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Growth and Gas Exchange by Lettuce Stands in a Closed, Controlled Environment

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Abstract. **Two studies were conducted in which 'Waldmann's Green' lettuce *(Lactuca sativa* L.) was grown hydroponically from seed to harvest in a large (20-m^2), atmospherically closed growth chamber for the National Aeronautics and Space Administration's controlled ecological life support system (CELSS) program. The first study used metal-halide (MH) lamps [280 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux (PPF)], whereas the second used high-pressure sodium (HPS) lamps (293 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Both studies used a 16-hour photoperiod, a constant air temperature (22 to 23C), and 1000 $\mu mol \cdot mol^{-1}$ CO_2 during the light period. In each study, canopy photosynthesis and evapotranspiration (ET) rates were highly correlated to canopy cover, with absolute rates peaking at harvest (28 days after planting) at 17 μmol CO_2/m^2 per sec and 4 liters$\cdot m^{-2} \cdot day^{-1}$, respectively. When normalized for actual canopy cover, photosynthesis and ET rates per unit canopy area decreased with age (between 15 and 28 days after planting). Canopy cover increased earlier during the study with HPS lamps, and final shoot yields averaged 183 g fresh mass (FM)/plant and 8.8 g dry mass (DM)/plant. Shoot yields in the first study with MH lamps averaged 129 g FM/plant and 6.8 g DM/plant. Analysis of leaf tissue showed that ash levels from both studies averaged 22% and K levels ranged from 15% to 17% of tissue DM. Results suggest that lettuce should be easily adaptable to a CELSS with moderate lighting and that plant spacing or transplant schemes are needed to maximize canopy light interception and sustain efficient CO_2 removal and water production.**

Lettuce is one of several candidate species under study for use in controlled ecological life support systems (CELSSs) proposed for human life support in space. Several criteria favor the use of lettuce as a life-support crop, including its versatility as a fresh salad crop, its adaptability to controlled-environment cultivation, and its low growth habit with a defined shoot shape (Tibbitts and Alford, 1982). In addition, an extensive information base is available on lettuce growth and environmental physiology in controlled environments (Barta and Tibbitts, 1991; Craker and Seibert, 1983; Hammer et al., 1978; Hicklenton and Wolynetz, 1987; Knight and Mitchell, 1983, 1988a, 1988b; Sager, 1984; Tibbitts et al., 1983), although not in closed systems.

In this paper we present results from two baseline studies conducted with lettuce in a large (20-m^2), atmospherically closed chamber analogous to what might be used in a functioning CELSS. The objective of these studies was to track gas, water, and nutrient balances along with productivity of entire lettuce stands from seeding to harvest. Environmental conditions for growth were selected after surveying the literature (references cited above), university laboratories, and commercial operations having experience with growing lettuce. Because of the exploratory nature of the studies, several conditions changed between the first and second studies—most notably, the use of high-pressure sodium (HPS) lamps instead of metal-halide (MH) lamps and the addition of nutrient solution temperature control. Results from these and related studies will be used to assess the feasibility and reliability of using higher plants and the associated hardware and control systems for human life support in space.

Materials and Methods

Studies were conducted in National Aeronautics and Space Administration's (NASA's) biomass production chamber (BPC) located at Kennedy Space Center, Fla. The cylindrical chamber (7.5 m high and 3.7 m in diameter) formerly served as a hypobaric test chamber during NASA's Mercury Project and has since been adapted for plant studies (Prince and Knott, 1989; Prince et al., 1987). The internal volume including air ducts equaled 113 m^3 and, when closed, atmospheric leakage was ≈10% of the volume per day (0.4% vol/h).

Plants were supported inside the chamber by four, vertically stacked annular shelves, with each shelf supporting 16 0.25-m^2 (10-cm-deep) acrylonitrile–butadiene–styrene (ABS) plastic culture trays. Trays provided a basal rooting area of 4 m^2 per shelf and 16 m^2 for the entire chamber. Direct measurements of projected groundcover throughout growth indicated that actual canopy area reached ≈20 m^2 at final harvest due to leaves extending beyond the basal tray dimensions.

