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dissertation entitled

PHOTOTHERMAL RATIO: RELATING PLANT
GROWTH AND DEVELOPMENT TO THE
RATIO OF LIGHT AND TEMPERATURE

presented by

BIN LIU

has been accepted towards fulfillment
of the requirements for

Ph. D degree in Horticulture

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Date May 7, 1999

PHOTOTHERMAL RATIO: RELATING PLANT GROWTH AND DEVELOPMENT TO THE RATIO OF LIGHT AND TEMPERATURE

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

1999

ABSTRACT

PHOTOTHERMAL RATIO: RELATING PLANT GROWTH AND DEVELOPMENT TO THE RATIO OF LIGHT AND TEMPERATURE

BY

Bin Liu

Photothermal ratio (PTR) is defined as the ratio of radiant energy (light) to thermal energy (temperature). It describes light energy available for photosynthesis per unit of developmental time. In this project, the relationship between PTR and poinsettia plant quality was studied. Poinsettia 'Freedom' plants were grown under 27 treatment combinations of 3 temperatures, 3 daily light integrals and 3 plant densities during the vegetative stage and 9 treatment combinations of one temperature, 3 daily light integrals and 3 plant densities during the reproductive stage. The effects of PTR on plant dry weight, stem diameter and strength, bract and cyathia size were quantified. Plant quality parameters were linearly correlated to PTR. A high PTR during vegetative development enhanced plant stem strength and reduced stem breakage at anthesis. A high PTR during reproductive development improved plant appearance by increasing bract and cyathia size and reduced cyathia abscission. A poinsettia plant growth and development model was also developed to examine the response of plant growth and development to PTR. The simulation results confirmed that PTR is a useful parameter for plant quality control. In separate experiments, light, plant density and temperature were adjusted to increase PTR in an attempt to improve plant quality. Temperature adjustment to regulate PTR and improve poinsettia plant quality did not prove practical. However, the potential for light

adjustment to increase PTR and plant quality was substantial. Reducing overhead shading and decreasing plant density improved light interception greatly and increased plant quality. The minimum daily light integral for acceptable poinsettia plant quality was about 10 to 12 mol m^{-2} day^{-1} at 20 °C with plant spacing of 25 x 25 cm. This minimum daily light integral increased as temperature increased and decreased as plant density decreased.

Affectionately Dedicated to

my loving

Grandfather, Zi-Yun Liu

and

Grandmother, Ai-Zhu Chen

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to all those individuals that in one way or another helped me to complete my doctoral program:

Dr. Royal D. Heins, my advisor, for his irreplaceable role in making my Ph.D. dream come true, for his consistent encouragement, support, and guidance.

Drs. Joe T. Ritchie, James A. Flore, and Jeffery A. Andresen, my guidance committee members, for their encouragement, help, and guidance.

Mr. Tom Wallace and Mr. Dan Tschirhart, for their assistance in conducting experiments; Mrs. Cara Wallace for her editing the manuscripts.

Drs. William Carlson and Arthur Cameron, and all graduate students, undergraduate helpers, and visiting scholars in the MSU floricultural group, for their encouragement, help, and friendship.

Drs. Ep Heuvelink and H. Chala of Department of Horticultural, Wageningen Agricultural University, the Netherlands, for their hosting my three-month-study in their laboratory and constructive discussions.

My husband, ShiYing Wang, and my daughter, Cindy (Xin) Wang, for their love, understanding, and support.

The financial support from the American Floral Endowment and growers supportive of the MSU floriculture research program is greatly appreciated.

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LIST OF SYMBOLS OR ABBREVIATIONS

ΣIDLI	cumulative intercepted daily light integral on the canopy (mol m^{-2})
ADP	average daily temperature (^oC)
APT	average plant temperature (^oC)
CDLI	cumulative daily light integral (mol m^{-2})
CTT	cumulative thermal time (degree-days)
D	duration (days)
DLI	daily light integral (mol m^{-2} day^{-1})
DTT	daily thermal time (degree-days day^{-1})
DW	dry weight (g $plant^{-1}$)
DWrep	dry-weight gain during the reproductive stage (g $plant^{-1}$)
Expt.	experiment
k	extinction coefficient
LAI	leaf area index
LA_{ls}	leaf area of lateral shoot (cm^2)
LA_{ms}	leaf area of the mother stem (cm^2)
LA_{tot}	total leaf area of a plant (cm^2)
LD	long day
LI%	percentage of light interception (%)
LN	leaf number on the second lateral shoot
LUR	leaf unfolding rate (leaves day^{-1})
MC	mostly cloudy
MSU	Michigan State University
PC	partly cloudy
PTR	photothermal ratio
PTR_{area}	photothermal ratio based on light available per unit area (mol degree-day^{-1} m^{-2})
$PTR_{intercept}$	photothermal ratio based on light intercepted by a plant (mol degree-day^{-1} $plant^{-1}$)
PTR_{plant}	photothermal ratio based on light available per plant (mol degree-day^{-1} $plant^{-1}$)
PTR^r	reproductive photothermal ratio (mol degree-day^{-1} $plant^{-1}$)
PTR^v	vegetative photothermal ratio (mol degree-day^{-1} $plant^{-1}$)
R_iRT_p	ratio of radiant to thermal energy based on light intercepted by a plant (mol degree-day^{-1} $plant^{-1}$)
RRT	ratio of radiant to thermal energy
RRT_a	ratio of radiant to thermal energy based on light available per unit area (mol degree-day^{-1} m^{-2})
RRT_p	ratio of radiant to thermal energy based on light available per plant (mol degree-day^{-1} $plant^{-1}$)

RUE	radiation use efficiency (g mol^{-1})
S	sunny day
SAS	Statistical Analysis Systems
SD	short day
SLW	special leaf weight (g cm^{-2})
T	average plant temperature (^{o}C)

Section I

Is Plant Quality Related to the Ratio of Radiant Energy to Thermal Energy?

IS PLANT QUALITY RELATED TO THE RATIO OF RADIANT ENERGY TO THERMAL ENERGY?[*]

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Abstract

Plant growth and development are driven by two forms of energy: radiant and thermal. Radiant energy drives photosynthesis and therefore dry weight gain, while thermal energy drives development rate. This study was undertaken to determine the effect of the ratio of radiant energy to thermal energy (RRT) on plant quality of *Euphorbia pulcherrima* 'Freedom'. From pinch to the onset of short-day flower induction, plants were grown under 27 combinations of three air-temperature settings (19, 23, or 27C), three daily light integrals (5, 10, or 20 mol$\cdot$m$^{-2}\cdot$day^{-1}), and three plant spacings (15 x 15, 22 x 22, or 30 x 30 cm). Plants were treated for 450 degree-days (base temperature of 5C) in Expt. 1 or five weeks in Expt. 2. The results showed that the measured plant quality parameters that can be associated with quality were closely related to RRT. Although modified by spacing, specific leaf weight increased 100% to 150%, stem dry weight increased 80% to 90%, and cross-sectional area of stems increased 35% to 45% as RRT increased from 0.2 to 1.2 mol$\cdot$m$^{-2}\cdot$degree-day^{-1}. Plant dry weight (total, leaf, and stem) gain increased with RRT at almost twice the rate for plants at the 30 x 30-cm spacing compared to that at the 15 x 15-cm spacing.

Additional index words: daily light integral, *Euphorbia pulcherrima,* plant temperature, poinsettia

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[*] This paper was presented in international society for horticultural science workshop in May 1996 and published in Acta Hort. 435:171-182, 1997.

1. Introduction

Production of high-quality plants requires a combination of appropriate genetics, cultural procedures, and environmental conditions. Of the five environmental factors affecting plant growth, light, temperature, water, nutrients, and gases, the first two are different forms of energy: i.e., radiant and thermal. Plant growth is an energetically uphill process. Growth in the form of dry-weight accumulation is driven by the amount of radiant energy (light) that a plant receives during development, i.e., the daily light integral (DLI). Growth defined as the maturation rate of leaf, stem, and flower cells (development) depends on the rate of biochemical reactions, which is controlled primarily by thermal energy (average daily temperature [ADT], or more appropriately, average plant temperature, [APT]). Horticulturists generally accept that the relationship between ADT and DLI greatly influences plant quality.

Several reports have shown that plant quality was affected by different combinations of radiant energy and temperature. For example, petunia developmental rate increased as temperature increased (Krizek et al., 1972); however, when the light level remained constant, the increased developmental rate resulted in lower plant quality because of increased plant height and less lateral branching (Kaczperski et al., 1991; Merritt and Kohl, 1982; Piringer and Cathey, 1960). Low light, high night temperatures, or both resulted in low carbohydrate reserves, which led to poor rose color (Post and Howland, 1946). During the first three weeks after potting, reduction of light by shading (Hagen and Moe, 1981; Kristoffersen, 1969), closer spacing (Hagen, 1980), or a later potting date (Hagen and Moe, 1981) caused a reduction in the number and growth rate of lateral breaks and flowering side shoots of poinsettia. Increasing temperature at low light reduced the number of laterals and promoted their excessive elongation, which resulted in poor-quality poinsettias (Kristoffersen, 1994).

There is no widely used system for quantifying the effect of temperature and light combinations on plant quality. The ratio of radiant energy ($mol \cdot m^{-2}$) to thermal energy (degree-days) (RRT) may be one of the parameters controlling plant quality of floral crops. The objective of this study was to investigate if--and then describe how--plant quality (e.g., dry weight, stem strength, and thickness) of *Euphorbia pulcherrima* is related to RRT.

2. Material and Methods

Rooted cuttings of *Euphorbia pulcherrima* 'Freedom' in 15-cm pots were obtained from a commercial poinsettia propagator. Upon receipt, plants were pinched and assigned randomly to 27 combinations of temperature, light, and spacing; i.e., three air-temperature settings (19, 23, or 27C), three daily light integrals (5, 10, or 20 $mol \cdot m^{-2} \cdot day^{-1}$, equivalent to 100, 200, or 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for a 14-h photoperiod), and three plant spacings (close [15 x 15 cm], medium [22 x 22 cm], or wide [30 x 30 cm]). Plants were arranged in a split-plot design with temperature as the main plot, daily light integral as the split plot, and plant spacing as the split split plot.

Greenhouse temperature was controlled by a greenhouse climate-control computer (Priva, Model CD750, De Lier, Holland). Average air temperature in each greenhouse zone was determined from 0800 to 1700 HR. The temperature necessary to achieve the desired ADT (19, 23, or 27C) between 1700 and 0800 HR the next day then was calculated, and the climate computer was set to maintain the greenhouse zone at that temperature. Zone temperatures were reset to 19, 23, or 27C at 0800 HR.

Photosynthetic photon flux was measured at canopy level with quantum sensors (Li-Cor, Inc, Lincoln, Nebraska) linked to Campbell Scientific CR-10 dataloggers (Logan, Utah). Different light levels were obtained through internal greenhouse shading (sunny days) with 50% shading screens (LS 15F, Ludvig Svensson; Kinna, Sweden) or by supplemental lighting (cloudy days) with high-pressure sodium lamps. Expected DLI was estimated each morning at 0800 HR based on the weather forecast. Screens or lamps were actuated as necessary based on the prediction. Actual DLI was reviewed at 1200 HR, and screens or lamps were adjusted. If the DLI was less than desired at 1700 HR, the number of hours supplemental lights needed to be operated was calculated and programmed into the climate computer. The desired DLI was adjusted up or down each day for any deviations from desired DLI the previous day.

In Expt. 1, all plants were grown to an identical accumulated thermal time of 450 degree-days (5C base temperature), which was reached about 32, 25, and 20 days after pinch at 19, 23, and 27C, respectively. The actual number of days to 450 degree-days varied among each treatment and was based on measured APT (Table 1). All plants in Expt. 2 were grown under treatments for five weeks.

The following data were collected weekly on five plants from each treatment: total, stem, and leaf dry weight; leaf number; plant height and diameter; leaf area; and stem length of each lateral shoot. Stem diameter was measured five weeks after pinch. Leaf number was recorded daily. Shoot-tip temperature, canopy air temperature at the same

Table 1. Plant leaf number and area in Expts. 1 and 2 at transfer to short days.

	Temperature		Light integral		Degree-days			Leaf	
Plant spacing	Setting (C)	Plant (C)	DLI (mol m^{-2} d^{-1})	CDLI (mol m^{-2})	DTT (degree-days.d^{-1})	CTT (degree-days)	RRT (mol m^{-2} degree-day^{-1})	Number	Area (cm^{2})
				Expt. 1					
Wide	19	18.5	5	170	13.5	450	0.37	4.4	802
		18.4	10	350	13.4	450	0.74	4.3	792
		21.1	20	540	16.1	450	1.24	4.8	1045
	23	21.0	5	135	16.0	450	0.31	4.8	985
		21.3	10	270	16.3	450	0.61	5.2	971
		24.6	20	440	19.6	450	1.02	5.6	1026
	27	26.6	5	105	21.6	450	0.23	4.8	1013
		27.4	10	200	22.4	450	0.45	5.0	1030
		28.5	20	380	23.5	450	0.85	5.2	1050
Close	19	17.8	5	170	12.8	450	0.39	4.0	788
		18.1	10	350	13.1	450	0.77	4.0	715
		19.5	20	540	14.5	450	1.38	5.2	885
	23	21.3	5	135	16.3	450	0.31	4.6	863
		20.1	10	270	15.1	450	0.66	4.6	995
		22.0	20	440	17.0	450	1.18	6.2	1154
	27	26.1	5	105	21.1	450	0.24	3.8	914
		27.1	10	200	22.1	450	0.45	4.6	965
		27.0	20	380	22.0	450	0.91	5.0	980
				Expt. 2					
Wide	19	18.5	5	175	13.5	474	0.37	4.6	837
		18.4	10	350	13.4	470	0.74	4.8	807
		21.1	20	700	16.1	565	1.24	7.6	1490
	23	21.0	5	175	16.0	560	0.31	7.4	1492
		21.3	10	350	16.3	569	0.61	7.0	1608
		24.6	20	700	19.6	687	1.02	9.4	2162
	27	26.6	5	175	21.6	756	0.23	9.6	2271
		27.4	10	350	22.4	785	0.45	11.0	2353
		28.5	20	700	23.5	824	0.85	11.0	2240
Close	19	17.8	5	175	12.8	474	0.39	4.4	844
		18.1	10	350	13.1	470	0.77	4.0	715
		19.5	20	700	14.5	565	1.38	5.6	1101
	23	21.3	5	175	16.3	560	0.31	5.8	1304
		20.1	10	350	15.1	569	0.66	5.8	1181
		22.0	20	700	17.0	687	1.18	7.0	1554
	27	26.1	5	175	21.1	756	0.24	7.8	1464
		27.1	10	350	22.1	785	0.45	8.0	1269
		27.0	20	700	22.0	824	0.91	8.8	1470

height that shoot-tip temperature was taken, and light data were collected continually in each treatment. Shoot-tip temperature was measured by inserting a thermocouple into the second shoot's apex.

The RRT was calculated as RRT = DLI / DTT, where DLI is daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$), and DTT is daily thermal time ($degree\text{-}days \cdot d^{-1}$) based on plant temperature instead of the temperature setting.

3. Results

In Expt. 1, plant dry weight (DW) increased as DLI increased at the close and wide plant spacings (Fig. 1A). Plant DW decreased as average plant temperature (APT) increased at the wide spacing, but was similar as APT increased at the close spacing (Fig. 1B). In Expt. 2, plant DW increased as both DLI and APT increased (Fig. 1D and 1E) for all wide-spaced treatments except the combination of high temperature (27C) and high light (20 $mol \cdot m^{-2} \cdot d^{-1}$), which did not follow the general pattern. For close-spaced plants, plant DW varied little, but tended to decrease as temperature increased from 23 to 27C. Plant DW was consistently lower at the close spacing than at the wide spacing for all DLI/APT treatment combinations in both experiments.

Dry weight of plants grown to a common thermal time (Expt. 1) increased linearly as RRT increased (Fig. 1C). Both the DW at any one RRT and the rate of DW increase to increasing RRT were significantly higher for wide-spaced plants compared to close-spaced plants (3.88 vs. 1.98 g per $mol \cdot m^{-2} \cdot degree\text{-}day^{-1}$). The DW of plants grown for a common number of calendar days (Expt. 2) increased linearly with RRT; however, DW

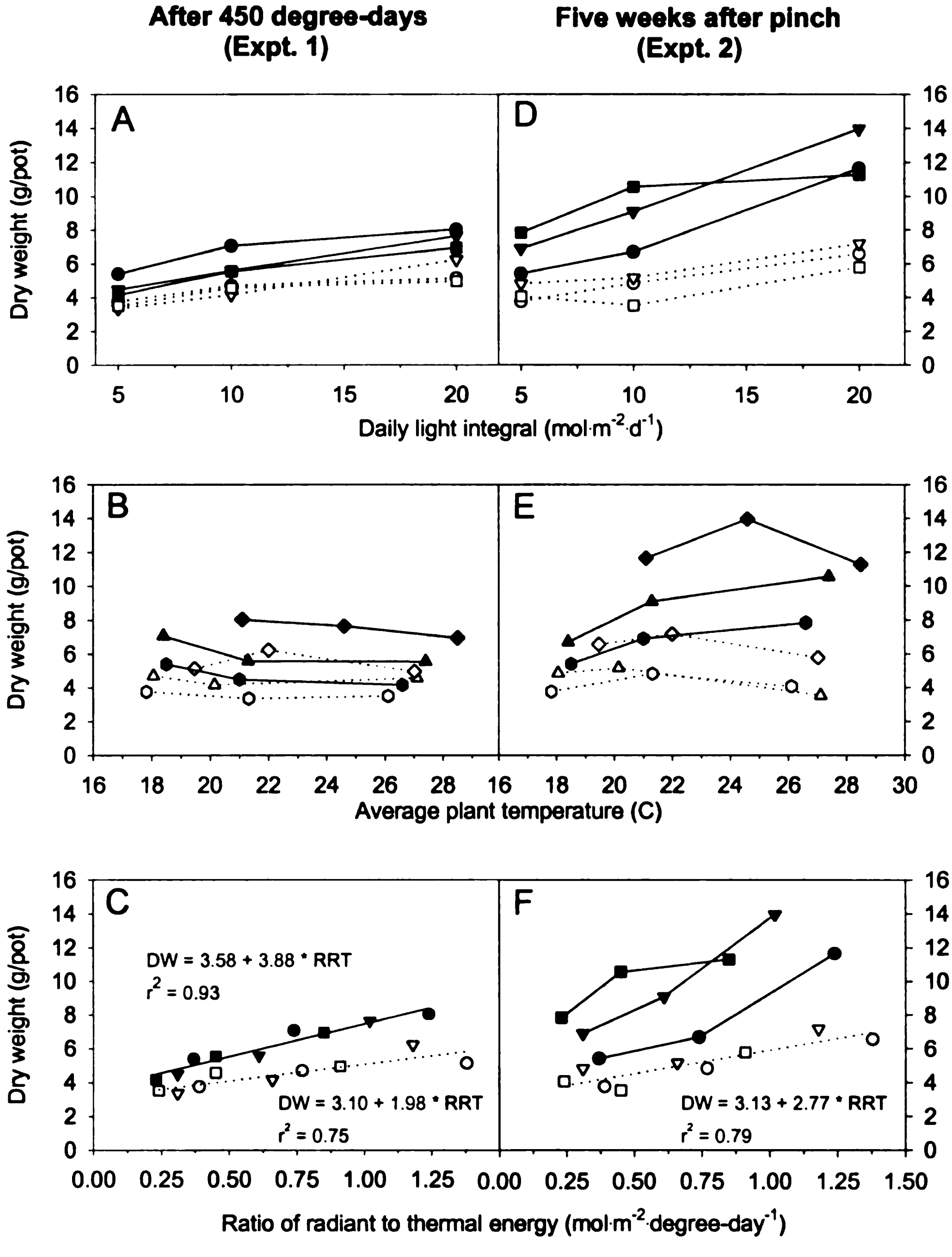

Fig. 1. Effect of daily light integral, average plant temperature, and ratio of radiant to thermal energy on poinsettia dry weight (spacing: close = C, wide = W).

