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Gas exchange rates of potato stands for bioregenerative life support

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Abstract

Plants can provide a means for removing carbon dioxide (CO_2) while generating oxygen (O_2) and clean water for life support systems in space. To study this, 20 m^2 stands of potato (*Solanum tuberosum* L.) plants were grown in a large (113 m^3 vol.), atmospherically closed chamber. Photosynthetic uptake of CO_2 by the stands was detected about 10 DAP (days after planting), after which photosynthetic rates rose rapidly as stand ground cover and total light interception increased. Photosynthetic rates peaked ca. 50 DAP near 45 μmol CO_2 m^{-2} s^{-1} under 865 μmol m^{-2} s^{-1} PPF (average photosynthetic photon flux), and near 35 μmol CO_2 m^{-2} s^{-1} under 655 μmol m^{-2} s^{-1} PPF. Short term changes in PPF caused a linear response in stand photosynthetic rates up to 1100 μmol m^{-2} s^{-1} PPF, with a light compensation point of 185 μmol m^{-2} s^{-1} PPF. Comparisons of stand photosynthetic rates at different CO_2 concentrations showed a classic C_3 response, with saturation occurring near 1200 μmol mol^{-1} CO_2 and compensation near 100 μmol mol^{-1} CO_2. In one study, the photoperiod was changed from 12 h light/12 h dark to continuous light at 58 DAP. This caused a decrease in net photosynthetic rates within 48 h and eventual damage (scorching) of upper canopy leaves, suggesting the abrupt change stressed the plants and/or caused feedback effects on photosynthesis. Dark period (night) respiration rates increased during early growth as standing biomass increased and peaked near 9 μmol CO_2 m^{-2} s^{-1} ca. 50 DAP, after which rates declined gradually with age. Stand transpiration showed a rapid rise with canopy ground cover and peaked ca. 50 DAP near 8.9 L m^{-2} d^{-1} under 860 μmol m^{-2} s^{-1} PPF and near 6.3 L m^{-2} d^{-1} under 650 μmol m^{-2} s^{-1} PPF. Based on the best photosynthetic rates from these studies, approximately 25 m^2 of potato plants under continuous cultivation would be required to support the CO_2 removal and O_2 requirements for one person.
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1. Introduction

The potential of plants for removing carbon dioxide (CO_2) and generating oxygen (O_2) for space life support systems has been studied for nearly 50 years (Myers, 1954; Gitelson et al., 1976; Salisbury, 1991). Through the process of photosynthesis, plants harvest light energy, which produces O_2 and biochemical energy (NADPH and ATP); the NADPH and ATP are then used to fix CO_2 into carbohydrate and other organic compounds (Govindjee and Coleman, 1990). By choosing plants that produce edible biomass (i.e., crops), they can also provide food. In addition, plant transpiration can be used as part of a water purification process, where for example, pre-treated waste water is fed to the crop production system and the resultant humidity from transpiration condensed as a source of clean water (Wolverton et al., 1983).

Characterizing plant gas exchange for life support can be achieved either directly or indirectly, depending on the experimental facilities and capabilities. The indirect approach involves growing plants and weighing the dry biomass at harvest. The carbon content of the biomass can then be determined and the equivalent amount of CO_2 needed to produce that biomass calculated (Wheeler, 1996). This approach is convenient but cannot monitor real-time responses to environmental perturbations or

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manipulations, such as temporary changes in light, photoperiod, CO_2 concentrations, etc., nor can it provide details on changes in gas exchange related to crop growth and development. On the other hand, direct measurements can track the effects of short-term events and system failures, as well as changes in gas exchange rates throughout crop growth. These can be taken by sampling individual leaves throughout the stand at regular intervals, which can then be used to estimate the whole stand rates, or by enclosing the entire stand inside a controlled environment chamber and measuring gas fluxes directly (Coombs et al., 1985). Measurements using the latter approach are less equivocal and have been reported for several crop species suggested for life support, including wheat (Bugbee and Monje, 1992; Wheeler et al., 1993; Monje and Bugbee, 1998; Barta and Henderson, 1998), lettuce (Knight and Mitchell, 1988; Wheeler et al., 1994), soybean (Dougher and Bugbee, 1997; Tako et al., 2001a; Wheeler et al., 2004), and rice (Tako et al., 2001a,b), as well as related crops such as aubergine (Hand et al., 1993).