Cultural approach. In each of the two studies reported, 'Waldmann's Green' lettuce plants were started by directly sowing dry seed between two nylon (Nitex) fabric wicks supported ≈4 cm above the bottom of culture trays. Wicks were supported by juxtaposing white-on-black polyethylene plastic strips suspended through 2.5-cm-diameter holes in white ABS plastic tray covers (Prince and Knott, 1989). All new wicks were prerinsed with ethanol and deionized water to remove potential phytotoxins (Wheeler et al., 1985). Two to three seeds were planted at each of six positions on the 0.25-m^2 tray covers. After planting, trays were

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covered with white, translucent acrylic covers for 2 days to maintain high humidity during seedling establishment. Seedlings were thinned to one per position (i.e., six per tray) 7 days after planting (DAP).

Nutrient solution was provided to each culture tray using the recirculating nutrient film technique (Graves, 1981) with a complete nutrient solution with nitrate as the sole N source (Table 1). Each of the four shelves with their 16 culture trays was supplied from a separate nutrient solution with circulating pumps and reservoirs situated immediately outside the chamber (Prince et al., 1987). Head spaces of the reservoirs were vented to the main chamber to maintain atmospheric closure. Solution pH was monitored continuously and maintained between 5.8 and 6.0 by automatically adding 0.4 M nitric acid. Solution electroconductivity was monitored continuously and maintained near 0.12 $S \cdot m^{-1}$ by automatically adding a complete nutrient stock solution. Water lost to evapotranspiration was replenished daily by adding deionized water to the reservoirs.

For the first study, nutrient solution temperatures were not controlled and averaged 26.3 ± 1.7C, ranging from 23 to 29C, depending on ambient temperature effects on external tanks and plumbing lines. For the second study, stainless-steel (alloy 316) coils were submersed into the reservoirs to control temperature. Nutrient solution temperatures were maintained constant, with a final average of 25.6 ± 0.6C

Environmental conditions. Lighting for the first study was provided by MH lamps (400-W Venture ProArc; Venture Lighting International., Cleveland) electronically dimmed with dimming ballasts (Wide-Lite, San Marcos, Texas), with the photosynthetic photon flux (PPF) averaging 280 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top of the plant canopy. Lighting for the second study was provided by HPS lamps (400-W Philips Ceramalux, Philips Lighting Corp., Bloomfield, N.J.; or GE Lucalox, General Electric Co., Cleveland), also dimmed with PPF averaging 293 $\mu mol \cdot m^{-2} \cdot s^{-1}$. PPF levels were monitored at each of 64 tray positions weekly using a quantum sensor (model LI-190, LI-COR, Lincoln, Neb.) and were adjusted as needed using dimming controls. A 16-h light/8-h dark photoperiod was used for both studies, providing 16 to 17 $mol \cdot m^{-2} \cdot day^{-1}$ PPF.

Air temperature (taken from four positions within the chamber) averaged 22.5 ± 0.5C (SD between the four sensor positions in the chamber) in the light and 22.1 ± 0.4C in the dark for the first study, and 22.6 ± 0.4C in the light and 22.4 ± 0.2C for the second study. Relative humidities averaged 80% ± 4% in the light and 81% ± 3% in darkness for the first study, and 71% ± 3% in the light and 75% ± 2% in darkness for the second study. Carbon dioxide concentration of the atmosphere was maintained at 1000 $\mu mol \cdot mol^{-1}$ (0.1 kPa) during light cycles by adding pure CO_2. Carbon dioxide levels were not controlled during dark cycles and rose in response to plant respiration (Wheeler, 1992). When lamps were started each day, CO_2 levels quickly decreased to the 1000 $\mu mol \cdot mol^{-1}$ setpoint, at which controlled additions of CO_2 were reinitiated. All CO_2 added to the chamber atmosphere was passed through columns of potassium permanganate-coated pellets (Air Repair Products, Stafford, Texas) to remove possible hydrocarbon contaminants (Morison and Gifford, 1984). Oxygen concentrations were monitored, but not controlled and generally remained near 21% (21 kPa) throughout the study. Although the chamber was closed for most of the study, O_2 concentrations did not increase because the chamber typically was entered daily for maintenance and measurements, which caused internal O_2 levels to equilibrate with external ambient levels.

Table 1. Nutrient solution composition for lettuce studies.

