

Stimulation of Lettuce Productivity by Manipulation of Diurnal Temperature and Light

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Abstract. ‘Salad Bowl’ and ‘Waldmann’s Green’ leaf lettuce (*Lactuca sativa* L.) were exposed to photosynthetic photon flux densities (PPFD) of 444 or 889 $\mu\text{mol s}^{-1}\text{m}^{-2}$ for 20 hours day^{-1} under a diurnal temperature regime of 25°C days/15° nights or 20° days/15° nights. Leaf dry weight of both cultivars was highest under the high PPFD/warm temperature regime and lowest under the low PPFD/cool temperature regime. ‘Waldmann’s Green’ yielded more than did ‘Salad Bowl’ at 889 $\mu\text{mol s}^{-1}\text{m}^{-2}$ and 25° days/20° nights. Under high PPFD, both cultivars yielded better with 25° days/25° nights than with 25° days/20° nights, although relative growth rates were the same under both temperature regimes.

The U.S. National Aeronautics and Space Administration (NASA) had identified a need to define optimum growth environments for crops capable of satisfying human nutritional requirements during long-term habitation of space (8, 10). Candidate species will be selected not only for food value and yield, but also potential for air revitalization, water purification, and waste recycling without accumulating a high proportion of nonedible biomass (4, 12).

Leaf lettuce is a candidate species with a relatively short production schedule, a favorable edible-to-nonedible biomass ratio, and a high photosynthetic activity throughout production; it also provides dietary vitamins, minerals, and fiber (4). In the present investigation, yield of 2 leaf lettuce cultivars was compared at 2 diurnal temperature regimes and high and low light levels.

Seeds of ‘Salad Bowl’ and ‘Waldmann’s Green’ leaf lettuce were germinated in automated nutriculture systems (14), which were placed in each of 2 reach-in growth chambers (Sherer-Gillett model 512–37). Each system supported growth of 20 lettuce plants spaced 20 cm apart within rows and 25 cm apart between rows. Germination procedures were modified after those of Knudson et al. (7), and cultural procedures were as described previously (6). Seeds were germinated in half-

strength modified Hoagland’s solution (3). Two days after sowing, seedlings were exposed to a PPFD of 444 $\mu\text{mol s}^{-1}\text{m}^{-2}$. After 4 days, the half-strength nutrient solution was switched to single-strength solution containing double-strength N as 5 mM NH_4^+ + 25 mM NO_3^- [supplied as KNO_3 , $\text{Ca}(\text{NO}_3)_2$, and NH_4NO_3]. Iron was supplied as 10 mM Sequestrene 330 Fe (Ciba-Geigy). PPFD was increased to 889 \pm 2 $\mu\text{mol s}^{-1}\text{m}^{-2}$ (high PPFD) at the top of the leaf canopy in one growth chamber and retained at 444 \pm 3 $\mu\text{mol s}^{-1}\text{m}^{-2}$ (low PPFD) in the other. Input wattage of 82% was provided by very high output Cool-White fluorescent lamps, with 18% from frosted incandescent lamps. One-half of the lamps were energized in the chamber maintained at low PPFD. Photoperiod in both chambers was 20 hr on a 24-hr cycle. Chamber floors were flooded during the dark period for additional humidification. Relative humidity was 64% \pm 2% in darkness (Bendix model 566 motor-driven psychrometer). Ambient temperature regimes of 20° \pm 2°C days/15° \pm 2° nights (cool temperatures) or 25° \pm 2° days/20° \pm 2° nights (warm temperatures) were maintained in combination with 444 or 889 $\mu\text{mol s}^{-1}\text{m}^{-2}$. Nutrient solution temperatures averaged 1° lower than ambient in light or darkness. A split-plot experimental design was used, in which each

nutriculture system represented a treatment group for a particular PPFD. Ten plants of each cultivar were randomized within a nutriculture system. Plants were harvested after 14.5 days of treatment.

Ten plants of each cultivar were exposed subsequently to similar, high PPFD under a 20-hr photoperiod in both chambers. The nutrient solution was identical to that already described. Ambient temperature was maintained at 25° \pm 2°C days/20° \pm 2° nights in one chamber and 25° \pm 2° days/25° \pm 2° nights in the other. Five plants per cultivar were harvested at days 8 and 12.5 of treatment. Relative growth rate was calculated as:

$$\overline{\text{RGR}} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \quad (11),$$

where $\overline{\text{RGR}}$ = mean relative growth rate ($\text{mg g}^{-1}\text{day}^{-1}$), $\ln W_2 - \ln W_1$ = difference between natural logarithms of whole plant dry weight (g) at second and first harvests, respectively, $t_2 - t_1$ = time interval between harvests (days). Harvests were performed during exponential growth for both cultivars, as determined from preliminary growth curves. This (night temperature) experiment was harvested 2 days earlier than the previous (PPFD/temperature) experiment because growth rates were greater and leaf tipburn would have become limiting had treatment continued.

