

acid synthesis and cell division in the plumular hook of pea after ethephon application.

Elevated levels of ethylene and ABA in ethephon-treated 'Redhaven' flower buds apparently delayed bloom in part by slowing the rate of floral development, possibly through effects on cell division.

Literature Cited

1. Addicott, F.T. 1983. Adscisic acid. Prager, New York.
2. Apelbaum, A. and S.P. Burg. 1972 Effect of ethylene on cell division and deoxyribonucleic acid synthesis in *Pisum sativum*. *Plant Physiol.* 50:117-124.
3. Couvillon, G.A. and D.A. Lloyd, II. 1978 Summer defoliation effects on peach spring bud development. *Hortscience* 13:53-54.
4. Crisosto, C.H., P.B. Lombard, and L.H. Fuchigami. 1986. Spring applications of ethephon and ethylene inhibitors on bloom delay, fruit set, and yield in 'Redhaven' peach. *Acta Hort.* 201:195-202.
5. Crisosto, C.H., P.B. Lombard, and L.H. Fuchigami. 1986. Effect of fall ethephon and hand-defoliation on dormant bud ethylene levels, bloom delay, and yield components of 'Redhaven' peach. *Acta Hort.* 201:203-212.
6. Dennis, F.G., Jr. 1976. Trials of ethephon and other growth regulators for delaying bloom in three fruits. *J. Amer. Soc. Hort. Sci.* 101:241-245.
7. Fuchigami, L.H. 1977. Ethephon-induced defoliation and delay of spring growth in *Cornus stolonifera* Michx. *J. Amer. Soc. Hort. Sci.* 102:452-454.
8. Fuchigami, L.H., M. Hotze, and C.J. Weiser. 1977. The relationship of vegetative maturity to rest development and spring budbreak. *J. Amer. Soc. Hort. Sci.* 102:450-452.
9. Fuchigami, L.H., C.J. Weiser., K. Kobayashi, R. Timmis, and L. Gusta. 1982. A degree growth state ($^{\circ}$ GS) model and cold acclimation in temperate woody plants, p. 93-116. In: P.H. Li and K. Sakai (eds.). *Plant cold hardiness and freezing stress*. Academic, New York.
10. Gianfagna, T.J., R. Marini, and S. Rachmiel. 1986. Effect of ethephon and GA₃ on time of flowering in peach. *HortScience* 21:69-70.
11. Levitt, J. 1980. Responses of plants to environment stresses. 2nd ed. vols. I. and II. Academic, New York.
12. Martin, G.C. and C. Nishijima. 1972. Levels of endogenous growth regulators in abscising and persisting peach fruits. *J. Amer. Soc. Hort. Sci.* 97:561-565.
13. Priestley, C.A. 1963. The importance of autumn foliage to carbohydrate status and root growth of apple trees. *Rpt. E. Malling Res. Sta.* p. 104-106.
14. Siebel, J.R. and L.H. Fuchigami. 1978 Ethylene production as an indicator of seasonal development in red-osier dogwood. *J. Amer. Soc. Hort. Sci.* 103:739-741.
15. Sigma Chemical Co. 1984. Sigma diagnostics glucose procedure no. 510. Sigma, St. Louis.
16. Weiler, E.W. 1982. An enzyme-immunoassay for cis (+)-abscisic acid. *Physiol. Plant.* 54:510-514.

J. AMER. SOC. HORT. SCI. 114(6):884-890. 1989.

Growth and Yield of Crisphead Lettuce under Various Shade Conditions

Charles A. Sanchez and Robert J. Allen

Everglades Research and Education Center, IFAS, University of Florida, P.O. Box 8003, Belle Glade, FL 33430

Bruce Schaffer

Tropical Research and Education Center, IFAS, University of Florida, 18905 S.W. 280 Street, Homestead, FL 33031

Additional index words. *Lactuca sativa*, photosynthesis, net CO₂ assimilation, photosynthetic photon flux, solar radiation

Abstract. Studies were conducted during five winter cropping periods in the Everglades, near Belle Glade, Fla., to determine effects of shade applied at various times throughout the growing period on the growth and yield of lettuce (*Lactuca sativa* L.). Ancillary studies also were conducted in a greenhouse to determine effects of shade on the light response of lettuce with respect to net CO₂ assimilation. The maximum net CO₂ assimilation rate (P_n) for lettuce decreased as the irradiance at which the plants were grown decreased. Continuous shading from thinning to harvest reduced crop growth approximately in direct proportion to the reduction in irradiance. Lettuce was most sensitive to reductions in radiation when growth and development were most rapid. These data suggest that lettuce growth from planting through the eight-leaf stage is not affected by small reductions in radiation that might occur in nature, but appears to be largely influenced by temperature. This observation is consistent with data collected during greenhouse experiments that showed that P_n at this early growth stage was low regardless of the shade treatment. Lettuce growth from the eight-leaf through the preheading stage was reduced by low shade levels (75% of prevailing solar radiation). Lettuce yield, however, generally was not affected by low shade levels through the preheading stage. Shading, regardless of the degree, reduced growth and yield during the heading stage of development. Results from greenhouse experiments indicated that the light saturation point of lettuce for photosynthesis during this latter growth stage could reach 800 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. This light level is higher than prevailing light that often exists during fall and winter growing seasons in southern Florida.

