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An Evaluation of Plant Growth and Development under Various Daily Quantum Integrals

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Abstract. **Plants of chrysanthemum [*Dendranthema × grandiflorum* (Ramat.) Kitamura], radish (*Raphanus sativus* L.), corn (*Zea mays* L.), and cucumber (*Cucumis sativus* L.) were grown under 8-, 12-, 18- or 24-hour daylengths and at three photosynthetic photon fluxes (PPF) within each daylength to evaluate growth and development responses to daily quantum integral (PPF x duration). For the same daily quantum integral, dry matter accumulation and leaf area development were less under 24-hour than under 18-hour daylengths with chrysanthemum and radish. With corn and cucumber, these values were similar under 12-, 18-, and 24-hour daylengths. In all of the species, leaf area and dry matter development were lowest under the 8-hour daylength. Continuous (24-hour) daylength produced some growth abnormalities in radish and chrysanthemum. Specific leaf weight in all species and flower node count in cucumber were linearly related to daily quantum integral up to the highest values examined (73.5 mol·day^{-1}·m^{-2}). All species showed expected photoperiod responses with respect to flowering, but the rate of floral development and number of flower buds formed were highest under the highest PPF (and highest daily quantum integral) treatments. The results indicate that field phenotypes can be obtained in controlled environment (CE) conditions, providing the field daylength and daily quantum integral conditions are reproduced.**

Developments in lighting technology have resulted in a shift away from the use of fluorescent tubes in CE lighting systems to the use of high intensity discharge lamps. Combinations of high intensity discharge and incandescent lamps can give good light distributions with fewer lamps, acceptable spectral quality, and, if needed, PPFs equivalent to peak natural daylight values (Bugbee and Salisbury, 1988; Warrington et al., 1978a, 1978b).

The ability to achieve high PPFs raises important questions with respect to the choice and management of lighting systems for CE experiments. Previously, Warrington et al. (1978b) showed that PPF operating levels of 650 to 750 µmol·s^{-1}·m^{-2} were adequate for most plant growth studies. The use of high PPF levels (≈2000 µmol·s^{-1}·m^{-2}), equivalent to peak sunlight values, for the entire 12-h light period resulted in abnormally high daily quantum integrals (PPF × duration) and plants that were not typical of greenhouse- or field-grown material. However, with dimming and switching systems, the capacity to achieve peak daylight PPF values can allow duplication of the diurnal flux patterns typical of natural daylight. Alternatively, the use of intermediate levels of PPF for longer periods may be more satisfactory for plant growth and CE operation than the use of very high PPF levels for shorter times, provided that plant responses to ‘daily quantum integral can be understood.

Some aspects of plant responses to daily quantum integral have been previously examined (Bugbee and Salisbury, 1988; Bunce, 1983; Chabot et al., 1979; Craker et al., 1983; Downs, 1975; Downs and Hellmers, 1975; Gislerod et al., 1989; Hurd and Thornley, 1974; Jurik et al., 1979), but only Bugbee and Salisbury (1988) have evaluated plant responses to integrals typical of the maximum values occurring naturally. These studies have shown that for similar daily quantum integrals, plants exposed to a low PPF for a long daylength generally accumulate more dry matter than plants exposed to a high PPF over a short daylength. However, growth abnormalities have been reported to occur when plants are grown under continuous light (Arthur et al., 1930; Hillman, 1956; Kristoffersen, 1963; Withrow and Withrow, 1949).

Our study was undertaken to provide more detailed information about the growth and development responses of several plant species to various daily quantum integrals. Continuous (24-h) daylength treatments were included to re-examine plant growth responses to these conditions. This information is required for the effective extension of results obtained in controlled environments to natural or field environments.

Materials and Methods

The experiments were carried out using the walk-in CE rooms in the Climate Laboratory at DSIR Fruit and Trees, Palmerston North, New Zealand.

Biological. Four species were chosen for the study. These had a range of daylength responses and included plants with both C3 and C4 photosynthetic pathways. Three species were sown as seed: radish CV. Early Scarlet Globe, cucumber CV. Triumph hybrid, and corn CV. DeKalb hybrid XL45. The fourth species, chrysanthemum CV. Resilience, was planted as rooted cuttings. Seeds were sown, up to nine per pot, 2 cm deep into 4.5-liter pots containing a growing medium of 70 coarse sand : 15 peat :15 vermiculite (by volume). For corn, cucumber, and radish, 15 pots were used in each PPF × daylength treatment.

The chrysanthemum cuttings were graded into three size classes with each class distributed equally across all treatments. Two cuttings were planted in each 4.5-liter pot. To assist establishment, the cuttings were held under low PPF conditions in a 16-h daylength for 7 days before the start of the treatments. Twelve pots (viz. 24 plants) were used in each treatment.

The plants were arranged within the CE rooms (daylength

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Abbreviations: CE, controlled environment; PPF, photosynthetic photon flux.

treatments) on trolleys. Each trolley accommodated one PPF treatment for a species. The trolleys were relocated within each room twice weekly to minimize the impact of any within-room positional effects.

All pots received daily up to five 200-ml applications of a half-strength Hoaglands's A nutrient 'solution, modified by the use of chelated iron (type ONC, Brooking, 1976). This amount was sufficient to ensure drainage from the pot at each application.

Environmental. Two separate experiments were carried out. Four CE rooms were used concurrently in the study with radish and chrysanthemum (expt. 1). ,Each room was set at one of four daylengths, viz. 8, 12, 18, and 24 h, and within each room there were three PPF treatments (Table 1). The standard lighting system used was four 1000-W Sylvania 'Metalarc' metal halide and four 1000-W ,Philips quartz halogen lamps (Warrington et al., 1978a). The various PPF treatments were achieved by using shade cloth to cover individual plant trolleys or by setting the plant trolleys at different heights. The PPF values achieved (Table 1) are means of nine measurements recorded across the CE room at the start and end of each experiment. The polypropylene shade cloth used did not alter the spectrum over the 400- to 800-nm range.

