoperiod improved tuberization under both short and long photoperiod, and that thermoperiods reduced injury from continuous light (Bennett et al., 1991; Cao et al, 1992b; Tibbitts et al., 1990). Using warm temperatures early in growth followed by cool temperatures later in growth also promoted good tuberization, but the reverse did not (Cao and Tibbitts, 1994a).

17.5.3 Carbon dioxide

Closed environments in space will require continuous control of atmospheric composition and pressure, including the partial pressure of carbon dioxide (CO_2). At the beginning of NASA's

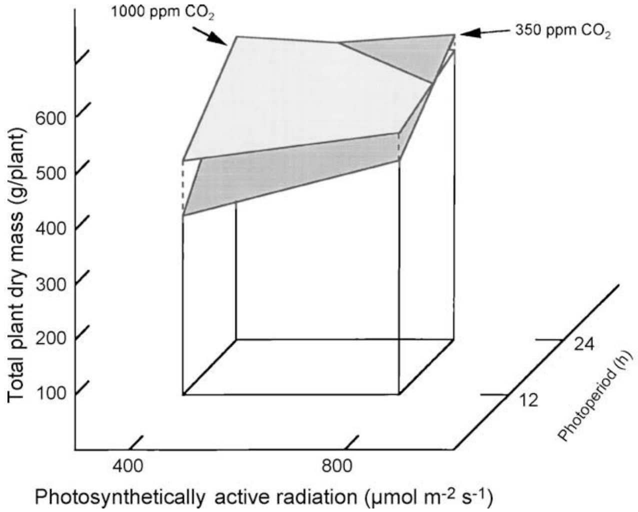

Figure 17.10: Total biomass of potato plants grown under two PARs (400 and 800 μmol m^{-2} s^{-1}), two CO_2 concentrations (350 and 1000 ppm), and two photoperiods (12 and 24 h). Data are averages for three cultivars, Norland, Russet Burbank, and Denali, grown for 90 days. Tuber yields showed a similar response pattern to total biomass. CO_2 enrichment showed the greatest proportionate benefit under the 12-h photoperiod and 400 μmol m^{-2} s^{-1} PAR, and no benefit or even had a negative effect under 800 μmol m^{-2} s^{-1} and 24 h lighting (Wheeler et al., 1991).

testing in 1982, 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., 1976), while whole-plant studies showed both positive (Collins, 1976) and negative effects (Goudriaan and de Ruiter, 1983). Initial studies at the Wisconsin showed that increasing the CO_2 from ~360 to 1000 ppm (0.036 to 0.10 kPa) increased single leaf photosynthetic rates for cv. Norland and increased tuber yields slightly for both cvs., but plants were grown under a 24-h photoperiod for those studies (Wheeler and Tibbitts, 1989). This led to a series of studies with cvs. Norland, Russet Burbank, and Denali where plants were grown for 90 days under 12- or 24-h photoperiods, 400 and 800 μmol m^{-2} s^{-1} PAR, and ambient (~360 ppm) and 1000 ppm CO_2. Total biomass and tuber yields increased with elevated CO_2 especially at the lower PAR and 12-h (short) photoperiod. In contrast, elevated CO_2 had had little or even a negative effect under continuous light (Wheeler et al., 1991) (Figure 17.10). These studies showed an average increase in yield of 39% when the CO_2 was enriched to 1000 ppm under the 12-h photoperiod with 400 μmol m^{-2} s^{-1} PAR and 27% increase under the 12-h photoperiod and 800 μmol m^{-2} s^{-1}. Free Air CO_2 Enrichment (FACE) studies in field plots in Europe found similar results – 40% increase in yield at 660 ppm (cv. Primura) and 32% increase in yield at 550 ppm (cv. Desirée) (Finnan et al., 2002; Miglietta et al., 1998). Subsequent studies investigating the effect of elevated CO_2 on cv. Denali plants showed a 29% increase in tuber yield from CO_2 enrichment (1000 ppm) under short days (Wheeler and Tibbitts, 1997). Collectively, the findings suggest

Figure 17.11: Neil Yorio at NASA's Kennedy Space Center taking leaf porometer measurements with potatoes to monitor stomatal conductance and transpiration rates. When measurements were taken at 400 ppm CO_2, a mask was worn to removed exhaled breath from the chamber to avoid elevating the CO_2 concentration.

the greatest benefits to potatoes from CO_2 enrichment occur at lower light levels and/or short photoperiods.