The extent to which temperature affects lettuce growth is cultivar-dependent (Scaife, 1973). Generally, a mean of 21C

over a 24-hr period appears to be the maximum and 4C appears to be the minimum for proper head development (Madariaga and Knott, 1951; Thompson and Knott, 1934). Temperatures higher than 21C promote seed stalk elongation, puffy heads, bitterness, and an increased tendency toward internal disorders (Whitaker et al., 1974). The relationship between lettuce growth and temperature is not simple and is affected by light level

Received for publication 11 Aug. 1988. Univ. of Fla. Agr. Expt. Sta. Journal Series no. 9181. 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.

(Bensink, 1958, 1961, 1971; Tibbitts and Kozlowski, 1980; Wiebe and Lorenz, 1977). Lettuce responds more favorably to increased temperature at high, but not low, irradiance (Bensink, 1971; Verkerk and Spitters, 1973).

Field crops generally are subjected to cloudy weather during some part of the Florida growing season. Artificial shading has been successful in identifying growth stages when high radiation is most critical for numerous crop species (Andrews and Burns, 1978; Barrios et al., 1986; Fischer, 1975; Pendleton and Weibel, 1965; Ferree and Stang, 1988). Little information is, however, available concerning the effects of shading on lettuce. Most research on effect of radiation on lettuce growth has been conducted in controlled environments (Knight and Mitchell, 1983a, 1983b; Tibbitts and Kozlowski, 1980). Furthermore, these studies were done with leaf or "Boston" types rather than with crisphead lettuce (Bensink, 1971; Knight and Mitchell, 1983a, 1983b). The objective of this study was to determine effects of shade applied at various times throughout the growing period on the growth and yield of crisphead lettuce.

Materials and Methods

Field experiments were conducted during five winter cropping periods in 1980, 1981, and 1982 in the Everglades, near Belle Glade, Fla. All experiments were conducted on Pahokee muck (Eucic, hyperthermic Typic Medisaprist) soil. The cultivars used were 'Montello' in 1980 and 'South Bay' in 1981 and 1982. Lettuce fields were fertilized according to soil test fertilizer recommendations (Thomas, 1970), and water was supplied by subsurface irrigation from field ditches. Lettuce was seeded in double-row beds with 0.9-m centers and thinned at the four-leaf stage to a 30-cm in-row spacing to give an approximate population of 54,320 plants/ha. Planting, thinning, and harvest dates for each experiment are given in Table 1. Field experiments are referred to as 80a, 80b, 81a, 81b, and 82.

Shading treatments of various levels and durations were applied at different stages of crop development (Table 1). Polyethylene cloth rated for 25%, 47%, or 73% shade was attached to conduit frames 0.75 m tall, 6 m long (along rows), and 3 m wide (across rows) to cover the entire top surface with drops 0.4 m down to block all prevailing sun angles. The first shade treatments were applied after lettuce thinning; subsequent shading treatments were applied at various times after thinning (Table 1). The shade structures were moved to different plots at

different stages of plant development to compare duration and timing of shading. All experiments consisted of four replications (except 80a, which had only three replications) in a randomized complete-block design.

Radiant flux (Q) (280–2800 nm) was measured with an Eppley pyranometer and photosynthetic photon flux (PPF) (400–700 nm) was measured with a Lambda quantum sensor (Model LI 185A). Because of the high correlation ($r = 0.99$) between Q and PPF, continuous on-site measurements were made using a stationary pyranometer and only periodic measurements were made using a portable quantum sensor.

Crop growth measurements were done in Expt. 80a and 80b by removing 10 plants from the center four rows of each plot at 11, 22, 33, and 48 days after thinning, which left one complete row for marketable yield determinations at maturity. In Expts. 80a and 80b, fresh and dry weights were determined. Only fresh weights were measured in Expts. 81a, 81b, and 82 because percentage dry matter did not change significantly with treatments and because lettuce is marketed by fresh weight. Total fresh weight at maturity was determined by removing 4 m of row from the center of the plots. Experiment 82 was harvested at 60 days after thinning, in addition to the first harvest made 49 days after thinning, to evaluate the possibility that the effect of shading was more a delay in growth rather than an absolute yield reduction. Total marketable yields were determined by separating marketable and unmarketable lettuce heads using standard marketing criteria for unwrapped lettuce (USDA, 1973). In these studies, the determination of marketable yield was largely based on lettuce head size, the presence of cracked stems, and ribbiness. Ribbiness is a condition in which lettuce wrapper leaves are twisted and leaf mid-ribs are overly prominent. When this condition occurs, the mid-ribs of lettuce wrapper leaves often break when the lettuce is packed for shipment.

Analysis of variance and regression analysis were done using SAS techniques (SAS, 1982). Although the shade structures were moved to different plots at different stages of development to compare early vs. late shading at various shading levels, we could not predict the exact time when the lettuce crop would mature; therefore, the shading intervals during the heading stage were of slightly longer duration than the others. For the purposes of comparing shade applied during pre-heading with shade applied during heading stages, shading periods were adjusted to lengths of exactly 11, 22, and 33 days by multiplying the shad-

Table 1. Experiments and treatments for field studies on the effect of shading on crisphead lettuce growth and yield.

