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Enhancement of Lettuce Yield by Manipulation of Light and Nitrogen Nutrition

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Abstract. **Several levels of photosynthetic photon flux density (PPFD) were tested for effects on growth of 4 cultivars of lettuce (*Lactuca sativa* L.) under controlled-environment conditions. Growth of 'Salad Bowl', 'Bibb', and 'Ruby' was greater at 932 μmol $s^{-1}m^{-2}$ than at ≤ 644 μmol $s^{-1}m^{-2}$ under a 16-hour photoperiod. Thirty mM NO_3^- or 5 mM NH_4^+ + 25 mM NO_3^- increased leaf dry weight while reducing leaf chlorosis in 'Salad Bowl' and 'Grand Rapids' relative to that with 15 mM NO_3^-, and reduced leaf purpling in 'Bibb' and 'Ruby' with little or no effect on yield. Continuous illumination with 455 or 918 μmol $s^{-1}m^{-2}$ stimulated yield of 'Salad Bowl' and 'Bibb' when 30 mM N as NH_4^+ + NO_3^- was used relative to that with 15 mM NO_3^-.**

Although production costs generally have prevented controlled-environment agriculture from becoming a superior economic alternative to open-field agriculture (15, 17), yield rate of crops grown in controlled environments is often greater than that in the field (4, 6, 19). For instance, it takes at least 55 days to produce a marketable leaf lettuce crop in the field, but only 22 days in a controlled environment (4, 8). Furthermore, fresh weight yield per cycle of 6.0 kg m^{-2} has been obtained in controlled environments vs. 2.4 kg m^{-2} in the field. Although controlled-environment production holds considerable promise for further improvements in yield of lettuce (7), lack of economic incentive has delayed identification of optimum cultural conditions for this and other crops. However, the U.S. National Aeronautics and Space Administration has initiated a program in which photosynthetic higher plants may be of central importance in a space-deployed, regenerative life-support system (13, 15, 16). Ground tests in the Soviet Union indicated that plants can provide part of the calories and all of the O_2 required by several humans over a 6-month period (9). Leaf lettuce is one candidate species being considered for a controlled ecological life-support system (CELSS) because it provides some of the minerals, vitamins, and fiber needed in the diet, has a high yield rate, has a favorable proportion of edible biomass, and sustains a high level of photosynthetic activity during production (11). In addition to seeking "optimum environments" for leaf lettuce growth, selection or development of superior cultivars will be important to realize the goal of crops approaching their genetic potential for edible biomass production in a CELSS.

Materials and Methods

Cultivars. Four cultivars of lettuce were compared for their growth response to various light and N treatments: 'Salad Bowl', 'Grand Rapids', and 'Ruby' are loose-leaf types, and 'Bibb' is a butterhead type.

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Illumination and photoperiod. The experiments were conducted in 2 Sherer-Gillett model 512-37 reach-in growth chambers (5.6 m^2). Illumination was provided by 82% input wattage from very high output Cool-White fluorescent lamps annd 18% from frosted incandescent lamps. Photon flux densities up to 950 $\mu mol\ s^{-1}m^{-2}$ were measured with a LI-COR model LI-185 Quantum Radiometer in the wavelength interval from 400 to 700 nm at 51 cm below the light cap. Shade cloth suspended above the leaf canopy reduced photon flux density 30% with all lamps energized. A reduction of 50% was achieved by energizing one-half the lamps in a chamber; a 70% reduction was achieved by using shade cloth under the latter lighting regime. Light level measurements were taken immediately before and after experimental treatment and once weekly during treatment. Photoperiod was either 16 or 24 hr on a 24-hr light/dark cycle.

Culture system and nutrient treatments. Two nutriculture systems (18) were installed within both growth chambers used in this study. Each system included 20 plant containers that shared a common, recirculating nutrient solution. The one-liter containers (9.5 × 9.5-cm top) were arranged 20 cm apart (center-to-center) within rows and 25 cm apart between rows. Aeration of nutrient solution (22 liters total) was achieved by recirculating the solution through the plant containers and into a 2-liter common reservoir at 220 ml min^{-1}. The system automatically replenished fresh nutrient solution as 25 liters day^{-1} dripped out of the common reservoir of each nutriculture system.