Each treatment was measured with radiometric and photometric sensors (LI-COR LI-185 quantum/radiometer/photometer; LI-COR, Lincoln, Neb.) to determine conversion factors for different light measurement systems and to allow general comparisons with earlier published work. The following relationships applied to the lamp combination used: 1 $\mu mol \cdot s^{-1} \cdot m^{-2}$ = 65 lux and 1 $\mu mol \cdot s^{-1} \cdot m^{-2}$ = 0.241 $W \cdot m^{-2}$ (400 to 700 nm).

The temperature and relative humidity conditions for expt. 1 were constant at 20 ± 0.3C and 78% ± 5% RH (0.5 kPa vapor pressure deficit), respectively. Carbon dioxide concentration was continuously monitored and remained at 340 ± 20 $\mu l \cdot liter^{-1}$ air throughout the study.

'One CE room was used for successive treatments in the study with corn and cucumber (expt. 2). Four daylengths and three PPF treatments at each daylength were used as in expt. 1. A high intensity light system consisting of 6 × 1500-W Sylvania 'Metalarc' metal halide and 8 × 1000-W Philips quartz halogen lamps (Warrington et al., 1978b) was used. The PPF values and corresponding daily quantum integrals achieved are shown in Table 2. The use of a plate glass–water thermal barrier between the lighting system and the plant growth chamber ensured that leaf temperature increases due to high PPF conditions were small (Warrington et al., 1978b).

Table 1. PPF and calculated daily quantum integral values recorded for each daylength × PPF treatment in expt. 1 (radish and chrysanthemum). Values are the mean values recorded at nine representative positions across the CE room at the start and end of each treatment.

Daylength (h)	PPF treatment		
	High	Medium	Low
	PPF ($\mu mol \cdot s^{-1} \cdot m^{-2}$)		
8	672	586	339
12	691	570	240
18	646	228	95
24	667	223	96
	Daily quantum integral ($mol \cdot day^{-1} \cdot m^{-2}$)		
8	19.4	16.9	9.8
12	29.9	24.5	10.4
18	41.9	14.8	6.2
24	57.6	19.3	8.3

Table 2. PPF and calculated daily quantum integral values recorded for each daylength × PPF treatment in expt. 2 (corn and cucumber).

Daylength (h)	PPF treatment		
	High	Medium	Low
	PPF ($\mu mol \cdot s^{-1} \cdot m^{-2}$)		
8	1209	609	431
12	822	295	123
18	1134	414	175
24	799	286	119
	Daily quantum integral ($mol \cdot day^{-1} \cdot m^{-2}$)		
8	34.8	17.3	12.4
12	35.5	12.7	5.3
18	73.5	26.8	11.3
24	69.0	24.7	10.3

The temperature and relative humidity conditions for expt. 2 were constant at 23 ± 0.3C and 78% ± 5% RH (0.6 kPa vapor pressure deficit), respectively. In other respects, the procedures were similar to those in expt. 1.

Experimental. Plants were harvested through the study to allow development to be assessed and compared at various times. Pot spacing ensured that no light competition occurred among remaining plants.

Radish plants were harvested 7, 14, 21, 24, and 29 days after sowing. The pots were thinned to four plants per pot at the day 7 harvest and two per pot at day 14. The day 21, 24, and 29 harvests each comprised 10, 10, and 9 individual plants, respectively, chosen at random across each treatment.

The chrysanthemum plants were harvested on days 9, 19,29, and 38 after transplanting. The cuttings were selectively harvested to reduce the numbers to one per pot following the second harvest and to ensure that two plants of each of the original large, medium, and small rooted cutting grades were included per harvest. Within these constraints, plants were selected at random across each treatment.

Corn and cucumber were harvested on days 8, 15, 22, and 29. Plants were thinned to two per pot on day 8 and the remaining harvests comprised 10, seven, and eight plants for corn and 15, seven, and eight plants for cucumber.

At harvests, the following were recorded: plant height or main stem length, total leaf area, main stem leaf number, tiller number (corn only), stage of floral development, length and diameter of the radish hypocotyl, and the dry weights of various shoot parts. Leaf areas were determined using an area meter (LI-COR LI-3000 with transparent belt conveyer), and dry weights were recorded after vacuum drying at 40C for 24 h.

Results

Dry weight. Dry matter production in each species increased with daily quantum integral but also depended on daylength (Fig. 1). For all species, the greatest relative changes in dry weight for a fixed change in daily integral generally occurred under long rather than short daylengths. The C3 plants, chrysanthemum and radish, produced highest dry weights for all daily quantum integrals under an 18-h daylength, and least under an 8-h daylength. Continuous lighting (24 h) produced plants with dry weights intermediate to the 12- and 18-h conditions. In cucumber and in the C4 species corn there were only small differences between the 12-, 18-, and 24-h daylengths, but dry matter accumulation was markedly lower under 8 h.

Leaf development. The responses of leaf area to daily quantum integral, especially with ‘radish and cucumber, were more curvilinear than the dry weight responses. Overall, however, leaf area and dry weight responses were similar. Highest leaf area values were recorded in the 12-, 18-, and 24-h daylengths and lowest under 8 h (Fig. 2).