Year	Experiment	Dates of			Shading periods, days from thinning	Percent of prevailing solar radiation ²
		Planting	Thinning	Harvest		
1980	80a	16 Jan.	12 Feb.	28 Mar.	0–45, 10–45, 22–45, 31–45	100, 75, 53
	80b	22 Oct.	14 Nov.	1 Jan.	0–11, 0–22, 0–33, 0–48, 11–48, 22–48, 33–48	100, 75, 53, 27
1981	81a	30 Nov.	9 Jan.	26 Feb.	0–11, 0–22, 0–33, 0–48, 11–48, 22–48, 33–48	100, 75, 53, 27
	81b	1 Nov.	28 Nov.	14 Jan.	0–21, 0–47, 21–47	100, 75, 53, 27
1982	82	8 Feb.	16 Mar.	20 Apr.	0–35	100, 75, 53

²Each level was represented during each interval.

ing level by the actual length of the shading period (Table 1) and dividing by 11, 22, or 33 days. An analysis was then made using adjusted shading intensities as a continuous variable and shading duration and shading time (pre-heading vs. heading) as class variables.

Two additional experiments were conducted in the air-conditioned greenhouse during May and Oct. 1987. To prevent heat build-up in the greenhouse, the entire greenhouse was covered with 40% and 25% shade cloth during the first and second experiments, respectively. The maximum daily photosynthetic photon flux (PPF) in the greenhouse was 1100 and 1400 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ for the first and second greenhouse experiment, respectively, as determined with a quantum sensor connected to a LICOR LI-1000 data logger. Mean daily temperature in the greenhouse was $19 \pm 3\text{C}$. 'South Bay' lettuce was seeded into 5-liter pots filled with Pahokee muck. At the four-leaf stage, the lettuce was thinned to one plant per pot and exposed to various shade levels to produce pretreatments of 100%, 75%, 53%, and 27% of prevailing solar radiation.

At 14-day intervals, from 10 days after thinning until harvest (52 days after thinning), the effect of irradiance on net CO_2 assimilation (P_n) of individual lettuce leaves was determined. P_n was determined in the laboratory for plants from each shade pretreatment after placing a portion of a single leaf on each plant in a Parkinson leaf chamber connected to a portable CO_2 analyzer (Analytic Development Co., Hoddesdon, Herts, U.K.) Outside air was supplied to the chamber via a pump at a flow rate of $365\text{ ml}\cdot\text{min}^{-1}$. The methods used have been described in detail (Schaffer et al., 1987). Light was provided by four 500-W reflector flood lamps that gave a maximum PPF of $800\text{ }\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. To measure the effects of irradiance on P_n , PPF was increased in nonconsecutive steps by placing cloths of different mesh sizes between the lights and the leaf chamber. Leaves were allowed to equilibrate in the chamber for 5 min before P_n determinations. This equilibration time was determined to be satisfactory according to preliminary experiments. Four single-plant replications per treatment were used for light response determination. To avoid the possibility of re-using a leaf that had been damaged by the leaf chamber, a different set of plants at the same stage of development was used for each P_n determination. Light saturation curves were determined using second-order polynomial regression (SAS, 1982).

Results and Discussion

The net CO_2 assimilation rate (P_n) of lettuce grown in the greenhouse 10 days after thinning (DAT) was low ($2\text{ }\mu\text{mol}\text{ CO}_2/\text{m}^2$ per sec), regardless of shade treatment. Therefore, photosynthetic response curves could not be determined during this early stage of development. Light response curves were determined at 24, 38, and 52 DAT. The hyperbolic shape of the curves relating P_n and PPF were similar to those for other crop species (Salisbury and Ross, 1978).

At 24 DAT, the maximum P_n of plants grown under full light was $9.4\text{ }\mu\text{mol}\text{ CO}_2/\text{m}^2$ per sec (Fig. 1). All shade pretreatments reduced the maximum net CO_2 assimilation rate of lettuce. Lettuce grown under pretreatments of 75%, 53%, and 27% of prevailing solar radiation for 24 DAT produced maximum P_n values of 7.6, 6.0, and $5.7\text{ }\mu\text{mol}\text{ CO}_2/\text{m}^2$ per sec, respectively. At harvest (52 DAT), maximum P_n of unshaded plants was $9.8\text{ }\mu\text{mol}\text{ CO}_2/\text{m}^2$ per sec. Lettuce grown under pretreatments of 75%, 53%, and 27% prevailing solar radiation for 52 DAT, produced maximum P_n values of 7.5, 4.7, and $4.4\text{ }\mu\text{mol}\text{ CO}_2/\text{m}^2$ per sec, respectively. These results generally agree with