Potato is often suggested as a crop for space life support applications (Tibbitts and Alford, 1982; Tibbitts et al., 1994; Masuda et al., 2005; Wheeler, 2006) and was the focus of several large-scale studies conducted at NASA's Kennedy Space Center from 1991 through 1996 (Stutte et al., 1999; Wheeler et al., 2003). Some data from these studies have been reported (Stutte et al., 1999; Wheeler et al., 2003; Wheeler, 2006), but complete details on CO_2, PPF (photosynthetic photon flux), and photoperiod effects on gas exchange rates from these studies have not been published. These findings can be used to develop management approaches with potato as a crop for bioregenerative life support systems in space.

2. Materials and methods

2.1. Plant chamber description

The Biomass Production Chamber located at Kennedy Space Center, FL, USA is a cylindrical steel vessel that was formerly used for hypobaric testing during NASA's Mercury and Gemini Programs (Prince and Knott, 1989). The chamber is 3.7 m in diameter, 7.5 m high, and is divided into upper and lower halves with two plant growing levels in each half (Fig. 1). Each of the four plant growth levels supports 16 trapezoidal-shaped plastic (acrylonitrile-butadiene-styrene) trays having a rooting area of 0.25 m^2 each. However, when the space between trays and the tendency of shoots to lean over the edges of the trays are considered, the effective canopy area of the chamber at full coverage was approximately 20 m^2 (0.3125 m^2 per tray). The entire atmospheric volume for both the upper and lower halves of the chamber including air ducting is 113 m^3.

Lighting for plant growth was provided by 96, 400-W high-intensity discharge (HID) lamps (3 lamps per 2 trays) separated from the plants by Pyrex glass barriers. High-pressure sodium (HPS) lamps (Philips Ceramalux, Philips Lighting Corp., Bloomfield, NJ, USA or GE Lucalox, General Electric, Cleveland, OH, USA) and metal halide (MH) lamps (Venture Pro-Arc, Venture Lighting, Cleveland, OH, USA) were used in the first study, and HPS only were used in the second and third studies (Table 1).

Fig. 1. NASA's Biomass Production Chamber located at Kennedy Space Center, Florida, USA. The chamber provided a closed atmospheric volume of 113 m^3 and 20 m^2 of growing area to study crops for life support applications.

Air circulation was provided by two 30-kW blowers (one each for the upper and lower halves of the chamber) connected to the chamber by steel ducting (Fig. 1). Motors were mounted external to the air ducts to minimize possible gaseous contaminants from electrical and lubricated components. The air handling systems provided three to four air exchanges (400 m^3) per minute with air velocities ranging from 0.2 to 1.5 m s^{-1} approximately 25 cm above the plant canopy. Heat rejection and humidity control were provided by a copper, chilled-water coils located after each blower. For the first few days in each study, supplemental humidification was provided by atomized streams of de-ionized water sprayed directly into the air ducts (Fig. 1).

Table 1
Lighting conditions for the three gas exchange studies with potato plants

Study	Lamp type	PPF (μmol m^{-2} s^{-1})	Photoperiod (h)	Daily PPF (mol m^{-2} d^{-1})
1	HPS/MH[a]	655	12	28.3
2	HPS	865	12	37.4
3	HPS	915	12[b]	42.2

[a] 2/3 of the lamps were high pressure sodium (HPS), 1/3 were metal halide (MH).

[b] Photoperiod switched to 24/0 for days 58, 59, and 60.

Fig. 2. Potato plants (35 days old) growing inside NASA's Biomass Production Chamber. Two of the four growing shelves are shown in the photo. Each shelf provided 5 m^2 of area.

2.2. Hydroponic growing system

Plants were grown using a nutrient film technique where solution was maintained about 0.5 cm deep and supplied at a rate of 1.0 to 1.5 L min^{-1} to each tray (Wheeler et al., 1990) Fig. 2. Each of the four growing levels was supplied by a separate external reservoir with the headspace atmospherically connected to the main chamber. Nutrient solution volume for each level was approximately 225 L, with 185 L in the reservoir and approximately 40 L in the trays and plumbing. A modified 1/2 Hoagland solution with nitrate as the only N source was used (Hoagland and Arnon, 1938). Solution pH in all systems was maintained automatically near 5.8 using 0.4 M nitric acid. Solution electrical conductivity (EC) was maintained automatically at a minimum of 0.12 S m^{-1} with additions of a complete stock solution. Solution volumes in each reservoir were adjusted to 225 L with de-ionized water added manually each day (typically from 08:00 to 09:00).