The experiment was repeated after shifting diurnal temperature regimes between chambers. This was done to check whether between-chamber variability (2, 9) would limit interpretation of diurnal temperature effects at high PPFD. Experimental design and manipulated variables were matched as closely as possible between chambers.

In both experiments, leaves \geq 1 cm in length were excised at harvest and dried for 3 days at 75°C in a forced-air oven. Samples were equilibrated to room temperature and humidity before weighing.

A significant interaction occurred between PPFD and diurnal temperature regime. At 444 or 889 $\mu\text{mol s}^{-1}\text{m}^{-2}$, 25°C days/20° nights resulted in greater yield of both leaf lettuce cultivars than did 20° days/15° nights (Table 1). Under the cooler temperature regime, neither cultivar responded significantly to change of PPFD. However, under the warmer regime, growth of both cultivars was stimulated at the higher PPFD. ‘Waldmann’s Green’, a dark-green cultivar, was more productive than ‘Salad Bowl’, a light-

Table 1. Effect of 20 hr day^{-1} of 2 different photosynthetic photon flux densities (PPFD) and light/dark temperature regimes on yield of leaf lettuce after 14.5 days of treatment. Plants were grown in a modified Hoagland’s solution containing 5 mM NH_4^+ + 25 mM NO_3^- .

PPFD ($\mu\text{mol s}^{-1}\text{m}^{-2}$)	Cultivar	Leaf dry wt (g plant ⁻¹)	
		Light/dark temp 25°/20°C	20°/15°C
444	Salad Bowl	1.98 a ² B ³	1.18 a A
	Waldmann’s Green	2.78 b B	1.38 a A
889	Salad Bowl	2.90 b B	1.33 a A
	Waldmann’s Green	5.06 c B	2.04 b A

²Mean separation within columns by Duncan’s multiple range test, 5% level (lower case).

³Mean separation within rows by Duncan’s multiple range test, 5% level (upper case).

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Table 2. Effect of dark temperature on yield of leaf lettuce grown for 20 hr day⁻¹ of 910 μmol s⁻¹m⁻² in chamber A or at 914 μmol s⁻¹m⁻² in chamber B after 12.5 days of treatment.

Light/dark temperature (°C)	Cultivar	Leaf dry wt (g plant ⁻¹)	
		Chamber A	Chamber B
25/25	Salad Bowl	3.48 ^{2b}	3.31 b
	Waldmann's Green	3.72 b	3.40 b
25/20	Salad Bowl	2.55 a	2.51 a
	Waldmann's Green	2.85 a	2.76 a

²All data within rows are nonsignificant according to F test at 5% level.

³Mean separation within columns by Duncan's multiple range test, 5% level.

Table 3. Effect of dark temperature on relative growth rate of leaf lettuce between 8 and 12.5 days of 20 hr day⁻¹ of 910 μmol s⁻¹m⁻² in growth chamber A or 914 μmol s⁻¹m⁻² in chamber B.

Light/dark temperature (°C)	Cultivar	Relative growth rate (mg g ⁻¹ day ⁻¹)	
		Chamber A	Chamber B
25/25	Salad Bowl	382 ²	369
	Waldmann's Green	367	372
25/20	Salad Bowl	398	388
	Waldmann's Green	362	364

²All data within columns and rows are nonsignificant according to F test, 5% level.

green cultivar, particularly when grown under the high PPF/D/warm temperature regime. In an unrelated study, lettuce growth measured as leaf number and area was not different between that at 25° days/17° nights and 21° days/13° nights if radiant energy was maintained at a low level of 1.1 cal hr⁻¹ cm⁻² (15).

Day temperature warmer than night temperature is used routinely in the culture of many plant species (1, 5, 15), including lettuce and tomato under low light levels (16, 17). Even under >900 μmol s⁻¹m⁻² provided by high-intensity discharge lamps, 'Grand Rapids' lettuce yielded better under 25°C days/20° nights than under 15° days/20° nights (13). However, in the present investigation, continuous 25° during the short dark period as well as the high-PPFD light period resulted in higher leaf dry weight of 'Salad Bowl' and 'Waldmann's Green' than if the 4-hr dark period was maintained at 20° (Table 2). Possible explanations for a warm dark period enhancing dry-weight gain during the subsequent light period over that of a cooler dark period include higher leaf-expansion rate, more rapid starch hydrolysis, and elevated sink demand at the warmer tem-

perature. Thus, diurnal temperature variation *per se* is not critical for high productivity of these lettuce cultivars under high-PPFD lighting with fluorescent + incandescent lamps. The data in Table 2 also indicate that between-chamber variability was not a significant factor in the reproducibility of these results.

RGR of both cultivars during exponential growth were not different with 25°C days/20° nights or 25° days/25° nights (Table 3), even though cumulative leaf dry weight was higher for continuous 25° at the last harvest date (Table 2). This apparent discrepancy is explained most easily by suggesting that the plants grown with continuous 25° entered exponential growth sooner than those grown with 25° days/20° nights, but sustained RGR for the duration of the treatment period. Reducing the lag phase of seedling development appears to be a promising area of exploration to shorten further the production schedule of these lettuce cultivars.

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