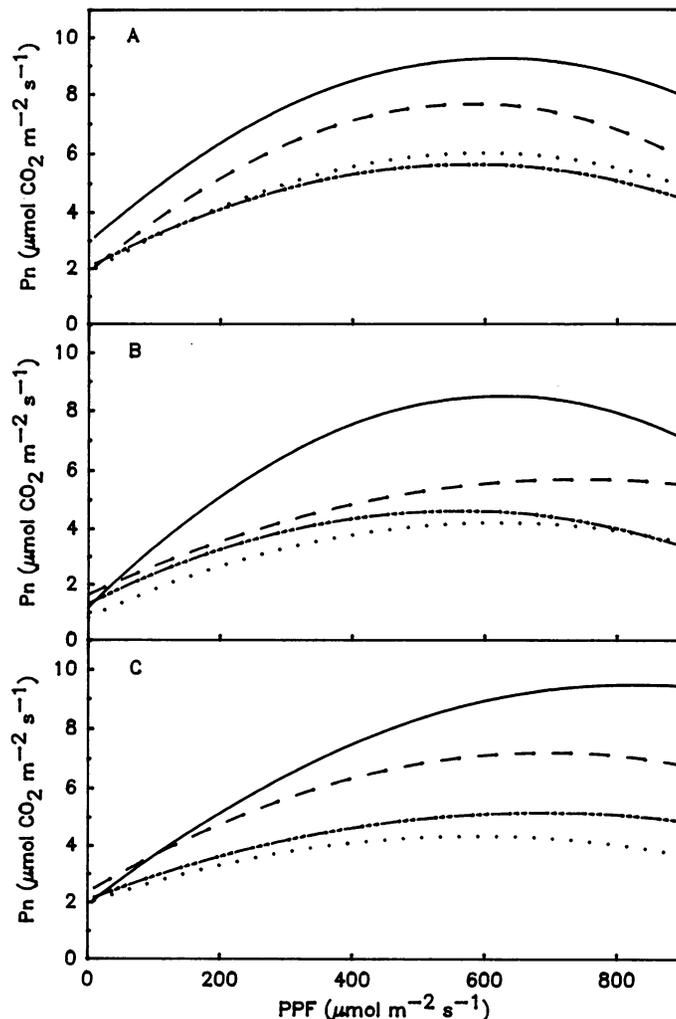


Fig. 1. Light response curves for net CO_2 assimilation of lettuce grown under 100% (—), 75% (---), 53% (-·-·-), and 27% (···) prevailing solar radiations at three times in the greenhouse. Lines were fit by quadratic regression using the following equations, $P < 0.01$:

(A) 24 days after thinning

% solar radiation	Equation	r^2
100	$y = 1.4 + 0.02\text{ PPF} - (1.6 \times 10^{-5})\text{ PPF}^2$	85
75	$y = 2.0 + 0.02\text{ PPF} - (1.7 \times 10^{-5})\text{ PPF}^2$	73
53	$y = 1.6 + 0.01\text{ PPF} - (1.2 \times 10^{-5})\text{ PPF}^2$	80
27	$y = 1.5 + 0.01\text{ PPF} - (1.1 \times 10^{-5})\text{ PPF}^2$	71

(B) 38 days after thinning

% solar radiation	Equation	r^2
100	$y = 1.6 + 0.02\text{ PPF} - (1.6 \times 10^{-5})\text{ PPF}^2$	88
75	$y = 1.6 + 0.01\text{ PPF} - (7.6 \times 10^{-6})\text{ PPF}^2$	75
53	$y = 0.8 + 0.01\text{ PPF} - (1.1 \times 10^{-5})\text{ PPF}^2$	85
27	$y = 1.2 + 0.01\text{ PPF} - (1.1 \times 10^{-5})\text{ PPF}^2$	69

(C) 52 days after thinning

% solar radiation	Equation	r^2
100	$y = 1.9 + 0.02\text{ PPF} - (1.1 \times 10^{-5})\text{ PPF}^2$	82
75	$y = 2.3 + 0.02\text{ PPF} - (1.3 \times 10^{-5})\text{ PPF}^2$	67
53	$y = 2.0 + 0.008\text{ PPF} - (7.0 \times 10^{-6})\text{ PPF}^2$	67
27	$y = 2.1 + 0.009\text{ PPF} - (7.2 \times 10^{-6})\text{ PPF}^2$	71

studies of other plant species where plants subjected to reduced PPF or shading have lower maximum P_n than plants grown under full light or high irradiance (Boller and Nosberger, 1985;

Teskey and Shrestha, 1985). There also was a highly significant ($P < 0.01$) trend for the PPF for maximum Pn of lettuce to increase with plant age. The unshaded plants at 24 DAT responded to increasing PPF up to $600 \mu\text{mol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$, whereas the same treatment near harvest required $800 \mu\text{mol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$ for maximum Pn.

Experimental periods in the field differed markedly in solar radiation and average high and low temperatures (Table 2). Unshaded treatments in Expts. 80a, 80b, 81a, 81b, and 82 yielded, respectively, 47.1, 71.6, 43.7, 45.5, and 61.2 Mg lettuce/ha. Lettuce yields in Expt. 80a were limited by high rainfall shortly after planting, which affected seedling emergence and stand establishment. Lettuce yields in 81a and 81b were limited by low temperatures and low solar radiation during the growing period. The effects of artificial shading on lettuce generally were more pronounced during periods when yields already were limited by ambient environmental conditions.

The reduction in crop growth with continuous shading from thinning to harvest was proportional to the reductions in irradiance (Table 3). Continuous shading from thinning to harvest resulted in the production of many small lettuce heads with pronounced mid-ribs, which substantially decreased marketable yields with increased shade level (Table 3). Marketable yield was not improved by delaying harvest an additional 12 days in Expt. 82. Although the additional time allowed the lettuce mass of the shaded treatments to increase, the lettuce heads remained small, were ribby, and had a high incidence of cracked stem (data not shown).

The effect of shade applied during selected periods on the growth of lettuce is shown in Fig. 2. Only the highest shade level (27% of prevailing solar radiation) significantly affected the growth of lettuce during the first 11 DAT (to the eight-leaf stage). It is reasonable to assume that only extreme shading would have reduced the growth between planting and thinning. This observation is consistent with data from the greenhouse study, which indicated the maximum Pn of lettuce 11 days after thinning was relatively low regardless of shade pre-treatment. Verkerk and Spitters (1973) indicated that lettuce growth during the seedling stage of development generally would not be limited by typical reductions in solar radiation that would occur in nature. Work by Bierhuizen et al. (1973) suggests that lettuce growth during early stages depends primarily on temperature. These observations are consistent with data collected in our study. In Expt. 81a it took 40 days from planting until thinning (four-leaf stage), while, in 81b, it took only 27 days. Interest-

ingly, degree-day accumulation (using a base of 5C) from planting to thinning was ≈ 400 for both experiments (data not shown).