2.3. Plant cultural procedures

Potato plants (*Solanum tuberosum* L.) cvs. Denali (1/2 of plants for first study) and Norland (1/2 of plants for first study and all plants for second and third studies) were propagated as nodal plantlets maintained on a modified Murashige-Skoog mineral medium with 0.7% agar, 2% sucrose, and no growth regulators (Tibbitts et al., 1994). Plantlets were grown under fluorescent lighting at 100 μmol m^{-2} s^{-1}, a 16-h photoperiod, and 23 °C. After approximately 28 days in vitro, plantlets were transplanted to the hydroponic culture trays covered with white-on-black polyethylene plastic sheets (Wheeler et al., 1990). Agar medium was rinsed from the roots and individual plantlets were wrapped in pliable, polyurethane foam plugs and placed in holes of the plastic sheets covering the hydroponic trays. Three plantlets were placed in each 0.3125 m^2 tray. At about 10 DAP (days after planting), one plant was culled from each tray leaving two plants per tray, or 6.4 plants m^{-2}. All trays were covered with white translucent covers for the first 72 h to maintain high humidity around the transplants.

2.4. Environmental conditions

For the first 3 days in each study, incident PPF (photosynthetic photon flux) was only about 15% of normal incident because of the shading by the germination covers. PPF readings were taken weekly with a quantum sensor (LiCor 185) at the top of the plant canopy at the center of each of the 16 trays on each of the four growing levels. Depending on the combination of metal halide and high-pressure sodium lamps used (see Yorio et al., 1995), instantaneous PPF values for the three studies averaged 655, 866, and 917 μmol m^{-2} s^{-1}, and daily PPF values averaged 28.3, 37.4, and 42.2 mol m^{-2} d^{-1}, respectively (Table 1). Lamps were cycled to provide a 12 h light (06:00 to 18:00) and 12 h dark (18:00 to 06:00) photoperiod. Previous studies suggest that increasing the photoperiod later in growth (after 56 DAP) can increase final tuber yields in potato (Wheeler and Tibbitts, 1997); hence four changes to the photoperiod were imposed during the third study to observe the effects on gas exchange rates: At day 58, the photoperiod was switched to 24 light/0 dark and then switched back to 12 h light and 12 h dark at day 61 (72 h duration); on day 64 to 16/8, and then back to 12/12 at day 65 (48 h duration); on day 68 to 20/04, and then back to 12/12 on day 69 (48 h duration); and on day 75 to 24/0, and then back to 12/2 on day 76 (48 h duration).

Temperature in the first study was maintained at 22 °C for the first 25 days and then dropped to 18 °C through day 105. Temperature for the second study was maintained at 20 °C in the light and 16 °C in the dark through day 90. Temperature in the third study was maintained at 20 °C in the light and 16 °C in the dark until day 58, after which the temperature was maintained at a constant 16 °C through day 105. Relative humidities were maintained near 70% for all of the studies, which resulted in vapor pressure deficits of 0.79, 0.70, 0.62, and 0.55 kPa for 22, 20, 18, and 16 °C, respectively.

Carbon dioxide concentrations were controlled at a minimum of 1000 μmol mol^{-1} (0.1 kPa) during the light cycle by automatic CO_2 additions. No attempts were made to suppress CO_2 increases from respiration during the dark cycles, which often exceeded 2000 μmol mol^{-1} by the end of the dark period. Likewise, no attempt was made to prevent oxygen (O_2) build-up during light cycles. However, O_2 concentrations seldom exceeded 22% because the chamber

was commonly entered daily for maintenance activities (normal ambient O_2 level is about 20.9%, or 20.9 kPa).

2.5. Gas exchange measurements

Beginning at about 10 DAP, CO_2 concentration showed a repeating pattern of dark-period increase followed by light period (''morning'') drawdown to the 1000 μmol mol^{-1} set point. The rates of stand respiration and photosynthesis could be calculated from the increase of CO_2 during the dark and subsequent drawdown in the light, i.e., closed gas exchange system measurements (Wheeler, 1992). (Note, ''stand'' is a more appropriate term than ''canopy'' for these types of measurements, since the data include contributions from roots and root-zone microflora, as well as from shoots; Hand et al., 1993). When the chamber was sealed, atmospheric leakage rate was approximately 10% vol. day^{-1} or 0.42% vol. h^{-1}. At this leakage rate, loss of CO_2 from the chamber at a set-point of 1000 μmol mol^{-1} amounted to only 0.2 μmol m^{-2} s^{-1} and hence was ignored for gas exchange calculations. Evapotranspiration (ET) rates were measured daily from condensed water collected from the heat exchange systems (cold coils) and also from the daily additions of make-up water, nutrient stock solution, and acid to each of the four nutrient systems. All gas exchange rates were calculated for the chamber as a single unit and based on a stand area of 20 m^2. On several occasions PPF levels were dimmed to different settings for 1-h intervals to study the effects on stand gas exchange rates. Gas exchange responses to CO_2 concentration were also studied by temporarily shutting off the CO_2 control system during the light period (at full light intensity) and allowing the plant stand to draw the CO_2 concentration down over several hours to a compensation point. The first derivative of this drawdown curve was then calculated to estimate net photosynthetic rates across the range of CO_2 concentrations (Wheeler, 1992).

