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Effects of Photosynthetic Rate Maximization on Chrysanthemum Growth and Development

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Abstract. **A 2nd order equation relating net photosynthesis (Pn) to photosynthetic photon flux density (PPFD), temperature, and CO_2 was determined from single leaf CO_2 depletion measurements made with an open gas analysis system. From this information, a photosynthetic optimization equation was used as the basis for computer regulation of greenhouse environment control using 2 strategies. In strategy 1, both temperature and CO_2 setpoints were reset every 15 min based on the PPFD in the greenhouse. In strategy 2, only the temperature setpoint was reset, CO_2 was ambient. The calculated setpoints represented temperature and/or CO_2 values, where predicted Pn was maximized at the particular PPFD. Both strategies were compared to a typical commercial chrysanthemum environment of 16/20/24°C (night/day/vent) with ambient CO_2. *Chrysanthemum morifolium* Ramat. ('Bright Golden Anne') grown in the temperature and CO_2 optimized environment had significantly greater leaf, stem, and total dry weight at flowering compared to the other 2 environmental strategies. The percentage of stem dry weight and the stem length also were increased. For all 3 planting dates the percentage of flower dry weight was reduced but statistically significant on 1 date only. Flowering date was not affected. No consistent statistical differences in plant development were observed between the temperature optimized environment and the traditional environment.**

Photosynthetic rate is influenced by a number of environmental (6) and plant factors (2), and photosynthetic potential is determined by genetic potential (9) and the effect of environment on previous plant growth (1, 7). Photosynthetic photon flux density (PPFD), temperature, and CO_2 concentration are 3 of the important environmental factors which influence photosynthetic rate, and they can be controlled to some extent in a geeenhouse. Photosynthetic studies typically have evaluated 1 or 2 factors at a time (14); however, specific mathematical responses generally have not been determined in greenhouse crops which relate photosynthesis to PPFD, temperature, and/or CO_2 concentration. Exception include the work on carnation (6) and cucumber (12, 13).

As temperature increases, photosynthesis increases up to a maximum after which it then decreases for any given PPFD and CO_2 concentration. A similar response has been observed for CO_2 when PPFD and temperature were fixed (6). When PPFD is fixed and CO_2 and temperature are varied over all combinations, a response surface is formed when all points are plotted. Only 1 combination of temperature and CO_2 concentration at a given PPFD should result in maximum photosythesis.

With greenhouse environmental control by computers (15), it is possible to sense the current PPFD and to control temperature and CO_2 based on a photosynthesis maximization equation. Therefore the objectives of this research were to: 1) develop a regression equation relating photosynthesis to light, temperature, and CO_2 concentration, 2) develop a photosynthetic maximization environmental-control strategy based on this equation, and 3) determine if short-term photosynthetic maximization would yield whole plant growth optimization.

Materials and Methods

Photosynthesis measurements. Individual 'Bright Golden Anne' rooted cuttings were potted in 10 cm pots and placed in a growth chamber at 20°C and a photosynthetic photon flux density (PPFD, 400–700 nm) of 325μmol $s^{-1}m^{-2}$ (8 hr dark day^{-1}) for 1 week. Plants were pinched, and the dark span was increased to 14 hr day $^{-1}$ to induce flowering. Thirty-five days later, net photosynthetic rate (Pn) was determined for the 5th leaf developed on the apical lateral shoot. Pn measurements were made using an open system described by Sams and Flore (11).

Pn was determined at different PPFD, temperature, and CO_2

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concentrations (Table 1) based on a central composite statistical design (3, 5, 8). PPFD and CO_2 concentration (Table 1) were determined on log transformed values to emphasize the lower part of the range for data collection, whereas temperature selection was linear to provide equal data collection emphasis on the entire temperature range.

Four replicates were exposed to each environmental treatment combination simultaneously, and Pn measurements were made sequentually after equilibrium had occurred. Actual PPFD, temperature, and CO_2 concentration values were recorded for regression analysis. Regression equations were calculated using the SPSS subprogram 'Regression' (10).

