J. Amer. Soc. Hort. Sci. 112(6):932–935. 1987.

Influence of Light- and Dark-period Air Temperatures and Root Temperature on Growth of Lettuce in Nutrient Flow Systems

Peter R. Hicklenton
Agriculture Canada Research Station, Kentville, N.S. B4N 1J5, Canada
Mark S. Wolynetz
Agriculture Canada, Engineering and Statistical Research Centre, Research Branch, Ottawa, Ont. K1A 0C6, Canada

Additional index words. hydroponics, nutrient film technique, solution culture, growth chambers, Lactuca sativa

Abstract. **Butterhead lettuce (*Lactuca sativa* L. 'Montana') plants were grown in recirculating solution culture in growth chambers under various combinations of day temperatures (TD; 12°, 15°, 19.5°, or 22.5°C) and night temperatures (TN; 5° or 14°) and root-zone temperature (TR; 20°, 23°, 26°, or 29°) Photosynthetic photon flux (PPF) was 3.8 mol·day^{-1}· m^{-2}. Leaf area and weight were determined at 7-day intervals. The final harvest followed 28 days of treatments. There were no significant interaction effects between TD and TN. An increase of TD from 12° to 19.5° increased fresh and dry leaf weight and leaf area at final harvest, but increasing TN from 5° to 14° had little effect. Specific leaf area and leaf area ratio increased with increasing TD and TN. Leaf weight ratio increased with TD but remained constant with TN. The overall effect of TR on plant size was minor. Dry weight of roots decreased with increasing TR at the 14- and 21-day harvests, but fresh and dry leaf weights were not affected. Leaf area increased with TR up to 26°. Increases in TR resulted in increased values for specific leaf area, leaf area ratio, and leaf weight ratio at final harvest. The results suggest that some butterhead lettuce cultivars may be grown satisfactorily under low daily PPF by allowing TN to decline to 5° while maintaining TD at ≈19°C. In 'Montana', increasing TR above 20° under those conditions had little beneficial effect on plant size at harvest.**

Commercial greenhouse production of butterhead lettuce has expanded significantly during the last decade in the northeastern United States and Canada. Crops typically are produced in small greenhouse ranges (11) using recirculating nutrient film systems (2). Butterhead crops produced during the winter compete successfully with field-grown lettuce imported from southern regions, provided that production costs can be minimized while quality and growth rate are maintained under low winter light conditions. Costs for greenhouse production can be reduced by lowering air temperature, particularly during the dark period. Production guidelines for lettuce (18) suggest day temperatures in the range from 16° to 19°C and night temperature from 7° to 10° with root-zone temperature maintained at 19° to 24°. Some studies (8, 13) indicate beneficial effects of heating the solution to 30° under low day and night air temperatures. The effects of different light- and dark-period air temperatures and root temperatures on growth of butterhead lettuce have received little attention. These effects are the subject of this study.

Materials and Methods

Pelletized seeds of 'Montana' lettuce were sown in polyurethane foam plugs (Smithers-Oasis, Kent, Ohio) and placed in plastic trays in growth chambers (Enconaire, Model GR36). Air temperature was maintained at 20° ± 0.5°C. Photosynthetic photon flux (PPF) was 200 ± 12 μmol·s^{-1}·m^{-2} at the surface of the plugs for 16 hr/day and was supplied from cool-white fluorescent and incandescent lamps (75% and 25% input wattage, respectively). Relative humidity was maintained at 65% ± 8%. About 95% of the seeds germinated within 3 days. After 6 days in the trays, the plants were moved to a recirculating nutrient system under similar environmental conditions. Composition of the nutrient solution is shown in Table 1. Electrical conductivity (Ec) and pH were determined and readjusted to Ec 2.0 dS·m^{-1} and pH 5.8 by addition of nutrient solution and 1 N HNO_3, respectively, at 3-day intervals. Nutrient solution temperature was maintained at 20° ± 1.5°. These conditions were maintained for 7 days, at which time a majority of the plants had attained a plastochron index (PI) of 4 or 5, based upon a reference length of 10 mm (5). The PI of individual plants was recorded.