Although a CO_2 concentration of 1000 ppm is elevated in comparison to current Earth ambient, CO_2 concentrations in the Space Shuttle and International Space Station typically range from ~2000 to 6000 ppm, with episodes even exceeding 10 000 ppm with large crews. Consequently, we were curious about plant responses to 'super-elevated' CO_2 levels, i.e., $CO_2 > 2000$ ppm. When cvs. Norland and Denali plants were grown under 400, 1000, and 10 000 ppm $CO_{2,}$ some bleaching was noted on leaves after 90 days growth at 10 000, but there was no difference in total biomass when compared to 1000 ppm-grown plants (Mackowiak and Wheeler, 1996). But transpiration and stomatal conductance measurements with a leaf porometer (Figure 17.11) showed significantly higher rates at 10 000 compared to 1000 ppm (Mackowiak and Wheeler, 1996), which was unexpected based on the research literature (Drake et al., 1997; Morison, 1987). Subsequent studies showed that stomatal conductance at 10 000 > 400 > 1000 ppm, and that the diurnal rhythms were damped at the super-elevated 10 000 ppm (Figure 17.12). Similar responses have been seen in soybean, sweetpotato, bean, and radish (Wheeler et al., 1999) and provide a good example of some unexpected and intriguing consequences of growing plants in space-like environments.

17.6 Further Testing for Space Environmental Physiology

An obvious concern for growing potatoes or any other plant in space is the different gravity environment. Watering plants in low gravity is a challenge but the typical problems associated

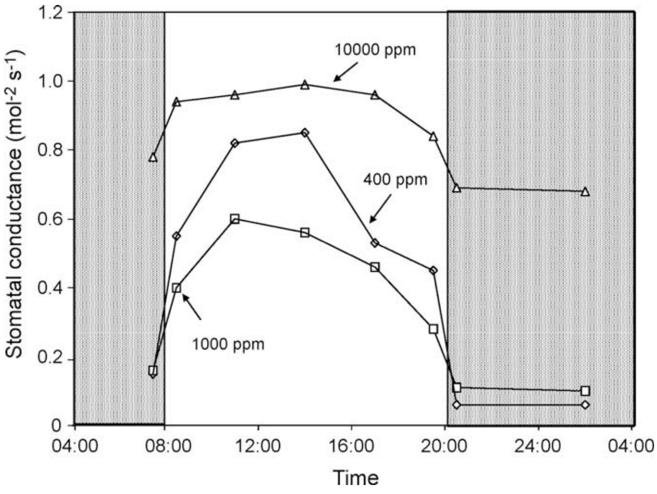

Figure 17.12: Stomatal conductance of potatoes grown at 400, 1000, and 10 000 ppm carbon dioxide. Conductance and transpiration were lowest at 1000 ppm and highest at 10 000 ppm. Super-elevated concentrations like 10 000 ppm might can occur in closed environments in space (source: Wheeler et al., 1999).

with this, such as poor aeration of roots zones, are secondary and not a direct effect of gravity on the plants (Hoehn et al., 2000; Morrow et al., 1995; Porterfield, 2002). Spaceflight conditions can cause some chromosomal aberrations (Krikorian and O'Connor, 1984) and affect some aspects of plant growth and development (Kiss et al., 2000; Musgrave et al., 1997), and initial tests to grow wheat plants in space resulted in heads with no seed (Levinskikh et al., 2000). But this was later determined to be a result of elevated ethylene on the Russian Mir space station and not weightlessness. Plant shoots can be oriented with light in the absence of gravity (Halstead and Dutcher, 1987), provided there is sufficient blue light (400–500 nm) for phototropism (Morrow et al., 1995). Thus if an adequate environment is provided for the plants, fractional or even microgravity do not appear to pose fundamental impediments (Monje et al., 2005; Stutte et al., 2005).