-●- 19C (W) ··○·· 19C (C) -⬢- 5 mol (W) ··⬡·· 5 mol (C)
-▼- 23C (W) ··▽·· 23C (C) -▲- 10 mol (W) ··△·· 10 mol (C)
-■- 27C (W) ··□·· 27C (C) -◆- 20 mol (W) ··◇·· 20 mol (C)

was higher for a particular RRT as treatment temperature increased for wide-spaced plants (Fig. 1F).

Leaf DW (Fig. 2A and 2D) and specific leaf weight (SLW) (Fig. 2B and 2E) increased as RRT increased for Expts. 1 and 2. As with plant DW, leaf DW increased at about twice the rate for wide-spaced plants as for close-spaced plants (2.84 vs. 1.49 g per $mol \cdot m^{-2} \cdot degree\text{-}day^{-1}$). The leaf DW of plants grown for a common number of calendar days (Expt. 2) followed the same pattern as that of total DW (Figs. 1F and 2D). Although leaf DW at a particular RRT increased with temperature, SLW decreased (Fig. 2D and 2E).

Stem DW increased linearly as RRT increased in Expts. 1 and 2 (Fig. 2C and 2F). As with plant and leaf DW, stem DW increased at about twice the rate for wide-spaced plants as for close-spaced plants (0.88 vs. 0.43 and 1.09 vs. 0.60 g per $mol \cdot m^{-2} \cdot degree\text{-}day^{-1}$ for Expts.1 and 2, respectively).

Shoot lengths of plants grown to 450 degree-days (Expt. 1) were similar, except that shoots on close-spaced plants growing at 27C tended to be taller (Fig. 3A and 3B). In contrast, shoot length of plants grown for five weeks (Expt. 2) increased as temperature increased (Fig. 3D and 3E); DLI had no consistent effect on shoot length, although wide-spaced plants grown in the 20 $mol \cdot m^{-2} \cdot d^{-1}$ treatments were consistently shorter than those in other treatments. There was no consistent relationship between shoot length and RRT (Fig. 3C and 3F).

Diameter of the second lateral shoot increased about 20% as RRT increased from about 0.2 to 1.2 (Fig. 4), an increase in stem cross-sectional area of 35% to 45%. Shoot

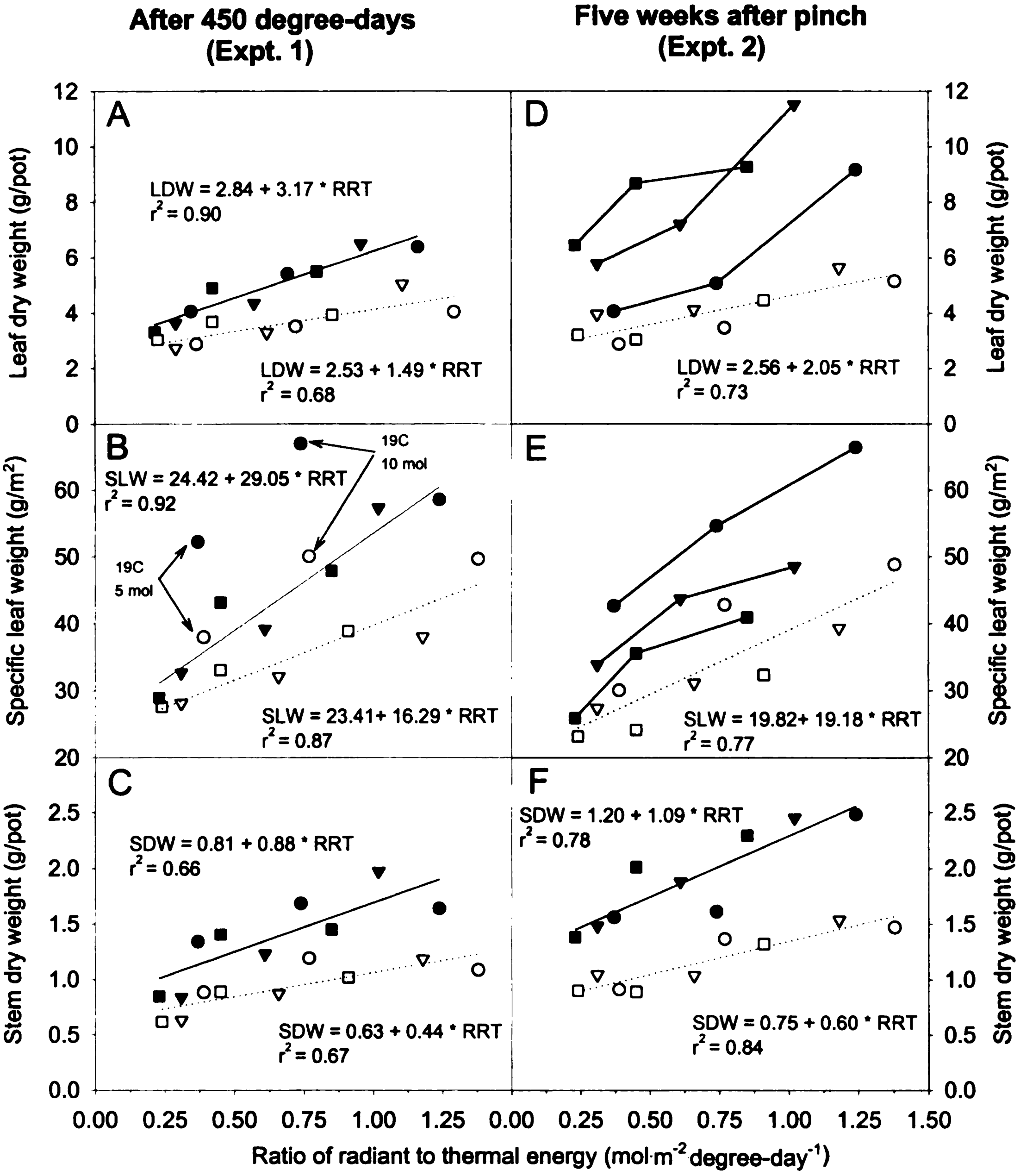

Fig. 2. Effect of the ratio of radiant to thermal energy on leaf dry weight, specific leaf weight, and stem dry weight of poinsettia (spacing: close = C, wide = W). Regression excluded marked points.

-●- 19C (W) ··○·· 19C (C)
-▼- 23C (W) ··▽·· 23C (C)
-■- 27C (W) ··□·· 27C (C)

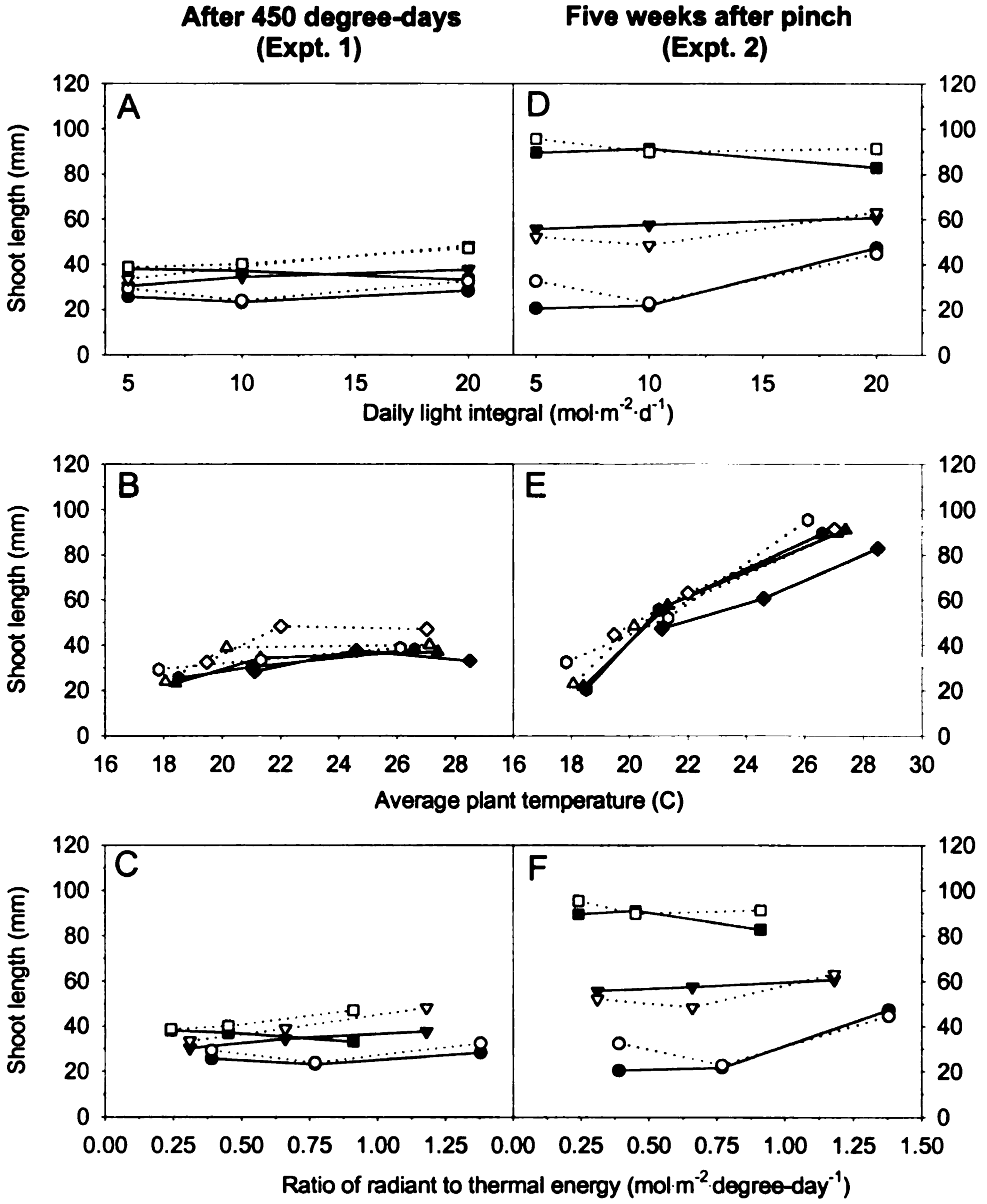

Fig. 3. Effect of daily light integral, average plant temperature, and ratio of radiant to thermal energy on poinsettia lateral shoot length (spacing: C = close, W = wide).

-●- 19C (W) ··○·· 19C (C) -⬢- 5 mol (W) ··⬡·· 5 mol (C)
-▼- 23C (W) ··▽·· 23C (C) -▲- 10 mol (W) ··△·· 10 mol (C)
-■- 27C (W) ··□·· 27C (C) -◆- 20 mol (W) ··◇·· 20 mol (C)

diameter was about 1 mm thicker (50% to 65% larger cross-sectional area) on plants grown at the wide spacing compared to the close spacing at all RRT. Cross-sectional area on stems from wide-spaced plants (1.2 RRT) was 120% larger than that of close-spaced plants (0.2 RRT).

4. Discussion

The effects of temperature (thermal energy) and light (radiant energy) on plant growth and development are well known. Radiant energy drives plant photosynthesis and, consequently, plant biomass production. The developmental rate of a crop is determined primarily by thermal energy. Plant biomass accumulation per unit of development therefore depends on the ratio of radiant to thermal energy. Plants receiving a large amount of radiant energy per unit of thermal energy should accumulate more biomass than those receiving a small amount. In Expt. 1, plants in all treatments accumulated the same thermal energy (450 degree-days) before the start of short days: about 32, 25, and 20 days for plants growing at 19, 23, and 27C, respectively. Therefore, plants growing under the same DLI received very different cumulative light integrals (CLI) before flower induction. For example, plants growing at 19C under 10 $mol \cdot m^{-2} \cdot d^{-1}$ (RRT of 0.74) received a CLI 75% greater (150 $mol \cdot m^{-2}$) than those growing at 27C (RRT of 0.45). The increased CLI resulted in 28% more plant DW at the start of short days for plants at the wide spacing. Overall, plant DW increased linearly as RRT increased (Fig. 1C).

Maturation of many crops requires a fixed amount of thermal time from the start of flower induction. Assuming that radiant energy is similar between years, crop yield has the potential to be larger in "cool" growing seasons compared with "warm" growing

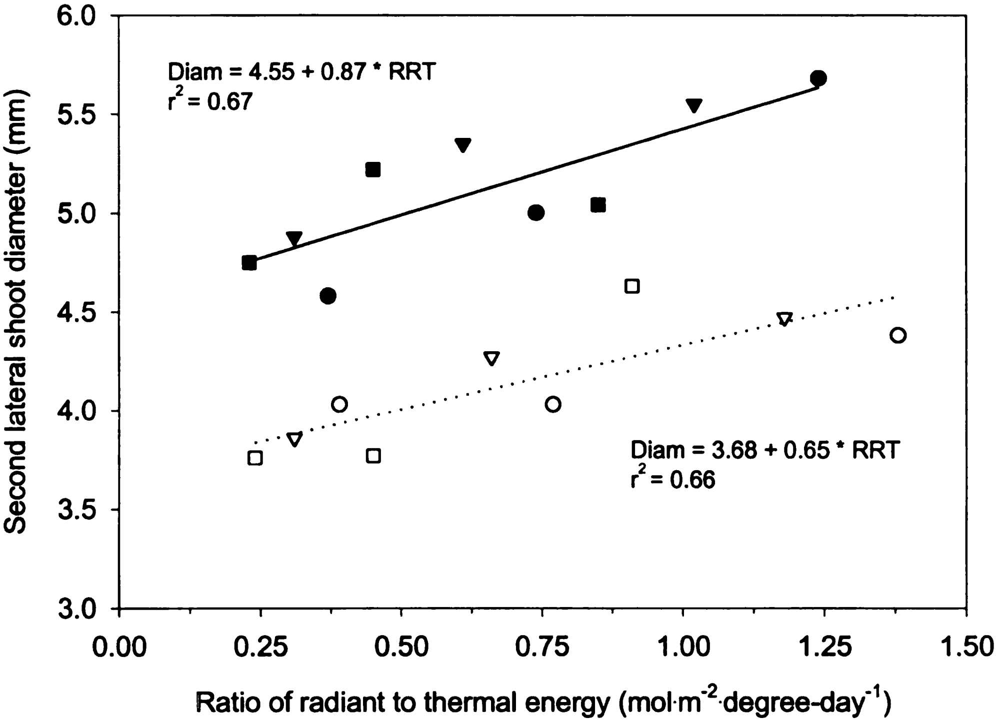

Fig. 4. Effect of the ratio of radiant to thermal energy on the diameter of the second lateral poinsettia shoot (spacing: close = C, wide = W).

-●- 19C (W)	··○·· 19C (C)
-▼- 23C (W)	··▽·· 23C (C)
-■- 27C (W)	··□·· 27C (C)

seasons because low temperatures slow plant developmental rate and extend the maturation duration. Such plants can harvest radiant energy for a longer period before maturation. This relationship has been observed in field crops such as corn, spring wheat, and soybean (Amir et al., 1991; Muchow et al., 1990; Spaeth et al., 1987). Harris and Scott (1968) also showed that a 20-day delay in anthesis allowed the dry weight of carnation flowers in a low-temperature, shaded treatment to approximate that of an unshaded, higher-temperature treatment.

In these experiments, RRT was not the only factor that influenced plant DW accumulation. Plants grown at the wide spacing accumulated more DW than those at the close spacing. Dry weight gain is not a function of radiant energy, but of absorbed radiant energy (Hay and Walker, 1989). Although closely spaced plants intercepted more light per unit bench area, plants at the wide spacing had more leaves fully exposed to the light throughout the developmental period and therefore absorbed more radiant energy per plant. The slope of the plant DW to RRT line gives a measure of radiant energy conversion efficiency per plant per degree-day over the course of the experiment; it was almost twice as large at the wide spacing than at the close spacing (3.88 vs. 1.98 g per $mol \cdot m^{-2} \cdot degree\text{-}day^{-1}$).

In Expt. 2, plants accumulated different amounts of thermal time under the same DLI. For example, plants at 27C accumulated about 60% more degree-days than those in the 19C treatment. Plant size became quite different. Higher temperatures promoted a faster leaf unfolding rate, which resulted in a larger leaf area per plant (Table 1). Plant and leaf dry weight at each DLI increased as temperature increased, especially at the wide plant spacing (Fig. 1E). However, plant parameters associated with higher plant quality such as SLW (Fig. 2E), stem DW (Fig. 2F), and stem diameter (Fig. 4) did not increase as temperature increased when DLI was held constant, instead, they decreased.