3. Results and discussion

Net photosynthesis (CO_2 uptake) and night respiration (CO_2 production) data for the first (655 μmol m^{-2} s^{-1} PPF) and second (865 μmol m^{-2} s^{-1} PPF) studies are shown in Fig. 3. Beginning at about 10 DAP, net photosynthesis of the stands was detectable. Following this, photosynthetic rates increased rapidly as canopy cover and total light interception increased (Fig. 3). This observation is consistent with field and related controlled environment studies that demonstrated a close linkage between ground cover, total light interception, and growth of potato crops (Khurana and McLaren, 1982; Haverkort et al., 1991; Klassen et al., 2003). Although canopy cover was nearly complete (100%) ca. 35 DAP, net photosynthetic rates continued to increase as the canopy grew closer to the lamps and the incident PPF at the upper canopy increased. Photosynthetic rates peaked near 36 μmol CO_2 m^{-2} s^{-1} in the first study around 40 days, remained relatively constant until about 65 days and then gradually declined as the stand matured (Fig. 3). Photosynthetic rates in the second study with a higher PPF peaked near 45 μmol CO_2 m^{-2} s^{-1} around 50 days, remained relatively constant until about 70 days and then gradually declined as the stand matured (Fig. 3). Related field studies with potato stands using either fixed sun-lit chambers or portable transparent enclosures reported peak net photosynthesis rates between 31 and 32 μmol CO_2 m^{-2} s^{-1} (Bhagsari et al., 1988; Vos and Groenwold, 1989; Fleisher et al., 2006), but these tests were carried out with 350–370 μmol mol^{-1} CO_2, which would result in reduced rates compared to the 1000 μmol mol^{-1} CO_2 used in our studies. Studies in which aubergine (eggplant) stands were enclosed in clear chambers in a glass house reported peak rates near 45 μmol CO_2 m^{-2} s^{-1} when measured at 900 μmol m^{-2} s^{-1} PPF and elevated CO_2—conditions very similar to our studies (Hand et al., 1993).

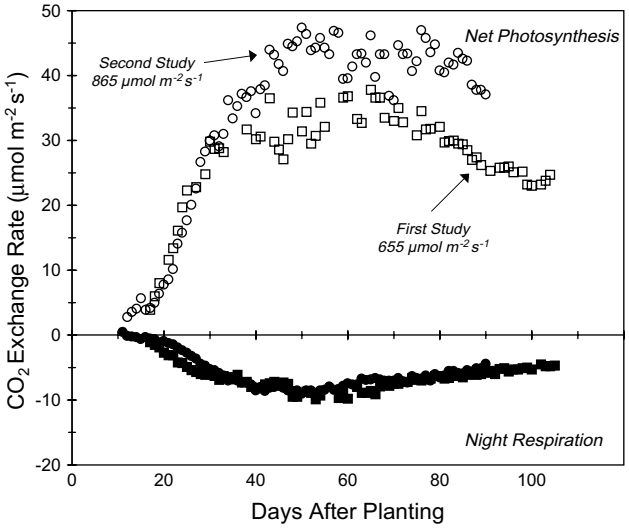

Fig. 3. Net photosynthesis (open symbols) and dark period respiration (filled symbols) of 20 m^2 potato stands throughout growth and development. Average photosynthetic photon flux for the first study was 655 μmol m^{-2} s^{-1} and for the second study was 865 μmol m^{-2} s^{-1}.

Although the peak photosynthetic rates in our studies were quite high, even higher rates of 60 and 70 μmol CO_2 m^{-2} s^{-1} have been measured for wheat stands grown under CO_2 enrichment and PPFs of 1400 and 2000 μmol m^{-2} s^{-1}, respectively (Bugbee and Monje, 1992; Monje and Bugbee, 1998). Whether such high PPFs could be used to increase photosynthetic rates of potato stands is unknown. Wheat canopies with their vertically inclined leaves seem to adapt well to high irradiance by developing high leaf area indices while maintaining relatively low light extinction coefficients (Bugbee, 1990; Bugbee and Monje, 1992). Thus light can penetrate deeper into the canopy allowing more efficient use of high irradiance. In contrast, potato canopies with their more horizontal leaves typically have higher light extinction coefficients (up to 1.0 in controlled environments, Wheeler and Tibbitts, unpublished). As a consequence, most of the incident

light is absorbed by the upper leaf layers, which become photosynthetically saturated.