Macronutrients (mM)		Micronutrients (μM)	
N	7.5	Cl	187.4
P	0.5	Fe	60.0[z]
K	3.0	Mn	3.7
Ca	2.5	Zn	0.64
Mg	1.0	Cu	0.52
S	1.0	B	4.75[y]
		Mo	0.01

[z]From HEDTA chelate.
[y]Decreased to 1.2 μM for second study.

Experimental measurements. Beginning 15 DAP, shoot (head) diameters were measured manually for each plant along two axes offset by 90°. Measurements were repeated at ≈2-day intervals thereafter. Total projected canopy cover was calculated by $\pi (d/2)^2 \times$ (no. plants), where d = the average shoot (head) diameter.

Plants were harvested at 28 DAP and shoot fresh mass (FM) was measured. Roots from all plants and one shoot from each of the 64 trays were oven dried at 70C for 48 h and the average percent dry mass (DM) for these shoots was then used to calculate the DM of the remaining, undried shoots. In addition to the final harvest at 28 DAP, four plants (one from each shelf) were harvested at 2-day intervals beginning at 16 DAP in the second study. Duplicate tissue samples from the final harvest for both studies were ground with a Wiley mill (2-mm screen) and analyzed for proximate nutritional composition (Nutrition International, Dayton, N.J.). Proximate analyses followed standard Association of Official Analytical Chemists procedures (1984) and included the following: moisture by vacuum oven, ash by muffle furnace, protein by Kjeldahl N (6.25 conversion factor), crude fiber by digestion and gravimetric technique, fat by ether extraction, and carbohydrate by difference. Dietary energy equivalents were calculated by assigning 4 $kcal \cdot g^{-1}$ carbohydrate, 4 $kcal \cdot g^{-1}$ protein, and 9 $kcal \cdot g^{-1}$ fat. Four dried tissue samples from each study also were analyzed in triplicate for elemental composition using inductively coupled plasma spectroscopy (Alexander and McAnulty, 1981).

Beginning at ≈15 DAP, plants were sufficiently large for stand respiration to cause a measurable increase in CO_2 concentration during the dark period. This rise in concentration was followed by a drawdown to the 1000 $\mu mol \cdot mol^{-1}$ setpoint after the lamps came on each day. Slopes of 1-h segments of these diurnal changes in CO_2 concentration were used to calculate stand respiration and net photosynthesis rates using a closed system approach (Wheeler, 1992). With a leakage rate of 0.4% chamber vol/h, CO_2 loss from the chamber was $<0.2\ \mu mol \cdot m^{-2} \cdot s^{-1}$; hence, leakage was ignored in CO_2-exchange calculations. Data from the first 20 min after the dark–light or light–dark transitions were avoided for calculations to allow adequate time for environmental equilibration and to avoid any pressure transients.

Stand evapotranspiration (ET) rates were tracked daily by recording the amount of water added to the nutrient solution to bring the reservoirs to a fixed volume plus the volume of nutrient concentrate and acid added. Stand CO_2 exchange and ET rates were expressed either on an absolute basis, assuming 20 m^2 was available for stand growth, or normalized for actual canopy cover when direct area measurements were available.

Results

Beginning at 15 DAP, shoot diameters and total canopy cover of the lettuce stands increased rapidly (Fig. 1). Shoot diameters and total canopy cover increased earlier in the second study with HPS

lamps than in the first study with MH lamps. The faster start by plants in the second study amounted to an advantage of 1 to 2 days in development compared to plants in the first study (Fig. 1).

Time-course net photosynthesis and dark-period respiration rates for the stands in each study are presented in Fig. 2. Net photosynthesis rates for the entire 20 m^2 of planted area (absolute rates) were low initially because of the low amount of photosynthetically active radiation intercepted by the canopy (Figs. 1 and 2). Beginning at ≈15 DAP, absolute rates increased steadily to ≈17 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at harvest for both studies (Fig. 2). The increase in photosynthetic rate with time slowed slightly near 23 days in the second study and 24 days in the first study, which corresponded closely to when leaves between adjacent plants began to overlap. As with net photosynthesis, absolute rates of dark-period respiration were low initially but gradually increased as stand biomass increased (Fig. 2). Normalized photosynthetic rates (i.e., rates per unit area of projected canopy cover) were highest at 16 DAP (≈25 $\mu mol \cdot m^{-2} \cdot s^{-1}$), when gas exchange was first detectable, and then showed a general decline until plants were harvested at 28 DAP (Fig. 2). Likewise, normalized dark-period respiration rates were highest when plants were young and then declined slightly with age (Fig. 2).