Our hypothesis was that plant quality was related to RRT. The results showed that the measured plant quality parameters were closely related to RRT (Figs. 2B, 2C, 2E, 2F, and 4). Although modified by spacing, SLW, stem DW, and stem thickness were closely correlated with RRT. The SLW increased 100% to 150%, stem DW increased 80% to 90%, and cross-sectional area of stems increased 35% to 45% as RRT increased from 0.2 to 1.2.

To achieve good plant quality, management of thermal and radiant energy is of great importance on a daily and crop-life basis. Currently, dynamic regulation of RRT is not actively practiced, in part because quantitative relationships between RRT and plant quality are not available. A further limitation on use of RRT as a dynamic regulation tool is that many crops must be marketed on specific dates; therefore, thermal time development must occur at some minimum rate or the crop will not be marketable when required. With such a limitation, maximum radiant energy interception, both by the greenhouse and by the crop, is essential. Since photons that fall on the growing media cannot be intercepted, one strategy to maximize radiant energy interception is to maximize development with high thermal energy (temperature) early in crop development in order to quickly obtain an adequate leaf area, then to minimize thermal energy within acceptable developmental rates to maximize RRT. Alternatively, when markets limit shipping dates and radiant energy from the sun is limiting, the only alternative is to supply supplemental radiant energy from electrical lamps. Continued research to define the minimum RRT necessary to meet market quality will assist growers in determining how much supplemental light is necessary to produce acceptable-quality crops on specified dates.

In summary, the results of these experiments show that poinsettia quality, defined as plant caliber, dry weight, stem strength, etc., is correlated with RRT and further research to develop dynamic climate regulation relationships is warranted.

5. Acknowledgments

The authors gratefully acknowledge the expert assistance of Tom Wallace, the valuable discussions of Shi-Ying Wang, and the helpful editing of Cara Wallace.

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Section II

Modeling Poinsettia Vegetative Growth and Development: The Response to the Ratio of Radiant to Thermal Energy

MODELING POINSETTIA VEGETATIVE GROWTH AND DEVELOPMENT: THE RESPONSE TO THE RATIO OF RADIANT TO THERMAL ENERGY[*]

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Abstract

The relationships between poinsettia vegetative growth/development and light/temperature have been modeled using the computer software STELLA II. The model development was based on greenhouse experiments conducted with 27 treatments; i.e., factorial number combinations of three levels of constant temperature (19, 23, or 27 °C), three levels of daily light integral (5, 10, or 20 mol m^{-2} day^{-1}), and three levels of plant spacing (15 x 15, 22 x 22, or 30 x 30 cm). Agreement between simulated and actual data for all 27 treatments is reasonably good ($R^2 > 0.94$) for all considered plant characteristics; i.e., plant dry weight, leaf number, leaf area index, and leaf area. Results from the simulation with different levels of daily light integral, temperature, and plant spacing confirm that the ratio of radiant to thermal energy (RRT) is a useful parameter for plant growth, development, and quality control. The RRT significantly affects leaf unfolding rate when RRT is lower than 0.025 mol $degree\text{-}day^{-1}$ $plant^{-1}$. Plant dry weight is highly correlated with RRT; it increases linearly as RRT increases.

Additional index words: light, poinsettia, simulation, temperature

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[*] This paper was presented in international society for horticultural science conference in August 1997 and published in Acta Hort. 456:133-142, 1998.

1. Introduction

Light and temperature are two environmental factors that have a direct and significant effect on plant production. Light (radiant energy) drives plant photosynthesis. Increasing radiant energy results in increased plant biomass. Temperature (thermal energy), which primarily affects plant developmental rate, also influences plant dry weight accumulation. Increased leaf area associated with faster plant development under warmer temperatures can result in greater light interception and, therefore, greater plant biomass. However, warmer temperatures may depress crop yield by causing accelerated development, which results in less cumulative radiant energy interception. Therefore, high yield of corn (Muchow et al., 1990) or spring wheat (Amir and Sinclair, 1991) is associated with low temperature and high solar radiation.

Temperature-driven developmental rate can be affected by light. A low daily light integral (DLI) can influence development by limiting the supply of photosynthates (Faust and Heins, 1993; Volk and Bugbee, 1991).

Much research has been directed at simulating the interaction between light and temperature on crop production (Amir and Sinclair, 1991; Larsen, 1990; Muchow et al., 1990; Spaeth et al., 1987). Liu and Heins (1997) have reported that the ratio of radiant to thermal energy (RRT) is a useful parameter in describing the combined effects of light and temperature on plant growth, development, and quality.

The objectives of this study were to 1) develop a model for quantifying the relationships between poinsettia vegetative growth/development and light/temperature, and 2) use the model to examine the response of poinsettia plant growth and development to RRT.

2. Materials and Methods

2.1. General experimental procedures

The experiment was conducted in glass greenhouses during the fall of 1996. Rooted cuttings of *Euphorbia pulcherrima* 'Freedom' in 15-cm pots were obtained from a commercial poinsettia propagator. Upon receipt, plants were pinched and assigned randomly to 27 combinations of temperature, light, and spacing; i.e., three air-temperature settings (19, 23, or 27 °C), three daily light integrals (5, 10, or 20 mol m^{-2} day^{-1}, equivalent to 100, 200, or 400 mol m^{-2} s^{-1} for a 14-h photoperiod), and three plant spacings (close [15 x 15 cm], medium [22 x 22 cm], or wide [30 x 30 cm]). Plants were arranged in a split-plot design with temperature as the main plot, daily light integral as the split plot, and plant spacing as the split-split plot.

Greenhouse temperature was controlled by a greenhouse climate-control computer (Priva, Model CD750, De Lier, Holland). Photosynthetic photon flux was measured at the top and bottom of the plant canopy with light bars (18 photodiodes on a 1-m bar) and recorded by CR-10 dataloggers (Campbell Scientific, Logan, Utah). Different light levels were obtained through internal greenhouse shading (sunny days) with 50% shading screens (LS 15F, Ludvig Svensson, Kinna, Sweden) or by supplemental lighting (cloudy days) with high-pressure sodium lamps. Greenhouse air temperature and plant shoot-tip temperature was recorded by the CR-10. Because plant temperature rather than air temperature plays an important role in control of plant developmental rate (Harris and Scott, 1969; Ritchie and NeSmith, 1991; Watts, 1972), all analyses were based on plant temperature instead of the greenhouse temperature setting.

Data (total plant, stem, and leaf dry weight; leaf area and number) were collected weekly on five plants from each treatment. The leaf number of each of the five plants from each treatment also was recorded daily.

2.2. Model description

2.2.1. Input variables and simulation period

The input variables in the model were plant temperature, daily light integral, plant spacing, initial dry weight, and leaf area of the cutting. We assumed a plant with six leaves on the second lateral shoot was an ideal size for the onset of short-day flower induction; therefore, the simulation stopped when the leaf number was six. All the abbreviations and parameters used in this paper are listed in Table 1.

2.2.2. RRT expression

RRT was calculated as:

$$RRT_a = DLI / DTT \qquad [1]$$

in our early report (Liu and Heins, 1997), where RRT_a is the ratio based on the amount of light intercepted daily by a unit area (mol degree-day^{-1} m^{-2}), DLI is the daily light integral (mol m^{-2} day^{-1}), and DTT is thermal time (degree-day·day^{-1}). In fact, RRT can be described further as:

$$RRT_p = DLI / DTT * spacing \qquad [2]$$

or

$$R_iRT_p = \Sigma\ IDLI / CTT * spacing \qquad [3]$$

where RRT_p is the ratio based on the amount of light intercepted daily by a plant (mol degree-day^{-1} plant^{-1}), R_iRT_p is the ratio based on the amount of light intercepted by a plant

Table 1. List of abbreviations and parameters.

Symbol	Description	Units
CTT	Cumulative thermal time	degree-days
DLI	Daily light integral	mol m^{-2} d^{-1}
DTT	Daily thermal time	degree-day·d^{-1}
DW	Total plant dry weight	g plant^{-1}
IDLI	Intercepted daily light integral in canopy	mol m^{-2} d^{-1}
LAI	Leaf area index	
LA_{ls}	Leaf area of all lateral shoots	cm^{2}
LA_{ms}	Leaf area of the mother stem	cm^{2}
LA_{tot}	Total leaf area of a plant	cm^{2}
LN	Leaf number on the second lateral shoot	leaves
LUR	Leaf unfolding rate	Leaves day^{-1}
k	Extinction coefficient	
R_iRT_p	The ratio based on the amount of light intercepted by a plant	mol degree-day^{-1} plant^{-1}
RRT_a	The ratio based on unit area	mol degree-day^{-1} m^{-2}
RRT_p	The ratio based on a plant	mol degree-day^{-1} plant^{-1}
RUE	Radiation use efficiency	g mol^{-1}
Spacing	Reciprocal of plant density	cm^{2} plant^{-1}
T	Average plant temperature	°C

during a certain development period (mol degree-day^{-1} plant^{-1}), IDLI is the interception of the daily light integral in the canopy, CTT is cumulative thermal time, and spacing is the reciprocal of plant density (cm^2 plant^{-1}).

2.2.3. Leaf unfolding rate (LUR) submodel

Data analysis from the 27 temperature, light, and spacing combinations showed that after first leaf appearance, poinsettia LUR increased as average plant temperature increased. However, under similar plant temperatures, LUR was reduced dramatically when plants were grown under low DLI and at a close spacing, especially under higher temperatures. Therefore, the relationship between LUR and plant temperature (T) was linear only when its slope was taken as a logistic function of RRT:

$$\mathrm{LUR} = a + b/(1 + c * \exp(-d * \mathrm{RRT_P}))T \qquad [4]$$

where a, b, c, and d are regression coefficients.

The pattern of leaf appearance observed in these experiments was different between the first leaf after pinch and the subsequent leaves. Therefore, the effect of average plant temperature (T) on LUR was described as two different functions:

$$\mathrm{LUR} = -0.2944 + 0.0302 * T - 0.0005483 * T^2, \qquad \mathrm{LN} \leq 1, (R^2 = 0.72) \qquad [5]$$

$$\mathrm{LUR} = -0.1137 + 0.0163/(1 + 0.5172 * \exp(-78.2 * \mathrm{RRT_P}))T, \mathrm{LN} > 1, (R^2 = 0.92) \qquad [6]$$

where LN is leaf number on the second lateral shoot.

2.2.4. Leaf area index (LAI) submodel

During vegetative growth, leaf area of all lateral shoots ($\mathrm{LA_{ls}}$ in cm^2) was a quadratic function of leaf number on the second lateral shoot (Fig. 1A):

$$\mathrm{LA_{ls}} = 19.74 * \mathrm{LN}^2, \qquad (R^2 = 0.94) \qquad [7]$$

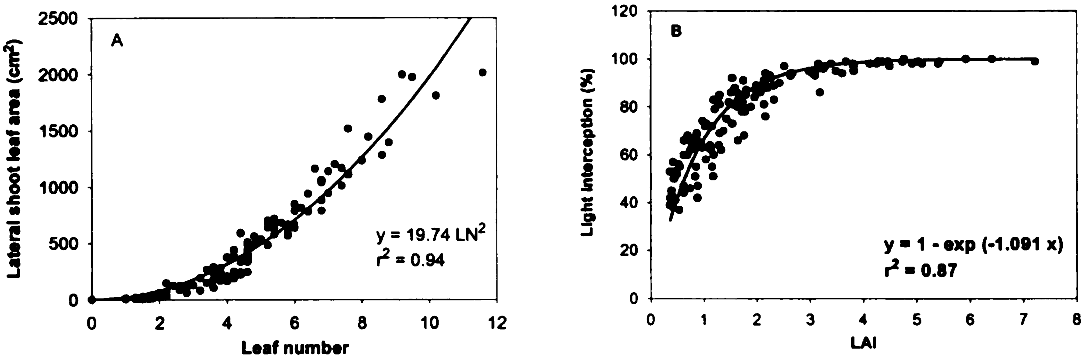

Fig. 1. A quadratic relationship (A) between the lateral shoot leaf area and the second shoot leaf number (LN), and an exponential relationship (B) between light interception and leaf area index (LAI) for extinction coefficient (k) estimation.

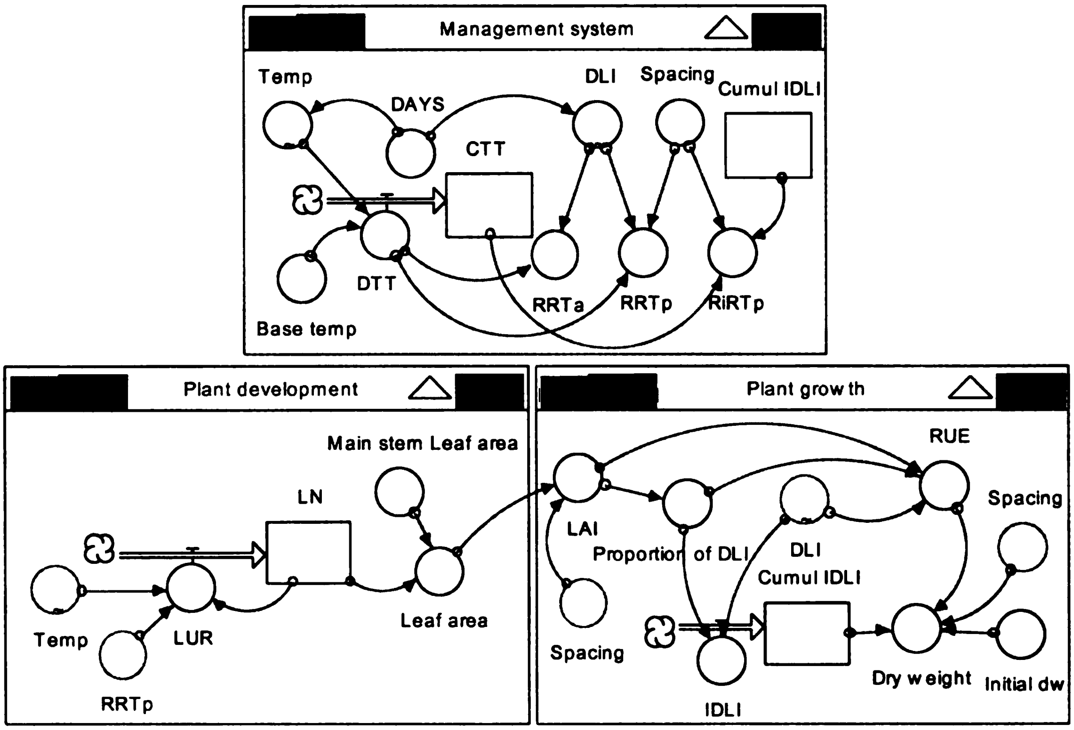

Fig. 2. A STELLA diagram showing the operation of the poinsettia growth and development model. Abbreviations are as described in the text.

The total leaf area of a plant (LA_{tot}) is the leaf area sum on all lateral shoots and the mother stem (LA_{ms}):

$$LA_{tot} = LA_{ls} + LA_{ms} \qquad [8]$$

Although LA_{ms} changed slightly after pinch, it was assumed to be a constant and assigned as an initial value in the model.

After LA_{tot} is determined, the LAI can be calculated as follows:

$$LAI = LA_{tot} / spacing \qquad [9]$$

2.2.5. Biomass accumulation submodel

Monteith (1977) showed that biomass production was linearly related to cumulative light interception for several crops grown with adequate water and nutrients. Therefore, total plant dry weight (DW in grams) can be calculated as:

$$\begin{aligned} DW &= RUE * spacing * \sum IDLI \\ &= RUE * spacing * \sum DLI * (1 - \exp(-k * LAI)) \qquad [10] \end{aligned}$$

where RUE is radiation use efficiency (g mol^{-1}), and k is an extinction coefficient that was fitted as 1.091 (Fig. 1B). Root dry weight was not taken into account in the current study.

According to Sinclair and Horie (1989), RUE is a function of the relative amounts of sunlit and shaded leaves. RUE is reduced at a low LAI because of the high fraction of the leaves that is light-saturated and therefore is less efficient photosynthetically than that in the shade. When the fraction of shaded leaf area increases, RUE increases. RUE is described as an exponential function of the ratio of LAI to IDLI:

$$RUE = 0.1449 * \exp(1.287 * LAI / IDLI) \qquad [11]$$

Based on this relationship, the regression between DW and $\sum$ IDLI resulted in an R^2 of 0.94.

2.3. Computer software

Computer software, STELLA II (High Performance Systems, Inc., N. H.), was used for simulation. As shown in Fig. 2, the current model includes three sectors; i.e., environment management, plant growth, and plant development.

2.4. Model Evaluation and Simulation

An independent data set was used to evaluate the model. The experiment was conducted in 1995 with the same 27 treatment combinations of light, temperature, and spacing. Simulations were run from pinch to day 35 for each treatment. The simulated leaf unfolding number, leaf area, LAI, and plant dry weight from all 27 treatments were regressed on the measured data. Intercepts and slopes of the resulting regressions were tested for significance from 0 and 1, respectively, by a *t*-test using associated standard errors. Ideally, the intercept and slope should be 0 and 1, respectively, and the regression should have a high coefficient of simple determination (R^2). Bias and RMSE (root mean squared error) also were used to evaluated the model's performance (Retta et al., 1991).

Simulations were conducted through varying daily mean temperature at 18, 20, 22, 24, 26, or 28 °C, DLI at 5, 10, 15, or 20 mol m^{-2} d^{-1}, and plant spacing at 15 x 15 cm (very close), 20 x 20 cm (close), 25 x 25 cm (medium), or 30 x 30 cm (wide). Simulated results were used to measure the responsiveness of days from pinch to unfolding of the sixth leaf on the second lateral shoot and plant dry weight to changes in RRT.