Derivation of control equations. The predictive Pn equation ultimately selected was a full 2nd order function in the form of:

$$\mathrm{Pn} = \beta_1 + \beta_2 I + \beta_3 T + \beta_4 C + \beta_5 I^2 + \beta_6 T^2 + \beta_7 C^2 + \beta_8 IT + \beta_9 IC + \beta_{10} TC, \qquad [1]$$

where I, C, and T were log PPFD, log CO_2 concentration and temperature, respectively, and $\beta_1, \beta_2, \ldots \beta_{10}$ were coefficients.

An equation that predicts either a maximum or stationary point of 1 variable for a given value of the other 2 variables can be calculated by taking the partial derivative with respect to each variable of (1), setting the partials to zero and then solving for the variable chosen for each partial. For any PPFD and CO_2 concentration, the temperature (t_{opt}) where the Pn slope equals zero (i.e., the Pn rate would be maximum) would be predicted by:

$$T_{opt} = -(\beta_3 + \beta_8 I + \beta_{10} C)/(2\,\beta_6); \qquad [2]$$

and, by simplification, $T_{opt} = \alpha_1 + \alpha_2 C + \alpha_3 I$, [2b]

where α_1, α_2, and α_3 are constants. Likewise, the CO_2 concentration where the Pn slope equals zero would be predicted by:

$$C = (\beta_4 + (\beta_9 I) + (\beta_{10} T)/(2\,\beta_7). \qquad [3]$$

By substitution of equation [2] into [3] and by simplification, one obtains equation [4] which predicts the optimum concentration of CO_2 (C_{opt}) for maximum Pn at any chosen PPFD (γ and δ are constants):

$$C_{opt} = {}_{\gamma I}\delta.$$

By substituting the calculated value of C from equation into equation [2], the optimum temperature for maximum Pn at the chosen PPFD is predicted.

Greenhouse control. The environmental control systems in 6 14.5 m^2 greenhouse sections were computerized (Oglevee Computer Systems, Connellsville, Pa.). The system controlled heating, cooling, and CO_2 concentration and monitored greenhouse temperature, PPFD, CO_2 concentration and relative humidity. The heating system consisted of 6 stages from no heating to full capacity, and the cooling system consisted of 11 overhead vent stages (closed to full venting) followed by fan cooling when the greenhouse temperature increased 3°C above the cooling setpoint. Fans continued to run until temperature dropped back to the cooling setpoint. CO_2 was injected into each section from cylinders of compressed CO_2. The injection time (T_i) used to raise the CO_2 concentration from an initial concentration (C_i) to a final concentration was based on equation [5]:

$$T_i = [(C_f - C_i) \cdot (V) \cdot (R)] \cdot [1 + (C_f - 330) \cdot (V) \cdot (R) \cdot E] \qquad [5]$$

Where C_f = final concentration ($\mu l\ l^{-1}$); C_i = initial concentration ($\mu l\ l^{-1}$); V = Volume of greenhouse (m^3); R = Reciprocal of injection rate (min ml^{-1}); E = Air exchange rate (air exchange min^{-1}).

Once C_f was reached, CO_2 concentration was maintained by continued pulse injections of CO_2 once per minute. Pulse time was calculated by:

$$T_p = (C_f - 330\ \mu l\ l^{-1}) \cdot V \cdot R \cdot E \qquad [6].$$

CO_2 enrichment was stopped when the vents were open more than 5 cm.

Environmental conditions in each section were recorded every 15 min and stored on magnetic disk. Once every 24 hr, the environmental factors and outside temperature were plotted for each section at the 15 min interval. Also for each section, hourly means were calculated and recorded.

Three greenhouse environmental control strategies were used, each with 2 replications. They were: a) traditional (T) environment for chrysanthemum production consisting of 16°/20°/24°C (night/day/vent) temperature setpoints and ambient CO_2 concentration, (330 ± 25 ppm); b) optimized temperature (OT) based on the photosynthesis equation, ambient CO_2 concentra-

Table 1. Central composite design coded values, actual values and observed and calculated Pn for each coded value.