Night respiration rates for the first and second studies rose steadily from day 15 to day 40, reaching a peak of 9.1 μmol m^{-2} s^{-1} in the first study and 8.9 μmol m^{-2} s^{-1} in the second study. Respiration rates remained relatively constant until about day 60, and then gradually declined as the stands matured (Fig. 3). Respiration rates for wheat stands grown under similar conditions but at a daily PPF 50 mol m^{-2} d^{-1} reached approximately 15 μmol CO_2 m^{-2} s^{-1} (Wheeler et al., 1993), while respiration of wheat stands grown at a much higher irradiance of 145 mol m^{-2} d^{-1} reached nearly 30 μmol m^{-2} s^{-1} (Bugbee and Monje, 1992). These examples demonstrate the strong influence of the native lighting environment on standing biomass and respiration rates.

The steady rise in respiration during early growth was likely linked to the steady increase in biomass and its associated "growth respiration" during this stage of development (Amthor, 2000). After day 60, shoot growth slowed and tuber bulking dominated biomass gains, and the slow decline in respiration after this likely reflects the diminished growth respiration component and a gradual shift to lower cost "maintenance respiration" (Amthor, 2000).

A plot of CO_2 exchange rates showing net photosynthesis and night respiration for the third study is shown in Fig. 4. As with the previous two studies, photosynthesis rose rapidly as canopy cover and light interception increased, with rates leveling off near 42 μmol CO_2 m^{-2} s^{-1} around 45 days after planting. Unlike the previous two studies, the photoperiod was changed from 12 h light/12 h dark to continuous light at day 58 (for 3 days) and then again at day 75 (for 2 days). The original intent of this change was to maintain continuous light from day 58 until the end of the study to increase final tuber yields (Wheeler and Tibbitts, 1997). But it was apparent that this change stressed the potato stand, as shown by a 35% drop in instantaneous photosynthesis rates that followed (Fig. 4). After 3 days of continuous light we chose to go back to a 12/12 photoperiod, which resulted in a 19% increase in photosynthetic rate. The change to continuous light was repeated at day 75 and maintained for 2 days to see if a similar response would occur (Fig. 4). As with the previous change, the photosynthetic rates dropped immediately (25%) following the switch to continuous light, and then increased (14%) following the return to a 12/12 photoperiod. Following each change to continuous light and subsequent return to 12/12, there was an increase in night respiration, which may be a consequence of increased carbon pools in the plant tissue from the continuous light. Note that no night respiration measurements were possible during the continuous light treatment and respiration measurements could only be resumed upon return to a 12/12 photoperiod (Fig. 4).

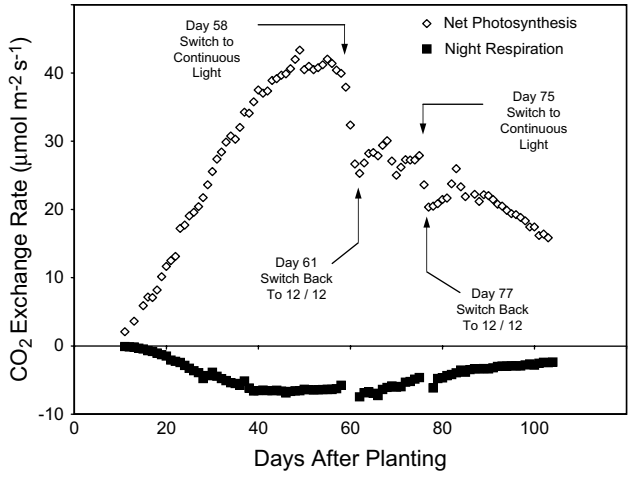

Fig. 4. Net photosynthesis (open symbols) and dark period respiration (filled symbols) of 20 m^2 potato stand throughout growth and development. Photoperiods were changed several times throughout the study to track the effects on instantaneous photosynthetic rates and dark period respiration.

In addition to the changes to continuous light on days 58 and 75, the photoperiod was increased from 12/12 to 16/8 on days 64 and 65, and then back to 12/12, and then again to 20/04 on days 68 and 69, followed by a return to 12/12. A slight decrease in photosynthetic rate seemed to occur on day 66 following the 2 days at 16/8, while a more noticeable decrease occurred on days 70 and 71, following the change to a 20/04 photoperiod (Fig. 4). Collectively, these results showed that long photoperiods decreased the instantaneous net photosynthetic rates, which may be due in part to increased background respiration. It is also possible that carbohydrate accumulation during the long photoperiods directly suppressed photosynthetic rates through feedback effects (Azcon-Bieto, 1983; Stutte et al., 1996), but no measurements (e.g., leaf starch content) were taken to confirm this.