Carbon dioxide uptake from stand photosynthesis was detectable sooner in the second study than in the first, following the trends in canopy cover between the two studies (Figs. 1 and 2). The correlation between stand CO_2 uptake and canopy cover could be described by the quadratic equations $y = 24.45x - 0.3x^2$ ($R^2 = 0.99$) in the first study, and $y = 29.42x - 0.79x^2$ ($R^2 = 0.99$) in the second study (Fig. 3). Before canopy cover reached 10 m^2 (≈22 DAP), CO_2 uptake showed a near-linear increase with increasing canopy cover (Figs. 1 and 3).

ET rates for the lettuce stands over time are shown in Fig. 4. As with stand CO_2 exchange, absolute ET rates increased quadratically with the increase in canopy cover: $y = 17.15 + 5.71x - 0.11x^2$ ($R^2 = 0.99$) for the first study and $y = 18.44 + 5.24x - 0.10x^2$ ($R^2 = 0.99$) for the second study (Fig. 5). When normalized for canopy

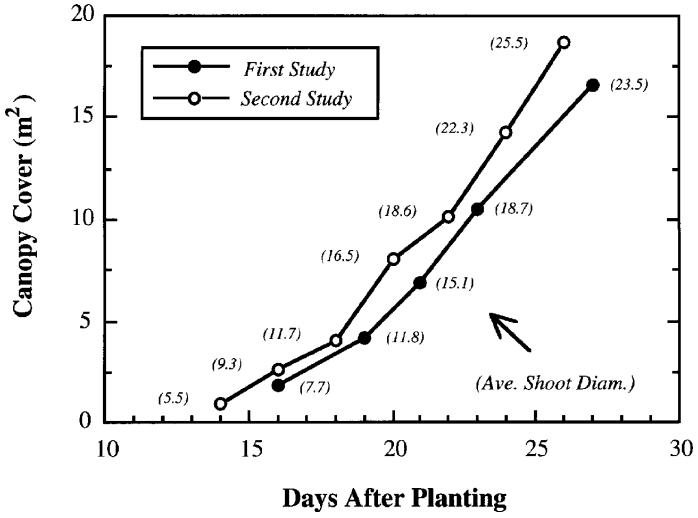

Fig. 1. Canopy cover over time for two lettuce plantings. Areas were determined by measuring shoot diameters (shown in cm) to calculate single plant canopy cover and then multiplying by the total number of plants.

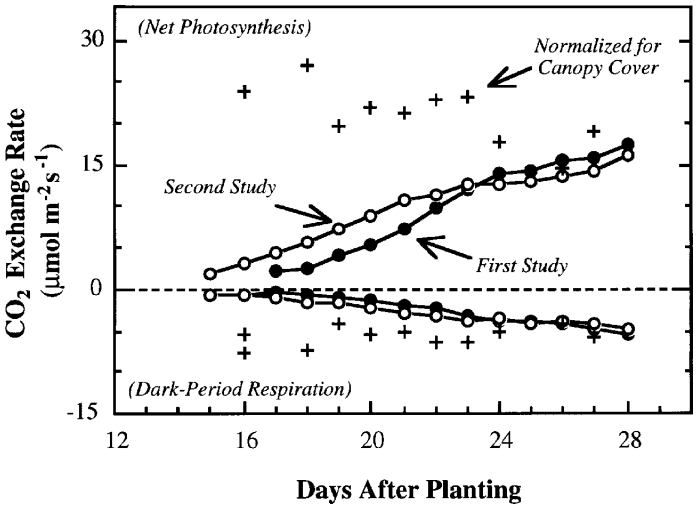

Fig. 2. Carbon dioxide-exchange rates for two lettuce plantings over time. Rates during the light period are shown as positive values (net photosynthesis), while rates during the dark period are shown as negative values (dark-period respiration). Rates for the entire 20-m^2 area of the chamber are shown with symbols connected by lines; rates normalized to the actual canopy cover for both studies are shown as unconnected + symbols.