Another unique but controllable aspect about space environments for both humans and plants will be atmospheric pressure. Recent missions on NASA's Space Shuttle, the International Space Station, and the Russian Mir Space Station all operated at 1 atm (101 kPa) with about 21% (21 kPa) of oxygen. But early NASA missions with Mercury, Gemini, and Apollo operated at 1/3 atm (34 kPa) with 100% oxygen (34 kPa), while Skylab, NASA's first Space Station, operated at 1/3 (34 kPa) total pressure with 70% (24.3 kPa) oxygen (Lange et al., 2005). NASA's future missions to the Moon and Mars will likely operate at 54 kPa (0.54 atm). By using lower pressures both structural mass and gas leakage can be reduced. In addition, EVAs (space walks) can occur without any pre-breath time, allowing rapid responses to emergencies. If pressures are sufficiently low, separate inflatable greenhouse structures might be possible for growing plants (Clawson et al., 2005). Pressure testing with plants to date has been sparse, but results suggest that plants tolerate pressures down to a 1/4 atm or less, provided sufficient oxygen is available for respiration and CO_2 for photosynthesis (Corey et al., 2002; He et al., 2007). Perhaps one of the more consistent responses of plants to reduced pressures is increased transpiration (Daunicht and Brinkjans, 1992; Massimino and Andre, 1999). This can be explained largely by increased gas diffusion rates at reduced pressures, which in turn can result in cooler temperatures of any surfaces associated with evaporating water, such as leaves (Rygalov et al., 2005).

One of the biggest risks for any living organisms in space will be the high energy radiation that can damage the molecular structure of cells. This includes galactic cosmic radiation (GCR), solar energetic particles (SEP), and so-called trapped radiation circulating planets with magnetic fields, such as Earth's Van Allen Belts (NRC, 2006). For spacecraft in low-Earth orbit, living organisms are inside the Van Allen Belts and somewhat shielded by the Earth's magnetic field, but in interplanetary travel or on the surfaces of the Moon or Mars, the effects of GCR and SEP can be serious. In addition, secondary radiation such as high energy neutrons can occur from collisions with surface regolith. Extensive interest and testing have focused on radiation effects on humans and astronaut safety (NRC, 2006), but less is known of plant responses to high energy radiation, and this remains an important area of research.

17.7 Atmospheric Regeneration Rates from Potato Photosynthesis

When potatoes were grown in the atmospherically closed Biomass Production Chamber at Kennedy Space Center, photosynthetic gas exchange rates could be tracked throughout growth for an entire 20 m^2 stand (Wheeler et al., 2003, 2008a). These measurements showed several distinctive features: First, stand (canopy) net photosynthetic rates increased rapidly as stand ground cover increased and approached 100% ground cover ca. 35 days-age (Figure 17.13). This has been observed with other crops as well and emphasizes the importance of light interception by the canopy (Monje and Bugbee, 1998; Wheeler et al., 1994). A closer look at Figure 17.13 shows that photosynthesis continued to rise after full canopy cover (ca. days 35–50), but this was a result of the canopy growing closer to the lamps and receiving greater light. A second observation was that stand photosynthetic rates were a strong function of incident light, with the study conducted at 865 $\mu mol\, m^{-2}\, s^{-1}$ PAR showing higher rates than the study at 655 $\mu mol\, m^{-2}\, s^{-1}$ (Figure 17.13). Short-duration tests where the light intensity was changed showed that photosynthetic rates increased linearly up to $\sim$1000 $\mu mol\, m^{-2}\, s^{-1}$ at 50 days after planting, with a light compensation point near 200 $\mu mol\, m^{-2}\, s^{-1}$ and stand respiration rates near 10 $\mu mol\, m^{-2}\, s^{-1}$ when grown at high light intensities (Wheeler et al., 2008a). Third, net photosynthetic rates decreased with age depending on the extent of leaf senescence (Figure 17.13). This was especially apparent in one test in which the photoperiod was changed from 12-h to continuous light (Figure 17.14). Immediately following this photosynthetic rates dropped but when the photoperiod

