Production of high-quality plants is affected by radiant energy (commonly referred to as light) and temperature (thermal energy). Radiant energy [defined in this paper as number of photosynthetic (400 to 700 nm) photons/m²] drives photosynthesis and, consequently, plant biomass accumulation. Thermal energy is the primary environmental factor that drives developmental rate. Plants grown under high radiant energy and low thermal energy become stocky but grow and develop slowly. In contrast, plants grown under low radiant energy and high thermal energy grow and develop rapidly but become thin and weak. Horticulturists often have an intuitive awareness of these responses, and attempt to balance radiant and thermal energy to maintain desired plant quality within an economically acceptable production time. The concept of a photothermal ratio (PTR), the ratio of radiant energy to thermal energy (degree-day) was proposed to describe the balance between plant growth and plant development in greenhouse crops. The objective of this study was to quantify the effect of PTR during vegetative (PTRv) or reproductive (PTRr) phases on finished plant quality of ‘Freedom’ poinsettia (Euphorbia pulcherrima Willd. ex Klotzsch). In Expt. 1, plants were grown under 27 combinations of three constant temperatures (19, 23, or 27 °C), three daily light integrals (DLIs) as measured by the number of photosynthetic (400 to 700 nm) photons (5, 10, or 20 mol·m⁻²·d⁻¹), and three plant spacings (15 × 15, 22 × 22, or 30 × 30 cm) from pinch to the start 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 moved to combinations of three DLIs (5, 10, or 15 mol·m⁻²·d⁻¹) and three plant spacings (25 × 25, 30 × 30, or 35 × 35 cm) at a constant 20 °C from the start of short days until anthesis. Both PTRv and PTRr affected final plant dry weight (DW). All components of DW (total, stem, leaf, and bract) increased linearly as PTRr increased, and responded quadratically to PTRv, reaching a maximum when PTRv was 0.04 mol/degree-day per plant. Stem strength depended more on PTRr than PTRv. When PTRv increased from 0.02 to 0.06 mol/degree-day per plant, stem diameter increased ~24%, while stem strength increased 75%. The size of bracts and cyathia increased linearly as PTRv increased, but was unaffected by PTRr. When PTRv 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.
Two experiments were conducted in four glass greenhouses in East Lansing, Mich., during Fall 1996. Rooted stem cuttings of ‘Freedom’ poinsettia in 15-cm-diameter (1.57-L) round pots were obtained from a commercial propagator on 23 Aug. for Expt. 1 and 29 Aug. for Expt. 2. Plants were pinched to six nodes 1 week after receipt.

**EXPERIMENT 1.** Plants were grown under various PTR treatments during the vegetative stage (PTRv) and a common PTR during the reproductive stage (PTRr). Immediately after pinch, plants were randomly assigned to one of 27 combinations of three constant air-temperature settings (19, 23, or 27 °C), three daily light integrals (DLIs) as measured by the number of photosynthetic (400 to 700 nm) photons (5, 10, or 20 mol·m⁻²·d⁻¹), and three plant spacings [close (15 × 15 cm), medium (22 × 22 cm), or wide (30 × 30 cm)]. plants were grown under the treatments for 5 weeks, then were moved to a glass greenhouse set to a constant 20 °C with natural short day (SD) (<12 h) and DLI conditions (average =10 mol·m⁻²·d⁻¹) for reproductive development at a common spacing of 30 × 30 cm.

**EXPERIMENT 2.** Plants were grown under a common PTR during the vegetative stage, and moved to different PTR treatments for reproductive development. Environmental conditions during vegetative growth for all plants in Expt. 2 were 23 °C, a DLI of 10 mol·m⁻²·d⁻¹, and 22 × 22 cm plant spacing. When 450 degree-days (5 °C base temperature) had accumulated after pinch, plants were selected randomly and assigned to one of nine combinations of three DLI (5, 10, or 15 mol·m⁻²·d⁻¹) and three plant spacings [close (25 × 25 cm), medium (30 × 30 cm), or wide (35 × 35 cm)] at 20 °C under natural short-day conditions (<12 h). Plant spacings were greater in Expt. 2 than in Expt. 1 because plants were larger at the onset of PTR treatments, having completed 25 d of vegetative growth. Daily duration of the supplemental lighting was always <11.5 h. The experiment was terminated at anthesis.