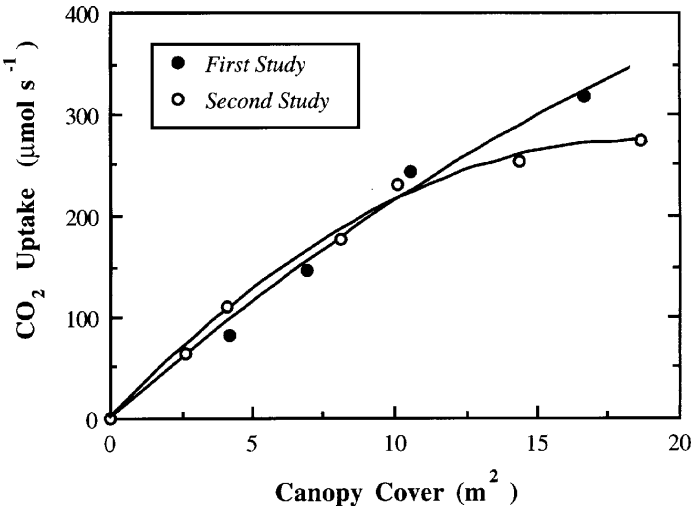

Fig. 3. Relationship between net photosynthetic CO_2 uptake and canopy cover for two lettuce plantings.

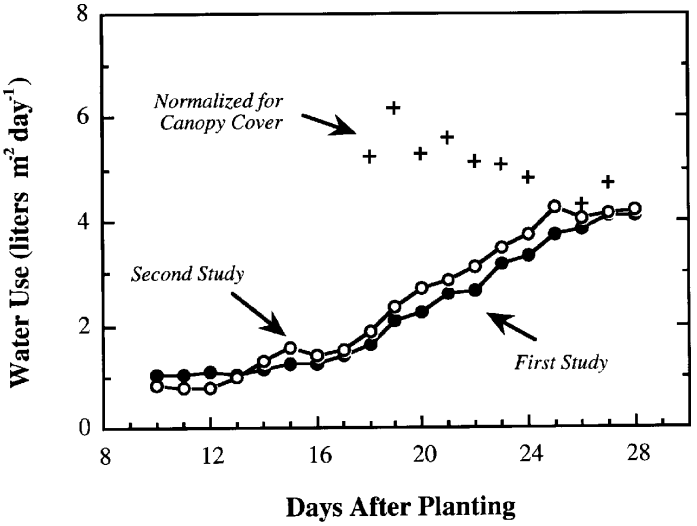

Fig. 4. Evapotranspiration for two lettuce plantings over time. Rates for the entire 20-m^2 area of the chamber are shown with symbols connected by lines; rates normalized to the actual canopy cover for both studies are shown as unconnected + symbols.

cover, ET rates per unit area of canopy showed a decline between 18 and 28 DAP (Fig. 4). Final ET rates at full canopy cover for both studies averaged ≈4 liters·m^{-2}·day^{-1}, which would equate to an average rate of 2.6 mmol·m^{-2}·s^{-1} over a 24-h period (Fig 4).

Time-course harvest data from the second study indicated that plant biomass increased rapidly between 16 DAP (≈5 g FM) and 28 DAP (≈180 g FM) (Fig. 6). Final harvest data for the two studies are shown in Table 2. Head FM averaged 129 g/plant and 5.3% DM for the first study, and 183 g FM/plant and 4.8% DM for the second study. Total plant DM averaged 7.4 g/plant in the first study and 9.4 g/plant in the second. Roots from both studies averaged 0.6 g DM/plant, accounting for ≈8% and 6% of total plant DM in the first and second studies (Table 2).

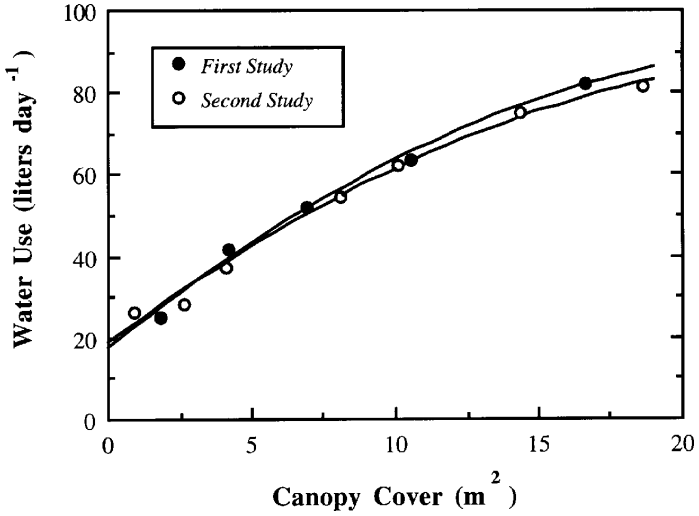

Fig. 5. Relationship between evapotranspiration and canopy cover for two lettuce plantings. The y intercept indicates the amount of direct evaporation from the hydroponic culture system before canopy establishment.