3. Results and discussion

3.1. Validation of the model

Agreement between simulated and actual data with all 27 treatments was relatively good ($R^2 > 0.94$) for all considered plant characteristics; i.e., leaf number, leaf area, LAI, and dry weight, although the intercepts were significantly greater than 0 and the slopes significantly less than 1 (Fig. 3 A to D). The model slightly underestimated all characteristics (bias < 0). Since both leaf area and LAI were calculated from leaf number, and dry weight calculation was related to LAI, the underestimation of leaf number was the main reason for the underestimation of all other characteristics. The leaf unfolding rate was a little faster in the model-evaluation data set than in the model-development data set. This difference might be attributable to the bias of data collection. Although leaf number was slightly underestimated, the average error in leaf number prediction was still less than one leaf (bias < -0.13 leaves and RMSE = 0.66 leaves). Generally, the model accurately simulated leaf area (slope = 0.93), LAI (slope = 0.94), and plant dry weight (slope = 0.90).

The simulated results and actual data points are showed in Fig. 3 E to H for three treatments. These treatments represent temperature, light, and spacing all at low, medium, and high levels; i.e., 19 °C x 5 mol x 232 cm^2, 23 °C x 10 mol x 466 cm^2, and 27 °C x 20 mol x 929 cm^2. The simulated results were close to the observed data. Therefore, the model constructed in the current study can be used for poinsettia plant growth, development, and quality control.

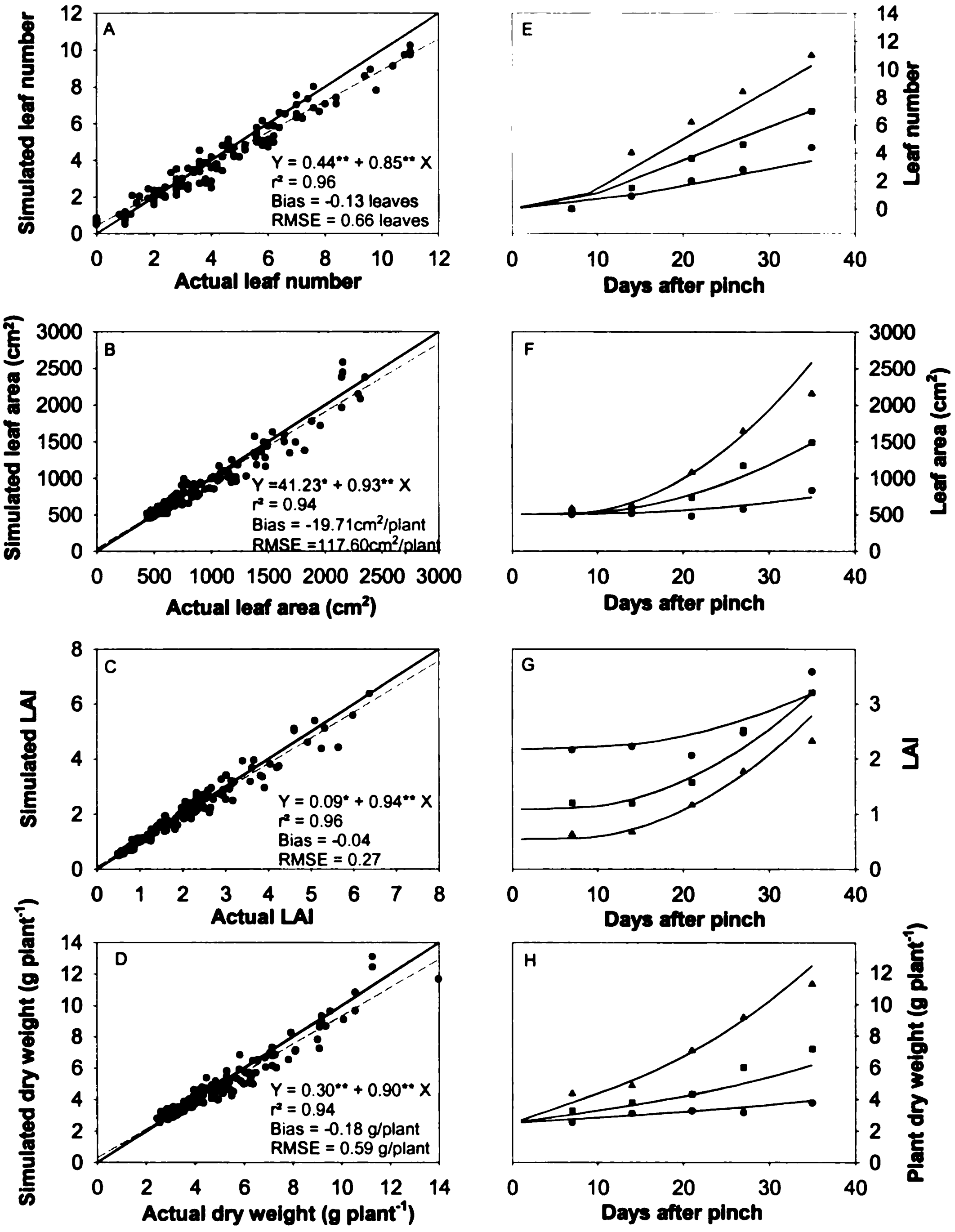

Fig. 3. Simulated vs. observed leaf number (A), leaf area (B), leaf area index (LAI; C) and plant dry weight (D) from all 27 treatments, and simulated (solid line) and observed (symbol) leaf number (E), leaf area (F), LAI (G) and plant dry weight (H) at different days after pinch from three treatments: 19°C x 5 mol x 232 cm^2 (●), 23°C x 10 mol x 466 cm^2 (■), 27°C x 20 mol x 929 cm^2 (▲). The variables x and y in A to D represent the x-axis and y-axis variables in each figures, respectively

3.2. Responsiveness to RRT

Days to unfolding of the sixth leaf increase sharply as RRT_p decreases from 0.025 to 0.005 mol degree-day^{-1} plant^{-1}. When the RRT_p value is greater than 0.025 mol degree-day^{-1} plant^{-1}, its effect on days to unfolding of the sixth leaf becomes minor (Fig. 4). At the same plant temperature, low light level will delay development by 3 to10 days, depending on the magnitude of RRT_p (Fig. 4), which indicates when the DLI available for each plant is lower than a certain level, plant developmental rate is not only a function of plant temperature, but also of RRT_p. The minimum DLI required for normal plant development (i.e., plant developmental rate is only related to plant temperature) increases as temperature increases. For instance, assuming plants are grown at a medium spacing (25 x 25 cm), a low DLI of 6 mol m^{-2} day^{-1} does not affect LUR when plants are grown below 21 °C. However, LUR will be affected at this DLI level when the temperature is higher than 21 °C. The effect of low DLI on LUR becomes larger as temperature increases. This interactive effect of light and temperature on plant development also was observed in tomato (Dieleman and Heuvelink, 1992). The decreased development rate likely is due to the limitation of assimilate supply under low DLI. Alternatively, lower temperatures slow plant development so that the low amount of assimilate (caused by a low light level) is not a limiting factor.

Plant dry weight is highly correlated with R_iRT_p; it increases linearly as R_iRT_p increases (Fig. 5). The simulated results are consistent with the observed data (Liu and Heins, 1997).

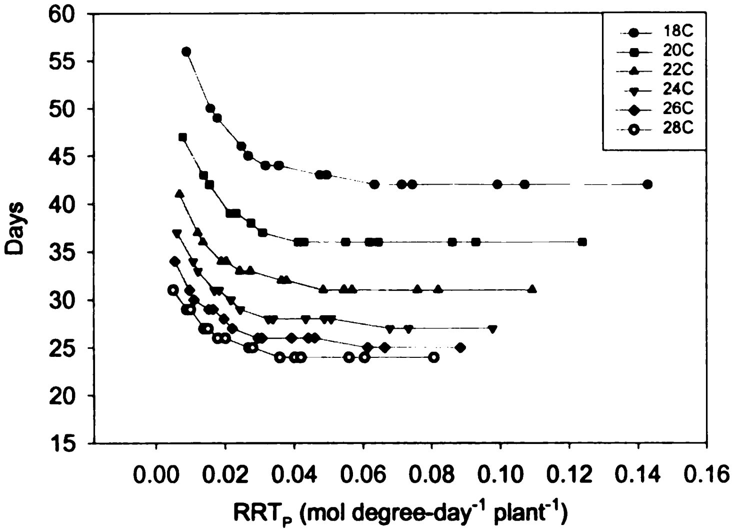

Fig. 4. Relationship between RRT_p, simulated days from pinch to unfolding of the sixth leaf, and temperature on the second lateral shoot.

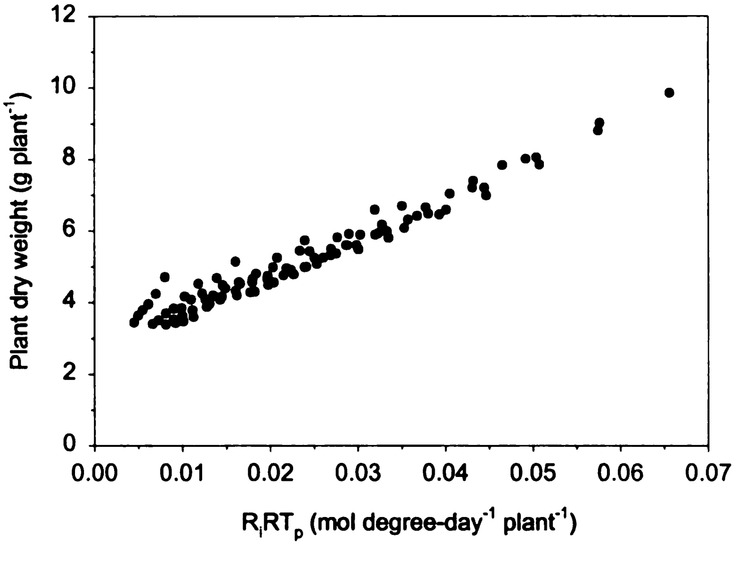

Fig. 5. Relationship between R_iRT_p and simulated plant dry weight.

4. Conclusion

The model constructed in the current study provides a means of predicting poinsettia plant dry weight, leaf number, LAI, and leaf area under different levels of temperature, light, and plant spacing. The simulation results confirm that RRT is an important parameter for plant growth, development, and quality control. RRT has a significant effect on plant developmental rate when plants are grown under low light levels combined with high temperatures; i.e., when RRT_p is lower than 0.025 mol degree-day^{-1} plant^{-1}. Moreover, RRT appears to be a predictor of plant dry weight. Since plant external quality (i.e., plant texture and stem firmness) is correlated with plant dry weight, plant quality can be predicted or controlled through RRT.

5. Acknowledgments

The authors gratefully acknowledge the American Floral Endowment for providing funding for this project, Tom Wallace for his assistance in conducting the experiments, Shi-Ying Wang for his comments, and Cara Wallace for her editing.

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Section III

Photothermal Ratio Affects Plant Quality in 'Freedom' Poinsettia (*Euphorbia pulcherrima* Willd.)

Photothermal Ratio Affects Plant Quality in 'Freedom' Poinsettia (*Euphorbia pulcherrima* Willd.)*

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Received for publication ____________. Accepted for publication ____________. This study was funded by the American Floral Endowment. We gratefully acknowledge the assistance of Tom Wallace in conducting the experiments. 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.

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[2] Professor.

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* The paper format was adopted for this section in accordance with "Journal of the American Society for Horticultural Science."

Production and Culture

Photothermal Ratio Affects Plant Quality in 'Freedom' Poinsettia (*Euphorbia pulcherrima* Willd.)

Additional index words. bract size, cyathia size, dry weight, ratio of radiant to thermal energy (RRT), stem strength

Abstract. Photothermal ratio (PTR) is defined as the ratio of radiant energy (light) to thermal energy (temperature). The objective of this study was to quantify the effect of PTR during the vegetative (PTR^v) and reproductive (PTR^r) phases on finished plant quality of 'Freedom' poinsettia *(Euphorbia pulcherrima* Willd.*)*. In Expt. 1, plants were grown under 27 combinations of three temperatures, three daily light integrals (DLI), and three plant spacings from pinch to the onset of short-day flower induction, and then moved to a common PTR until anthesis. In Expt. 2, plants were grown under a common PTR during the vegetative stage and then assigned to nine combinations of one temperature, three DLI, and three plant spacings after the onset of short-day flower induction. Both PTR^r and PTR^v affected final plant dry weight. All components of dry weight (total, stem, green leaf, and bract) responded linearly to PTR^r and quadratically to PTR^v. Stem strength depended more on PTR^v than PTR^r. When PTR^v increased from 0.02 to 0.06 mol/degree-day per plant, stem diameter increased about 24%, while stem strength increased 75%. The size of bracts and cyathia was correlated linearly to PTR^r but unaffected by PTR^v. When PTR^r increased from 0.02 to 0.06 mol/degree-day per plant, bract area, inflorescence diameter, and cyathia diameter increased 45%, 23%, and 44%, respectively.

Both light (radiant energy) and temperature (thermal energy) affect production of high-quality plants when they are grown with adequate nutrients and water and are free of pests and diseases. Radiant energy drives plant photosynthesis and, consequently, plant biomass production. Thermal energy is the primary environmental factor driving developmental rate. Plants grown under high radiant energy and low thermal energy become "husky" but develop slowly. In contrast, plants grown under low radiant energy and high thermal energy develop rapidly but become thin and weak. Horticulturists have tried to balance radiant and thermal energy intuitively to maintain adequate plant quality while minimizing production time. The concept of relating radiant energy (mol m^{-2}) and thermal energy (degree-day) as a ratio (RRT) was proposed to measure the balance between plant growth and development in greenhouse crops (Liu and Heins, 1997, 1998).

A similar concept termed photothermal quotient (PTQ) has been applied in field crops. Nix (1976) described photothermal quotient as a ratio of mean daily irradiation to mean temperature above a base temperature in units of cal cm^{-2} $degree\text{-}day^{-1}$, a definition similar to that of RRT. In order to avoid terminology confusion, we have changed "radiant energy to thermal energy" to "photothermal" in this paper. However, we believe "ratio" is more appropriate than "quotient." Photothermal ratio (PTR), therefore, will replace RRT in future reports and will represent PTQ in the discussion.

Islam and Morison (1992) believed that PTR was more meaningful physiologically than either temperature or radiation as an independent variable and should be considered a derived variable in regression analysis for crop yield prediction. The PTR has been used to predict seed number and yield with good results for different crops, such as wheat (Fischer, 1985; Magrin et al., 1993; Ortiz-Monasterio et al., 1994; Rawson, 1988; Savin and Slafer, 1991), rice (Islam and Morison, 1992), and sunflower (Cantagallo et al., 1997).

In contrast to field crops whose targeted crop yield is the number and size of seeds or kernels, ornamental crops typically have a high vegetative component. Several reports showed different combinations of light level (radiant energy) and temperature (thermal energy) affected floral plant quality (Hagen, 1980; Hagen and Moe, 1981; Harris and Scott, 1968; Kaczperski et al., 1991; Kristoffersen, 1994, 1969; Merritt and Kohl, 1982; Piringer and Cathey, 1960). However, none of these authors attempted to explain their results based on the PTR concept. In 1996, we proposed that the ratio of radiant energy (mol m^{-2}) to thermal energy (degree-days) (RRT) might be one of the parameters controlling quality of floral crops. Our initial studies showed that RRT or PTR was a useful parameter for predicting plant growth and quality control (Liu and Heins, 1997, 1998).

Based on different calculations for radiant energy, RRT was defined further into three forms; i.e., RRT_a, RRT_p, and R_iRT_p (Liu and Heins, 1998). The RRT_a (mol degree-day^{-1} m^{-2}) was based on the amount of incident light on a unit area. It is used most appropriately when plants are widely spaced and are not shading each other, and the amount of light available for each plant depends only on light intensity. When the plant canopy overlaps and becomes solid, light available for each plant depends on light intensity and plant spacing. In this situation, RRT_p (mol/degree-day per plant), which is based on the amount of light available for a plant, is more appropriate. Since photosynthesis is related directly to the amount of light intercepted by a plant, plant spacing and leaf area index should be considered. Therefore, R_iRT_p (mol/degree-day per plant), based on the amount of light intercepted by a plant, can be used in any situation. When the term PTR is applied in this paper, PTR_{area}, PTR_{plant}, and $PTR_{intercept}$ will be assigned the same meaning as RRT_a, RRT_p, and R_iRT_p, respectively.

We previously reported the effects of PTR on poinsettia vegetative growth and development (Liu and Heins, 1997 and 1998). The current work focuses on the effect of PTR on subsequent reproductive growth and development. The objective of this study was to quantify the effect of PTR during the vegetative and reproductive phases on poinsettia plant quality at anthesis. Plant quality was characterized through plant dry weight, bract size, flower size and lateral-shoot strength.

Materials and Methods

Two experiments were conducted in glass greenhouses in East Lansing, MI, during the fall of 1996. Rooted cuttings of *Euphorbia pulcherrima* 'Freedom' in 15-cm pots were obtained from a commercial poinsettia propagator on August 23 for Expt. 1 and August 29 for Expt. 2. Plants were pinched to leave six nodes and leaves on the mother stem one week from receipt. Immediately after pinch, plants in Expt. 1 were assigned randomly to one of 27 different combinations of temperature, light, and spacing; i.e., three air-temperature settings (19, 23, or 27 °C), three daily light integrals (DLI) (5, 10, or 20 mol m^{-2} day^{-1}), and three plant spacings (close [15 x 15 cm], medium [22 x 22 cm], or wide [30 x 30 cm]). Plants, which had been grown under the 27 treatments for five weeks, then were moved to a glass greenhouse at 20 °C with natural photoperiods (<12 h) and light conditions and grown until anthesis. Guard rows consisting of plants at comparable spacing surrounded treatment plants to avoid edge effects.

In Expt. 2, all plants were grown under the same condition, i.e., 23 °C, 10 mol m^{-2} day^{-1} DLI and 22 x 22 cm plant spacing during the vegetative stage. When thermal time was accumulated to 450 degree-days, plants were transferred randomly to one of nine combinations of temperature, light, and spacing; i.e., one temperature setting (20 °C), three DLI (5, 10, or 15 mol m^{-2} day^{-1}), and three plant spacings (close [25 x 25 cm], medium [30 x 30 cm], or wide [35 x 35 cm]). The photoperiod was kept shorter than 11.5 h. The experiment was stopped at anthesis. A split-plot design was used in both Expts. 1 and 2. Temperature was assigned as the main plot, DLI as the split plot, and plant spacing as the split split plot.