Seeds were germinated in a trough lined with black cloth wicking half-strength nutrient solution from the container below (12) and darkened by a lid with transparent slits to ensure upright growth of seedlings. Two days after sowing, lids were removed, exposing seedlings to half-maximal light for 16 hr day^{-1}. After 2 days of adaptation, 2 transplants were inserted through holes in the polyvinyl chloride cover of each container. Each seedling was supported through the center of a black foam plug fitted snugly through the hole. Two days after transplanting, seedlings were thinned to one per container, the germination solution was changed to the nutrient test solution, and environmental treatments were initiated.

Nutrient solutions modified after those used by Hoagland and Arnon (10) were used as test solutions. Elemental composition of test solutions is summarized in Table 1. Nitrogen was supplied either as NO_3^- alone at 15 or 30 mM, or as 25 mM NO_3^- + 5 mM NH_4^+. Solution pH was maintained at 6.0 ± 0.4 pH units (Corning portable pH/Temp meter 4) by addition of 1 N HNO_3 or 1 N KOH. Ionic strength was maintained at initial value ± 5% (Barnstead conductivity bridge) by addition of deionized H_2O or nutrient solution.

Temperature and humidity. Ambient temperature regimes of 25°C ± 2° days/20° ± 2° nights or continuous 25° ± 2° (in continuous light) were maintained in the chambers during treatment. Solution temperatures averaged 1° less than air tempertures in light and darkness. Relative humidity was 71% ± 3% in both chambers during the light cycle and 64% ± 2% during the dark cycle (Bendix motor-driven psychrometer, model 566).

Experimental design and growth analysis. A split-plot design was used in which each nutriculture system within a growth chamber constituted a (light or nutrient) treatment group. Experiments included either 5 plants each of 4 cultivars, or 10 plants each of 2 cultivars, arranged randomly within the 20 containers of a nutriculture system.

Upon termination of experimental treatment, leaves ⩾ one cm in length were stripped as close to the stem as possible, counted, and dried for 3 days at 75°C in a forced-air oven. Dry weights of stems and roots as well as leaves were determined. Edible harvest is reported as total leaf dry weight per plant and percentage of plant dry weight.

Table 1. Elemental composition of modified single-strength (1 ×) and double strength (2 ×) Hoagland's nutrient solutions (NS) used for experimental treatments.

Element	Nutrient solution (N source)			
	1× NS (1× NO_3^-)	1× NS (2× NO_3^-)	1× NS (2× [NO_3^- + NH_4^+])	2× NS (2× NO_3^-)
	Element concn (mM)			
N	15	30	30	30
P	1	1	1	2
K	6	11	11	12
S	2	2	2	4
Ca	5	10	5	10
Mg	2	2	2	4
	Element concn (μM)			
B	46	46	46	92
Fe	44	44	44	88
Cl	18	18	18	36
Mn	9.2	9.2	9.2	18.4
Zn	0.77	0.77	0.77	1.54
Cu	0.32	0.32	0.32	0.64
Mo	0.11	0.11	0.11	0.22

Results and Discussion

The lettuce test cultivars were initially screened for their growth response to 4 different levels of PPFD when cultured in single-strength (1 ×) nutrient solution. Leaf dry weight of all cultivars was greater with 932 $\mu mol\ s^{-1}m^{-2}$ of photosynthetically active radiation than with 452 or 261 $\mu mol\ s^{-1}m^{-2}$ after 25.5 days of exposure for 16 hr day^{-1} (Table 2). This high value of PPFD (for a fluorescent- + incandescent-illuminated growth chamber) also increased leaf dry weight of 'Salad Bowl' and 'Ruby', but not of 'Grand Rapids' relative to that at 644 $\mu mol\ s^{-1}m^{-2}$.

Table 2. Effect of different values of photosynthetic photon flux density (PPFD) on total leaf dry weight per plant and leaf percent dry weight of the entire plant for 4 cultivars of lettuce treated for 25.5 days in single-strength nutrient solution containing 15 mM NO_3^-. Photoperiod was 16 hr on a 24-hr light/dark cycle. Ambient temperature was 25°C days/20° nights.