Design Code			Design Values			Photosynthesis ($mg\ CO_2\ dm^{-2}h^{-1}$)	
PPFD ($\mu mol\ s^{-1}m^{-2}$)	CO_2 ($\mu l\ l^{-1}$)	Temp (°C)	PPFD ($\mu mol\ s^{-1}m^{-2}$)	CO_2 ($\mu l\ l^{-1}$)	Temp (°C)	Observed	Calculated
1	1	1	1090	1580	26	29.4	29.7
1	1	−1	1090	1580	16	12.7	15.2
1	−1	1	1090	440	26	22.4	23.8
1	−1	−1	1090	440	16	18.0	18.5
−1	1	1	180	1580	26	1.7	4.3
−1	1	−1	180	1580	16	1.7	2.1
−1	−1	1	180	440	26	6.8	4.1
−1	−1	−1	180	440	16	7.5	10.5
0	0	0	450	830	21	20.1	18.3
−1.682	0	0	1000	830	21	2.3	2.3
1.682	0	0	2000	830	21	33.8	35.0
0	−1.682	0	450	300	21	15.2	15.4
0	1.682	0	450	2500	21	16.0	12.0
0	0	−1.682	450	830	13	12.1	10.2
0	0	1.682	450	830	29	17.9	17.1

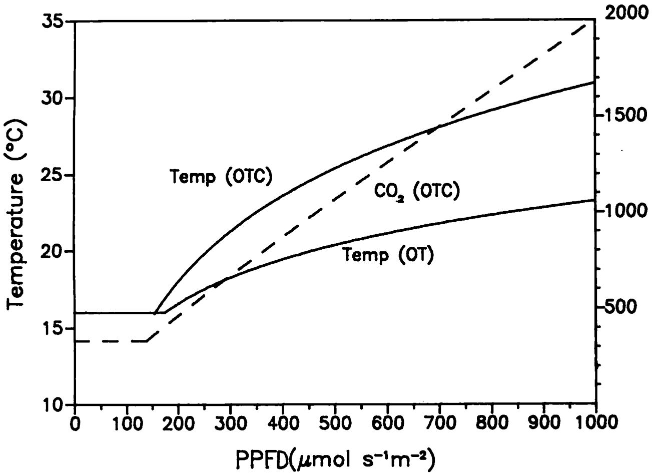

Fig. 1. Relationship between predicted setpoint temperatures and PPFD for the OT and OTC environments and the relationship between predicted setpoint CO_2 concentration and PPFD for the OTC environment.

tion (330 ± 25 ppm); and c) optimized temperature and CO_2 (OTC) based on the photosynthesis control equation. Temperature and CO_2 were reset every 15 min. Temperatures were not allowed to drop below 16° or CO_2 below 330 ppm.

Equations [2] and [4] were used to calculate setpoints based on PPFD for the OTC environment. The CO_2 concentration was set to 330 ppm and equation [2] was used to calculate temperature for the OT environment. Actual temperatures and CO_2 concentrations achieved during the experiments are presented in the Results.

Data collection. Leaf area, number of leaves, stem length, and flower diameter were collected on each shoot of 5 plants from the 6 different greenhouse sections both 5 and 10 weeks after the start of short days. Leaf, stem, flower, and root dry weight were determined for each plant by drying the tissue for 72 hr at 50°C. Data were analyzed using a randomized complete block design using experimental error rather than sampling error to determine treatment significance. Sampling error typically is used in greenhouse experiments because greenhouse sections are not replicated. In this analysis, however, it was possible to use experimental error because each treatment was replicated in 2 greenhouse sections.

Results and Discussion

Photosynthetic response. Average Pn varied from 1.7 to 33.8 mg CO_2 dm^{-2} hr^{-1} depending on the PPFD, CO_2, temperature combination (Table 1). A 2nd order equation based on log transformed PPFD and CO_2 values was calculated on the data (R^2 = 0.89). Coefficients for equation [1] are listed below.

$\beta_1 = -21.92$	$\beta_6 = -0.07$
$\beta_2 = -23.94$	$\beta_7 = -22.98$
$\beta_3 = -4.78$	$\beta_8 = 1.51$
$\beta_4 = 64.29$	$\beta_9 = 13.05$
$\beta_5 = -4.83$	$\beta_{10} = 1.55$

A comparison of calculated Pn and observed Pn for each treatment combination is shown in Table 1. Calculated values are within 20% of actual values except for the 0, 1.682, 0 treatment, and the 4 treatment combinations with PPFD coded −1. The larger deviation under the −1 PPFD conditions (180 µmol $s^{-1}m^{-2}$) probably is due to the increase in observed Pn when CO_2 concentration decreased from 830 µl l^{-1} to 440 µl l^{-1}. This increase may be due to increased stomata aperture. Also, increasing CO_2 from 300 to 2500 ppm (0, −1.682, 0 to 0, 1.682, 0) only slightly increased Pn, possibly due to PPFD being limiting.