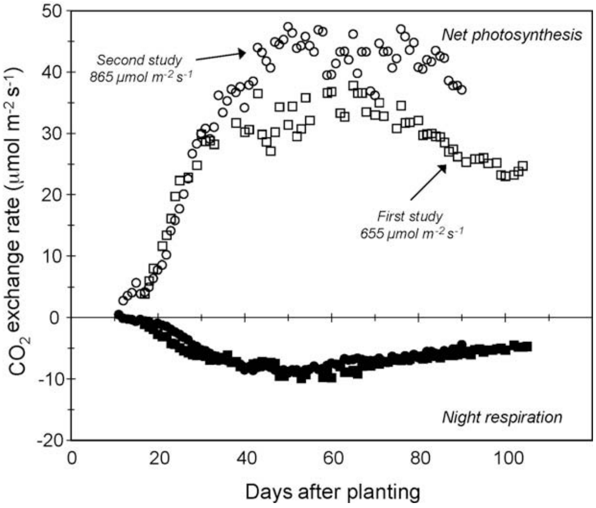

Figure 17.13: Carbon dioxide exchange rates of 20 m^2 potato stands grown at 865 or 655 $\mu mol\,m^{-2}\,s^{-1}$ PAR. Positive values reflect net photosynthetic rates during the light period and negative values reflect respiration rates during the dark period (source: Wheeler et al., 2008a).

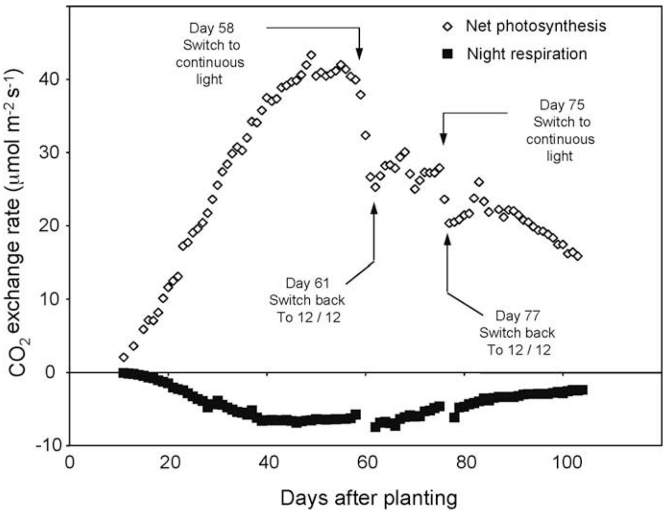

Figure 17.14: Effect of changes in photoperiod on the carbon dioxide exchange rate of a 20 m^2 potato stand. On day 58, the photoperiod was changed from 12-h to 24-h (i.e., continuous light), which resulted in drop in the instantaneous photosynthetic rates. Switching back to 12 h at day 61 allowed photosynthetic rates to slowly increase. A similar effect was observed between days 75 and 77 (source: Wheeler et al., 2008a).

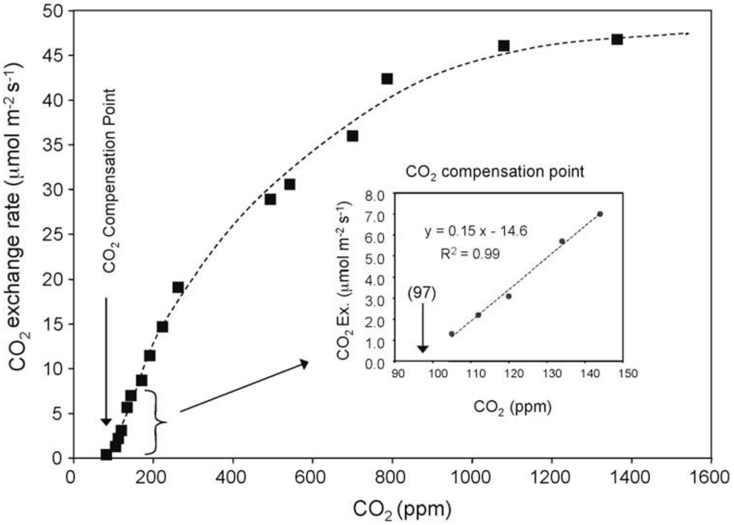

Figure 17.15: Carbon dioxide exchange rate (net photosynthetic rate) of a 20 m^2 potato stand at different CO_2 concentrations. The photosynthetic rates saturated above 1200 ppm while the CO_2 compensation point occurred at 97 ppm (source: Wheeler et al., 2008a).

was returned to 12 h, photosynthetic rates increased again. This suggested some feedback inhibition on instantaneous photosynthetic rates under the long photoperiod (Wheeler et al., 2008a). A fourth observation was that photosynthetic rates of potato stands showed a classic C_3 response to CO_2, where rates increased rapidly as CO_2 was increased up to ~400–500 ppm and saturated near ~1200 ppm (Drake et al., 1997; Wheeler et al., 2008a) (Figure 17.15).