All shade levels reduced lettuce growth during the first 22 or 33 days after thinning (Fig. 2). Furthermore, growth rates for all shade levels in the 22-DAT treatment were significantly lower than the unshaded treatment 10 days after the shades were removed (on day 33). By maturity (on day 48), however, only the highest shade level (27% of prevailing solar radiation) for the 22- and 33-DAT treatments produced significantly less lettuce mass than did the unshaded treatment (Fig. 2). The growth of lettuce for 75% and 53% of solar radiation recovered to the same level as the unshaded treatment imposed from 33 to 48 days after the shades were removed. Generally, marketable yields were reduced only by the 27% of solar radiation treatment applied during the first 11, 22, or 33 days after thinning (Table 4). It appears that, despite the fact that low-PPF growing conditions lower Pn, lettuce will adjust with time to recover from the effects of moderate shade levels (to 53% of prevailing solar radiation) applied during early growth stages.

Shade applied during all intervals immediately before harvest (through the heading stage) reduced the growth of lettuce even at the lowest shading level (Fig. 2). Marketable yields also were substantially reduced with shading of various durations applied during heading (through 48 DAT; Table 4). Yield reduction was especially pronounced in Expt. 81a, during which ambient environmental conditions already were limiting lettuce yields. Reduction in marketable yield was due both to smaller head size and the presence of pronounced ribs and cracked stems.

The results of regression analysis using adjusted shading levels clearly indicate that lettuce mass and yield are affected more ($P < 0.01$) by shading during the heading stage of development than during preheading stages. A comparison showing the effect of shading 21 days after thinning and 21 days before harvest on lettuce mass in Expt. 81a is shown in Fig. 3. Where the shade was applied the 21-day period after thinning, lettuce mass decreased only when irradiance was reduced $>50\%$. However, when the shade was applied the 21-day period before harvest, lettuce mass decreased linearly across all shade levels. Zink and Yamaguchi (1962) found that lettuce produced 70% of its fresh weight during the heading stage of development, and it is not surprising that lettuce growth was most affected by shading during this period. Data from the greenhouse study indicate that during the heading stage, the light saturation level of photosynthesis might exceed $800 \mu\text{mol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$. Ambient light conditions during the fall and winter growing seasons in southern

Table 2. Mean air and soil temperatures ($^{\circ}\text{C}$) and solar radiation ($\text{J} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$), during experimental periods in the field.

Experiment	Air temp 2 m above ground level				Mean soil temp at 10 cm		Solar radiation ($\text{J} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$) ^a	
	Night		Day		Night	Day	Mean	Range
	Mean	Range	Mean	Range				
80a	11.9	-0.6-20.0	24.1	10.0-31.1	19.7	22.7	176	(25.4-301)
80b	14.4	5.0-23.3	25.0	10.0-32.2	22.0	23.6	140	(24.3-237)
81a	9.4	-2.2-21.1	21.9	10.0-30.6	17.8	19.8	157	(27.7-261)
81b	12.1	0-22.2	24.2	8.3-28.9	20.0	21.9	147	(34.7-213)
82	15.5	5.0-21.1	28.1	21.1-32.2	21.3	25.1	211	(37.0-302)

^aMeasured with an Epply pyranometer (280-2800 nm). Mean is for entire experimental period and range represents daily averages during experiment period. An estimation of total irradiance within the photosynthetically active waveband (400-700 nm) can be obtained from measurements of total solar radiations by using the ratio ($2.2 \mu\text{mol} \cdot \text{J}^{-1}$).

Table 3. The effect of continuous shading from thinning to harvest on mean lettuce head mass and marketable yield.

Percent of prevailing solar radiation	Lettuce mass (g/head)					Marketable yield (Mg·ha ⁻¹)				
	80a	80b	81a	81b	82	80a	80b	81a	81b	82
100	866	1318	804	838	1126	47.1	71.6	43.7	45.5	61.2
75	692	994	700	693	911	10.0	54.0	10.2	10.8	49.5
53	563	958	633	619	769	0	44.2	0	10.8	41.8
27	---	420	442	---	---	---	0	0	---	---
	L**Q**	L**Q**	L**Q**	L**Q**	L**Q**	L**Q**	L**Q**	L**Q**	L**Q**	L**Q**