Photosynthetic photon flux was measured at the top and bottom of the plant canopy with line quantum sensors including 18 G2711 photodiodes (Hamamatsu, Japan) on a 1-m bar and CR10 dataloggers (Campbell Scientific, Logan, Utah). Intercepted light was calculated by light transmitted to the bottom of the canopy subtracted from incident light on the top of the canopy. Different DLI were obtained through internal greenhouse shading (sunny days) with 50% shading screens (LS 15F, Ludvig Svensson, Kinna, Sweden) or by supplemental lighting (cloudy days) from high-pressure sodium lamps that were controlled automatically by dataloggers to the designed DLI. Expected DLI was estimated each morning at 0800hr based on the weather forecast. Screens or lamps were actuated as necessary based on the prediction. Actual DLI was reviewed at 1400hr, and screens or lamps were readjusted. The desired DLI was adjusted up or down each day for any deviations from the desired DLI of the previous day.

Greenhouse temperature was controlled by a greenhouse climate-control computer (Priva, Model CD750, De Lier, Holland). Both air temperature and plant shoot-tip temperature, which were different (Table 1), were recorded by the CR10. Because plant temperature rather than air temperature plays an important role in control of plant developmental rate (Harris and Scott, 1968; Ritchie and NeSmith, 1991; Watts, 1972), all analyses were based on the actual plant temperature instead of the greenhouse temperature.

Table 1. Difference between air temperature and plant shoot-tip temperature under different light levels and plant spacings

Air temperature (°C)	DLI (mol m^{-2} day^{-1})[z]	Plant shoot-tip temperature (°C)		
		Close spacing	Medium spacing	Wide spacing
20.0	5	19.0	18.6	19.2
	10	19.5	19.8	19.6
	20	21.8	22.0	21.4
23.4	5	20.6	21.0	21.0
	10	21.6	21.7	22.1
	20	23.7	24.9	25.7
27.0	5	25.7	25.8	26.0
	10	25.3	25.5	25.3
	20	25.8	25.3	27.3

[z] Daily light integral.

Data were collected at anthesis. The observation items included plant height, shoot and internode length on the second lateral shoot, dry weight (total, stem, bract, and green leaf [including transitional leaf]), stem diameter (average diameter of the first three nodes from the bottom), stem strength, cyathia and inflorescence diameter on the second lateral shoot, and total leaf and bract area. Bracts were defined as leaves with over 80% red color and transitional leaves were colored leaves between the green leaves and the bracts. Stem strength was measured by using a force-gauge meter (Hunter Spring Company, Lansdale, PA). The force gauge meter reading was recorded when a lateral shoot was broken from the main stem by using the meter to push vertically downward. The higher the force-gauge reading, the stronger the stem.

Dry-weight data (total, stem, and leaf) also were collected at the onset of short day (SD). Dry-weight gain during the reproductive stage (DW_{rep}) was calculated by final dry weight minus dry weight at the onset of SD.

Different PTRs were applied during vegetative development in Expt. 1. We use "vegetative PTR (PTR^v) " to describe this situation. In Expt. 2, different PTRs were used after the onset of SD induction. Therefore, we term this treatment "reproductive PTR (PTR^r)."

Regression and general linear models were fitted using the Statistical Analysis Systems Institute (SAS) PROC GLM routine (SAS Institute, Inc., Cary, N.C.). The least square principle was applied to fit the general linear models.

Results

The relationships between PTR (i.e., PTR_{area}, PTR_{plant}, or $PTR_{intercept}$) in the two experiments and plant quality parameters were analyzed by using linear regression (Table 2). Plant final dry weight (total, stem, green leaf, and bract) and stem diameter were correlated significantly to PTR^v and PTR^r. Strength of the sixth lateral shoot was related to PTR^v, while cyathia diameter, inflorescence diameter, and bract area were related to PTR^r. The linear regression for each PTR form showed a different coefficient of determination (r^2). The r^2 for $PTR_{intercept}$ was generally higher than that for PTR_{plant} and greater than that for PTR_{area}. In Expt. 2, r^2 values for either PTR_{plant} or $PTR_{intercept}$ were almost identical. Therefore, $PTR_{intercept}$ was chosen as an independent variable in the following analysis.

Table 2. The coefficient of determination (r^2) of the linear regression between the photothermal ratio (PTR) and the parameters related to plant quality at anthesis for Expt. 1 (n = 27) and Expt. 2 (n = 9)

Parameter	Lateral shoot	PTR^v			PTR^r		
		PTR_{area}	PTR_{plant}	$PTR_{intercept}$	PTR_{area}	PTR_{plant}	$PTR_{intercept}$
Total dry weight	-	0.35^{**}	0.46^{***}	0.59^{***}	0.61^{*}	0.94^{***}	0.94^{***}
Stem dry weight	-	0.29^{**}	0.29^{**}	0.41^{***}	0.78^{**}	0.82^{***}	0.89^{***}
Leaf dry weight	-	0.35^{**}	0.52^{***}	0.63^{***}	0.56^{**}	0.94^{***}	0.93^{***}
Bract dry weight	-	0.31^{**}	0.39^{***}	0.47^{***}	0.55^{*}	0.95^{***}	0.93^{***}
Stem diameter	2^{nd}	0.39^{***}	0.48^{***}	0.59^{***}	0.59^{*}	0.77^{**}	0.75^{**}
Lateral shoot breakage	1^{st}	0.19^{*}	0.10^{NS}	0.16^{*}	0.04^{NS}	0.07^{NS}	0.02^{NS}
force	2^{nd}	0.10^{NS}	0.09^{NS}	0.13^{NS}	0.00^{NS}	0.15^{NS}	0.11^{NS}
	3^{rd}	0.03^{NS}	0.13^{NS}	0.14^{NS}	0.23^{NS}	0.19^{NS}	0.23^{NS}
	4^{th}	0.09^{NS}	0.15^{*}	0.18^{*}	0.00^{NS}	0.06^{NS}	0.03^{NS}
	5^{th}	0.01^{NS}	0.24^{**}	0.28^{**}	0.05^{NS}	0.06^{NS}	0.05^{NS}
	6^{th}	0.20^{*}	0.66^{***}	0.63^{***}	0.19^{NS}	0.04^{NS}	0.05^{NS}
Cyathia diameter	2^{nd}	0.07^{NS}	0.05^{NS}	0.08^{NS}	0.50^{*}	0.90^{***}	0.82^{***}
Inflorescence diameter	2^{nd}	0.09^{NS}	0.08^{NS}	0.15^{*}	0.66^{**}	0.78^{**}	0.82^{***}
Bract area	-	-	-	-	0.64^{**}	0.95^{***}	0.94^{***}
Plant height	-	0.11^{NS}	0.10^{NS}	0.16^{*}	0.06^{NS}	0.02^{NS}	0.02^{NS}
Lateral shoot length	2^{nd}	0.05^{NS}	0.04^{NS}	0.08^{NS}	0.07^{NS}	0.33^{NS}	0.29^{NS}
Internode length	2^{nd}	0.00^{NS}	0.07^{NS}	0.03^{NS}	0.04^{NS}	0.26^{NS}	0.17^{NS}
Plant diameter	-	0.00^{NS}	0.00^{NS}	0.00^{NS}	0.05^{NS}	0.06^{NS}	0.05^{NS}

$^{NS, *, **, ***}$ Nonsignificant or significant at $P = 0.05, 0.01,$ or 0.001, respectively.

The $\mathrm{PTR}^{r}_{\mathrm{intercept}}$ and $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ affected plant final dry weight (total, stem, green leaf, and bract) differently (Fig. 1, solid symbols). In Expt. 2, all components of dry weight increased linearly as $\mathrm{PTR}^{r}_{\mathrm{intercept}}$ increased (Fig. 1E-1H, solid symbols). The slope of the linear regression in Fig. 1 can be interpreted as the increase in dry weight per mol of photons for each degree-day. Of the different organs, the bract dry weight increased at the largest rate, 62.8 g per mol/degree-day (Fig. 1H). Stem and green leaf dry weight increased at 22.4 and 49.75 g per mol/degree-day (Fig. 1F-1G), respectively. In Expt. 1, all final dry weight components responded to $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ quadratically (Fig. 1A-1D, solid symbols). Plant dry weight increased as $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ increased up to about 0.04 mol/degree-day per plant. After which, increasing $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ did not improve plant dry-weight accumulation (Fig. 1A-1D, solid symbols).

Analyzing the relationship between $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ and plant final dry weight in Expt. 1 might be an oversimplified procedure because plants were treated differently before and after the onset of SD. At the onset of SD (start of common PTR), plants had accumulated different dry weights (total, stem, and leaf) following growth under different PTR^{v}s for five weeks (Fig. 1A-1C, open symbols). The net gain in plant dry weight during the SD flowering period was plotted with $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ and the relationships were fitted as a quadratic relationship within each temperature regimen (Fig. 2A-2C). The positive aftereffect of $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ on net plant-dry weight gain during reproductive development was obvious. The most dry-weight net gain was achieved when $\mathrm{PTR}^{v}_{\mathrm{intercept}}$ was about 0.05 mol/degree-day per plant at 19 °C, 0.055 at 23°C, and 0.035 at 27 °C. In Expt. 2, the effect of $\mathrm{PTR}^{r}_{\mathrm{intercept}}$ on net plant dry-weight gain during reproductive development (Fig. 2D-2F) was the same as that showed in Fig. 1F-1G (solid symbols).

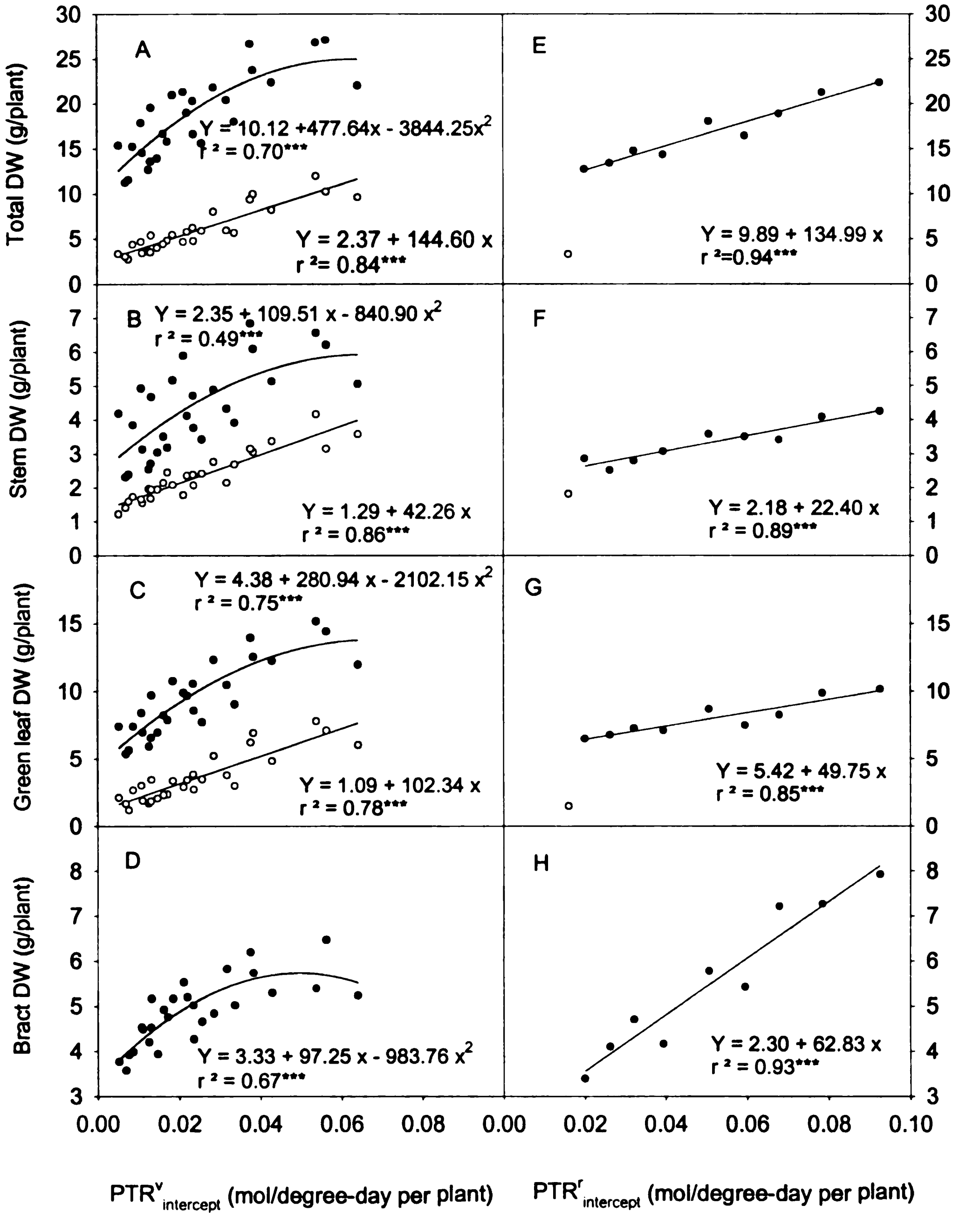

Fig. 1. Effects of $PTR^{v}_{intercept}$ (Expt. 1) and $PTR^{r}_{intercept}$ (Expt. 2) on plant dry weight (DW) accumulation at anthesis (solid symbols) and at the onset of short-day induction (open symbols).

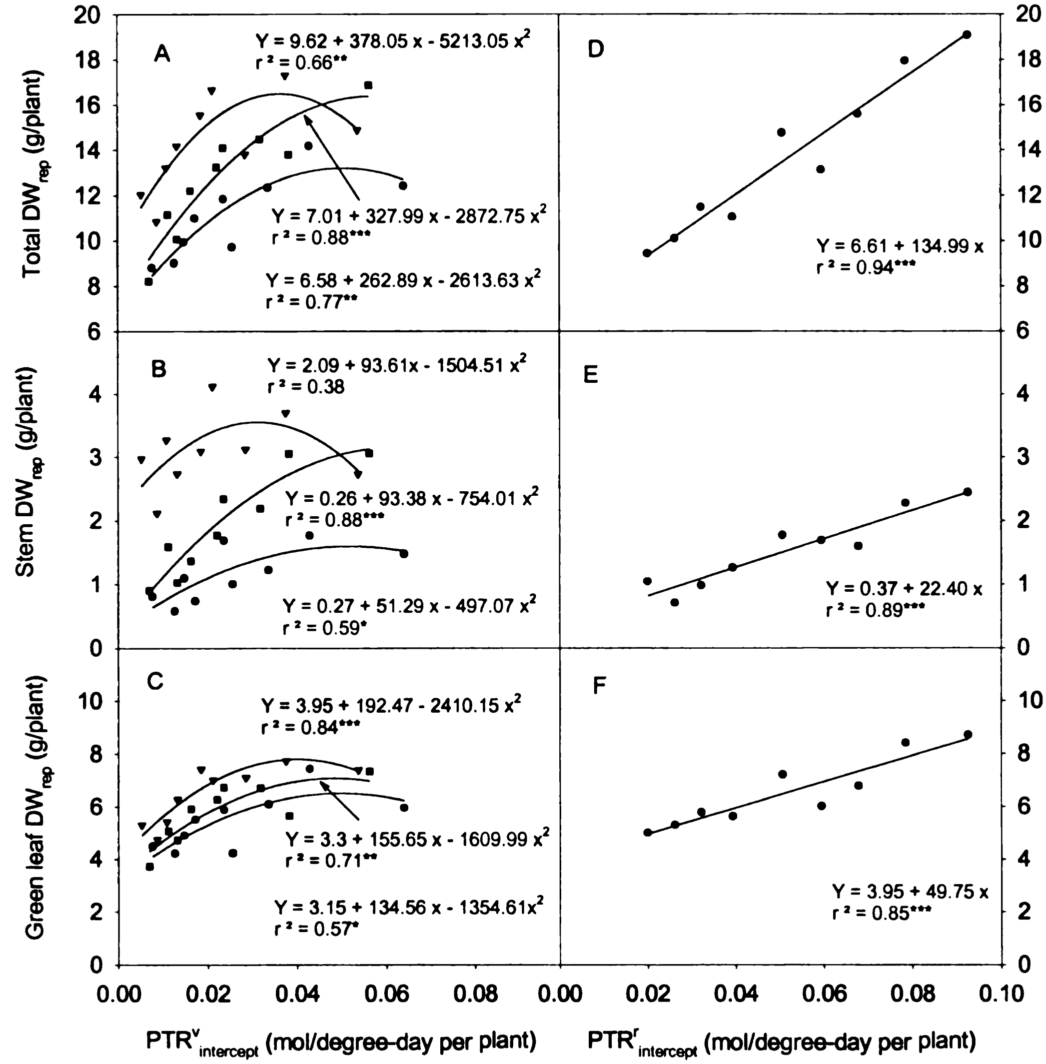

Fig. 2. Effects of $PTR^{v}_{intercept}$ (Expt. 1) and $PTR^{r}_{intercept}$ (Expt. 2) on plant dry-weight gain during the reproductive stage (DW_{rep}). In A, B, and C, non-linear regressions were fitted to the three different temperatures (● 19 °C, ■ 23 °C, and ▼ 27 °C).

The $PTR^{v}_{intercept}$ had more influence on stem strength than the $PTR^{r}_{intercept}$ (Table 2). Generally, the basal lateral shoots were more sensitive to PTR than apical shoots. There was a significant linear relationship between stem strength on the sixth lateral shoot and $PTR^{v}_{intercept}$ (Fig. 3B). When $PTR^{v}_{intercept}$ increased from 0.02 to 0.06 mol/degree-day per plant, the breakage force increased from 310 to 547 g, a 75% increase in stem strength.