PPFD ($\mu mol\ s^{-1}m^{-2}$)	Leaf dry wt			
	Salad Bowl	Bibb	Grand Rapids	Ruby
	(g plant^{-1})			
261	1.13 a C[z]	0.78 a B	0.80 a B	0.52 a A
452	1.68 b B	1.39 b A	1.09 a A	1.18 b A
644	2.03 b B	1.93 b B	1.93 b B	0.86 b A
932	3.67 c C	2.95 c B	2.00 b A	1.90 c A
	(% of plant)			
261	80 a B	71 a A	81 b B	83 a B
452	81 a B	71 a A	73 a A	80 a B
644	81 a A	78 a A	83 b A	81 a A
932	81 a B	75 a A	78 ab AB	77 a AB

[z]Mean separation by Duncan's multiple range test, 5% level (lowercase for columns, uppercase for rows).

'Salad Bowl' also yielded better than all other cultivars at 261 or 452 μmol $s^{-1}m^{-2}$, but was not superior to 'Bibb' at 644 or 932 μmol $s^{-1}m^{-2}$. 'Ruby' consistently yielded lower than 'Salad Bowl' at all values of PPFD tested.

The proportion of plant dry weight comprised by leaves was unaffected by PPFD except for 'Grand Rapids', but PPFD and cultivar interacted significantly for this parameter, and differences did occur among cultivars at a given PPFD (Table 2). 'Salad Bowl' had a higher proportion of leaf dry weight than did 'Bibb' at all light levels tested except for 644 μmol $s^{-1}m^{-2}$. Leaf number per plant also was greater for all cultivars at the highest vs. the lowest PPFD tested (Fig. 1). Plants grown at 932 μmol $s^{-1}m^{-2}$ tended to develop more leaves than those grown at 644 or 452 μmol $s^{-1}m^{-2}$. There also was a significant interaction between light level and cultivar for leaf number. At least part of the increased leaf dry weight caused by increasing increments of light (Table 2) appears to be due to greater leaf number (Fig. 1).

All lettuce cultivars developed stresslike symptoms when grown at high but not low PPFD in 1 × nutrient solution (Table 3). 'Salad Bowl' and 'Grand Rapids' developed yellow leaves at 644 or 932 μmol $s^{-1}m^{-2}$, but not at 261 or 452 μmol $s^{-1}m^{-2}$, whereas 'Bibb' and 'Ruby' developed extreme leaf purpling only at 932 μmol $s^{-1}m^{-2}$. The general chlorosis of leaves particularly resembled N-deficiency symptoms.

Growth of lettuce at high PPFD in 1 × nutrient solution containing double-strength (2 ×) N, or in 2 × nutrient solution (both providing 30 mM N as NO_3^-) prevented leaf yellowing in 'Grand Rapids' and reduced it in 'Salad Bowl' (Table 4). The same N regimes stimulated leaf dry weight gain in those cultivars (Table 5). When 2 × N was supplied as 5 mM NH_4^+ + 25 mM NO_3^- in otherwise 1 × nutrient solution, leaf chlorosis of 'Salad bowl' was eliminated under high PPFD (Table 4); leaf dry weight was 31% greater than when N was supplied as 30 mM NO_3^- alone (Table 5). Yield of 'Grand Rapids' also was improved by the mixed N source, but much less than for 'Salad Bowl'. Leaf purpling of 'Bibb' and 'Ruby' was reduced by doubling N in the nutrient solution (Table 4), but leaf dry weight was unaffected substantially (Table 5). Increasing N level from 15 to 30 mM either by doubling ionic strength of the entire nutrient solution or by manipulating only N concentration and source also increased leaf number under high PPFD in most cases (Fig. 2). However, doubling N as NO_3^- alone had no effect on leaf number of 'Salad Bowl' relative to that in 1 × nutrient solution. Since total leaf dry weight of 'Salad Bowl' did increase in response to 30 mM NO_3^- in 1 × nutrient solution at high PPFD (Table 5), the effect must have been due to larger and/or denser leaves for this treatment combination. 'Salad Bowl' was the only cultivar in which 30 mM N as NH_4^+ + NO_3^- increased leaf number relative to treatments in which 30 mM NO_3^- alone was used (Fig. 2). Although leaf number was similar for 'Bibb' and 'Salad Bowl' using the mixed N source, leaf dry weight was significantly greater for 'Salad Bowl' (Table 5), suggesting once again that size and/or density of leaves were promoted by growing this cultivar in 2 × N as NH_4^+ + NO_3^- at high PPFD.