**Significant linear (L) or quadratic (Q) response at $P = 0.01$.

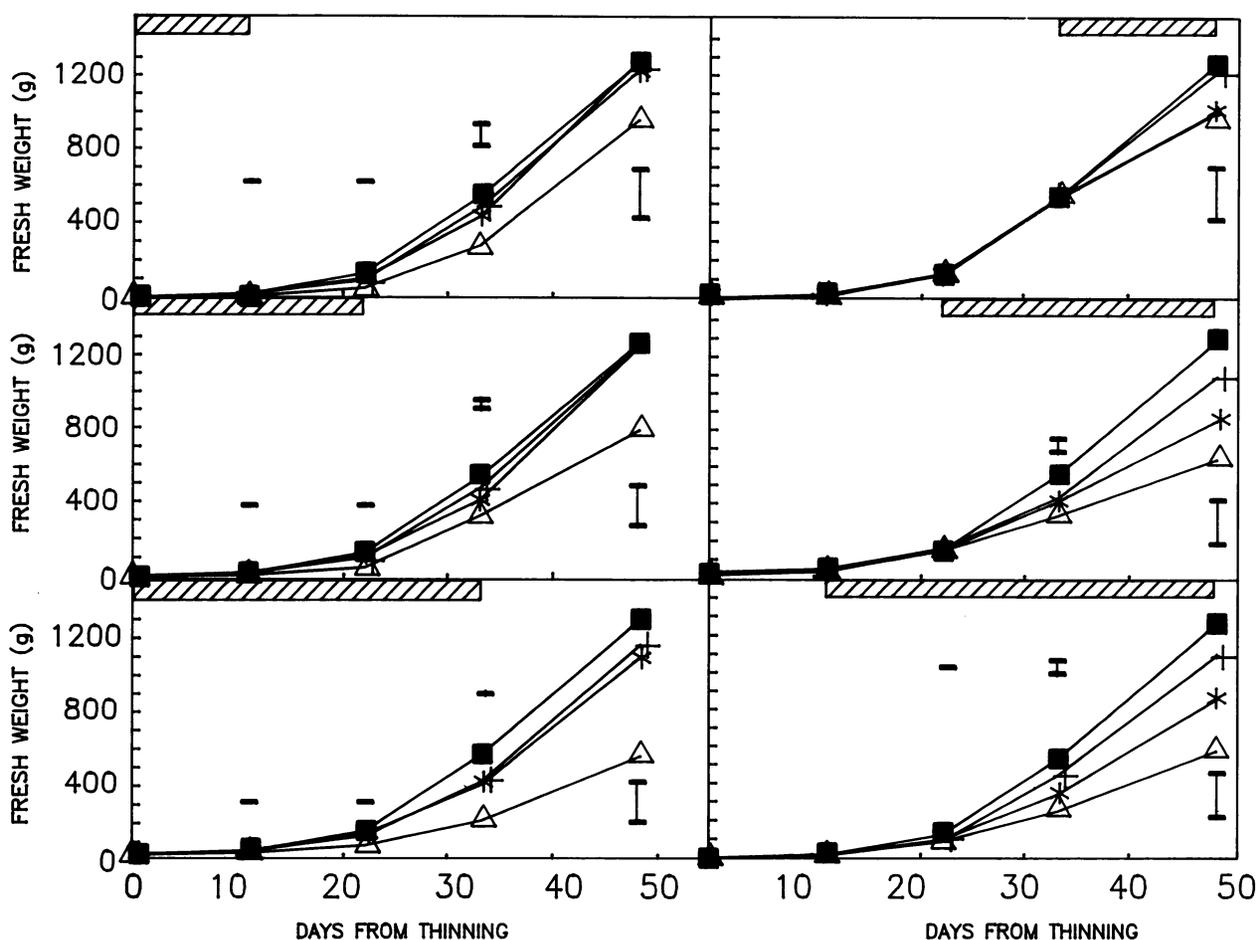


Fig. 2. Effect of different levels of shading applied at selected periods of crop development during Expt. 80b on the growth of lettuce. ■ = 100% solar radiation, + = 75% solar radiation, * = 53% solar radiation, △ = 27% solar radiation, ▨ = shading period. Error bars I show LSD at each sampling time.

Florida often are below this light saturation level (Table 2). It is reasonable that any reduction in radiation during this period would reduce lettuce growth and yield.

Multiple regression analysis of the data combined from the five field experiments showed that total plant mass and marketable yields were primarily a function of mean temperature, average solar radiation, and the period of shading (Table 5). These factors accounted for 85% and 72% of the variation in total lettuce mass and marketable yield, respectively. Several studies have shown increased lettuce growth with increased temperature at constant light intensity, and increased growth with

increased light intensity at constant temperature (Knight and Mitchell, 1983b; Tibbits and Kozlowski, 1980). Furthermore, Bensink (1958, 1961, 1971) found that temperature and light interact to influence the heading of Boston lettuce; under high irradiance or long days, leaves become increasingly broad, which is concurrent with head formation. The effect of temperature was, however, dependent on light. At high irradiance, leaf width increased with increased temperature. At low irradiance, leaf length increased and leaf width decreased with increased temperature. Because of the wide variability in temperatures within the experimental periods, light-temperature interactions could

Table 4. The effects of shading for different periods of time (days after thinning) on lettuce yield for Expts. 80b and 81a.

Shade after thinning (days)	Percent of prevailing solar radiation	Marketable yield (Mg·ha ⁻¹)	
		Expt. 80b	Expt. 81a
0	100	71.6	43.7
0-11	75	70.0	62.2
0-11	53	71.8	43.3
0-11	27	54.5	43.0
0-22	75	69.2	47.9
0-22	53	70.8	45.8
0-22	27	37.0	10.1
0-33	75	64.9	32.0
0-33	53	59.3	42.9
0-33	27	0	0
11-48	75	61.0	0
11-48	53	48.7	0
11-48	27	0	0
21-48	75	59.4	0
21-48	53	47.1	0
21-48	27	0	0
33-48	75	68.6	9.9
33-48	53	47.2	0
33-48	27	52.3	0
0-48	75	44.2	10.2
0-48	53	53.0	0
0-48	27	0	0
Shading intensity		L**Q**	L**Q**
Shading time		0.01	0.01
LSD (P = 0.05)		22.9	15.2