Although extending the photoperiod from 12 h to 24 h dropped the instantaneous photosynthetic rates 35%, the additional 12 h of light each day would still increase the daily totals of CO_2 removed and O_2 produced. But the radiation use efficiency for gas exchange (i.e., CO_2 removed per unit of light provided) decreased under the long photoperiods. Thus if a life support system has ample power for electric lighting, long photoperiods could be used to increase gas exchange and reduce the amount of planted area, but if energy is limited, shorter photoperiods would be more efficient for a crop like potato.

On several occasions PPF levels were changed for 1-h intervals and the stand net photosynthetic responses were monitored. An example of such a test conducted at 50 DAP in the second study is shown in Fig. 5. The results show a linear response in stand CO_2 exchange vs. light intensity up to nearly 1100 μmol m^{-2} s^{-1} PPF. In this case, the light (PPF) compensation point (x-intercept) occurred near 185 μmol m^{-2} s^{-1} (Fig. 5). This indicates that a PPF of 185 μmol m^{-2} s^{-1} was required to offset the background (dark) respiration of the standing biomass before any net photosynthesis occurred. Light compensation points up

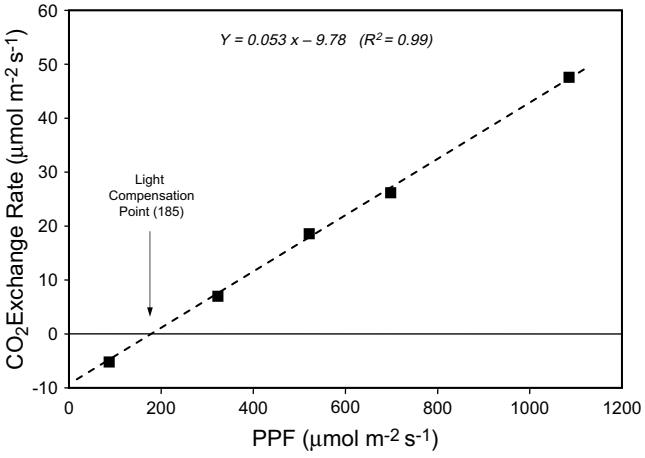

Fig. 5. Net photosynthesis rates of a 20 m^2 potato stand in response to different photosynthetic photon flux (light intensity). The test was conducted at 50 days after planting.

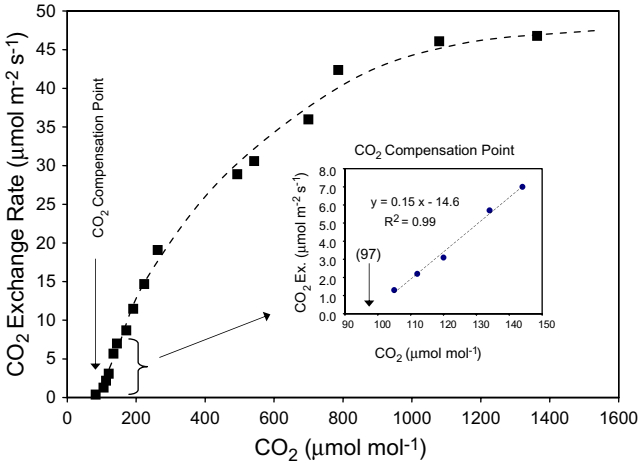

Fig. 6. Net photosynthesis rates of a 20 m^2 potato canopy at different concentration of atmospheric CO_2. The test was conducted at 62 days after planting by shutting off the CO_2 supply for the chamber and allowing the stand to draw the CO_2 concentration down to a compensation point. The net photosynthetic rates were calculated as the first derivative (slope) of the CO_2 drawdown sequence.

to ~140 µmol m^{-2} s^{-1} were reported for stands of aubergine grown in clear enclosures placed in a glasshouse (Hand et al., 1993), while a compensation point of 190 µmol m^{-2} s^{-1} was reported for a wheat stand grown at 38.5 mol m^{-2} d^{-1} (Wheeler et al., 1993), which is similar to the irradiance in our studies with potato. In contrast, light compensations points for wheat stands grown under very high irradiance (~145 mol m^{-2} d^{-1}) were near 600 µmol m^{-2} s^{-1} (Bugbee, 1990). Thus crops that develop under high irradiance and generate large amounts of biomass will have high stand respiration rates, which in turn result in high light compensation points.