Fourteen days after seeding, 72 plants were transferred to each of four growth chambers. Each chamber was equipped with four recirculating nutrient systems each consisting of a single vinyl trough, 50-liter nutrient reservoir, pump, and supply and

Table 1. Elemental composition of nutrient solution.

Element	Concentration
	(mM)
N	11
P	2
K	5
Ca	3
Mg	1
S	1
	(μM)
Fe	46
B	53
Mn	9.2
Zn	2.3
Mo	1.1
Cu	0.8

Received for publication 20 Jan. 1987. Contribution nos. 1888 and I-912 of Agriculture Canada, Research Station, Kentville, and Agriculture Canada, Engineering and Statistical Research Centre, Research Branch, Ottawa, respectively. Partial funding for this project was provided by the Canada/Nova Scotia Agri-Food Development Agreement. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-04 via Open Access. This is an open access article distributed under the CC BY-NC-ND license (https://creativecommons.org/licenses/by-nc-nd/4.0/). https://creativecommons.org/licenses/by-nc-nd/4.0/

Table 2. Experimental day and night temperatures.

Expt.							
1	2	3	4	5	6	7	8
15°/5°[z]	15°/5°	12°/5°	12°/5°	12°/5°	12°/14°	12°/5°	12°/14°
15°/14°	15°/14°	12°/14°	12°/14°	15°/5°	15°/14°	15°/5°	15°/14°
19.5°/5°	19.5°/5°	22.5°/5°	22.5°/5°	19.5°/5°	19.5°/14°	19.5°/5°	19.5°/14°
19.5°/14°	19.5°/14°	22.5°/14°	22.5°/14°	22.5°/5°	22.5°/14°	22.5°/5°	22.5°/14°

[z]Day temperature (°C; 0800 to 1700 HR)/night temperature (°C; 1700 to 0800 HR).

Table 3. The effect of day temperature (TD) on dry (DLW) and fresh leaf weight (FLW) and leaf area (LA) of 'Montana' lettuce.

Period of treatment (days)	TD (°C)[z]	DLW (g)	FLW (g)	LA (cm^2)
	12	0.096	1.64	62.6
7	15	0.106	1.79	76.9
	19.5	0.117	2.32	90.7
	22.5	0.120	2.29	94.1
SE[y]		0.007	0.1	7.4
14	12	0.24	4.18	144.7
	15	0.27	4.62	195.4
	19.5	0.33	6.92	255.2
	22.5	0.35	6.90	278.0
SE		0.03	0.36	25.5
21	12	0.51	9.39	313.4
	15	0.60	11.12	440.6
	19.5	0.82	17.27	625.9
	22.5	0.85	17.49	674.6
SE		0.09	1.29	57.4
28	12	0.96	18.32	601.2
	15	1.20	22.89	856.1
	19.5	1.61	33.49	1186.5
	22.5	1.72	35.50	1384.2
SE		0.13	1.51	108.4

[z]For each parameter, values are least squares means adjusted for initial differences by using plastochron index as a covariate. Data represent TD effects over all levels of TN and TR, expressed on a per-plant basis.
[y]Standard error of the difference, n = 32, df = 17, except for FLW, where n = 20, df = 11.

Table 4. Specific leaf area (SLA), leaf weight ratio (LWR), and leaf area ratio (LAR) of 'Montana' lettuce in relation to day temperature following 28 days in treatments.

Day temp (°C)	SLA ($cm^2 \cdot g^{-1}$)[z]	LWR ($g \cdot g^{-1}$)	LAR ($cm^2 \cdot g^{-1}$)
12	621.5	0.864	537.7
15	712.3	0.871	622.8
19.5	743.2	0.881	655.6
22.5	788.5	0.891	703.1
SE[y]	38.2	0.007	30.9

[z]Values are least square means, adjusted for initial diferences by using plastochron index as a covariate. Data represent TD effects over all levels of TN and TR, expressed on a per-plant basis.
[y]Standard error of the difference, n = 32, df = 17.