During these same closed chamber studies, concentrations of ethylene gas could be monitored throughout growth and development. Ethylene is a plant hormone that is produced during normal metabolism (Abeles et al., 1992) but it can accumulate in tightly closed atmospheres. Ethylene production by potato stands was generally low in comparison to wheat, soybean, and lettuce but even a relatively low concentration of 40 ppb caused epinasty in young expanding leaves (Wheeler et al., 2004) (Figure 17.16). When 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} stand area 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 transpiration rates for 20 m^2 stands using the NFT approach ranged from 3.4 to 5.2 L m^{-2} day^{-1} (3.4–5.2 mm day^{-1}) throughout growth, while maximum rates for canopies exceeded 9 L m^{-2} day^{-1}, or 9 mm day^{-1} (Figure 17.17) (Wheeler, 2005; Wheeler et al., 2008a). Higher transpiration rates occurred at higher PAR but it is not clear whether this was due to increased leaf

Figure 17.16: Epinastic potato leaves on secondary branches that developed in an atmosphere containing about 40 ppb ethylene (source: Wheeler et al., 2004).

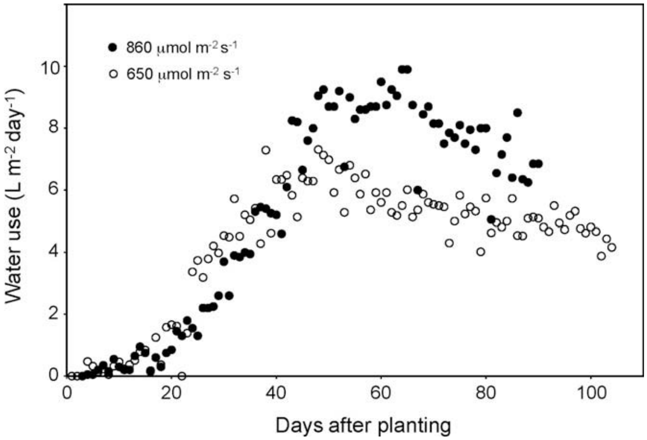

Figure 17.17: Water use (transpiration) of 20 m^2 potato stands grown at different PAR (light) intensities. Peak rates exceeded 9 $L\,m^{-2}\,day^{-1}$ (9 $mm\,day^{-1}$) under high PAR.

temperatures, increased stomatal opening, or both. As with stand CO_2 exchange, time course measurements of transpiration 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 (Figure 17.17).

Figure 17.18: Tuber yields from cv Norland plants grown under 12 h (3.6 kg) and 24 h (4.9 kg) photoperiods of 400 μmol m^{-2} s^{-1} PAR. Plants were harvested at 147 days.

17.8 Potatoes for Food in Space

There will be no ‘growing seasons’ in space and crop cultivation can be continuous. Thus estimating yield rates or productivities (g m^{-2} day^{-1}) is more meaningful than traditional yield per unit area (g m^{-2}, t ha^{-1}, etc.). These productivities can then be used to estimate the crop area needed to meet the food and oxygen requirements for a given number of people. An additional consideration is when to harvest. Sequential harvests with cv. Norland plants showed that yields continued to increase up to 148 days but that maximum productivity (i.e., g m^{-2} day^{-1}) 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 kg $plant^{-1}$ and 4.3 kg $plant^{-1}$ fresh mass under 12-h photoperiod and continuous light, respectively (Figure 17.18). This equaled 0.57 kg $plant^{-1}$ and 0.79 kg $plant^{-1}$ dry mass (DM) with 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 and area of 0.2 m^2 using screen cages, plants received 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 (Figure 17.19). When this was done with cv. Norland, productivities were 21.9 g DM m^{-2} day^{-1} at 110 days (Wheeler and Tibbitts, 1989), which is 23% less than the 28.5 g DM m^{-2} day^{-1} observed with

Figure 17.19: Ann Fitzpatrick of the University of Wisconsin taking leaf photosynthetic measurements from a closed stands of potatoes in a large growth room at the Biotron.

individually caged plants harvested at a similar age (Wheeler and Tibbitts, 1987). This points out the importance of getting accurate measurements of harvested areas and light provided to the plants.