Equations [2b] and [4] took the following forms:

$$T_{opt} = -30.2 + 4.27 \ln C + 4.153 \ln I;$$
$$C_{opt} = 3.65\ I^{.9129}$$

Optimum temperatures and CO_2 concentrations based on the equations are shown in Fig. 1. The equation predicted optimum temperatures below 16°C when the PPFD was less than 160 µmol $s^{-1}m^{-2}$ for the OTC environment and 190 µmol $s^{-1}m^{-2}$ for the OT environment. As 16° is the minimum night temperature typically recommended for chrysanthemum production (4), temperatures during night or day were controlled to 16°, even when the equation predicted a lower temperature. Similarly, when CO_2 concentration was predicted lower than 330 µl l^{-1}, it was controlled at 330 µl l^{-1}.

The unrealistic prediction values from these equations below about 150 µmol $s^{-1}m^{-2}$ were not unexpected, as the minimum PPFD used in experimentation was 100 µmol $s^{-1}m^{-2}$. Therefore, values below 100 µmol $s^{-1}m^{-2}$ would be an extrapolation beyond the experimental data.

The optimum temperatures at PPFD above 200 µmol $s^{-1}m^{-2}$ were always greater for the OTC environment compared to the OT environment; differences became greater as irradiance increased. In both instances, however, the optimum temperature continued to increase, but at a reduced rate, as PPFD increased, suggesting a positive interaction between CO_2 concentration and temperature. In carnation, Enoch and Hurd (6) did not report such a positive interaction.

These data show the difficulty in accurate environmental control in a greenhouse, even with a computer control system. Researchers typically report day and night temepratures heating setpoints and less frequently venting or cooling setpoints. Actual average, maximum and minimum temperature seldom are reported. The actual temperatures to which plants are exposed may be quite different than the setpoint temperatures. Greenhouse CO_2 concentration data are normally lacking except in CO_2 research, and then the concentration setpoint is often only reported. Actual CO_2 concentration may be much lower than desired due to venting, as Table 3 shows. An exact knowledge of the actual environment will be necessary in the future to utilize research from different experiments and institutions together in models for environmental control strategies.

Even with the low degree of environmental control accuracy under high PPFD in the OTC environment, sufficient improvement in environmental setpoints over the traditional environmental strategy occurred, offering a significant increase in net dry weight production. We conclude from these data that use of a photosynthetic optimization model to increase stem dry weight is a valid procedure for an environmental control strategy in chrysanthemum production. Significant increases in dry weight occurred in all 3 crops under the OTC environment (Table 2). Pot chrysanthemums, however, are not sold by dry weight, and the concomitant increase in stem height was undesirable for potted chrysanthemum production. Application of additional growth retardant would be necessary for potted chrysanthemum production using this strategy. How much remains a question, as ultimate height may be related to the number of high temperature days.

Greenhouse plant response. Plants grown in the OTC environment had significantly greater leaf, stem, and total dry weight

Table 2. Influence of greenhouse environment on plant development of *Chrysanthemum morifolium* 'Bright Golden Anne' after 10 weeks of growth under short days.