discharge tubing. The flowing nutrient solution was thermally isolated from the chamber environment with 1.2-cm-thick expanded polystyrene board. The PPF at plant height in each chamber was maintained at 170 ± 12 $\mu mol \cdot s^{-1} \cdot m^{-2}$ from 0930 to 1530 HR each day. Photoperiod was 9 hr, with a progressive increase and decrease in PPF from 0800 to 0930 HR and from 1530 to 1700 HR, respectively. Total daily PPF was 3.8 $mol \cdot day^{-1} \cdot m^{-2}$. A series of eight experiments was conducted to investigate effects of day (TD) and night (TN) air temperatures and root-zone temperature (TR) on lettuce growth. The TD (maintained between 0800 and 1700 HR) treatments were 12°, 15°, 19.5° or, 22.5°C and the TN (1700 to 0800 HR) was 5° or 14°. The nutrient solution in each reservoir was maintained at 20°, 23°, 26°, or 29° in all experiments by means of a simple proportional control system (17). The TR was measured frequently with thermocouples placed in the developing root mass and was ±0.5° of reservoir temperature under all air temperature conditions. Relative humidity could not be held constant under all temperature conditions and varied between 55% and 75%. Nutrient solution composition and maintenance was the same as that during the pre-treatment phase of the experiment.

Table 5. The effect of night temperature (TN) on dry (DLW) and fresh leaf weight (FLW) and leaf area (LA) of 'Montana' lettuce.

Period of treatment (days)	TN (°C)	DLW[z] (g)	FLW (g)	LA (cm^2)
7	5	0.104	1.96	75.1
	14	0.116	2.05	87.0
SE[y]		0.007	0.20	5.3
14	5	0.28	5.16	200.4
	14	0.31	6.14	236.2
SE		0.03	0.40	18.93
21	5	0.68	12.63	470.3
	14	0.71	15.00	556.9
SE		0.04	1.60	44.5
28	5	1.31	24.57	916.5
	14	1.43	30.52	1097.6
SE		0.09	1.77	84.2

[z]For each parameter, values are least square means adjusted for initial differences by using plastochron index as a covariate. Data represent TN effects over all levels of TD and TR, expressed on a per-plant basis.
[y]Standard error of the difference, n = 64, df = 17, except for FLW, where n = 40, df = 11.

Table 6. Specific leaf area (SLA), leaf weight ratio (LWR), and leaf area ratio (LAR) in relation to night temperature following 28 days of treatment of 'Montana' lettuce.

Night temp (°C)	SLA ($cm^2 \cdot g^{-1}$)[z]	LWR ($g \cdot g^{-1}$)	LAR ($cm^2 \cdot g^{-1}$)
5	661.1	0.877	582.4
14	771.7	0.877	677.2
SE[y]	29.7	0.005	23.9

[z]Values are least squares means adjusted for initial differences by using plastochron index as a covariate. Data represent TN effects over all levels of TD and TR, expressed on a per-plant basis.
[y]Standard error of the difference, n = 64, df = 17.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-04 via Open Access. This is an open access article distributed under the CC BY-NC-ND license (https://creativecommons.org/licenses/by-nc-nd/4.0/). https://creativecommons.org/licenses/by-nc-nd/4.0/

Table 7. The effect of root-zone temperature (TR) and dry (DLW) and fresh leaf weight (FLW), dry root weight (DRW), and leaf area (LA) of 'Montana' lettuce.

Period of treatment (days)	TR (°C)	DLW[z] (g)	FLW (g)	DRW (g)	LA (cm^2)
7	20	0.108	1.99	0.031	82.1
	23	0.106	1.99	0.029	79.6
	26	0.108	2.06	0.029	81.8
	29	0.104	2.00	0.030	80.8
SE[y]		0.002	0.04	0.003	1.5
14	20	0.28	5.58	0.058	209.3
	23	0.29	5.64	0.055	213.4
	26	0.30	5.72	0.053	226.3
	29	0.30	5.67	0.051	224.3
SE		0.01	0.15	0.002	3.9
21	20	0.69	14.08	0.111	495.4
	23	0.68	13.72	0.106	503.3
	26	0.73	14.26	0.108	540.6
	29	0.68	13.21	0.097	515.1
SE		0.02	0.32	0.004	11.1
28	20	1.35	27.34	0.178	964.1
	23	1.33	26.86	0.180	989.6
	26	1.42	28.56	0.176	1042.2
	29	1.38	27.12	0.176	1032.2
SE		0.03	0.71	0.007	24.1

[z]For each parameter, values are least squares means adjusted for initial differences using plastochron index as a covariate. Data represent TR effects over all levels of TD and TN, expressed on a per-plant basis.
[y]Standard error of the difference, n = 32, df = 71, except for FLW, where n = 20, df = 47.