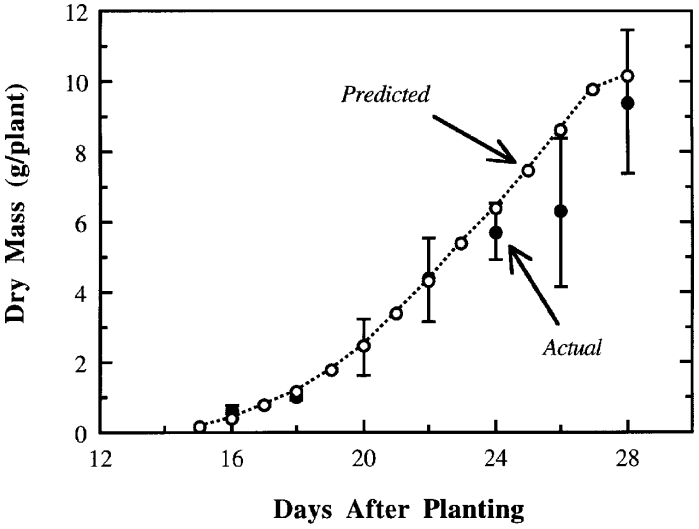

Fig. 6. Growth of lettuce plants over time in the second study. Closed symbols show actual harvest data, and open symbols with a dotted line show predicted dry mass based on canopy CO_2-exchange measurements. Harvest data represent averages for four plants at each date except for final harvest at day 28, which represents the average of 360 plants. Final harvest occurred 6 h into the light period on day 28. Vertical lines indicate SDS.

Table 2. Yield parameters of lettuce plants grown for 28 days in NASA's biomass production chamber.

Study	Shoot fresh mass	Shoot dry mass	Root dry mass	Total plant dry mass
		(g/plant)		
First[z]	129 ± 32	6.81 ± 1.66	0.57 ± 0.14	7.38 ± 1.78
Second[y]	183 ± 39	8.80 ± 1.93	0.61 ± 0.15	9.41 ± 2.05

[z]Averages of 384 plants ±SDS; all plants grown under metal-halide lamps.
[y]Averages of 360 plants ±SDS; all plants grown under high-pressure sodium lamps.

Protein and crude fiber values were higher in the first study, while carbohydrate values were higher in the second study (Table 3); however, no statistical comparisons were made between studies since there were only two replicates from each study. Elemental analysis of leaves showed high tissue concentrations of K in both studies (15% to 17%), whereas P, Fe, and B were higher in tissues from the first study (Table 4). No deficiencies or toxicities were apparent for any of the essential elements. Nutrient solutions in both studies were similar, with the exception of B, which was higher during the first study (Table 1). Leaf tipburn injury was first apparent at 21 DAP in the first study and at 20 DAP in the second study. At final harvest, tipburn was apparent on 49% of the plants from the first study and on 48% of the plants in the second study.

Discussion

Data from both studies indicated a trend of increasing CO_2 uptake from stand photosynthesis throughout growth. The increased CO_2 uptake closely followed the increase in canopy cover, suggesting that photosynthesis was limited primarily by canopy interception of PAR. During early development, each 1 m^2 increase in canopy area resulted in an increase in stand CO_2 uptake of 20 to 25 μmol·s^{-1} (Fig. 3). Normalizing chamber CO_2 exchange rates for actual canopy cover indicated that photosynthesis per unit canopy area declined slightly between 16 and 28 days (Fig. 1). One likely cause for this decline in photosynthetic efficiency was increased mutual shading of leaves within and between individual plants.