Differences in main-stem leaf number among the PPF and daylength treatments were generally much smaller than the differences in leaf area. Leaf count for corn and cucumber was about linearly related to the daily quantum integral and no marked differences occurred among the different daylengths (Fig. 3). Leaf number for radish on day 24, before advanced floral de-

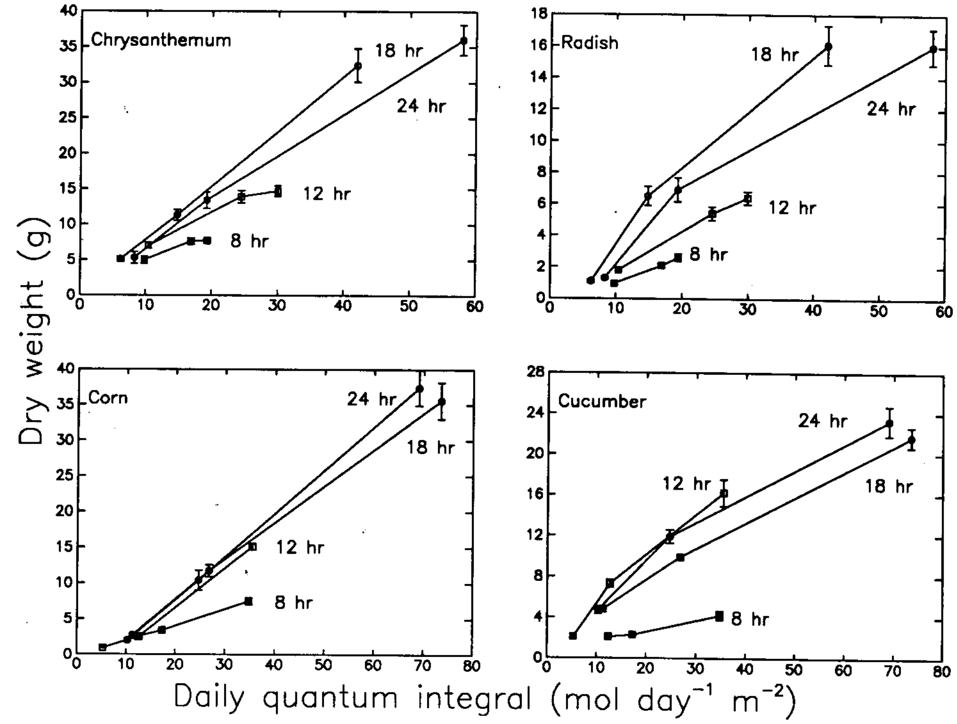

Fig. 1. Shoot dry matter accumulation in chrysanthemum (day 38), radish (day 29, including hypocotyl), corn (day 29), and cucumber (day 29) grown under 8-, 12-, 18-, or 24-h daylengths at various daily quantum integrals. Bars represent ±SE.

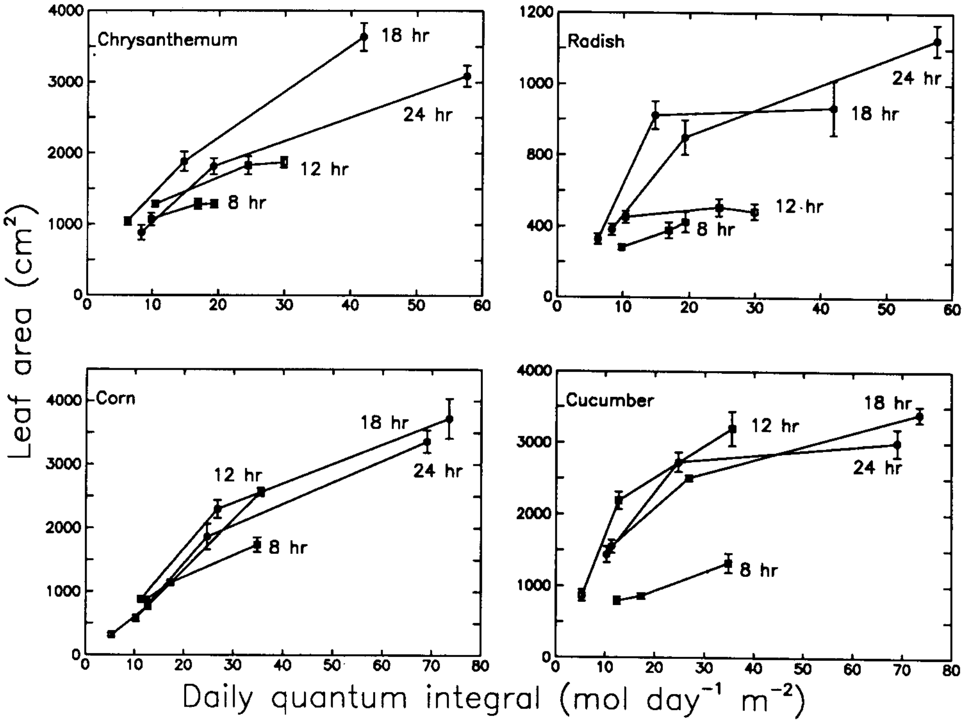

Fig. 2. Total leaf area of chrysanthemum, radish, corn, and cucumber under 8-, 12-, 18-, or 24-h daylengths at various daily quantum integrals. Bars represent ± SE.