Table 8. Specific leaf area (SLA), leaf weight ratio (LWR), and leaf area ratio (LAR) of 'Montana' lettuce in relation to root temperature following 28 days of treatment.

Root temp (°C)	SLA ($cm^2 \cdot g^{-1}$)[z]	LWR ($g \cdot g^{-1}$)	LAR ($cm^2 \cdot g^{-1}$)
20	696.0	0.874	609.6
23	716.2	0.872	627.0
26	716.0	0.881	632.4
29	737.3	0.881	650.3
SE[y]	4.4	0.002	5.9

[z]For each ratio, values are least squares means adjusted for initial differences by using plastochron index as a covariate. Data represent TR effects over all levels of TD and TN, expressed on a per-plant basis.
[y]Standard error of the difference, n = 32, df = 71.

Each plant was alloted ≈660 cm^2 of growing area with 22 cm separating plants in a trough and 30 cm between troughs.

Two or three plants were chosen at random and harvested from each nutrient system following 7, 14, 21, and 28 days of treatments. The first harvest was thus 21 days from seeding. The polyurethane medium was removed carefully from individual root systems, and plants were separated into leaf and root tissue. Leaves were blotted and weighed prior to area measurement. All tissue was dried at 90° for 24 hr and reweighed. The primary responses recorded were dry leaf weight (DLW), dry root weight (DRW), leaf area (LA), and fresh leaf weight (FLW). Three derived criteria were calculated: specific leaf area (SLA), the ratio of LA to DLW; leaf weight ratio (LWR), the ratio of DLW to total dry weight (DLW + DRW); and leaf area ratio (LAR), the ratio of LA to total plant dry weight.

Since only four growth chambers were available, only four day/night air temperature combinations could be evaluated simultaneously. In order to provide adequate replication, eight experiments were carried out with each day/night temperature combination repeated three or four times. (Table 2). The 12° and 22.5°C TD treatments in Expts. 3 to 8 were in response to patterns in growth observed during the first two experiments. Since TD and TN are partially confounded with experiments, their effects were assessed by fitting a hierarchial model to the data, with TD and TN introduced into the model after removing experiment variation; such an approach should be conservative in attributing effects to these two factors. The data from each harvest were analyzed separately. The PI was a measure of plant size prior to the initiation of the treatments and was used as a covariate in the model (14).

For the data from each harvest, a split-split model was used. The among-chamber-within-experiment term (Error A) was used to test the importance of experiments, TD, TN, and the TD x TN interaction. The nutrient system-within-chamber-within-experiment term (Error B) was used to test the significance of Error A, TR, and the two- and three-way interactions involving TR. The residual among plant within nutrient system variation was used to evaluate Error B (among nutrient solution-within-chamber-within experiment). Unless specifically stated, effects were considered to be significant whenever $P < 0.05$.

Results and Discussion

For the primary responses (DLW, DRW, LA, and FLW), with the exception of DRW in harvest 1, the covariate PI reduced the residual mean squares ($P < 0.001$) in each harvest. For the secondary responses (SLA, LWR, LAR), the covariate generally did not reduce the residual mean square ($P < 0.05$). For consistency, however, the results of the analysis of covariance are presented.