	Planted 19 Jan. 1983			Planted 5 Feb. 1983			Planted 17 Feb. 1983		
Variable	OTC[z]	OT[z]	TRAD[z]	OTC	OT	TRAD	OTC	OT	TRAD
Leaf DW (g)	5.17	4.26	4.34	6.44 a	4.93	4.95 b	6.46 a	5.42 b	4.96 b
Stem DW (g)	7.74 a[y]	4.67 b	5.15 b	7.86 a	4.70 b	4.48 b	6.34 a	4.31 b	4.88 b
Root DW (g)	1.68	1.49	1.10	3.50	2.86	2.32	2.15	1.61	1.36
Flower DW (g)	4.73	4.16	4.42	4.90	4.17	4.21	5.96	6.62	5.85
Total DW (g)	19.32	14.58	15.01	22.70 a	16.66 b	15.97 b	20.92 a	18.53 b	16.47 c
Leaf DW (%)	26.9 b	29.4 a	29.1 a	28.4	31.0	29.7	30.8	29.3	30.2
Stem DW (%)	40.1 a	32.2 b	34.3 b	34.7	28.1	28.1	30.3 a	26.3 b	26.2 b
Root DW (%)	8.9	10.0	7.4	15.4	17.0	14.4	10.3	8.7	8.3
Flower DW (%)	24.2	28.5	29.3	21.4	25.2	26.5	28.6 a	35.7 b	35.4 b
Shoot DW (%)	91.1	90.0	92.6	87.9	91.3	91.4	89.7	91.3	91.7
Stem length (cm)[x]	41.2 a	32.0 b	34.9 b	24.3 a	22.5 a	20.4 b	22.7 a	18.2 b	19.0 b
Flower diameter (cm)	12.1	12.2	12.0	10.3	11.8	11.5	11.6	12.5	11.8
Leaf number	9.7	9.5	9.8	11.6	10.1	10.1	12.2 a	10.7 b	10.7 b
Total leaf area (cm^2)	1615	1489	1492	1435	1296	1304	1600 a	1388 b	1328 b
Specific leaf area (m^2/kg)	29.5	34.3	33.5	22.2	26.3	26.3	29.4	29.2	30.7

[z] OTC — Optimized temperature and CO_2, OT — optimized temperatue and ambient CO_2, TRAD — traditional temperatures and ambient CO_2.
[y] Means separation within each planting date and variable by Duncan's multiple range test, 5% level. Means without letters are not significantly different.
[x] Second lateral shoot from apex of mother shoot.

Table 3. Distribution of the actual temperatures and CO_2 concentrations plants were exposed to in each environmental strategy compared to the calculated setpoint. Comparison between setpoint and actual value was made by comparing the setpoint at time zero with the actual value 15 min later. This process was repeated every 15 min on a 24 hr basis.

Environmental strategy	PPFD $\mu mol\ s^{-1}m^{-2}$	Temperature (°C)[z]					CO_2 ($\mu l\ l^{-1}$)[y]				
		$< -3°$	$-3°$ to $-1°$	$-1°$ to $1°$	$1°$ to $3°$	$>3°$	< -150	-150 to -50	-50 to 50	50 to 150	>150
				Crop 1 (1 Feb. through 6 April)							
OTC	0–32	0	0	52	35	13	1	<1	55	24	20
	32–500	<1	<1	40	42	17	13	8	52	10	16
	500+	3	16	45	25	11	67	7	9	4	12
OT	0–32	0	0	53	37	8	3	<1	58	20	19
	32–500	0	<1	41	44	14	<1	1	69	15	14
	500+	1	2	17	46	35	<1	2	55	23	16
T	Night	1	<1	68	14	16	1	<1	68	14	16
	Day	1	9	68	19	2	2	9	49	24	16
				Crop 3 (24 Feb. through 5 May)							
OTC	0–32	0	0	48	36	16	2	<1	49	28	22
	32–500	<1	<1	35	41	23	21	9	45	10	15
	500+	6	17	39	21	7	82	3	4	3	8
OT	0–32	<1	<1	50	38	12	2	0	52	24	21
	32–500	<1	<1	35	44	21	2	1	65	15	17
	500+	<1	2	10	39	49	0	1	53	21	21
T	Night	1	1	59	20	20	1	1	59	20	20
	Day	6	17	61	15	0	3	10	58	27	2

[z] Percentage of time actual temperatures were within the indicated temperature range compared to actual setpoint.
[y] Percentage of time the actual CO_2 concentrations were within the indicated CO_2 concentration range compared to the actual setpoint.

compared to the OT and T environments at flowering (Table 2). No significant differences in root or flower dry weight were observed.