The light response data in Fig. 5 indicate that during this stage of growth the stand was not light-saturated even at 1100 µmol m^{-2} s^{-1} PPF. But it is important to note that these tests only measured short-term responses to changes in PPF, and longer duration changes in PPF (e.g., days or weeks) would likely cause adjustments in overall standing biomass and background respiration levels. For example, Wheeler et al. (1993) reported a rapid drop in net photosynthesis of a 20 m^2 wheat stand following a reduction in PPF, but that net photosynthetic rates gradually increased at the lower PPF over the next week as dark respiration rates decreased. This suggested that the wheat stand acclimated to the new PPF environment, perhaps through senescence of leaves lower the canopy under the lower PPF (Wheeler et al., 1993).

An interesting capability of atmospherically closed chambers is that the CO_2 supply can be turned off temporarily and the "drawdown" of CO_2 concentration tracked over time. Provided the drawdown is sufficiently slow to allow stomatal adjustment to the changing CO_2 concentration, the slope (first derivative) from this drawdown can be used to calculate the photosynthetic rate across that entire range of CO_2 concentration (Wheeler, 1992). An example of such a test conducted on day 62 in the second study is shown in Fig. 6. The results show a classic C_3 photosynthetic response and confirm at the stand level what has been reported from single leaf measurements with potato for many years (Chapman and Loomis, 1952; Ku et al., 1977). The findings showed that saturation of stand photosynthesis occurred near 1200 µmol mol^{-1} in this study, while the CO_2 compensation point (Γ) occurred at 97 µmol mol^{-1} (Fig. 6). Similar results were observed in drawdown tests from the other studies (data not shown).

In contrast to light compensation points, which are strongly dependent on the standing biomass and background respiration, CO_2 compensation points at a given temperature should not be affected much by standing biomass and total respiration (Bauer et al., 1983). At 20 °C and 21 kPa of O_2 (similar to our study), single leaf CO_2 compensation points for C_3 species are typically near 30 µmol mol^{-1} (Bauer et al., 1983), and Häusler et al. (1999) reported dark-respiration adjusted CO_2 compensations points (Γ*) of 38 µmol mol^{-1} for potato cv. Désirée leaves measured at 22 °C. The CO_2 compensation points measured for whole stands in our study were higher than these single leaf values. This difference may be related to inadequate air mixing through the dense canopy, where for example some leaves may have experienced different CO_2 concentrations than that measured for the whole chamber volume. But no attempts were made to sample CO_2 gradients through the canopy profile and verify this.

As with any short duration tests to assess photosynthetic rates at different CO_2 levels (Fig. 6), one must be cautious about projecting these rates to different "native" CO_2 environments due to biochemical acclimation events, which can include changes in Rubisco content (Moore et al., 1999). Yet in a comparison of five C_3 species, Sage et al. (1989) reported a slight positive effect on A/C_i responses of potatoes grown at CO_2 levels enriched to 0.10 kPa, suggesting that potatoes do not acclimate negatively to prolonged

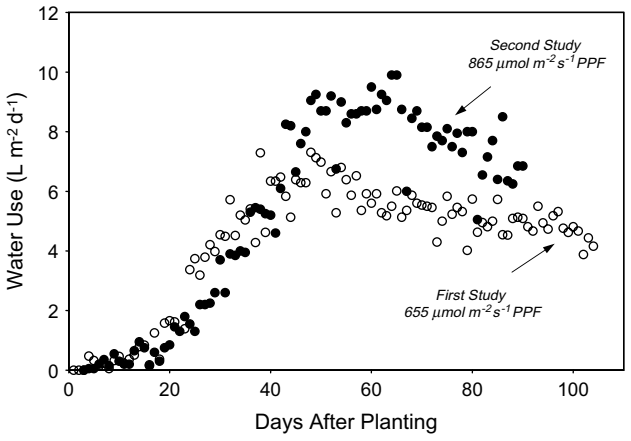

Fig. 7. Water use rates from evapotranspiration from two 20 m^2 potato stands over time. Average photosynthetic photon flux for the first study was 655 µmol m^{-2} s^{-1} and for the second study was 865 µmol m^{-2} s^{-1}.

exposures of elevated CO_2, as has been reported for some other species (Moore et al., 1999).

Beginning about 15 DAP, stand water use (evapotranspiration) increased rapidly as canopy cover increased (Fig. 7), similar to stand photosynthesis. A comparison of water use between the first study (655 µmol m^{-2} s^{-1} PPF) and the second study (865 µmol m^{-2} s^{-1} PPF) showed slightly higher rates up until ca. day 35 for the first study. After about day 40, water use in the first study leveled off near 6.3 L m^{-2} d^{-1}, while water use continued to increase in the second study until about day 50, where it leveled off near 8.9 L m^{-2} d^{-1}. After about 60 days, water use rates in both studies showed a gradual decline as the stand matured (Fig. 7). The higher water use later in growth in the second study may be related to the increased stomatal conductance at the higher PPF (Sharkey and Raschke, 1981), although the higher PPF stand showed generally less water use prior to 40 days. Another possibility was that leaves of the higher PPF stand became warmer as they grew closer the lamp barriers, thereby increasing the leaf-to-air vapor pressure deficit. Because the temperature regimes were slightly different between the studies and no direct canopy temperature measurements were possible after about 40 days age, it is difficult to assess the exact effects of PPF on stand water use from these studies.