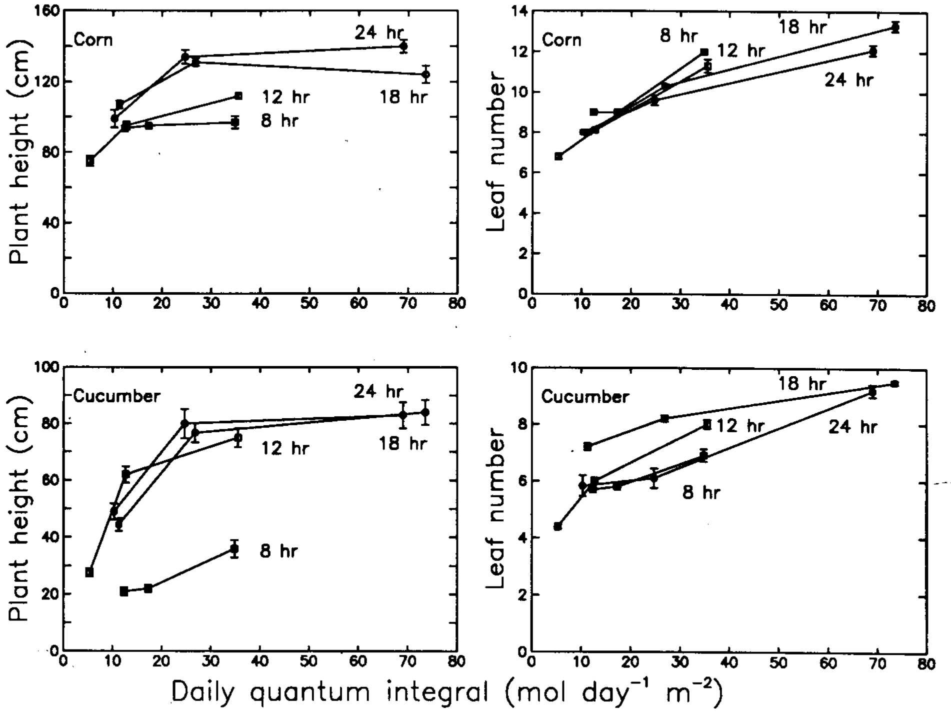

Fig. 3. Plant heights and main stem leaf. numbers of corn and cucumber, measured 29 days after sowing, for plants grown under 8-, 12-, 18-, or 24-h daylengths at various daily quantum integrals. Bars represent ± SE.

velopment, was similar under each daylength treatment but was consistently lower under the low PPF treatment at each daylength (6. 1 ± 0.5 leaves in high and medium PPF treatments and 5.5 ± 0.3 leaves under low PPF conditions).

In contrast to leaf number, the responses of specific leaf weight (leaf dry weight per unit leaf area) to the treatments were substantial. Specific leaf weight increased with increasing daylength and increasing PPF in all species. As a consequence, specific leaf weight was linearly related to daily quantum integral in each of the four species studied (Fig. 4).

Plant height and lateral branching. Cucumber main stem length and corn height (tip of uppermost extended leaf) were both strongly curvilinear in response to daily quantum integral (Fig. *3).* Differences between plants growing under the 18- and 24-h daylengths were small, but the shortest plants were consistently found under the 8-h conditions; this effect was particularly marked in cucumber. Height responses measured in chrysanthemum at the end of the treatments (day 38) were confined to two types; in the 8- and 12-h daylengths, where floral induction occurred and normal terminal flower buds were formed, the plants were 30 to 40 cm high while under 18 and 24 h, they were 43 to 52 cm high. Differences among PPF treatments were small, but tallest plants were produced under the medium-PPF conditions at each daylength. Chrysanthemum growth in the 18- and 24-h high-PPF treatments was further characterized by a trend for the main stem to develop at an angle 20” to 30° from the vertical and for the leaves to be markedly epinastic.

The PPF and daylength treatments strongly affected lateral shoot development. Chrysanthemum plants growing under the 18- and 24-h daylength and high-PPF treatments produced a large terminal “crown” floral bud. This response inhibited further leaf development on the main stem but resulted in considerable lateral branch formation (Table 3). Long-day conditions are normally assumed to inhibit reproductive development in chrysanthemum. Under the reproductively inductive 8- and 12-h daylengths, lateral branch development occurred in all PPF treatments and was greatest under the highest daily quantum integrals. In cucumber the development of lateral stems was also generally related to daily quantum integral in the 12-, 18-, and 24-h daylengths but, as with the height growth response (Fig. 3), development of laterals was much reduced under 8 h (Table 3). Corn produced tillers only in the high PPF treatments under 18- (1.63 tillers per plant) and 24-h (0.75 tillers per plant) daylengths.

Reproductive development. The daylength responses of the species selected were consistent with their previous photoperiod classifications (Salisbury, 1963). Chrysanthemum initiated flower buds under 8- and 12-h (quantitative short-day plant) but generally not under 18- and 24-h daylengths (see below). Radish flowered under 18 and 24 but not under 8 and 12 h (qualitative long-day plant). Corn flowered under all daylengths, but flower initiation occurred earlier and there were fewer leaves initiated under shorter days (quantitative short-day plant). Cucumber flowered under all daylengths (day-neutral plant).

The flowering response was unaltered by PPF, but the rate of floral development was generally increased as either PPF or daily quantum integral was increased. Hence, the number and size of flower buds on chrysanthemum and the rate of floral development (radish) or flower initiation (corn) were all greatest at the highest PPFs studied (Table 4).

Chrysanthemum plants growing at 18- and 24-h daylengths and under high-PPF conditions developed terminal floral buds that were 6.0 and 3.0 mm in diameter, respectively, on day 38. Although extensive lateral branch development occurred, no floral development on the axillary meristems was detected at that time.

The number of flowering nodes (either distillate flowers or total flowers) in cucumber showed a strong positive response to daily quantum integral. Flower node count followed the same response curve regardless of daylength (Fig. 5). In addition, the