TD and TN exerted independent influences on lettuce growth at each harvest; that is, the TD x TN interaction was not significant for any primary response variables. The effects of TD on LA, FLW, and DLW were highly significant even after 7 days (Table 3). An increase in TD from 12° to 19.5°C resulted in average increases of 73% and 120%, respectively, in DLW and FLW at final harvest. A further increase in TD to 22.5° had no significant effect on DLW or FLW. Leaf area (LA), however, continued to increase with TD up to 22.5°. These data contrast with previous results in which dry weight gain over a 40-day period increased nearly exponentially with temperature between 10° and 22° for several cultivars (16). In that work, however, plants were grown at irradiance levels about four times as high as those used in present experiments. The discrepancy in results between these two studies indicates the difference in temperature response that may be expected between plants cultured under low and high irradiance conditions, and underlines the fact that results and conclusions drawn from the present study may apply only to winter production conditions at northern latitudes.

The capacity of plants to accumulate dry matter depends to a large extent on the size of the assimilatory surface in relation to overall size of the plant. The LAR provides a measure of this relationship and may be used in assessing effects of environmental conditions on the relative size of the assimilatory apparatus (12). LAR is the product of the ratios SLA and LWR. After 28 days, the lowest values for SLA were obtained in plants grown at 12°C TD (Table 4), indicating an accumulation of dry matter by leaves under conditions that tended to severely limit

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-04 via Open Access. This is an open access article distributed under the CC BY-NC-ND license (https://creativecommons.org/licenses/by-nc-nd/4.0/). https://creativecommons.org/licenses/by-nc-nd/4.0/

leaf area expansion. Conversely, SLA was large at a TD of 22.5°. In addition to altering the distribution of dry matter of leaf tissue, increasing TD resulted in greater partitioning of dry matter to the leaves, as indicated by the increasing values for LWR (Table 4). Overall, LAR increased with TD. A similar relationship had been described previously for lettuce grown under low irradiance conditions (3, 4), where temperature in excess of 20°C resulted in a significantly increased LAR but prevented head formation. Strong negative correlations between LAR and heading have been confirmed experimentally (9), although critical values of LAR are cultivar-specific. Since the experiments were terminated before commencement of head formation, it was impossible to determine whether the LAR values observed after 28 days of growth at 22.5°, or even 19.5°, indicate reduced potential for heading at harvest. Culture at TD 22.5° rather than at 19.5° is contraindicated, however, by lack of significant improvements in DLW as well as by the high LAR values.

An increase in TN from 5° to 14°C did not affect DLW, although FLW and LA were increased by the higher TN after 28 days (Table 5). SLA and LAR were reduced at 5° compared to 14°, but LWR was not affected ($P < 0.05$) by TN (Table 6). Thus, while TN influenced the distribution of dry matter within the leaves, there was no change in dry matter partitioning between root and shoot biomass. Previous studies with carnation (10) and tomato (6) under diurnally fluctuating temperatures have shown that dry matter accumulation is either increased or not affected by a decrease in TN from the established TD. The present results are consistent with the observations of those studies. Increased average levels of nonstructural carbohydrate during darkness in plants grown at low TN may increase proportionally the quantity of respiratory energy available for growth as compared with that for maintenance (7). It appears, however, that this advantage is offset by a reduction in respiratory rate at low TN, so that rates of dry matter accumulation do not vary greatly. Proof of performance of similar mechanisms in lettuce will require analysis of the temporal distribution of nonstructural carbohydrates in relation to TN.

The effect of TR on leaf weight gain was minor over the four harvest dates. Neither DLW or FLW was affected by increasing TR from 20° to 29°C (Table 7). DRW, however, decreased slightly with increasing TR for harvests 2 and 3, whereas LA increased up to 26°. This observation contrasts with the results of a previous study with the cultivar Ostinata (13), which indicated significant increases in leaf and root weight over a 20° to 30° TR range, when plants were subjected to low air temperatures (13° day and 4° night) in greenhouses.

The effects of TR on plant growth observed in the present work are not explainable from the available data. A high respiratory rate in root tissue at 29°C TR is a possible reason for the lower DRW in that case. Increases in TR, however, also affect leaf weight and the distribution of dry matter within the plant. At higher TR, increased SLA and LAR values were obtained, as well as increased partitioning of dry matter to the leaves (LWR; Table 5). Similar effects on partitioning over the range of root temperatures used in this study have been described for strawberry (15), whereas changes in shoot morphology, mediated by alterations in dry matter distribution with increasing root temperature, have been reported for blueberry (1). It seems unlikely that such changes in dry matter partitioning can be explained entirely on the basis of changes in root respiration. Alterations in other aspects of root physiology, such as the metabolism of chemical growth regulators, their synthesis, and translocation, may be responsible.