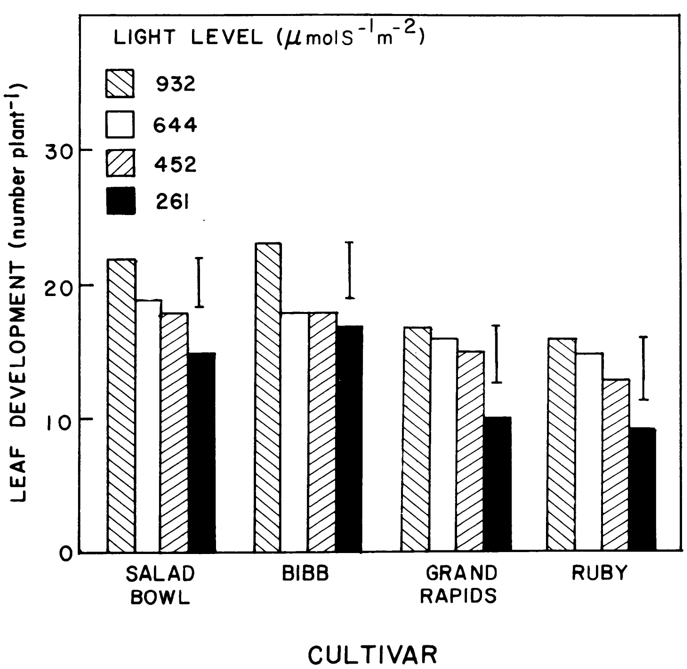

Fig. 1. Leaf number of 4 lettuce cultivars grown for 25.5 days under one of 4 different levels of photosynthetic photon flux density (PPFD) in single strength (1×) Hoagland's solution and an ambient temperature regime at 25°C days/20° nights. Vertical lines indicate significant differences between treatments within a cultivar according to Duncan's multiple range test, 5% level.

Table 3. Visual evaluation of leaf discoloration symptoms for lettuce treated for 25.5 days under 4 different values of photosythetic photon flux density (PPFD) in single-strength nutrient solution containing 15 mM NO_3^-. Photoperiod was 16 hr day^{-1} on a 24-hr light/dark cycle. Ambient temperature was 25°C days/20° nights.

PPFD (μmol $s^{-1}m^{-2}$)	Degree of stress			
	Salad Bowl[z]	Grand Rapids[z]	Bibb[y]	Ruby[y]
261	–	–	+	+
452	–	–	+	+
644	+ +	+	+ +	+ +
932	+ +	+	+ + +	+ + +

[z]+ + = extreme yellowing; + = yellowing; – = no yellowing (green).
[y]+ + + = extreme purpling; + + = slight purpling; + = normal purpling (background).

Table 4. Visual evaluation of leaf discoloration symptoms for lettuce treated for 22 days at 889 μmol $s^{-1}m^{-2}$ and 4 different N regimes in nutrient solution (NS). Photoperiod was 16 hr day^{-1} on a 24-hr light/dark cycle. Ambient temperature was 25°C days/20° nights.

NS strength and N form	Degree of stress			
	Salad Bowl[z]	Grand Rapids[z]	Bibb[y]	Ruby[y]
1 × NS				
15 mM NO_3^-	+ +	+	+ + +	+ + +
30 mm NO_3^-	+	–	+ +	+ +
5 mM NH_4^+ + 25 mM NO_3^-	–	–	+ +	+ +
2 × NS				
30 mM NO_3^-	+	–	+ +	+ +

[z]+ + = extreme yellowing; + = yellowing; – = no yellowing (green).
[y]+ + + = extreme purpling; + + = slight purpling; + = normal purpling (background).

Table 5. Effect of different N regimes in nutrient solution on yield of 4 cultivars of lettuce treated for 22 days at 918 μmol $s^{-1}m^{-2}$ for 16 hr day^{-1}. Ambient temperature was 25°C days/20° nights.