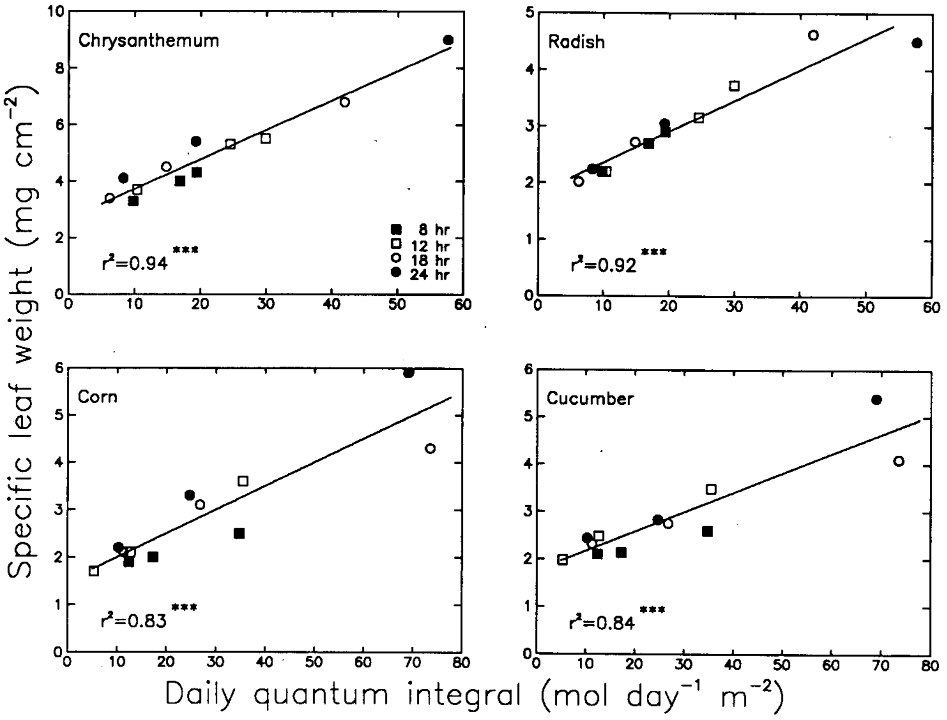

Fig. 4. Specific leaf weights of chrysanthemum, radish, corn, and cucumber grown under 8-, 12-, 18-, or 24-h daylengths at different daily quantum integrals. The linear regression equations are: chrysanthemum, $y = 2.69 + 0.10x$; radish, $y = 1.81 + 0.06x$; corn, $y = 1.50 + 0.05x$; cucumber, $y = 1.76 + 0.04x$.

Table 3. Total length of lateral shoots of chrysanthemum and cucumber under each PPF and daylength treatment (SE value in parentheses).

Species and daylength (h)	Lateral length (cm) PPF treatment High	Medium	Low
Chrysanthemum			
8	40 (11)	47 (11)	18 (11)
12	102 (10)	106 (13)	42 (11)
18	131 (34)	7 (5)	5 (5)
24	108 (24)	0 (0)	0 (3)
Cucumber			
8	28 (4)	9 (1)	7 (1)
12	105 (10)	33 (4)	3 (1)
18	163 (14)	44 (3)	14 (3)
24	119 (16)	53 (9)	6 (1)

proportion of distillate (fruiting) nodes increased as the daily quantum integral increased.

Radish hypocotyl development. Radish hypocotyl diameter and length showed marked increases in response to increases in daily quantum integral (Fig. *6)*. For any particular daily integral, largest diameters and lengths occurred under 18-h and lowest under 8-h daylengths with 12- and 24-h values being intermediate. Differences in diameter growth among daylength treatments "were smaller than the differences in length growth. An allometric relationship was determined between hypocotyl dry weight (Rw) and shoot (leaf plus petiole) dry weight (Sw). It was not altered by either daylength or time from planting and could be defined by the general equation log Rw = log a + K log Sw (Hunt, 1978), where K, the allometric constant, was 0.672 (± 0.094***). However, the intercept did change and could be described by the specific equation log Rw = $[A_{\text{day no.}}$ + blog (day no. × daily integral)] + K log Sw, where b = 1.790 (± 0.113***) and A = –12.33, –11.84, and – 11.39 for days 21, 24, and 29, respectively.

Under all daylength conditions, a harvestable hypocotyl (length : diameter ratio < 2) was obtained under all high- and medium-PPF conditions. In the 12-, 18-, and 24-h daylengths this was achieved within 21 days of sowing. No harvestable hypocotyls developed under any of the low PPF conditions, indicating that the minimum daily light integral required was ≈15 $\text{mol}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$.

Discussion

The effects of light on plant growth and development have previously been studied in considerable detail, but while the majority of research has focused on determining the effects of either PPF or daylength alone, only a few studies have evaluated the influence of daily quantum integral. Plant species show considerable phenotypic acclimation to the light environment under which they are growing and may respond to the quantity, quality, and duration of radiation being intercepted. For flower initiation and development (Vince-Prue, 1975) and stem elongation (Morgan and Smith, 1981), these responses are well-defined for some species. Significant questions remain, however, as to how the different features of the radiation environment, which change in space and time, are detected by a plant and are used to determine the adaptive changes that occur.

Changes in leaf morphology in response to daily quantum integral, including changes in specific leaf weight, have been determined in several studies (e.g., Bjorkman et al., 1972; Bunce, 1983; Chabot et al., 1979). These have shown that peak instantaneous PPF has little influence over changes in leaf morphology but that the daily quantum integral is the primary stimulus for the changes that occur. Chabot et al. (1979) and Nobel and Hartsock (1981) interpeted these morphological changes as being

Table 4. Reproductive development of chrysanthemum, radish, and corn (SE value in parentheses).

Species and daylength (h)	PPF treatment		
	High	Medium	Low
Chrysanthemum (Day 38)			
		Terminal bud diam (mm)	
8	10.6 (0.4)	10.0 (0.6)	8.2 (0.5)
12	12.0 (0.5)	12.3 (0.3)	8.7 (0.5)
		Flower bud no./plant	
8	10.5 (1.4)	10.2 (1.1)	3.0 (1.0)
12	19.0 (0.5)	17.5 (0.4)	7.2 (0.7)
Radish (Day 29)			
		Flower development stage[w]	
18	4 to 5	4	2 to 3
24	5	3 to 4	3
		Flower stem length (mm)	
18	2.4 (0.7)	3.7 (0.7)	2.2 (0.5)
24	27.4 (4.7)	3.8 (1.1)	3.2 (0.7)
Corn			
		Time to tassel initiation (days)	
8	18	20	22
12	---[y]	---	---
18	18	22	27
24	20	25	29+[z]
		Final leaf no.	
8	15[x]	15	15
12	15	14 to 15	14 to 15
18	19	18 to 19	18
24	19	20	18+

[z] Growth stage not reached by day 29.