**Significant linear (L) or quadratic (Q) response at P = 0.01.

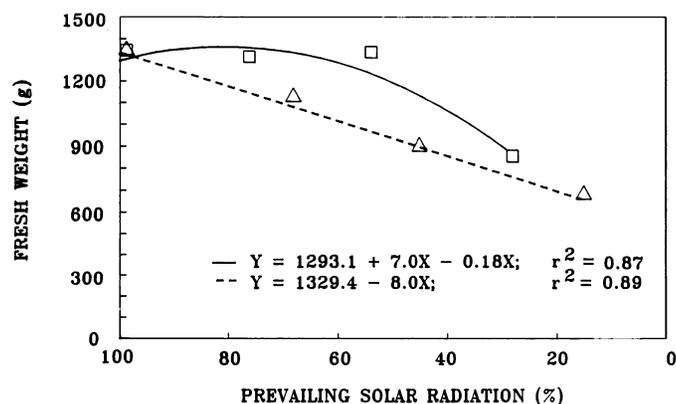


Fig. 3. Effect of period and level of light for 21 days on lettuce fresh weight in Expt. 80b. 0 = shading 21 days after thinning, Δ = shading 21 days before harvest.

not be determined. Additional work is needed to evaluate the effect of light and temperature on the heading of crisphead lettuce.

The multiple regression analysis also showed that days to maturity was primarily a function of total solar radiation intercepted and temperature accumulated using a degree-day base of 5C (Table 5). The fact that solar radiation has a large influence on lettuce growth explains why previous attempts to predict time to lettuce maturity based only on temperature summations have been unsuccessful (Madariaga and Knott, 1951). Additional work is needed to explore the possibility of using a combined temperature and solar radiation accumulation model to predict the growth and development of lettuce.

Table 5. Summary of multiple linear regressions for total mass, marketable yield, and days to maturity on mean temperature (°C), average solar radiation (PPF), shading period (SP), degree-day accumulation (DD_s), and total radiation intercepted (SR) for lettuce over five growing periods.

Response	Model variables	Percentage of total sums of squares			R ²
		Variable			
		First	Second	Third	
Lettuce mass	C, PPF, SP	48**	33**	4**	85**
Marketable yield	C, PPF, SP	30**	35**	7**	72**
Days to maturity	DD _s , SR	41**	40**	---	81**

**Significant at P = 0.01.

Sensitivity of lettuce to high shade (27% of prevailing solar radiation) throughout growth and low shade (73% of prevailing solar radiation) during heading is consistent with the observation that extended periods of cloudy weather in the Everglades either slow or completely halt lettuce growth. Growers frequently assume that slow growth is the result of a soil fertility deficit caused by leaching from the rainfall that usually accompanies cloudy weather. These growers often respond with sidedress fertilizer applications. Overall, a better understanding of the relationship between solar radiation and lettuce growth should enable us to improve management of fertilizer inputs.

Data from this study demonstrate the sensitivity of lettuce growth to low light during most periods of development after the four-leaf stage. Even though high productivity of lettuce often is attained in the Everglades, the existing crop genotypes may not be ideal for winter production in this region, where irradiance is variable and daylength is short. Most cultivars used are selections made from crosses between cultivars developed for summer months in northern latitudes of the United States, where irradiance is high and days are long. It could be possible to select lettuce germplasm capable of using solar radiation more efficiently in subtropical and tropical regions.

Literature Cited

- Andrews, R.H. and M. Burns. 1978. Effect of shade applied at consecutive periods on sweet corn development. *J. Amer. Soc. Hort. Sci.* 103:658-661.
- Barrios, E.P., F.J. Sundstrom, D. Badcock, and L. Leger. 1986. Quality and yield response of four warm-season lawngrasses to shade conditions. *Agron. J.* 78:270-273.
- Bensink, J. 1958. Morphogenetic effects of light intensity and night temperature on the growth of lettuce (*Lactuca sativa* L.). with special reference to the process of heading. *Proc. R. Netherlands Acad. Sci. Ser. C.* 61.
- Bensink, J. 1961. Heading of lettuce (*Lactuca sativa* L.) as a morphogenetic effect of leaf growth. *Proc. 15 Intl. Hort. Congr. Advances in Hort. Sci.* vol. 1 Pergamon, New York. p. 470-475.
- Bensink, J. 1971. On morphogenesis of lettuce leaves in relation to light and temperature. *Meded. Landouwhogeschool, Wageningen* 71:1-93.
- Bierhuizen, J.F., J.L. Ebbens, and N.C.A. Koomen. 1973. Effects of temperature and radiation on lettuce growing. *Neth. J. Arg. Sci.* 21:110-116.
- Boller, B.C. and J. Nosberger. 1985. Photosynthesis of white clover leaves as influenced by canopy position, leaf age, and temperature. *Ann. Bot.* 56:19-27.
- Ferree, D.C. and E.J. Stang. 1988. Seasonal planting, shading, growth,