Both vegetative and reproductive $PTR_{intercept}$ were correlated positively with stem diameter at anthesis (Fig. 3A and 3C, solid symbols). However, the stem diameter increased at about twice the rate with a $PTR^{v}_{intercept}$ increase than with a $PTR^{r}_{intercept}$ increase (32.8 vs. 17.0 mm per mol/degree-day). The $PTR^{v}_{intercept}$ had a significantly greater effect on stem diameter than the $PTR^{r}_{intercept}$. With the same $PTR_{intercept}$ increment of 0.02 to 0.06 mol/degree-day per plant during both developmental phases, the stem diameter increased about 1.3 mm in Expt. 1 but only 0.7 mm in Expt. 2.

Bract and cyathia size were affected by $PTR^{r}_{intercept}$, not $PTR^{v}_{intercept}$ (Fig. 4). Plants developed larger bracts and cyathia as $PTR^{r}_{intercept}$ increased. Plants grown under a $PTR^{r}_{intercept}$ of 0.0926 mol/degree-day per plant produced a 39-cm-diameter inflorescence and 17-mm-diameter cyathia. These diameters were about 10 cm and 8 mm larger than those for plants grown at a $PTR^{r}_{intercept}$ of 0.0200 mol/degree-day per plant. There was a similar tendency in total bract area (Fig. 5), which were 0.32 m^2 in the high $PTR^{r}_{intercept}$ and 0.16 m^2 in the low $PTR^{r}_{intercept}$.

All other investigated plant characteristics, such as plant diameter and height and lateral shoot and internode length, were not affected by either PTR^{v} or PTR^{r} (Table 2).

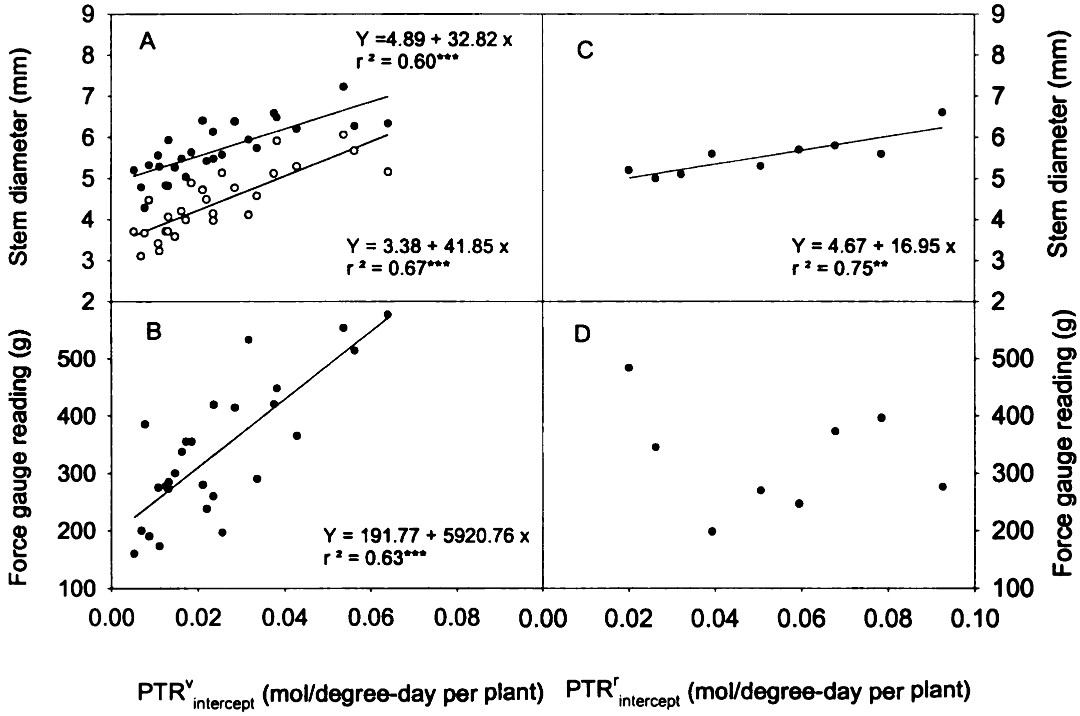

Fig. 3. Effects of $PTR^{v}_{intercept}$ (Expt. 1) and $PTR^{r}_{intercept}$ (Expt. 2) on stem diameter of the second lateral shoot and stem strength of the sixth lateral shoot at anthesis (solid symbols) and at the onset of flower induction (open symbols).

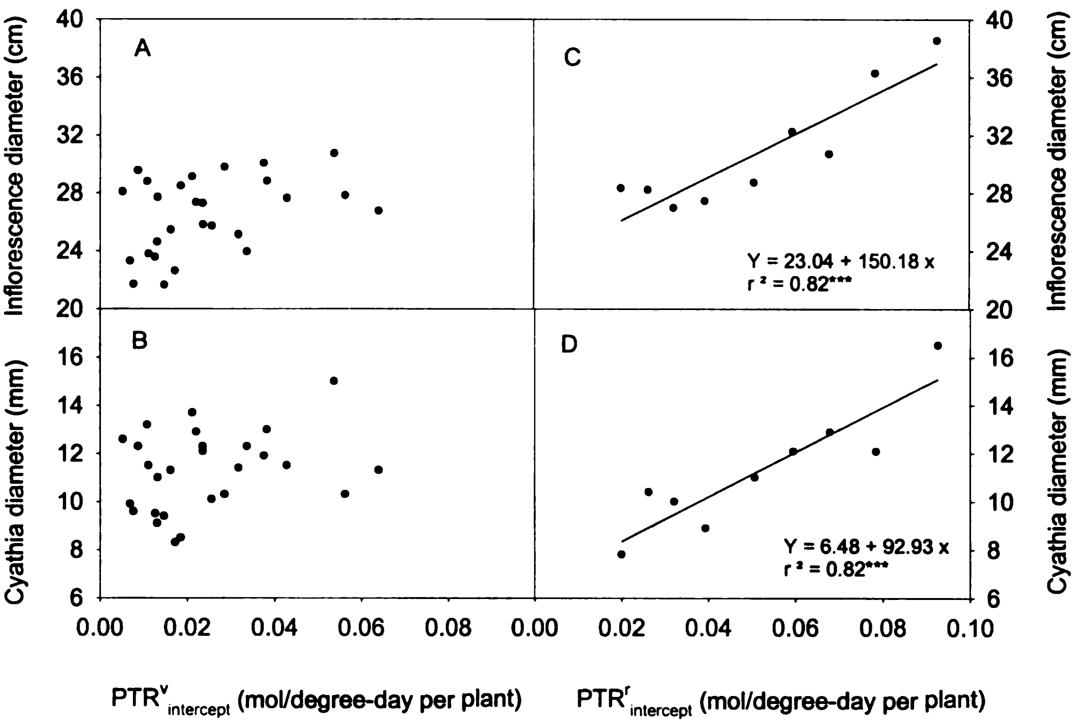

Fig. 4. Effects of PTR$^{v}_{intercept}$ (Expt. 1) and PTR$^{r}_{intercept}$ (Expt. 2) on inflorescence and cyathia diameter of the second lateral shoot at anthesis.

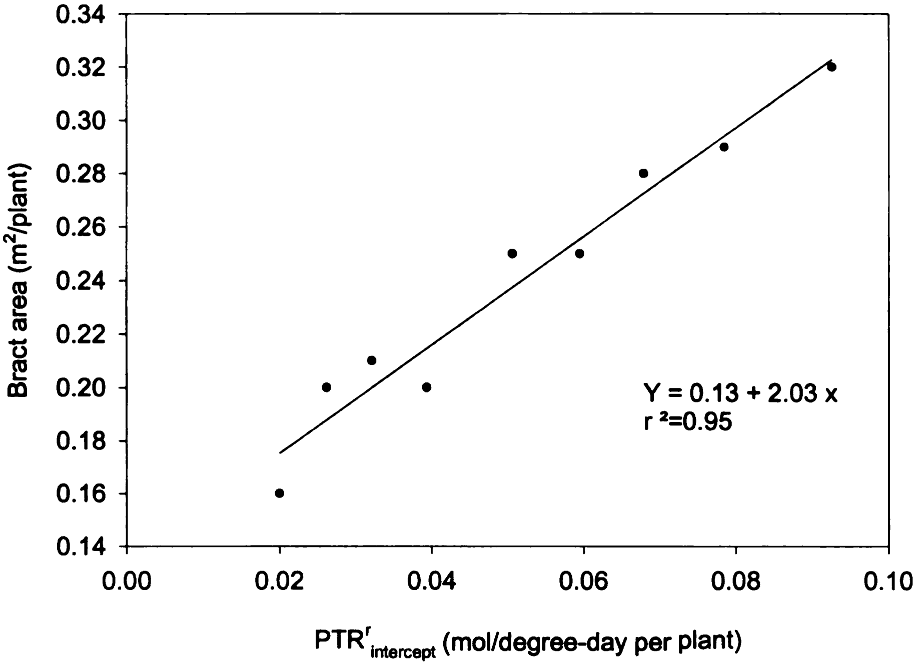

Fig. 5. Effects of PTR$^{r}_{intercept}$ (Expt. 2) on bract area at anthesis.

Discussion

The PTR concept describes light energy available for photosynthesis per unit of developmental time. Plant photosynthesis and dry-matter accumulation increase as intercepted light increases, while plant developmental rate increases as temperature increases. Plant biomass accumulation per unit of development, therefore, depends on PTR. A large $PTR_{intercept}$ means that plants intercept more photons, thus accumulating more biomass, for each unit of development. This relationship has been quantified in our previous (Liu and Heins 1997, 1998) and present studies (e.g., Fig. 1A-1C, open symbols; Fig. 1E-1H, solid symbols).

Further examination of the effect of PTR on total dry-weight accumulation before (Fig. 1A-1C, open symbols) or after (Fig. 1E-1H, solid symbols) the onset of SD induction showed that total dry weight increased at a similar rate (144.6 vs. 135.0 g per mol/degree-day). The slightly lower rate during reproductive development may be due to shading of leaves by developing bracts. However, stem growth and development was related more to the PTR^v. Stem dry weight increased at about twice the rate during vegetative development than reproductive development (42.3 vs. 22.4 g per mol/degree-day). Compared to that of PTR^r, the PTR^v's effect on stem dry weight resulted in a much greater increase in stem diameter as PTR^v increased (17.0 vs. 41.9 mm per mol/degree-day, respectively; Fig. 3A, open symbols, and 3C). Moreover, this effect lasted to anthesis (Fig. 3A, solid symbols). The final stem diameter of the second lateral shoot increased about 24% as PTR^v increased from 0.02 to 0.06 mol/degree-day per plant, an increase in stem cross-sectional area of about 50%.

It is clear that PTR^{r} affected bract dry-weight accumulation more than that of other organs (Fig. 1F-1H). After flower induction, assimilate partitioning patterns change. The reproductive sink becomes strong, which limits the assimilate partitioned for additional leaf, stem and root growth (Gardner et al., 1985). Bracts are part of the reproductive organs in poinsettia, and their dry weight increased faster than that of other organs as PTR^{r} increased (i.e., 62.8, 49.8, and 22.4 g per mol/degree-day for bracts, green leaves, and stems, respectively).

The effect of PTR^{v} on dry-weight gain can last to anthesis (Fig. 2). However, the aftereffect was more prominent on stem dry weight than on green leaf and bract dry weight (Fig. 2B, 2C; Fig. 1D). The aftereffect of PTR^{v} on dry weight varied with temperature because plant leaf area was different at the onset of SD after plants were treated under different temperatures for five weeks. For plants under the same environmental and spacing conditions, those with large leaf area intercepted more light and accumulated more biomass than those with small leaf area.

Lateral stem breakage is problematic in poinsettia production, since stem breakage reduces plant marketability and economic value. Many factors, including genetics, nutrition, and cultural practices, could cause lateral stem breakage (Leonard and Nell, 1998). We found that PTR was one of the factors that affect stem breakage significantly, especially on the lower lateral shoots (Table 2; Fig. 3B). The higher the PTR^{v}, the stronger the lateral shoots. In contrast, the PTR^{r} had little or no effect on stem breakage, probably because the joint between the lateral shoot and the main stem was established before flower induction. Another important reason is that PTR^{v} profoundly affected stem growth and development. Stem dry-weight accumulation increased significantly as the PTR^v increased, making thick strong stems.

Recently, Leonard and Nell (1998) reported that stem diameter at planting was one of the major factors that influenced stem breakage. Thinner cuttings (<4.5 mm in diameter) had twice as much breakage as thicker cuttings (>7.5 mm in diameter). Since plants grown under a high PTR would develop thick strong stems, the effect of PTR on stem breakage might start as early as the stock-plant stage.

Although a higher $PTR_{intercept}$ during the reproductive stage did not help reduce stem breakage, a higher reproductive $PTR_{intercept}$ did improve the finished plant quality by increasing bract and cyathia size. Bract area, inflorescence diameter, and cyathia diameter increased linearly as $PTR^r_{intercept}$ increased (Fig. 4C-4D; Fig. 5). When PTR^r increased from 0.02 to 0.06 mol/degree-day per plant, bract area, inflorescence diameter, and cyathia diameter increased about 45%, 23%, and 44%, respectively. The higher dry-weight accumulation in a higher PTR^r may not be the only reason for the larger bract size. According to Hall (1992), bract size increases linearly as average temperature increases from 15 to 24 °C. In our experiment, average plant shoot-tip temperature was about 1 °C higher under the high light level treatment (15 mol m^{-2} day^{-1}) than the low light level (5 mol m^{-2} day^{-1}). Larger temperature differences would occur during the day when supplemental lights (high-pressure sodium lamps) were turned on in the high light level treatment. The larger bracts may result from both high PTR and warmer day temperature.

Cyathia abscission is another parameter related to poinsettia plant quality. Increasing temperature and reducing irradiance in a greenhouse promoted cyathia abscission (Miller and Heins, 1986). Cyathia abscission increased under low light with high temperature; i.e., low PTR. Therefore, it can be inferred that cyathia abscission also is related to PTR. Cyathia abscission should be reduced by increasing PTR near anthesis.

The results presented in this report further confirm that poinsettia plant quality is related to the photothermal ratio (PTR). A high PTR during the vegetative stage will enhance plant stem strength, reducing stem breakage at anthesis. During reproductive development, a high PTR improves plant appearance by increasing bract and cyathia size and reducing cyathia abscission.

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Section IV

Improving Poinsettia Plant Quality through Adjustment of the Photothermal Ratio

Improving Poinsettia Plant Quality through Adjustment of the Photothermal Ratio*

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Received for publication _____________. Accepted for publication ____________. This study was funded by the American Floral Endowment. We gratefully acknowledge the assistance of Dan Tschirhart, Mark Yelanich, Robert Milks, and Shawn Koepnick in conducting the experiments. 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.

[1] Graduate Assistant.
[2] Professor.

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* The paper format was adopted for this section in accordance with "Journal of the American Society for Horticultural Science."

Production and Culture

Improving Poinsettia Plant Quality through Adjustment of the Photothermal Ratio

Additional index words. light adjustment, photothermal ratio regulation, plant spacing, temperature adjustment

Abstract. Photothermal ratio (PTR) that describes light energy available for photosynthesis per unit of developmental time is a useful parameter for plant quality control. The present study was focused on regulating PTR through adjustment of temperature, light, and plant spacing to improve poinsettia plant quality. Three strategies of temperature adjustment were tested: temperature adjusted every day based on the weather forecast; temperature adjusted twice a week based on the previous three or four days' cumulative daily light integral and degree-days; a higher constant temperature during the vegetative stage with a lower day/night temperature during the reproductive stage. The PTR of three different commercial greenhouses, i.e., glass, double poly, and double poly with hanging baskets and their corresponding plant quality were compared. The results showed that practical PTR regulation through temperature adjustment played a limited role in improving poinsettia plant quality. However, the potential for light adjustment to increase PTR and plant quality was substantial. Reducing overhead shading and widening plant spacing improved plant light interception greatly and increased plant quality. The minimum light level for an acceptable plant quality in poinsettia was about 10 to 12 mol m^{-2} day^{-1} at 20 °C with plant spacing of 25 x 25 cm. This level increased as temperature increased and decreased as plant spacing increased.

Photothermal ratio (PTR) is the ratio of radiant energy to thermal energy. The PTR concept describes light energy available for photosynthesis per unit of developmental time. Poinsettia plant quality, such as plant dry weight, stem strength, and bract and cyathia size, is correlated linearly to the PTR, which increases as PTR increases (Liu and Heins, 1997, 1999). A higher PTR during the vegetative stage will produce stronger and larger stems; during the reproductive stage, larger bracts and cyathia (Liu and Heins, 1999).

If the PTR is a useful parameter for plant quality control, the key issue is how to implement the PTR concept in commercial greenhouse production. Both temperature and light are components of PTR. Other than problems associated with greenhouse temperature control, high PTR values associated with high light levels are not a problem requiring grower intervention. A more likely problem is that low light levels and, therefore, low PRT values adversely affect plant quality.

To correct a low PTR value, light must be increased or temperature must be decreased. However, supplemental lights are not used in commercial greenhouses unless a grower believes their use will be profitable. Alternative ways to improve each plant's light interception include adjusting plant spacing before the plant canopy becomes too close, reducing overhead shade, or both. Major temperature changes to adjust PTR are not realistic because most plants are shipped to market on a fixed date and lowering temperature delays flowering. However, it is possible to adjust temperatures dynamically within an acceptable developmental rate over a plant's life cycle to match the light level. Discounting the daily fluctuation, the light intensity generally decreases during the poinsettia production period in the northern United States (Table 1). Therefore, an easy

Table 1. Average daily light integral changes during the poinsettia crop production period in Grand Rapids, Michigan, U.S.A. over 30 years (1961-1990, Latitude 43 °N; Weather Report, Michigan Agricultural Department, 1997).

	Daily light integral (mol m^{-2} day^{-1})	
	Outside greenhouse	Inside greenhouse (assuming transmissivity = 0.63)
August	38.3	24.1
September	29.2	18.3
October	19.7	12.4
November	11.8	7.4
December	9.2	5.8

way to maintain the designed PTR might be to apply higher temperatures during the vegetative stage and lower ones during the reproductive stage.

Our long-term objective is to develop a practical way to produce high-quality poinsettia plants through PTR adjustment. In this study, three PTR adjustment strategies were tested in a research greenhouse, and three commercial greenhouse PTRs and their corresponding plant quality were compared.