[y] Not determined.

[x] Final leaf number assessed by dissection on day 29 (refer Warrington and Kanemasu, 1983).

[w] 1 = vegetative; 2 = first stage of floral initiation, flower parts indistinguishable; 3 = floral parts visible; 4 = initial stem elongation; 5 = first florets visible microscopically, definite stem visible.

determined by changes in daily net photosynthesis, on the basis that variation in PPF throughout the course of a day could be integrated through the flow of carbon from photosynthesis. However, this explanation is constrained by the assumption that variation in PPF above that saturating for photosynthesis would have little influence on leaf development. In support of that contention, Chabot et al. (1979) presented evidence of a plateauing of specific leaf weight above 27 mol·day^{-1}·m^{-2}. In contrast, the responses to different PPFs and durations determined by Bunce (1983) could not be fully explained by differences in daily photosynthesis alone. Similarly, such a mechanism would not account for the responses determined in this study where no plateau was reached with specific leaf weight for any of the species studied up to daily quantum integrals in excess of natural values (Fig. 4). Bunce (1983) extended the hypothesis of the photosynthetic characteristics of individual leaves being determined by an energy-dependent feedback relationship, by showing that the effective rate of energy supply was influenced by the rate of leaf expansion as well as by daily net photosynthesis. In keeping with this proposal, others have shown that leaf expansion is very responsive to instantaneous PPF during early development (Jurik et al., 1979). Such a mechanism would account for the specific leaf weight responses determined in our study.

The relationships between daily quantum integral and either plant dry weight or total leaf area were less direct than those between quantum integral and specific leaf weight. Plant dry weight and total leaf area were strongly dependent on other factors, including the influence of both daylength and PPF on flowering and lateral shoot development. The highest dry-matter accumulation in chrysanthemum and radish occurred under the 18-h daylength, and 24 h provided no greater growth in corn and cucumber than 12 or 18 h. Gislerod et al. (1989) similarly found with five ornamental species, including chrysanthemum, that maximum dry-matter growth occurred under a 20-h daylength.

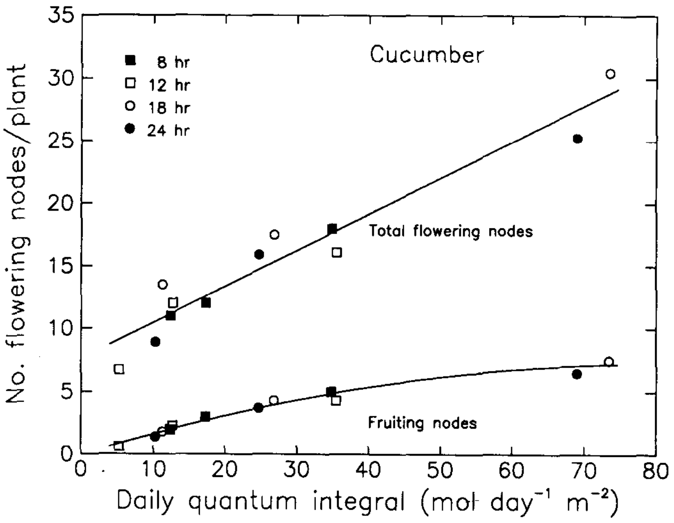

Fig. 5. Total number of flowering and fruiting nodes of cucumber; measured 29 days from sowing, for plants grown under 8-, 12-, 18-, or 24-h daylengths at various daily quantum integrals. The equations for the fitted regressions were: total number of flowering nodes, $y = 7.56 + 0.29x$; fruiting node count, $y = -0.08 + 0.18x - 0.001x^2$.

The lower dry-matter production under the 8-h daylength in this study appears to have been due to poorer leaf area development (Fig. 2) arising from smaller individual leaves and fewer branches (Table 3) being formed under these conditions. Banga and Smeets (1956) observed larger leaf areas under long daylengths with radish, and enhancement of lateral branch development under long days has been observed previously with chrysanthemum (Cockshull, 1976, 1979; Cockshull and Kofranek, 1985; Stefanis and Langhans, 1983). Overall, the results confirm previous observations (Downs and Hellmers, 1975; Went, 1957) that plants exposed to a low PPF for a long daylength generally accumulate more dry matter than plants exposed to a high PPF over a short daylength.

Dry matter accumulation in corn was approximately linearly related to daily quantum integral for each particular daylength. In contrast, these responses for the other three species were curvilinear with smaller changes in dry matter occurring at the higher integrals. Similar differences among species have been observed where growth rates have been determined. In tomato, relative growth rates (g·g^{-1}·day^{-1}, were shown to increase with increasing daily quantum integral up to values of ≈7 MJ·day^{-1}·m^{-2} (≈35 mol·day^{-1}·m^{-2}) beyond which rates declined, particularly in older plants (Hurd and Thornley, 1974). In contrast, crop growth rates obtained for dense, CO_2-enriched stands of wheat grown to grain maturity continued to increase in response to increases in daily quantum integral up to a very high value of 150 mol·day^{-1}·m^{-2} (Bugbee and Salisbury, 1988).

In the present study, there were few unusual growth symp-

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Species and daylength (h)	PPF treatment		
	High	Medium	Low
Chrysanthemum (Day 38)			
		Terminal bud diam (mm)	
8	10.6 (0.4)	10.0 (0.6)	8.2 (0.5)
12	12.0 (0.5)	12.3 (0.3)	8.7 (0.5)
		Flower bud no./plant	
8	10.5 (1.4)	10.2 (1.1)	3.0 (1.0)
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		Flower development stage[w]	
18	4 to 5	4	2 to 3
24	5	3 to 4	3
		Flower stem length (mm)	
18	2.4 (0.7)	3.7 (0.7)	2.2 (0.5)
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Corn			
		Time to tassel initiation (days)	
8	18	20	22
12	---[y]	---	---
18	18	22	27
24	20	25	29+[z]
		Final leaf no.	
8	15[x]	15	15
12	15	14 to 15	14 to 15
18	19	18 to 19	18
24	19	20	18+

[z] Growth stage not reached by day 29.