Follow-up studies were conducted with cv. Denali using stands where only the center plants were harvested. Plants in the first study were given short days for the first 40 days to initiate strong tuber sinks followed by continuous light for 92 days to promote tuber bulking (Wheeler, 2006). Plants were spaced closely (0.02 m^2 $plant^{-1}$) and grown at lower light for the first 18 days to reduce overall area use, after which they were transplanted to larger pots spaced at 0.25 m^2 $plant^{-1}$ 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 17.1). These yields are roughly twice that for record field yields (Knowles and Thornton, 2000). Adjusting for the reduced area requirement prior to transplanting, the tuber productivity in this study was 37.5 g DM m^{-2} day^{-1} (Table 17.1). 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 17.1) (Wheeler, 2006). When a second study was conducted but with a 12-h photoperiod for 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.

Assuming one human requires about 2500 kcal day^{-1} and there are ~3.7 kcal g^{-1} DM 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 $person^{-1}$ day^{-1} by 141 kcal m^{-2} day^{-1} ≈ 17.8 m^2 of potatoes would be required to continuously provide the food (dietary energy) for one person (Wheeler, 2006). 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

Table 17.1: Some high yields from potatoes grown in controlled environments (source: Wheeler, 2006)

	Study Duration	Tuber FM	Tuber DM	Total DM Productivity	Tuber DM Productivity	PAR	Radiation Use Efficiency (Total)	Radiation Use Efficiency (Tuber)
	(days)	(kg m^{-2})	(kg m^{-2})	(g m^{-2} day^{-1})	(g m^{-2} day^{-1})	(mol m^{-2} day^{-1})	(g mol^{-1})	(g mol^{-1})
Univ. Wisconsin (12 h photperiod)	132	18.01	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

FM = fresh mass; DM = dry mass; PAR = photosynthetically active radiation.

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 17.1); 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 $person^{-1}$ day^{-1}) / 63.9 g CO_2 m^{-2} day^{-1} $\approx$ 15.6 m^2 of potatoes 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).

17.9 Spaceflight Testing

With the relatively short supply line to spacecraft in low-Earth orbit, food can be replenished easily 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, including potatoes (Levinskikh et al. 2000; Musgrave 2002; Nechitailo and Mashinsky, 1993; Stutte et al., 2005). The first potato study involved flying 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 (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 enlarged (Kordyum et al., 1997). The third experiment used excised leaves with axillary buds to determine whether photosynthetically driven tuber formation could occur under space flight conditions (see Ewing, 1985; Wheeler et al., 1988a). 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 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 $\mu mol\ m^{-2}\ s^{-1}$ PAR (Croxdale et al., 1997). In-flight data showed that CO_2 concentrations in the chamber rose in the dark, and then drew down to a set-point of 500 $\mu mol\ mol^{-1}$ during the light, indicating the leaves were respiring and photosynthetically active (Brown et al., 1997). After 16 days in space the leaves had senesced significantly but tubers developed at all five leaf axils (Figure 17.20) (Cook et al., 1998; Croxdale et al., 1997). The size and shape of tubers from space were similar to those grown in a ground