Materials and Methods

Experiments were conducted in the research greenhouses of Michigan State University (MSU) in East Lansing, MI (42.2 °N) and three commercial greenhouses in different locations with different construction types and production arrangements. The experiments at MSU were focused on regulating the PTR through temperature adjustment based on the dynamic changes of natural light. Research in commercial greenhouses was aimed at clarifying the PTR changes in current commercial greenhouses and the possible PTR adjustment.

1. Temperature adjustment treatments at MSU

Rooted cuttings of *Euphorbia pulcherrima* Willd. 'Freedom' in 15-cm pots were obtained from a commercial poinsettia propagator on 15 August 1997. Plants were pinched to leave six nodes and leaves on the mother stem five days after receipt. Immediately after pinch, plants were assigned randomly to different treatments (Table 2) based on the strategies of the PTR adjustment. Plants in all treatments were grown under long days (LD) from 18 August until the sixth leaf on the second lateral shoot unfolded, then moved to a short-day (SD) photoperiod. A plant spacing of 25 x 25 cm during LD and 30 x 30 cm during SD was used. Plants in all treatments received natural light.

Table 2. Temperature (°C) adjustment in different treatments at MSU. In treatment 1, the temperature setting was adjusted based on the daily weather forecast. The weather types were grouped into sunny (S), partly cloudy (PC), and mostly cloudy (MC). In treatment 2, the temperature setting was adjusted based on the cumulative daily light integral (CDLI) and cumulative degree-days (CTT) in the cumulative duration (D). Constant temperature settings were used in treatment 3.

Treatment	Vegetative stage			Reproductive stage		
1	27 (S)	23 (PC)	19 (MC)	20/20 (S)	20/18 (PC)	20/16 (MC)
2	23 + [(CDLI-CTT)/D]			20 °C in first 4 weeks, then 20 + [(CDLI-CTT)/D]		
3	24			20/16		

In treatment 1, the greenhouse temperature setting was adjusted every day based on the weather forecast. During the vegetative stage (from the middle of August to the middle of September), the temperature was adjusted to 27 °C on sunny days, 23 °C on partly cloudy days, and 19 °C on mostly cloudy days. During the reproductive stage (from the middle of September to the end of November), only the night temperature was adjusted based on the weather forecast. Day temperature was maintained at 20 °C. A night temperature of 20, 18, or 16 °C was applied following a sunny, partly cloudy, or mostly cloudy day, respectively (Table 2).

In treatment 2, the greenhouse temperature setting was adjusted twice a week (every Monday and Thursday) based on the previous three or four days' weather conditions. The new temperature (T_{new}) was calculated by the following formula:

$$T_{new} = T_{ref} + [(CDLI - CTT)/D]$$

where T_{ref} is the reference temperature and CDLI and CTT were the cumulative daily light integral and cumulative degree-days (base temperature = 5 °C) in the calculated duration (D, days), respectively. During the vegetative stage, T_{ref} was set to 23 °C and the range of T_{new} was from 19 to 27 °C; i.e., if the calculated T_{new} was lower than 19 °C or higher than 27 °C, the T_{new} was set to 19 or 27 °C, respectively. During the reproductive stage, the temperature was set at 20 °C for first 4 weeks, then adjusted based on the above formula. The T_{ref} was 20 °C and the range of T_{new} varied from 18 to 22 °C (Table 2).

In treatment 3, a higher constant greenhouse temperature setting (24 °C) during the vegetative stage and a lower day/night temperature setting (20/16 °C) during the reproductive stage was used (Table 2).

2. Environmental conditions in the commercial greenhouses

Three greenhouses were chosen based on their geographic location, greenhouse type, and poinsettia production arrangement. Greenhouse A was a glass house oriented north-south in Grand Rapids, MI (42.9 °N). Greenhouse B was a double-poly north-south house in Fletcher, NC (35.3 °N). Greenhouse C was a poly-covered north-south house in Oberlin, OH (41.3 °N) and had hanging baskets. All three greenhouses were set at a constant 20 °C during the production period. Plant spacing was 30 x 34 cm, 25 x 25 cm, and 25 x 25 cm in greenhouses A, B, and C, respectively. In greenhouse C, the overhead hanging basket lines were on 61-cm centers with 48 baskets (25 cm each) per line and three lines per bay. Six plants from each greenhouse were shipped to MSU at anthesis for the final quality comparison.

3. Data collection

All environmental and plant data were collected identically in the MSU research and commercial greenhouses. Both air temperature and plant shoot-tip temperature were recorded by the CR10 dataloggers (Campbell Scientific, Logan, Utah). The difference between average air and plant temperature among treatments was about 0.1 to 0.7 °C. Because plant temperature rather than air temperature plays an important role in control of plant developmental rate (Harris and Scott, 1968; Ritchie and NeSmith, 1991; Watts, 1972), all analyses were based on actual plant temperatures instead of greenhouse temperatures.

Photosynthetic photon flux was measured at the top and bottom of the plant canopy with line quantum sensors constructed with 18 G2711-photodiodes (Hamamatsu, Japan) on a 1-m bar and linked to the CR10 dataloggers. Intercepted light was calculated by light transmitted to the bottom of the canopy subtracted from incident light on the top of the canopy.

Plant data were collected at anthesis. The observations included plant height, dry weight (total, stem, bracts, and green leaves [including transitional leaves]), stem diameter (average stem diameter of the first three nodes from the bottom), stem strength, cyathia and inflorescence diameter on the second lateral shoot, total leaf and bract area, and date of anthesis. Bracts were defined as leaves with over 80% red color and transitional leaves were colored leaves between the green leaves and the bracts. Stem strength was measured by using a force-gauge meter (Hunter Spring Company, Lansdale, PA). The force gauge meter reading was recorded at the point when a lateral shoot was broken from the main stem by using the meter to push downward vertically. The higher the force-gauge reading, the stronger the stem.

Previous results showed that PTR in different stages affected different parameters of plant quality (Liu and Heins, 1999). Therefore, vegetative PTR (PTR^v) and reproductive PTR (PTR^r) were calculated separately in the present study.

Results

1. Temperature adjustment treatments

Under the same natural light conditions, different strategies of temperature adjustment created different plant temperature patterns (Fig. 1). In treatment 1, greenhouse temperature adjustment based on the daily forecasted natural light conditions and plant temperatures generally changed with the daily light integral. However, although greenhouse temperature could be raised during sunny days, it could not be lowered during cloudy days the first two weeks after the experiment started because of high outside temperatures. Plant temperature change in treatment 2 depended on the light level the previous three or four days. Therefore, a higher plant temperature sometimes occurred the same day the plant was exposed to lower light. Plant temperature in treatment 3 fluctuated around 24 °C during the vegetative stage and around 18 °C during the reproductive stage, except when outside temperature rendered those in the greenhouse uncontrollable.

Different plant temperature patterns did not result in significantly different PTR. Table 3 showed the differences in average plant temperature, DLI, and PTR of the two developmental stages among different treatments. The difference in average temperature among treatments was less than 1 °C. Treatments 1 and 2 had a similar PTR. In treatment 3, PTR was slightly lower during the vegetative stage but slightly higher during the reproductive stage compared with that in treatments 1 and 2. Because plant spacings were the same and plant sizes were close, all three different forms of PTR (Liu and Heins, 1999), i.e., PTR_{area}, PTR_{plant}, and $PTR_{intercept}$, showed a parallel change.

The PTR during the vegetative stage was relatively low in all the temperature adjustment treatments (Table 3). During the vegetative stage, the average daily light integral (DLI) inside the greenhouse was about 9.9 to 11.7 mol m^{-2} day^{-1} and the average plant temperature was around 23 °C. Values of $PTR_{intercept}$ for all treatments changed between 0.018 to 0.022 mol/degree-day per plant (range from 0.005 to 0.065 mol/degree-day per plant).

There was no significant difference in any plant quality parameters, except cyathia diameter and green leaf dry weight, among the temperature adjustment treatments (Fig. 2, solid boxes). Cyathia diameter was significantly lower and green leaf dry weight was significantly higher in treatment 3 than in other treatments. Plant dry weight, stem diameter, and bract and cyathia size were similar between treatments 1 and 2. The highest total dry weight was in treatment 3 but the highest stem dry weight was in treatment 1. The average force gauge readings were higher in treatment 1 than in treatments 2 and 3, but not significantly.

Table 3. Average temperature (T), daily light integral (DLI), interception of daily light integral (IDLI), and photothermal ratio (PTR) in the vegetative stage and the reproductive stages.

Treatment	T (°C)	DLI (mol m^{-2} day^{-1})	IDLI (mol m^{-2} day^{-1})	Spacing (cm)	PTR_{area} (mol degree-day^{-1} m^{-2})	PTR_{plant} (mol/degree-day per plant)	$PTR_{intercept}$ (mol/degree-day per plant)
Vegetative stage							
Treatment 1	23.3	11.7	6.1	25 x 25	0.639	0.041	0.022
Treatment 2	22.6	11.1	5.7	25 x 25	0.631	0.041	0.021
Treatment 3	23.6	9.9	5.3	25 x 25	0.532	0.034	0.018
Greenhouse A	22.2	10.5	5.2	30 x 34	0.610	0.064	0.032
Greenhouse B	22.9	-	-	25 x 25	-	-	-
Greenhouse C	23.1	6.8	3.9	25 x 25	0.376	0.024	0.014
Reproductive stage							
Treatment 1	20.0	11.7	10.7	30 x 30	0.780	0.072	0.066
Treatment 2	20.2	11.5	10.4	30 x 30	0.757	0.070	0.064
Treatment 3	19.2	11.5	10.5	30 x 30	0.810	0.075	0.069
Greenhouse A	19.8	9.0	7.9	30 x 34	0.608	0.064	0.056
Greenhouse B	19.7	9.8	8.8	25 x 25	0.667	0.043	0.039
Greenhouse C	19.2	6.4	5.3	25 x 25	0.451	0.029	0.024

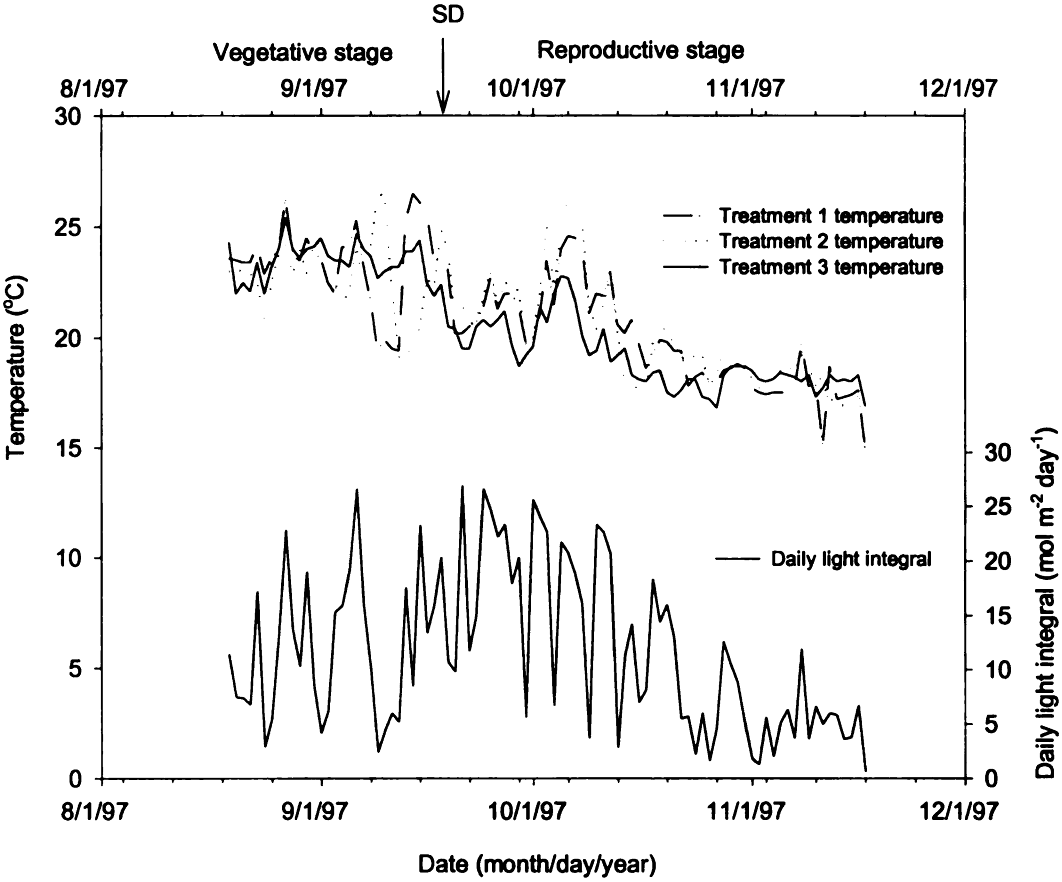

Fig. 1. Dynamic changes of daily light integral and plant temperature in three temperature adjustment treatments during the 1997 poinsettia growing season.

2. Commercial greenhouses

Light levels among the three commercial greenhouses were different (Fig. 3). The DLI in greenhouse B was slightly higher than in greenhouse A. The average difference was about 0.8 mol m^{-2} day^{-1} (Table 3). Greenhouse C with overhead hanging baskets had the lowest light level (Fig. 3). Its average DLI was 6.4 mol m^{-2} day^{-1} (Table 3), which was about 30% less incident light on the plant canopy than that in greenhouse A or B.

The different light levels, plant temperatures, and plant spacing among the three commercial greenhouses resulted in different PTR (Table 3). The lowest light condition and PTR were in greenhouse C. Although plants in greenhouse B had a higher PTR_{area} than that in greenhouse A, the latter had a higher PTR_{plant} and $PTR_{intercept}$. Plants in greenhouse A had a wider spacing, and therefore each plant received more light. When plant spacing changed from 25 x 25 cm to 30 x 34 cm, the light interception of individual plants increased by at least 30% during the reproductive stage.

Plant quality was significantly different among the three commercial greenhouses (Fig. 2). Plants produced in greenhouse A had the highest plant dry weight (total, stem, green leaf, and bract), stem and inflorescence diameter, and force gauge reading. In contrast, plants produced in greenhouse C had the lowest. Plants grown in greenhouse A were about 50% heavier (plant dry weight), 20% thicker and 44% stronger (stems), and 17% larger (bract size) compared to plants grown in greenhouse C. Based on the experts' evaluation, plant quality was graded as excellent, acceptable, and poor for plants produced in greenhouse A, B, and C, respectively.

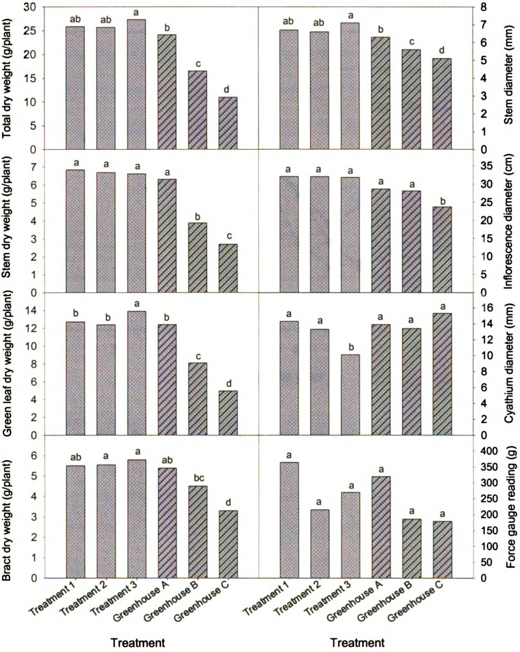

Fig. 2. Comparison of plant quality parameters at anthesis between temperature adjustment treatments and commercial greenhouses. Bars with the same letters were not significantly different at P = 0.05 according to Duncan's multiple range test.

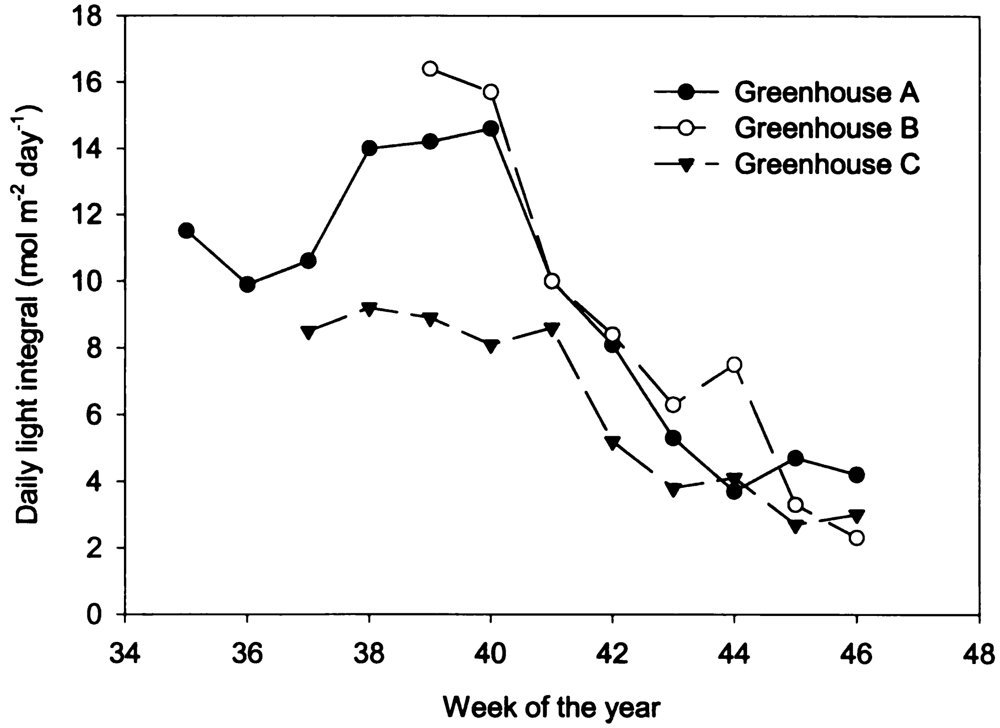

Fig. 3. Weekly average daily light integral in three commercial greenhouses.