[y] Not determined.

[x] Final leaf number assessed by dissection on day 29 (refer Warrington and Kanemasu, 1983).

[w] 1 = vegetative; 2 = first stage of floral initiation, flower parts indistinguishable; 3 = floral parts visible; 4 = initial stem elongation; 5 = first florets visible microscopically, definite stem visible.

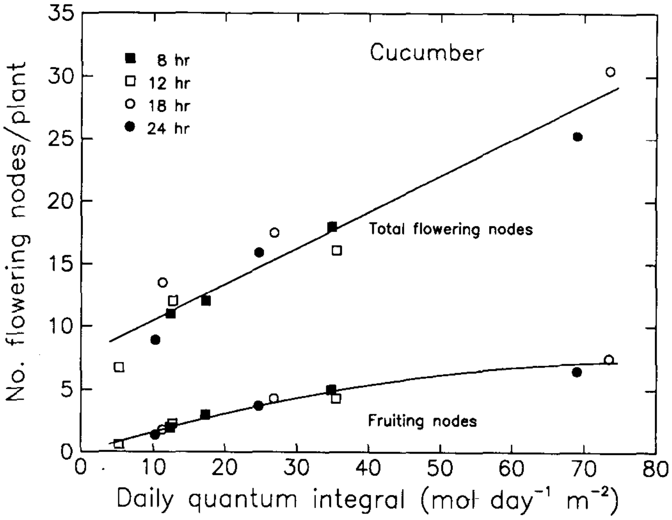

Fig. 5. Total number of flowering and fruiting nodes of cucumber; measured 29 days from sowing, for plants grown under 8-, 12-, 18-, or 24-h daylengths at various daily quantum integrals. The equations for the fitted regressions were: total number of flowering nodes, $y = 7.56 + 0.29x$; fruiting node count, $y = -0.08 + 0.18x - 0.001x^2$.

determined by changes in daily net photosynthesis, on the basis that variation in PPF throughout the course of a day could be integrated through the flow of carbon from photosynthesis. However, this explanation is constrained by the assumption that variation in PPF above that saturating for photosynthesis would have little influence on leaf development. In support of that contention, Chabot et al. (1979) presented evidence of a plateauing of specific leaf weight above 27 mol·day^{-1}·m^{-2}. In contrast, the responses to different PPFs and durations determined by Bunce (1983) could not be fully explained by differences in daily photosynthesis alone. Similarly, such a mechanism would not account for the responses determined in this study where no plateau was reached with specific leaf weight for any of the species studied up to daily quantum integrals in excess of natural values (Fig. 4). Bunce (1983) extended the hypothesis of the photosynthetic characteristics of individual leaves being determined by an energy-dependent feedback relationship, by showing that the effective rate of energy supply was influenced by the rate of leaf expansion as well as by daily net photosynthesis. In keeping with this proposal, others have shown that leaf expansion is very responsive to instantaneous PPF during early development (Jurik et al., 1979). Such a mechanism would account for the specific leaf weight responses determined in our study.

The relationships between daily quantum integral and either plant dry weight or total leaf area were less direct than those between quantum integral and specific leaf weight. Plant dry weight and total leaf area were strongly dependent on other factors, including the influence of both daylength and PPF on flowering and lateral shoot development. The highest dry-matter accumulation in chrysanthemum and radish occurred under the 18-h daylength, and 24 h provided no greater growth in corn and cucumber than 12 or 18 h. Gislerod et al. (1989) similarly found with five ornamental species, including chrysanthemum, that maximum dry-matter growth occurred under a 20-h daylength.

The lower dry-matter production under the 8-h daylength in this study appears to have been due to poorer leaf area development (Fig. 2) arising from smaller individual leaves and fewer branches (Table 3) being formed under these conditions. Banga and Smeets (1956) observed larger leaf areas under long daylengths with radish, and enhancement of lateral branch development under long days has been observed previously with chrysanthemum (Cockshull, 1976, 1979; Cockshull and Kofranek, 1985; Stefanis and Langhans, 1983). Overall, the results confirm previous observations (Downs and Hellmers, 1975; Went, 1957) that plants exposed to a low PPF for a long daylength generally accumulate more dry matter than plants exposed to a high PPF over a short daylength.

Dry matter accumulation in corn was approximately linearly related to daily quantum integral for each particular daylength. In contrast, these responses for the other three species were curvilinear with smaller changes in dry matter occurring at the higher integrals. Similar differences among species have been observed where growth rates have been determined. In tomato, relative growth rates (g·g^{-1}·day^{-1}, were shown to increase with increasing daily quantum integral up to values of ≈7 MJ·day^{-1}·m^{-2} (≈35 mol·day^{-1}·m^{-2}) beyond which rates declined, particularly in older plants (Hurd and Thornley, 1974). In contrast, crop growth rates obtained for dense, CO_2-enriched stands of wheat grown to grain maturity continued to increase in response to increases in daily quantum integral up to a very high value of 150 mol·day^{-1}·m^{-2} (Bugbee and Salisbury, 1988).