	Leaf dry wt (g $plant^{-1}$)			
	Single-strength nutrient solution			Double-strength nutrient solution
Cultivar	15 mM NO_3^-	30 mM NO_3^-	5 mM NH_4^+ + 25 mM NO_3^-	30 mM NO_3^-
Salad Bowl	2.95 bc A[z]	5.75 c C	7.54 c D	4.41 c B
Bibb	3.62 c A	4.22 b A	4.17 b A	3.83 bcA
Grand Rapids	1.94 a A	4.21 b B	4.07 b B	3.52 b B
Ruby	2.12 ab A	2.45 a A	2.35 a A	2.26 a A

[z]Mean separation by Duncan's multiple range test, 5% level (lowercase for columns, uppercase for rows).

Enhancement of lettuce productivity by high PPFD for 16 hr day^{-1} and enriched N nutrition (Table 5) prompted investigation of the same treatment combination under continuous 455 or 918 μmol $s^{-1}m^{-2}$ with 'Salad Bowl' and 'Bibb', the 2 highest-yielding cultivars. Single-strength nutrient solution was included as a standard for making relative comparisons of growth due to N source and level. Leaf dry weight of 'Bibb' was not different between 455 and 918 μmol $s^{-1}m^{-2}$ when grown in nutrient solution containing 15 mM NO_3^- or 30 mM N as NH_4^+ + NO_3^-, whereas that of 'Salad Bowl' was increased when grown at continuous 918 μmol $s^{-1}m^{-2}$ (Table 6). At either level of continuous light, yield of 'Salad Bowl' was far superior to that of 'Bibb'. Neither N treatment nor PPFD affected the proportion of plant dry weight comprised by leaves for either cultivar, but leaf percentage of plant dry weight was significantly greater for 'Salad Bowl' than for 'Bibb' with all treatment combinations. However, continuous 918 μmol $s^{-1}m^{-2}$ caused 'Salad Bowl' growing in nutrient solution containing 15 mM N as NO_3^- to develop leaf necrosis, and 'Bibb' to bolt prematurely (data not presented). We found that 30 mM N as NH_4^+ + NO_3^- reduced but did not prevent either response with continuous, high PPFD. A minimum daily period of darkness may be required to prevent development of stress symptoms or bolting in leaf lettuce, at least when high PPFD is used.

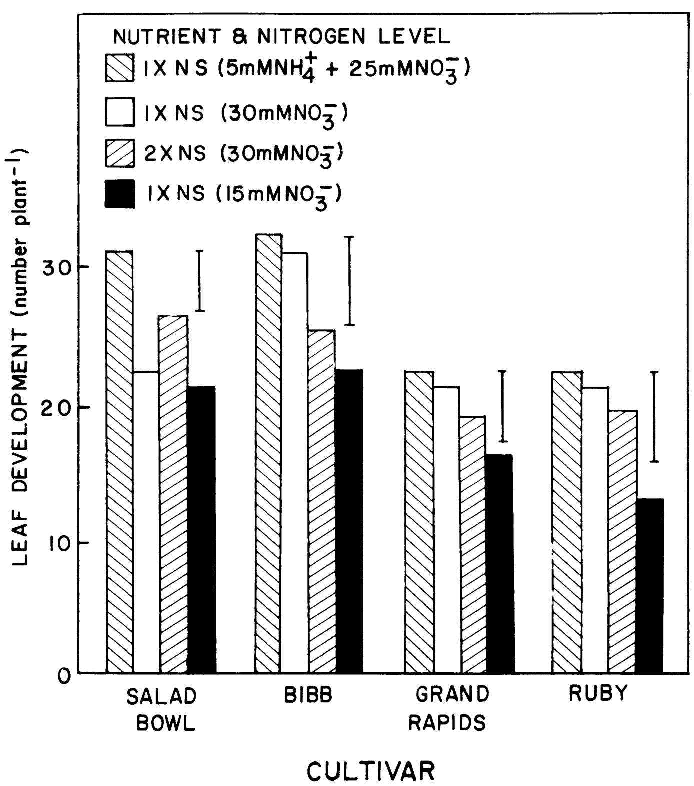

Fig. 2. Leaf number of 4 lettuce cultivars grown for 22 days at one of 4 levels of nitrogen under 16 hr day^{-1} of 889 μmol $s^{-1}m^{-2}$ and 25°C days/20° nights. Vertical lines indicate significant differences between treatments within a cultivar according to Duncan's multiple range test, 5% level.