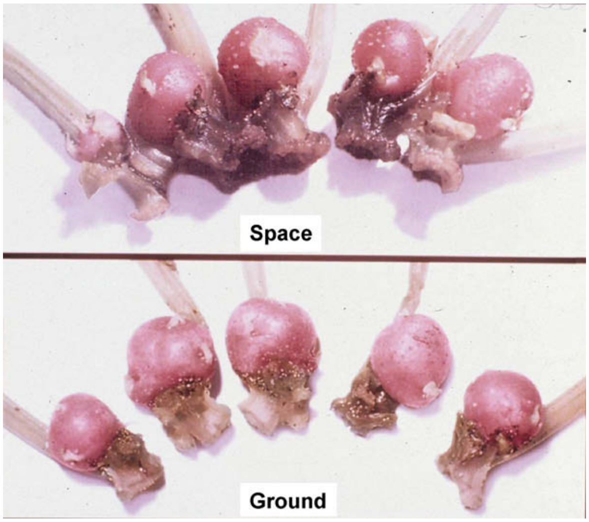

Figure 17.20: Potato tubers (1.5 cm in diameter) formed at the axils of leaf cuttings sent into space for 16 days on NASA's Space Shuttle (source: Croxdale et al., 1997; Tibbitts et al., 1999). Tubers formed in the μ-gravity environment of space with no negative effects.

control chamber, as were the distributions of starch grains and proteinaceous crystals (Cook and Croxdale, 2003). There were more small starch grains in the space-grown tubers (Cook et al., 1998; Croxdale et al., 1997), similar to results reported in experiments on the Russian Mir Space Station by Kordyum et al. (1997). Collectively the results indicate that gravity is not required for tuber formation.

17.10 Bioregenerative Systems for the Future in Space

It is still unclear whether electric lamps, direct solar lighting, or some combination of the two will be used for crops in space. The use of solar lighting will depend on the setting: For example, on the moon there are roughly 14 days of dark and 14 days of light (Salisbury, 1991). On Mars, the diurnal cycle is 24.6 h, similar 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, 1991; Wheeler, 2004). In addition, techniques for capturing solar 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 selecting optimal color combinations of LEDs for growing plants needs further study (Bula et al., 1991; Goins et al., 1997).

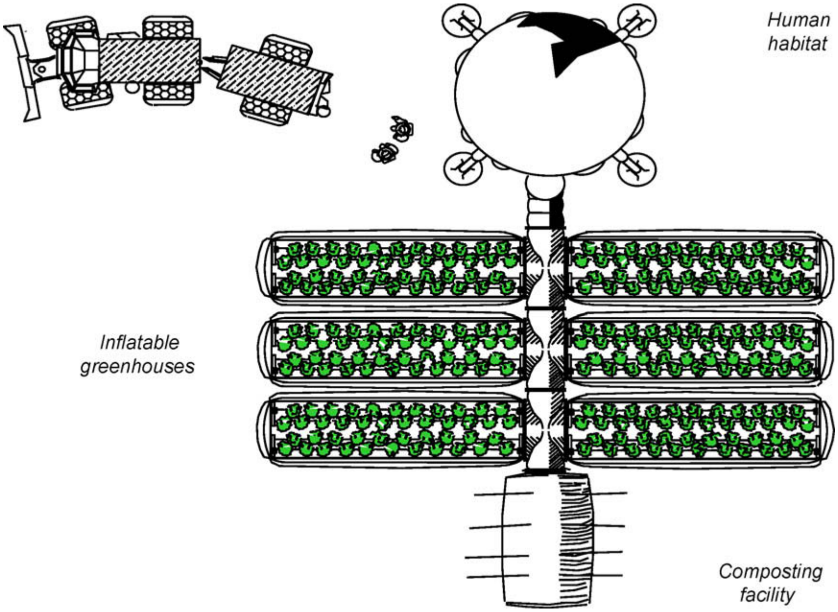

Figure 17.21: A concept for inflatable greenhouses (overhead view) that might be deployed on the surface of Mars (source: Sadler and Giacomelli, 2002). Inflatable structure are light weight and could be stowed in a small volume, but will require materials that are air tight, transparent, and tolerant of the UV radiation on the surface of Mars.