Partitioning of dry weight also varied among environments. The percentage of stem dry weight was greater on plants in the OTC environment compared to plants in the OT and T environments. The percentage of leaf dry weight was significantly less on plants in the OTC environment compared to the OT and T environments in the 1st planting, but not on OTC grown plants in the 2nd and 3rd plantings. The percentage of flower dry weight was less on plants in the OTC environment for all plantings but only significantly less in the 3rd planting. The increased stem length, stem dry weight, and percentage of stem dry weight in the OTC environment was most likely due to high air (plant) temperatures that occurred in this environment on sunny days (Karlsson and Heins, unpublished data). The Pn maximization equation calculates temperatures greater than 26°C when PPFD exceeds 575 $\mu mol\ s^{-1}m^{-2}$ (Fig. 1). Plants potted on 19 Jan.

and grown in the OTC environment were exposed to day temperatures of 26° or greater for at least 1 hr on 35 different days during their development. In separate growth chamber experiments, plants grown at 26° day temperature flowered with stem lengths of 30 cm, whereas shoots on plants grown at 14° day temperature were only 16 cm in length (Karlsson and Heins, unpublished data).

Whereas stem length increased for all 3 planting dates on plants in the OTC environment, the absolute difference was greatest on plants potted on 19 Jan. The short stems on plants in the last 2 potting dates is due to 2 factors. First, plants were sprayed with SADH 4 times instead of 2. Second, on 2 Mar. maximum setpoint temperatures in the OTC environment houses were set at 26°C. This maximum was set because flower petal necrosis was observed after bright sunny days on flowering plants. The maximum temperatures to which plants were exposed in the last 2 plantings were reduced.

No difference in flower diameter was observed after 10 weeks of growth. While the percent flower dry weight was consistently lower for the OTC environment grown plants, the actual dry weight of these flowers was greater than flowers in the other 2 environments in all but 1 instance.

Greenhouse control. Average day temperatures (0800 HR to 1600 HR) over the life of each crop varied from 1.6° to 0.7°C less for the OT environment and 1.0° to 1.6° greater for the OTC environment, compared to the T environment (21.8°, 21.8°, and 22.2° for the 3 planting dates). CO_2 in the OTC environment averaged 575, 550, and 490 $\mu l\ l^{-1}$ for the 3 planting dates, respectively. Temperature increases for each respective crop were attributed to increased PPFD levels (320, 340, and 370 $\mu mol\ s^{-1}m^{-2}$), whereas decreased average CO_2 concentrations were attributed to decreased time before venting each day as the outside temperature increased.

The actual environmental control achieved in the greenhouse is shown in Table 3 for the Crop 1 (planted 19 Jan.) and Crop 3 (planted 17 Feb.). Temperature control was slightly more precise on Crop 1 than Crop 3, due to increased outdoor temperatures and average solar radiation loads during the latter part of the Crop 3 development which made precise temperature control difficult. Temperatures ran above the setpoint more frequently than below setpoint for both crops, because of a programmed "dead band" of 3°C between the heating setpoint and the venting setpoint where neither heating or cooling occurred. This differential was set to prevent wasteful heating or cooling due to any temperature overshoot when in the cooling or heating mode. Temperature control in the T houses was more precise than temperature control in the OT and OTC environments. This difference was not unexpected, as the day setpoint remained constant in the T environment while the day temperature setpoint fluctuated over 13° in the OTC house depending upon the PPFD (Fig. 1). Precise control on variably cloudy days was especially difficult as more than 15 minutes was necessary for complete cooling when the temperature setpoint dropped from 26° to 20°.

Control of CO_2 concentration was also more precise on Crop 1 than Crop 3 for the same reasons associated with temperature control. The calculated CO_2 concentration was achieved within 50 $\mu l\ l^{-1}$ 52% and 45% of the time when the PPFD was between 32 and 500 $\mu mol\ s^{-1}m^{-2}$ in the OTC environment during the 2 cropping periods. This precision, however, was only achieved 9% and 4% of the time, when the PPFD was greater than 500 $\mu mol\ s^{-1}m^{-2}$ and the concentration was more than 150 ppm low 67% and 82% of the time, respectively. A significant portion of the time that the CO_2 was more than 150 $\mu l\ l^{-1}$ low occurred because venting was necessary for cooling.

In summary, Pn maximization equations were developed to predict optimum temperature and CO_2 concentration setpoints based on PPFD. Greenhouse temperature and CO_2 concentration setpoints were updated every 15 min using a greenhouse environmental control computer based on these equations. Total DW on plants grown under these environmental conditions was 27% to 42% greater than plants grown under traditional temperature and ambient CO_2 conditions. Time to flower was not influenced by environmental strategy; shoot length, however, was significantly increased on plants grown under the OTC environment.

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