In the present study, there were few unusual growth symp-

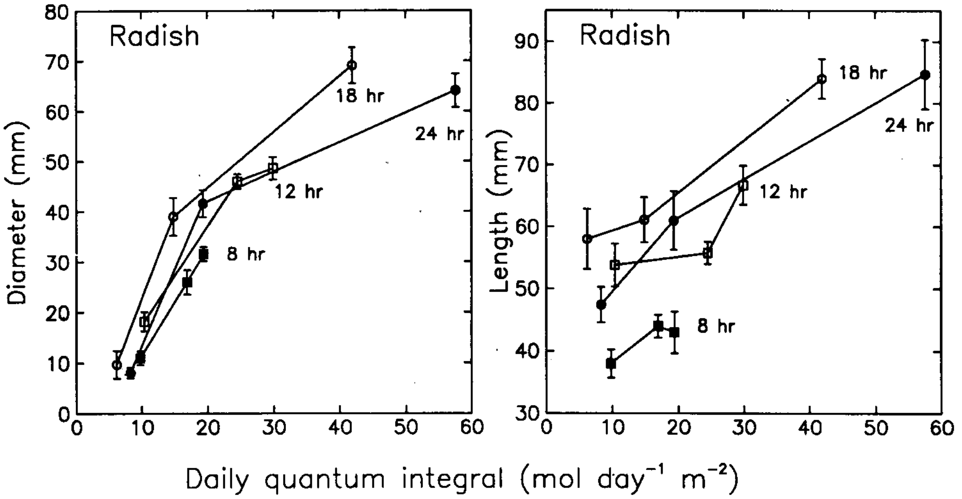

Fig. 6. Hypocotyl diameter and length of radish, measured 29 days after sowing, for plants grown under 8-, 12-, 18-, or 24-h daylengths at various daily quantum integrals. Bars represent ± SE.

toms under continuous daylengths. Some temporary partial chlorosis (mottling) was noted in the early development of radish, and leaf epinasty was observed in chrysanthemum. In many previous studies, some plants (particularly tomato) grown under continuous light (Arthur et al., 1930; Hillman, 1956; Hurd and Thornley, 1974; Kristoffersen, 1963; Withrow and ,Withrow, 1949) or under long light/dark (24/24 h) cycles (Highkin and Hanson, 1954) have shown very poor growth and abnormal symptoms, including a characteristic leaf chlorosis. Kristoffersen (1963) concluded that a dark period was required during the growth of tomato to restore plant water status. In our study, the satisfactory growth obtained under continuous lighting may have been due in part to the favorable watering and mineral nutrition regimes under which the plants were maintained. The mechanisms responsible for adverse growth under continuous light, however, require further study to account for these responses.

The floral initiation and development observed in this study are consistent with previously determined responses for each of the species. While the terminal “crown” bud formation in chrysanthemum grown under continuous long-day conditions was unusual, it is consistent with responses recorded previously by Cockshull (1976, 1979), Cockshull and Kofranek (1985), and Schwabe (1950). Similarly, Cantliffe (1981) found that altering the length of the photoperiod had no effect on sex expression in cucumber but that the number of distillate flowers was greater under the highest PPF conditions evaluated.

Higher rates of floral development were observed in this study at high than at low daily quantum integrals. Similar responses have also been observed in tomato (Kinet, 1977) and geranium (White and Warrington, 1988), and a threshold minimum integral has been identified for some grass species (Foggo and Warrington, 1989). The larger chrysanthemum bud diameters recorded under high-PPF conditions may have been due to a combination of earlier flower induction and greater development, as Karlsson and Heins (1986) and Karlsson et al. (1989) recorded earlier flowering and larger flower sizes when chrysanthemum was grown at high PPF under inductive short-day conditions.

The results of this study may have some important implications with respect to the management of many flower induction studies carried out in CE facilities. In many such studies, plants are grown under conditions that provide a basic 8-h photosynthetic lighting period that is extended with low light from incandescent lamps to provide the different daylength conditions required. In all of the species studied here, growth was markedly restricted under the 8-h daylength and, although floral induction responses may be relevant under such conditions, floral development and reproductive yield responses are likely to provide atypical data with respect to field responses. Most field crops in the world are grown at latitudes <45° where photoperiods are never <9 h (Francis, 1972). In fact, photoperiods <8 h only occur at latitudes >55°. For studies on many temperate crop species, therefore, a 9- or 10-h minimum daylength (depending on latitude) would be more realistic. Such a daylength would provide better growth at most PPF conditions than would 8 h. Further, because the rate of flower development was influenced by PPF (Table 4), care should be taken to maintain similar PPF values across different daylength treatments.

These results indicate that the operation of CEs for commercial crop production, including the use of supplementary lighting in greenhouses, can be maximized by using daylengths of 18 to 20 h and that continuous lighting provides no advantages. It may be possible to schedule the lighting period to take advantage of the off-peak demand rate structures of some utility companies or to schedule the 4 to 6-h dark phase to avoid maximum energy tariffs. However, it is equally clear that high PPF values should be used if maximum growth rates are required. Under 14- to 16-h daylengths, PPF values of 650 to 750 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$, which are typical of those used in many modern CE facilities, provide daily quantum integral values of 33 to 43 $\text{mol}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$ These are similar to values obtained in natural light conditions in middle latitude temperate zones (40 to 45 $\text{mol}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$; Bjorkman, 1981) but are lower than those for tropical zones (e.g., 60 $\text{mol}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$; Bjorkman and Ludlow, 1972). The approximate proportionality of many of the growth and development responses to daily integrals up to 60 $\text{mol}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$ in this study, and of wheat crop growth rates up to 150 $\text{mol}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$ (Bugbee and Salisbury, 1988), indicates that there are advantages to using higher instantaneous PPF values than those currently in use if maximizing productivity is the primary objective. In contrast, if the primary objective is to produce a phenotype under controlled conditions that is similar to a field type, then providing daylength and daily quantum integral conditions similar to the field conditions would be desirable. In this regard, the distribution of PPF throughout the lighting period might be an important factor. In the field, high daily quantum integrals are closely related to the magnitude of the peak PPF and it may be necessary to provide a similar daily PPF distribution in controlled conditions. No differences in plant growth have been detected when square and sinusoidal lighting regimes have been compared (Hughes and Cockshull, 1971; Raper et al., 1975) but in these instances the highest PPF used was ≈850 $\mu mol \cdot s^{-1} \cdot m^{-2}$. Responses under regimes with peak PPF values similar to those that occur in natural environments, therefore, remain to be examined.

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