Integrating the total CO_2 fixed during the light cycles and subtracting the total lost during the dark cycles indicated a net fixation of 107 and 122 mol CO_2 in the first and second studies, respectively. Combustion analysis showed that the lettuce leaf tissue was ≈40% C by weight, which matches the percentage of C in the generic formula for carbohydrate, i.e., CH_2O (Charles-Edwards et al., 1986). Assuming that each mole of CH_2O in the biomass came from one mole of CO_2, the final amount of biomass (DM) can be estimated as follows: 107 mol $CH_2O \times 0.03$ kg·mol^{-1} CH_2O, or 3.21 kg of biomass would have been produced in the first study, and 122 mol $CH_2O \times 0.03$ kg·mol^{-1} CH_2O, or 3.66 kg of biomass would have been produced in the second study. Actual DM yields from the first and second studies were 2.83 kg and 3.46 kg, respectively (including DM from sequential harvests in the second study before the final harvest at 28 days). Thus, biomass predictions from CO_2 exchange were ≈13% high in the first study and 6% high in the second study. A comparison of CO_2 exchange estimates of biomass with the sequential harvests in the second study is shown in Fig. 6. Early estimates of standing biomass matched actual harvest data rather closely, but gas-exchange predictions overestimated yields with increasing canopy age.

Several possible sources of error may account for the overestimation of biomass from gas-exchange measurements: because gas-exchange measurements were taken from a 1-h period early in the day, rates may not have represented the average photosynthetic rates across the entire photoperiod (Wheeler, 1992). In addition, photosynthetic rates calculated from morning drawdown measure-

Table 3. Proximate analysis of lettuce leaves grown in NASA's biomass production chamber. Data are expressed on a dry-weight basis.[z]

Study	Protein[y] (%)	Fat (%)	Carbohydrate (%)	Ash (%)	Crude fiber (%)	Energy content ($kcal \cdot g^{-1}$)
First	30.0 ± 0.8	4.1 ± 0.3	32.7 ± 1.6	22.0 ± 0.4	11.1 ± 0.1	2.88 ± 0.01
Second	27.2 ± 0.2	4.5 ± 0.1	37.0 ± 0.3	21.8 ± 0.3	9.4 ± 0.2	2.98 ± 0.01

[z]Data represent averages of two samples ±SDS.
[y]Total Kjeldahl N × 6.25.

Table 4. Elemental composition of lettuce leaves grown in NASA's biomass production chamber. Data are expressed on a dry-weight basis.[z]

Study	K	N	P	Ca	Mg	Zn	Cu	Fe	Mn	B	Mo
					($\mu g \cdot g^{-1}$)						
First	171,000 ± 24,000	48,000 ± 1200	4010 ± 240	9110 ± 1260	2950 ± 160	36.3 ± 6.8	6.00 ± 1.3 1	128 ± 18	53.8 ± 11 2	32.1 ± 7.6	0.41 ± 0.08
Second	147,000 ± 17,000	43,500 ± 400	3630 ± 230	9000 ± 1270	2890 ± 200	30.2 ± 5.1	5.75 ± 1.01	68 ± 23	41.1 ± 7.2	16.9 ± 3.4	na[y]

[z]Data represent averages of four samples ±SDS.
[y]Not available.

ments taken later in growth (e.g., 25 to 28 DAP) starting near 1500 $\mu mol \cdot mol^{-1}$ CO_2 may have been higher than those at a steady-state level of 1000 $\mu mol \cdot mol^{-1}$ CO_2. Related studies of CO_2 effects on canopy gas exchange suggest that canopy photosynthetic rates of some C_3 species are not yet saturated at 1000 $\mu mol \cdot mol^{-1}$ and may be increased by raising CO_2 to 1500 $\mu mol \cdot mol^{-1}$ (Wheeler et al., 1993). An additional source of error could have been actual DM losses resulting from tissue respiration or decarboxylation during oven drying, which would result in an overestimation of biomass by gas-exchange calculations.

As for CO_2 uptake, ET rates were highly dependent on canopy cover. Extrapolating ET rates to zero canopy cover gave a background rate of ≈20 liters·day^{-1} (Fig. 5). This most likely occurred from direct evaporation from exposed germination wicks and gaps between tray covers where nutrient solution was exposed to air. As the lettuce canopies reached complete closure, it is likely that most of the water flux was directly attributable to transpiration (Wheeler, 1992). Although relative humidity was higher in the first study, ET rates were similar between studies. Infrared temperature measurements indicated that leaves in the second study were ≈1C cooler than in the first. This temperature difference tended to equalize the leaf-to-air water vapor-pressure deficits between the two studies, which may explain the similar ET rates.