- and fruiting in 'Earlingrow' strawberry. *J. Amer. Soc. Hort. Sci.* 113:322-327.
- Fischer, R.A. 1975. Yield potential in a dwarf spring wheat and the effect of shading. *Crop Sci.* 15:607-613.
- Knight, S.L. and C.A. Mitchell. 1983a. Enhancement of lettuce yield by manipulation of light and nitrogen nutrition. *J. Amer. Soc. Hort. Sci.* 108:750-754.
- Knight, S.L. and C.A. Mitchell. 1983b. Stimulation of lettuce productivity by manipulation of diurnal temperature and light. *Hort-Science* 18:462-463.
- Madariaga, F.J. and J.E. Knott. 1951. Temperature summations in relation to lettuce growth. *Proc. Amer. Soc. Hort. Sci.* 58:147-152.
- Pendleton, J.W. and R.O. Weibel. 1965. Shading studies on winter wheat. *Agron. J.* 5:292-293.
- Salisbury, F.B. and C.W. Ross. 1978. *Plant physiology*. Wadsworth, Belmont, Calif.
- SAS Institute, Inc. 1982. *SAS user's guide: Statistics*. 1982 ed. SAS Institute, Inc., Cary, N.C.
- Scaife, M.A. 1973. The early growth rates of six lettuce cultivars as affected by temperature. *Ann. Applied Biol.* 74:119-128.
- Schaffer, B., L. Ramos, and S.P. Lara. 1987. Effect of fruit removal on net gas exchange of avocado leaves. *HortScience* 22:925-927.
- Teskey, R.O. and R.B. Shrestha. 1985. A relationship between carbon dioxide, photosynthetic efficiency and shade tolerance. *Physiol. Plant.* 63:126-132.
- Thomas, F.H. 1970. Sampling and methods used for analysis of soils in the soil testing laboratory of the Everglades experiment station. Everglades Sta. Res. Rpt. EV65-18.
- Thompson, H.C. and J.E. Knott. 1934. The effect of temperature and photoperiod on the growth of lettuce. *Proc. Amer. Soc. Hort. Sci.* 30:507-509.
- Tibbitts, T.W. and T.T. Kozlowski. 1980. Growth of crop plants under high levels of HID irradiation in the Wisconsin biotron. *Phytotron Nwsl.* 21:68-74.
- USDA. 1973. *USDA standards for grades of lettuce*. USDA Agr. Mktg. Serv. Washington, D.C.
- Verkerk, K. and C.J.Th. Spitters. 1973. Effects of light and temperature on lettuce seedlings. *Neth. J. Agr. Sci.* 21:102-109.
- Whitaker, T.W., E.J. Ryder, V.E. Rubatsky, and P.V. Vail. 1974. *Lettuce production in the United States*. USDA Hdbk. 221.
- Wiebe, H.J. and J.P. Lorenz. 1977. Influence of changing temperature and light-dependent temperature control on the growth of lettuce. *Gartenbauwissenschaft* 42:42-45.
- Zink, F.W. and M. Yamaguchi. 1962. Studies on the growth rate and nutrient absorption of head lettuce. *Hilgardia*. p. 471-485.

J. AMER. SOC. HORT. SCI. 114(6):890-893. 1989.

Solution Depth Affects Root Morphology and Growth of Cucumber Plants Grown in Circulating Nutrient Solution

Gap C. Chung¹, Richard N. Rowe², and Roger J. Field³

Lincoln University College, Christchurch, New Zealand

Additional index words. *Cucumis sativus*, nutrient film technique, shoot : root ratio, root number : root length ratio, hydroponics, Richards function

Abstract. Defruited cucumber (*Cucumis sativus* L.) plants were grown hydroponically for 28 days in containers with 4.5 liters of capacity, in which constant solution depths of 1, 5, 50, and 170 mm were maintained. The plants grown in the 1- and 5-mm-deep solutions grew more slowly than those in the deeper solutions. Both root and shoot growth were reduced at the shallow depths, but shoot growth was affected more than root growth. Thus, the shoot : root ratios were considerably smaller in the shallower than in the deeper solutions. The root systems in the shallower solutions, initially, were relatively more branched than in the deeper solutions. The shallow solutions caused the plants to allocate a higher proportion of their photosynthetic resources to the root at the expense of leaf growth. In the shallow solutions, a progressively higher proportion of this root growth became exposed above the solution, and, therefore, could not contribute to the absorption of water and nutrients. Control of solution depth may be a useful tool for controlling the vigor of the shoots of cucumber and the data presented may explain why growth problems have been experienced with this crop, particularly where a very thin film of nutrient is used, as in nutrient film technique.

One of the main physical characteristics of the nutrient film technique (NFT) is the shallow depth of the circulating nutrient solution (Cooper, 1975). Unlike plants grown in soil or in conventional hydroponics, the proportion of the root system immersed in the solution becomes progressively smaller with time,

and a higher proportion of roots becomes exposed to the air. With time, the increased exposure of roots to air in plants grown in NFT would be expected to be accentuated where the physical dimensions of the troughs and the growth of competing plants confine the volume of solution available to each plant grown in the system. It would be expected, therefore, that the depth of solution would affect the proportion of the root system directly involved in the absorption of water and mineral ions.

In the case of cucumber, it is generally recommended that more care be given to plants growing in NFT compared to other greenhouse production methods (Winsor, 1978). Graves (1983) suggested that some of the difficulties experienced in growing cucumber in NFT might be due to a fast growth rate of the root system, which blocks the flow of nutrient solution and causes partial root death and subsequent poor shoot growth. However, the literature does not reveal any work that attempts to examine

Received for publication 11 Oct. 1988. A portion of a thesis submitted by G.C.C. as partial fulfillment of the requirements for the PhD at the Lincoln Univ. College. We appreciate the computer program supplied by David R. Causton (Dept. of Botany and Microbiology, University College of Wales, Aberystwyth), for curve fitting. 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.

¹Present address : Dept. of Horticulture, College of Agr., Chonnam National Univ., Kwangju, Chonnam, Korea.

²Professor and Head, Dept. of Horticulture.

³Professor, Dept. of Plant Science.