Crops grown in the field in full sunlight may be exposed to values of PPFD of the order of 2000 μmol $s^{-1}m^{-2}$, whereas those grown in conventional controlled-environment facilities seldom receive more than 25% of this radiant flux density at any given time (20). It remains to be determined for any crop what value(s) of PPFD will allow maximum crop productivity, and under what associated environmental conditions. Some investigators have found 350 to 450 μmol $s^{-1}m^{-2}$ to be adequate for good photosynthetic productivity (3), whereas others recommend 650 to 750 μmol $s^{-1}m^{-2}$ (6). Statistically greater dry weight gain has been reported for several crop species grown at 800 than at 350 μmol $s^{-1}m^{-2}$ (20). In our study, PPFD values of about 900 μmol $s^{-1}m^{-2}$ consistently stimulated photosynthetic productivity of 'Salad Bowl' leaf lettuce above that obtained in the range from 250 to 650 μmol $s^{-1}m^{-2}$, especially in combination with elevated N (Table 2 and 6). It remains to be determined whether further elevation of PPFD will be useful, particularly if used in combination with CO_2 enrichment and growth regulators.

Effects of different N sources on yield have been investigated for various crop species (1, 2, 5). Growth rate and yield of wheat, maize, oats, and potatoes cultured in nutrient solutions containing NH_4^+ as well as NO_3^- exceeded those in media containing either N source alone (5, 14). In our study, all test cultivars of lettuce tolerated NH_4^+ in combination with NO_3^- very well, and growth of 'Salad Bowl' was particularly stimu-

Table 6. Effect of source and concentration of N in nutrient solution on yield of 2 cultivars of lettuce grown for 16 days under continuous illumination at a photosynthetic photon flux density (PPFD) of 445 or 918 μmol $s^{-1}m^{-2}$. Ambient temperature was constant 25°C.

	Leaf dry wt			
	N regime			
	15 mM NO_3^-		5 mM NH_4^+ + 25 mM NO_3^-	
PPFD (μmol $s^{-1}m^{-2}$)	Salad Bowl	Bibb	Salad Bowl	Bibb
	(g $plant^{-1}$)			
455	2.16 a B[z]	1.39 a A	3.09 a C	1.72 a AB
918	3.26 b C	1.37 a A	4.48 b D	2.03 a B
	(% of plant)			
455	80 a B	71 a A	79 a B	72 a A
918	80 a B	68 a A	79 a B	72 a A

[z]Mean separation by Duncan's multiple range test, 5% level (lowercase for columns, uppercase for rows).

lated by this mixed N source (Tables 5 and 6; Fig. 2). Ammonium tolerance may be an important attribute of candidate species for a regenerative life-support system, where recycled biological waste products may be incorporated into plant nutrient solutions.

Dry rather than fresh weight of lettuce leaves was used as the yield parameter in this study because the emphasis of controlled-environment production in the CELSS program is high photosynthetic productivity of the edible portion while minimizing accumulation of nonedible tissue (11). With its favorable proportion of edible biomass (70–80% of plant dry weight), leaf lettuce in general—and 'Salad Bowl' in particular ($\geq$ 80%)—fits this selection criterion particularly well (Tables 2 and 6). Of the 4 lettuce cultivars surveyed, 'Salad Bowl' had the highest relative yield rate and percentage of leaf dry weight in response to long exposures (16 or 24 hr day^{-1}) to values of PPFD 2 to 3 times higher than those usually obtained with fluorescent + incandescent lamps in a conventional growth chamber. This study indicated that doubling 1 $\times$ N from 15 to 30 mM N as NO_3^- alone or as NH_4^+ + NO_3^- enhanced yield, particularly of 'Salad Bowl', under elevated PPFD when a slow drip-out (turnover) of nutrient solution was used. Demand for N likely increased with greater photosynthetic activity. Additional optimization of N source and level, as well as other nutrient solution components, remains to be determined for lettuce grown in modified controlled environments.

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