At full canopy cover, stand water-use efficiencies (CO_2 uptake/ET) were (17.4 μmol CO_2/m^2 per sec)/(2.65 mmol H_2O/m^2 per sec) or 6.57 mmol CO_2/mol H_2O for the first study, and (16.1 μmol CO_2/m^2 per sec)/(2.70 mmol H_2O/m^2 per sec) or 5.96 mmol CO_2/mol H_2O for the second study. These values equate to ≈15 g CO_2 fixed/kg water transpired, or ≈10 g DM/kg water.

A comparison of total yields showed that shoot FM was 42% greater in the second study compared to the first, while total plant DM was 28% greater. Equivalent yield from the first study occurred at ≈26.5 days on the time-course harvest curve for the second study (Fig. 6), suggesting that the plants in the second study were ≈1.5 days more advanced than those in the first (Fig. 2). Records for CO_2-exchange rates and measurements of canopy cover showed that plants in the second study grew more during the first 2 weeks than plants in the first study. Because seed lots and planting techniques were similar between studies (seed was slightly older in the second study), the faster establishment was likely a result of environmental difference between the studies. PPF was ≈7% higher in the second study, which could account for much of the greater growth. Root-zone temperature was controlled and not allowed to fluctuate in the second study, which also may have promoted more rapid growth. However, Hicklenton and Wolynetz (1987) reported little effect on the growth of 'Montana' lettuce plants when root-zone temperatures were varied between 20 and 29C. Previous studies have reported little difference between HPS- and MH-grown lettuce plants at 24C, but noted that the influence of long-wave radiation and resultant effects on leaf temperatures caused differences in growth (Sager, 1984). Differences in lamp emission spectra may have contributed to differences in growth, particularly the low amount of blue in the HPS spectrum. Lack of sufficient blue radiation has been shown to promote more rapid hypocotyl and stem elongation of lettuce and other species (Tibbitts et al., 1983; Wheeler et al., 1991). This may have caused leaves under HPS lighting to expand rapidly and intercept more light during early growth. This hypothesis is supported by findings by Koontz et al. (1987), who reported greater growth of lettuce with HPS lamps compared to relatively blue-rich cool-white fluorescent lamps at 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF.

Proximate analyses of leaves indicated that the tissue contained high levels of protein (28% to 30%) and ash (22%). Protein and ash content of field-grown lettuce typically range from 19% to 26% and 9% to 20%, respectively (Duke and Atchely, 1986). The high ash levels were substantiated by direct elemental analyses, which indicated K concentrations of 15% to 17% in the leaf tissue (Table 4). The results suggest that the plants accumulated luxuriant levels of some nutrients under the conditions of these studies. It is likely that tissue nitrate levels of the hydroponically grown plants from our studies were higher than those of field-grown plants (Blom-Zandstra, 1989), although no direct nitrate measurements were taken. The Kjeldahl approach used to estimate total N and crude protein would be affected by tissue nitrate and, hence, tend to raise protein estimates.

Leaf tipburn was apparent on about one-half of the plants in both studies, although the amount of injury was considered mild. Tipburn has been related to Ca deficiencies in rapidly expanding lettuce leaves enclosed in heads; however, only analyses of mature shoot tissues were conducted in our studies, which would not be informative regarding Ca deficiency during early expansion (Barta and Tibbitts, 1991). Differences in tissue Ca and other elements

occurring between studies generally were small.

Implications for CELSS. Results from these closed chamber studies suggest that lettuce should do well under controlled environment production systems that may be used in a CELSS. Although the dietary nutritional value of lettuce is considered low, its short shoot height (hence low volume requirement), ease of culture in recirculating hydroponics systems, relatively low energy requirements for lighting, and few processing requirements are notable advantages compared to other crops often discussed for CELSS. However, the relatively short harvest cycles for lettuce would require efficient space use to minimize lighting loss. For a production system, it would not be advisable to start lettuce plants at the final spacing anticipated at harvest, as was done in our studies. Future CELSS studies should explore transplant schemes or automated plant spacing systems that could be used to minimize growing area requirements and maximize light interception by crop canopies.

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