3. Plant quality and PTR

Although each treatment and each greenhouse had a different growing condition, plant quality was closely related to PTR (Fig. 4 and Fig. 5). A higher plant quality was associated with a higher PTR. Plant total dry weight, stem dry weight, stem diameter, and inflorescence diameter at anthesis was correlated to $PTR^{r}_{intercept}$ (Fig. 4). The force gauge reading was correlated to $PTR^{v}_{intercept}$ (Fig. 5). However, cyathia size was not affected by $PTR^{r}_{intercept}$ (Fig. 4).

Discussion

Plant quality was not significantly different between treatments 1 and 2. Although dynamic temperature change in those two treatments was different (Fig. 1), the average PTR over time was very close (Table 3), as was plant quality. The initial reason for having treatment 1 was to change the temperature setting every day to correspond with light conditions and maintain a designed PTR. Since the greenhouse environment control had to be adjusted every day based on the weather forecast, it would be difficult to use in the most commercial greenhouses. Temperature adjusted twice a week based on light conditions the previous three or four days (treatment 2) can be programmed and controlled automatically by a computer. It should not be difficult to adopt this temperature adjustment strategy in the industry. However, the current study showed that plant quality was not affected by short-term PTR regulation.

The temperature adjustment strategy in treatment 3 was based on the seasonal change of natural light levels. Using a higher temperature by taking advantage of high light levels during the vegetative stage promotes leaf expansion and enhances light

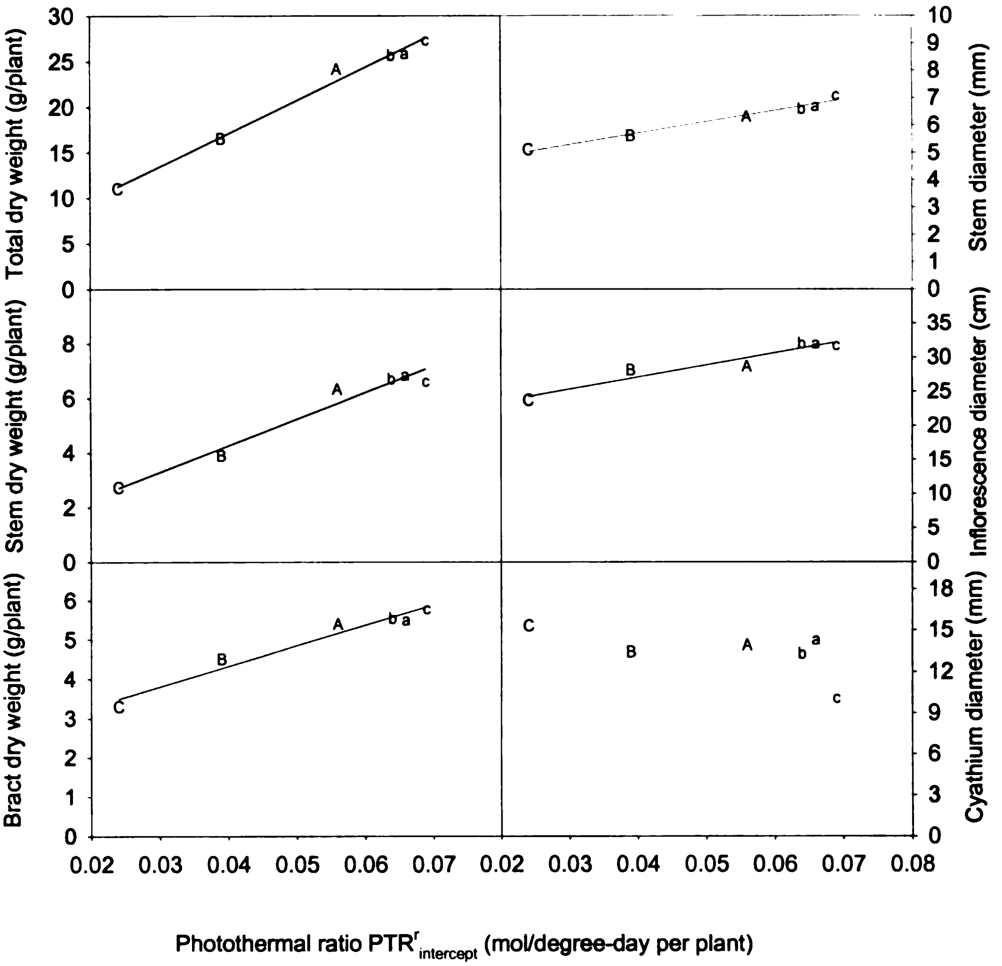

Fig. 4. Relationship between PTR$^r_{intercept}$ and plant dry weight (total, stem, bract and green leaf) and diameter of the stem, inflorescence and cyathia. The letters a, b, and c represent treatments 1, 2, and 3, respectively; the letters A, B, and C represent commercial greenhouses A, B, and C, respectively.

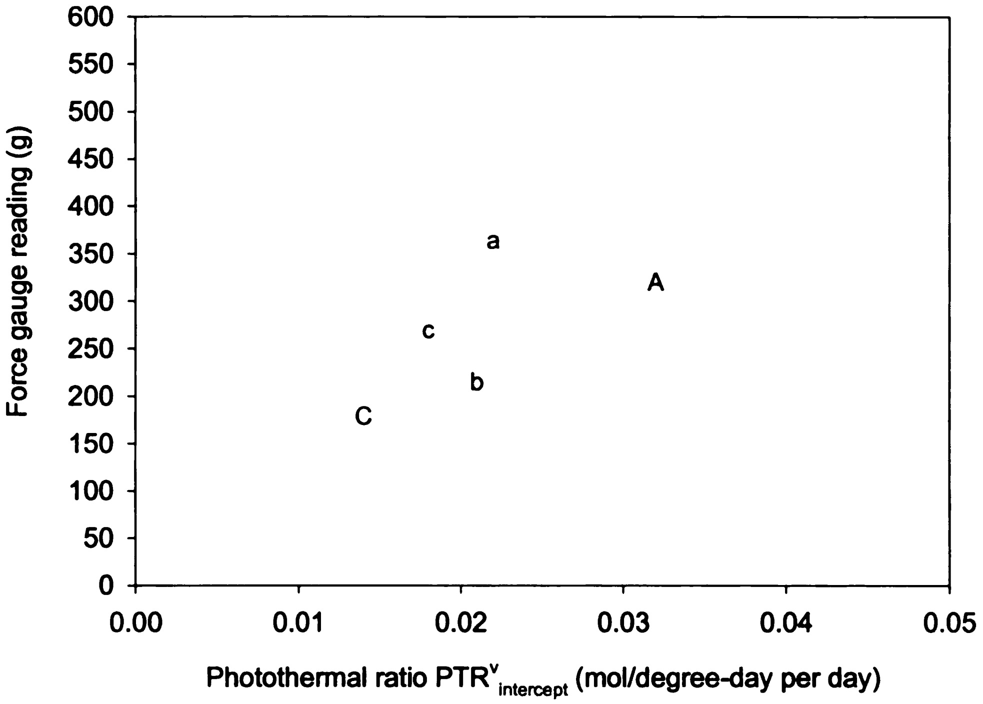

Fig. 5. Relationship between PTR$^{v}_{intercept}$ and force gauge reading. The letters a, b, and c represent treatments 1, 2, and 3, respectively; the letters A and C represent the commercial greenhouses A and C, respectively.

interception in young plants (Challa, et al., 1995). Higher temperature also increases plant developmental rate in the vegetative stage and gives flexibility during the reproductive stage. Compared with 20 °C, temperature of 24 °C can reduce the vegetative stage by about one week. During the reproductive stage, a lower night temperature decreased average daily temperature, prolonged developmental duration, and increased PTR. Among the three temperature adjustment treatments, treatment 3 had the highest PTR^r and the highest plant total dry weight and bract size.

The strategy used in treatment 3 was based on having high light levels during the vegetative stage. If the actual light level is lower than expected, the higher temperature will result in a low PTR^v and, consequently, a weak stem. In the present experiment, the actual average DLI was 9.9 mol m^{-2} day^{-1}, which was far below the thirty-years' average (i.e., 15-20 mol m^{-2} day^{-1}). Therefore, there was a relative low force gauge reading in the treatment's plants (Fig. 2).

As a whole, temperature adjustment treatments did not improve average PTR over time. Average temperature was close between temperature adjustment treatments and the commercial greenhouses (without temperature adjustment) (Table 3). During the vegetative stage, higher temperature was designed in treatment 3 and expected in treatments 1 and 2 because of high light intensity. The average temperature was about 22.6 to 23.6 °C. On the other hand, in commercial greenhouses, although temperature was set at 20 °C, hot weather eradicated greenhouse temperature control. The average temperature was 2 to 3 °C higher than the temperature setting. During the reproductive stage, a lower temperature was expected to correspond to low light levels in temperature adjustment treatments. However, there is a narrow range for temperature adjustment.

Temperatures should average between 18 and 20 °C during flower initiation and not be lower than 16°C after visible color for proper bract development (Hall, 1992). The average temperature adjustment was set between 18 and 20 °C. Because temperature control sometimes was lost during hot weather, the actual average temperature from all temperature adjustment treatments was around 20 °C during the reproductive stage, which was close to the temperatures in commercial greenhouses (Table 3). Therefore, it seems that regulation of PTR through temperature adjustment plays a limited role in improving poinsettia plant quality. The higher PTR^r that resulted in heavier final plant dry weight and bigger bracts (Fig. 4) may be attributed mostly to higher light levels in the MSU greenhouse. The average DLI at MSU was higher: consequently, the higher PTR in the MSU treatments compared to that in the commercial greenhouses.

In comparison with the temperature adjustment to correct a low PTR, there is a big potential for improvement in commercial greenhouses' light condition. Light levels at the canopy were quite different in different greenhouse types. With a similar latitude, average DLI was about 29% higher in greenhouse A (a glass house) than in greenhouse C (a double poly with hanging baskets) (Table 3). Glasshouses have better light transmission (transmissivity = 0.63 for Venlo-type glasshouse; Heuverlink etc. 1995) than double poly houses (transmissivity = 0.5; Hanan, 1998). Assuming the light level outside the greenhouses is the same, plants grown in a glass greenhouse should receive about 13% more light. In the current study, greenhouse B (double polyhouse) had a higher DLI than greenhouse A (glass greenhouse) because greenhouse B was located 7.6 degrees south of greenhouse A. Compared with greenhouse A, greenhouse C had a 13% transmission difference and about a 16% reduction of incident light because of the overhead hanging baskets. When the same plant spacing was used in greenhouse A as in greenhouse C (e.g., 25 x 25 cm), $PTR_{intercept}$ increased 33% (from 0.024 to 0.036 mol/degree-days per day).

Plant spacing adjustment plays an important role in improving individual plant light interception, increasing PTR, and enhancing plant quality. Although the incident light in commercial greenhouse A was lower than in greenhouse B, plant quality in greenhouse A was much better. The major difference was plant spacing. Greenhouse A used a spacing of 30 x 34 cm, while greenhouse B used 25 x 25 cm. Light interception for each plant as well as $PTR_{intercept}$ in greenhouse A increased about 30% (0.056 vs. 0.039 mol/degree-day per plant) compared with greenhouse B. Plant total and stem dry weight and stem diameter increased 32%, 38%, and 10%, respectively (Fig. 4).

There are several basic questions that need to be answered for active implementation of the PTR concept in commercial poinsettia production. There is no question that higher plant quality is associated with higher PTR, but what is the minimum PTR for acceptable plant quality? How much light do plants require to meet this quality? It is difficult to give an exact boundary between acceptable and unacceptable quality, because most plant quality parameters have not been quantified in the floriculture industry. Based on our experiments and experiences, it seems appropriate to use a range from 0.025 to 0.030 mol/degree-day per plant for the minimum $PTR^{v}_{intercept}$ ($minPTR^{v}_{intercept}$) from 0.040 to 0.045 mol/degree-day per plant for the minimum $PTR^{r}_{intercept}$ ($minPTR^{r}_{intercept}$) to produce poinsettia plants with acceptable quality.

According to the definition of $PTR_{intercept}$ (Liu and Heins, 1999), the minimum DLI required for acceptable plant quality at different plant spacing and temperatures can be calculated (Table 4, Appendix). When plants are grown at 20 °C, the minimum light level for the 25 x 25 cm spacing is about 10 to 12 mol m^{-2} day^{-1} for both developmental stages. As the temperature increases, the light level should be increased to meet the requirement of a designed PTR and acceptable plant quality. For example, when temperature increases from 20 to 22 °C, the minimum light level has to increase 1 to 2 mol m^{-2} day^{-1}, depending on plant spacing. When this minimum light level cannot be achieved, wider plant spacing should be used. If plant spacing is increased from 25 x 25 cm to 30 x 30 cm, the minimum DLI requirement decreases about 1 mol m^{-2} day^{-1} during the vegetative stage and 2 to 3 mol m^{-2} day^{-1} during the reproductive stage. For "dark" greenhouses (e.g., double poly with hanging baskets), where the average DLI is lower than 9 mol m^{-2} day^{-1} during the early growing season and 6 mol m^{-2} day^{-1} later on, the widest spacing (35 x 35 cm) is recommended.

In summary, practical PTR regulation through temperature adjustment plays a limited role in improving poinsettia plant quality. There is a much larger potential in light adjustment to increase PTR and plant quality in commercial greenhouses. Reducing overhead shading and widening plant spacing improves light interception greatly and increased plant quality. When plants are grown at 20 °C and a spacing of 25 x 25 cm, the minimum light level for acceptable plant quality is about 10 to 12 mol m^{-2} day^{-1}. This level will increase as temperature increases and decrease as plant spacing increases.

Table 4. Minimum daily light integral (minDLI) for an acceptable poinsettia plant quality at different plant spacing and temperatures.

minPTR$_{intercept}$ (mol/degree-day per plant)	Temperature (°C)	Spacing (cm)	light interception (%)^{z}	minDLI (mol m^{-2} day^{-1})
Vegetative stage				
0.025	20	25 x 25	58.2	10.0
		30 x 30	45.2	8.9
		35 x 35	36.2	8.2
	21	25 x 25	58.2	10.7
		30 x 30	45.2	9.5
		35 x 35	36.2	8.7
	22	25 x 25	58.2	11.3
		30 x 30	45.2	10.1
		35 x 35	36.2	9.3
	23	25 x 25	58.2	12.0
		30 x 30	45.2	10.7
		35 x 35	36.2	9.8
0.030	20	25 x 25	58.2	12.0
		30 x 30	45.2	10.7
		35 x 35	36.2	9.8
	21	25 x 25	58.2	12.8
		30 x 30	45.2	11.4
		35 x 35	36.2	10.5
	22	25 x 25	58.2	13.6
		30 x 30	45.2	12.1
		35 x 35	36.2	11.2
	23	25 x 25	58.2	14.4
		30 x 30	45.2	12.9
		35 x 35	36.2	11.8
Reproductive stage				
0.040	20	25 x 25	94.8	9.8
		30 x 30	91.4	7.1
		35 x 35	86.5	5.5
0.045	20	25 x 25	94.8	11.0
		30 x 30	91.4	8.0
		35 x 35	86.5	6.2

^{z} See appendix for details.

Appendix

$PTR_{interception}$ is defined as

$$PTR_{intercept} = CIDLI * spacing / CTT$$

where CIDLI is the cumulative light interception during the period, and CTT is cumulative thermal time (Liu and Heins, 1998). Assume that a standard plant has six unfolded leaves on the second lateral shoot at the end of the vegetative stage and 16 to 18 total leaves at anthesis. The cumulative light interception (CIDLI) at the end of the vegetative stage and at anthesis under different plant spacings can be simulated based on the model (Liu and Heins, 1998). The percentage of light interception (LI%) per unit area over developmental stage can be calculated:

$$LI\ \% = CIDLI / CDLI$$

where CDLI is the cumulative daily light integral during the period. The relationship between LI% and plant spacing can be plotted and regressed (Fig. 6). Therefore, the minCDLI can be achieved by

$$minCDLI = minPTR_{intercept} * CTT / (spacing * LI\%)$$

The average minDLI is equal to minCDLI divided by the days of developmental duration.

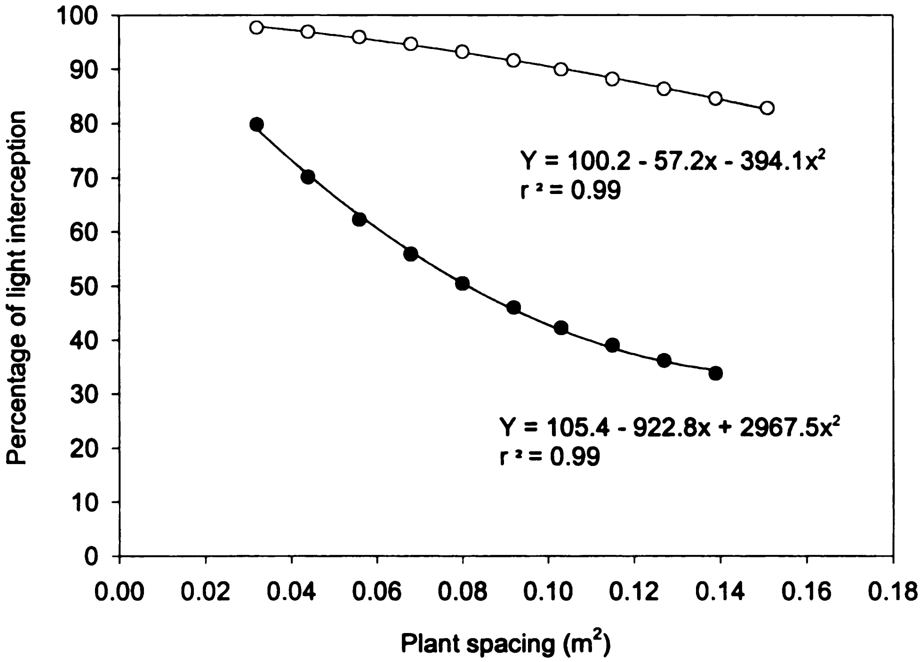

Fig. 6. Simulated relationship between percentage of light interception and plant spacing during the vegetative stage (from pinch to the sixth leaf unfolded on the second lateral shoot; solid symbols) and the reproductive stage (from onset of short days to anthesis; open symbols).

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