The results of this study permit the formulation of cultural guidelines for temperature conditions for butterhead crops during northern winter production. If temperatures during natural daylight hours are maintained at ≈19°C, nighttime temperature may drop to 5° with only minor effects on harvest weight. Under a 19.5° TD/5° TN regimen, maintenance of solution temperature above 20° may have little beneficial effect on harvest weight or quality, although individual cultivar response to higher temperatures in the root zone should be investigated.

Literature Cited

1. Bailey, J.S. and L.H. Jones. 1941. The effect of soil temperature on the growth of cultivated blueberry bushes. Proc. Amer. Soc. Hort. Sci. 38:462–464.
2. Cooper, A. 1979. The ABC of NFT. Grower Books, London.
3. Dullforce, W.M. 1956. Growth of lettuce seedlings. Nature (London) 177:1244–1245.
4. Dullforce, W.M. 1963. Analysis of growth of winter lettuce varieties. Rpt. Univ. Nottingham School Agr. 1962:57–64.
5. Erickson, R.O. and R.J. Michelini. 1957. The plastochron index. Amer. J. Bot. 44:297–305.
6. Gent, M.P.N. 1984. Carbohydrate level and growth of tomato plants.1. The effect of carbon dioxide enrichment and diurnally fluctuating temperatures. Plant Physiol. 76:694–699.
7. Gent, M.P.N. and H.Z. Enoch. 1983. Temperature dependence of vegetative growth and dark respiration: A mathematical model. Plant Physiol. 71:562–567.
8. Graves, C.G. 1981. Nutrient film technique. Hort. Rev. 5:2–37.
9. van Holsteijn, H.M.C. 1980. Growth of lettuce: II. Quantitative analysis of growth. Meded. Landbouwhogeschool, Wageningen 80(13):1–24.
10. Hurd, R.G. and H.Z. Enoch. 1976. Effect of night temperature on photosynthesis, transpiration and growth of spray carnations. J. Exp. Bot. 27:695–703.
11. Killenberg, C. Take a look at hydroponic realities. Amer. Veg. Grower 33(11):19–22.
12. Kvet, J. J.P. Ondok, J. Necas, and P.G. Jarvis. 1971. Methods of growth analysis, p. 343–391. In: Z. Sestak, J. Catsky, and P.G. Jarvis (Eds.). Plant photosynthetic production. Manual of methods. Junk, The Hague, Netherlands.
13. Mongeau, R. and K.A. Stewart. 1984. Effect of solution temperature on the growth and development of lettuce cv. Ostinata. Proc. Sixth Intl. Congr. Soilless Cult. ISOSC, Wageningen. p. 387–392.
14. Ormrod, D.P., D.T. Tingey, and M. Gumpertz. 1983. Covariate measurements for increasing the precision of plant response to O_3 and SO_2. HortScience 18:896–898.
15. Proebsting, E.L. 1957. The effect of soil temperature on the mineral nutrition of the strawberry. Proc. Amer. Soc. Hort. Sci. 69:278–281.
16. Scaife, M.A. 1973. The early relative growth rates of six lettuce cultivars as affected by temperature. Ann. Applied Biol. 74:119–128.
17. Spomer, L.A. 1982. A simple, inexpensive proportional water-bath temperature controller. J. Phys. E: Sci. Instrum. 15:1163–1164.
18. Wilcox, G.E. 1981. Lettuce growing in the nutrient film system. Purdue Univ. Coop. Ext. Serv. Publ. Yard and Garden HO-169.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-04 via Open Access. This is an open access article distributed under the CC BY-NC-ND license (https://creativecommons.org/licenses/by-nc-nd/4.0/). https://creativecommons.org/licenses/by-nc-nd/4.0/