The costs associated with lighting tend to be the major economic factor in trade studies of plant-based life support approaches (Drysdale et al., 2003). For example, highly productive plant systems for life support might require about 200 W m^{-2} (~1000 μmol m^{-2} s^{-1}) of photosynthetically active radiation (PAR) (Wheeler et al., 2001). Assuming a lighting system is 20% efficient for converting electric power to PAR reaching the plants (Cathey and Campbell, 1977), then1 kW of electric power would be required per m^2 of plant growing area. Studies done to date with planting of multiple species indicate that about 50 m^2 of plant growing area would be required to meet the food needs (daily calories) for one human (Gitelson et al., 1989; Tako et al., 2005; Wheeler et al., 2001), thus 50 m^2 $person^{-1} \times 1$ kW $m^{-2} = 50$ kW $person^{-1}$ just for the electric lighting. This does not include the power for cooling, air circulation, water pumps, sensors, etc., which might double the number to 100 kW $person^{-1}$. Thus hundreds of kilowatts or perhaps even megawatts of power might be required for large, plant based life support systems with electric lighting. Alternatively, solar light might be used. This would cut the electric power requirements significantly but would require a means for delivering the light into the protected growing environment. This might be possible with transparent structures, such as inflatable 'greenhouses' (Figure 17.21) or perhaps solar collectors connected to fiber optic or light conduits (Figure 17.22) (Cuello et al., 2000; Sadler and Giacomelli, 2002; Wheeler, 2004). The former approach would require durable transparent materials that are gas tight, resistant

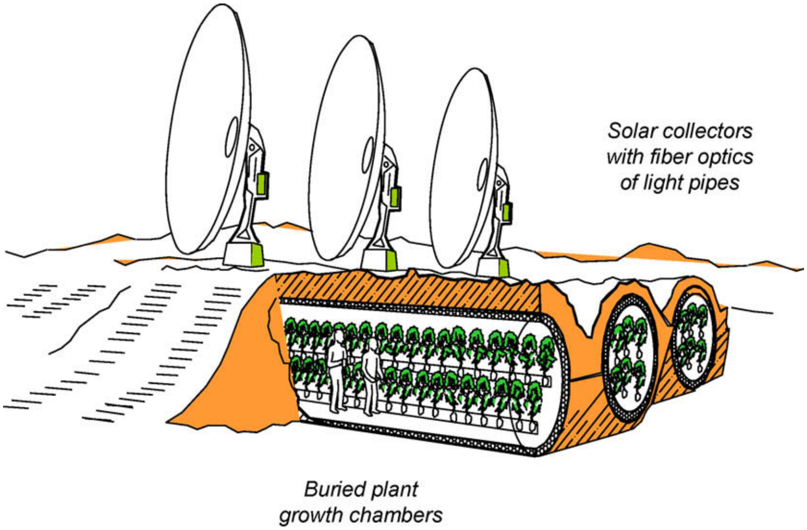

Figure 17.22: A concept of plant growth chamber covered with surface regolith for radiation shielding. Light could be collected with solar concentrators and piped into the plant chamber (source: Sadler and Giacomelli, 2002).

to the high energy radiation of space, and provide at least some thermal insulation (Clawson et al., 2005). These are substantial challenges but might be assisted by dropping the internal atmospheric pressure to reduce the force on the structure and/or by using external covers at night to provide insulation (Boston, 1981). Regardless of the configuration, solar lighting approaches would be possible only in settings that receive sufficient light. Use of solar lighting only at low latitudes on the Moon would not be practical because of the long (14-day) dark period (Salisbury, 1991). But at higher latitudes, such as the rim of Shackleton Crater on the South Pole of the Moon, sunlight is available for all but a few days each month and use of solar light for plant cultivation should be possible. Mars receives only 43% of the sunlight that reaches Earth and has a diurnal rotation cycle similar to Earth's (Salisbury, 1991). In addition, certain areas of Mars are prone to dust storms, which would interfere with transparent structure and solar collector approaches. Nonetheless, analyses of dust events and light transmittance data from Mars suggest that some Martian settings receive up to 25 to 30 mol m^{-2} day^{-1} of PAR (Clawson, 2007), which is comparable to many settings on Earth (Albright et al., 2005). Dealing with these various lighting constraints will pose an interesting challenge for agriculture engineers of the future.

17.11 Concluding Comments

Findings from controlled environment studies for NASA were consistent with many previous physiological studies with potatoes, but also revealed some interesting phenomena, including physiological intolerance of some cvs. 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 potatoes will one day supply food and oxygen to humans living on other planets, just as they have for hundreds of years on Earth.

Acknowledgments

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