3.1. Life support implications

The total amount of CO_2 fixed (removed) from the air, and the equivalent amount of O_2 produced for the three potato studies are shown in Table 2. The oxygen values were calculated assuming a 1:1 molar ratio of CO_2 fixed to O_2 produced, or an assimilation quotient of 1.0 (Wheeler, 1996). This is a reasonable assumption for a crop like potato that produces large amounts of carbohydrate, and is close to values empirically determined for rice by Tako et al. (2001a). Assuming humans produce about 1.0 kg of CO_2 $person^{-1}$ day^{-1} and require about 0.83 kg O_2 $person^{-1}$ day^{-1} (Stutte et al., 1999), the best results from these studies show that an area of about 25 m^2 of potato plants under continuous cultivation would be required to sustain one person. These rates might be improved with different horticultural approaches, such as staggered plantings (Stutte et al., 1999), different rooting media (Tibbitts et al., 1994), or increased lighting (Tibbitts et al., 1994; Wheeler, 2006). The latter could be achieved by either increasing the instantaneous PPF or extending the photoperiod (Wheeler and Tibbitts, 1997). Extending the photoperiods for potatoes after tubers have initiated can increase total biomass and tuber yields in some cultivars, but tends to reduce harvest indices (Wheeler and Tibbitts, 1986, 1997). And as observed in our third study, instantaneous photosynthetic rates can drop under longer photoperiods, thereby dropping the radiation use efficiency. Thus the benefits of increased total production from potato stands under long photoperiods must be weighed against possible reductions in the conversion efficiency of light and the associated electrical power costs.

4. Conclusions

Net photosynthesis, respiration, and water use (evapotranspiration) rates were monitored throughout growth and development for 20 m^2 potato stands in three separate studies. Results showed a rapid increase in all three parameters during early growth as the canopy cover increased, reaching maximum rates between 40 and 50 DAP: ~45 µmol CO_2 m^{-2} s^{-1} for photosynthesis; ~9 µmol CO_2 m^{-2} s^{-1} for respiration, and ~9 L m^{-2} d^{-1} for evapotranspiration. After about 60–70 DAP, rates showed a gradual decline as the stands matured

Table 2
Carbon dioxide removal, oxygen production, and equivalent areas of potato plantings required to support one human[a]

	Study 1 (g m^{-2} d^{-1})	Study 2 (g m^{-2} d^{-1})	Study 3 (g m^{-2} d^{-1})	Human requirement [b] (g d^{-1})	Area per Person (Best Rate)[c,d] (m^2)
CO_2 Removed	32.6	42.3	39.6	1000	23.6
O_2 Produced[e]	23.7	30.8	28.8	830	26.9

[a] Data estimated from biomass yields assuming a 41% carbon content and confirmed within 10% by totaling gas exchange rates Wheeler et al. (2003).
[b] From NASA SSP 30262 Space Station ECLSS Architectural Control Stutte et al. (1999).
[c] Best rates taken from the second study.
[d] Difference in areas for CO_2 removal and O_2 required adjusted for a human respiration quotient of 0.88.
[e] Assuming an assimilation (photosynthetic) quotient of 1.0 for CO_2 removed : O_2 produced Wheeler (1996).

and upper canopy leaves began to senesce. Stand photosynthetic rates showed a linear response to short-term changes in PPF up to ~1100 μmol m^{-2} s^{-1}, with a light compensation point during full canopy cover occurring at 185 μmol m^{-2} s^{-1}. Short term changes in CO_2 concentration showed a classic C_3 photosynthetic response with saturation occurring near 1200 μmol mol^{-1} and a CO_2 compensation point near 100 μmol mol^{-1}. Temporary (2–3 day) increases in the photoperiod from 12/12 to 24/0 caused a decline in instantaneous photosynthetic rates, which could be partially restored by returning to the original 12/12 photoperiod. Gas exchange rates and radiation use efficiencies for potato stands in these studies were as high or higher than those for wheat, soybeans, and lettuce plantings grown in the same chamber (Wheeler et al., 1993, 1994, 2004), suggesting that potatoes are an excellent candidate for bioregenerative life support systems on future space missions.

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