Expt. 1 was a split-plot experiment design with temperature as the main plot, DLI as the split plot, and plant spacing as the split-split plot. A split-split plot design was used in Expt. 2 with DLI the main plot, and plant spacing the split plot. There were five plants in each treatment. Guard rows consisting of plants at comparable spacing surrounded the treatment plants to avoid edge effects.

Photosynthetic photon flux (PPF) was measured at the top and bottom of the plant canopy with line quantum sensors constructed of 18 G2711 photodiodes (Hamamatsu, Japan) on 1-m bars, connected to dataloggers (CR10; Campbell Scientific, Logan, Utah). Intercepted light was calculated by subtracting light transmitted to the bottom of the canopy from incident light on the top of the canopy. Various DLI 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) of ~200, 200, 80, or 40 mmol·m⁻²·s⁻¹ PPF for the 20, 15, 10, or 5 mol·m⁻²·d⁻¹ treatments, respectively, from high-pressure sodium lamps. Expected DLI was estimated each morning at 0800 HR based on the weather forecast, and screens or lamps were actuated as necessary based on the prediction. Dataloggers were programmed to calculate DLI as it accumulated throughout the day. Actual DLI was reviewed at 1400 HR, and shading screens or lamps were readjusted at that time. Actual DLI was reviewed again at 1700 HR, and if further supplemental lighting was needed, the necessary duration was calculated manually and entered into the computer controlling the lamps. The desired DLI was adjusted up or down each day to compensate for any deviations from the target DLI of the previous day. Maximum variation in DLI was <0.5 mol·m⁻²·d⁻¹.

Greenhouse air temperature was controlled by a climate-control computer (model CD750; Priva, De Lier, Holland). Shoot-tip temperature was measured by inserting a 36-gauge (0.127-mm) thermocouple into the apex of the second lateral shoot from the top of the plant. Values are the mean of 35 d of the treatment ± SE.

### Table 1. Actual average daily air temperature, daily light integral (DLI) and plant shoot-tip temperature under various light levels and plant spacings (Expt. 1). Plant temperatures were measured with a thermocouple inserted into the apex of the second lateral shoot from the top of the plant. Values are the mean of 35 d of the treatment ± SE.

| Air temp (°C) | DLI (daily moles photons/m²) | Close spacing (15 × 15 cm) | Medium spacing (22 × 22 cm) | Wide spacing (30 × 30 cm) |
|---------------|-----------------------------|---------------------------|-----------------------------|---------------------------|
| 20.0 ± 0.2    | 5.2 ± 0.2                   | 19.0 ± 0.2                | 18.6 ± 0.2                  | 19.2 ± 0.2                |
| 10.1 ± 0.3    | 10.1 ± 0.3                  | 19.5 ± 0.2                | 19.8 ± 0.2                  | 19.6 ± 0.2                |
| 19.7 ± 0.3    | 21.8 ± 0.3                  | 21.4 ± 0.2                | 21.0 ± 0.2                  | 21.4 ± 0.2                |
| 23.4 ± 0.1    | 20.6 ± 0.2                  | 21.6 ± 0.2                | 21.7 ± 0.2                  | 22.1 ± 0.2                |
| 10.2 ± 0.2    | 20.3 ± 0.4                  | 23.7 ± 0.2                | 24.9 ± 0.1                  | 25.7 ± 0.1                |
| 5.0 ± 0.2     | 25.7 ± 0.1                  | 25.8 ± 0.1                | 26.0 ± 0.1                  | 26.0 ± 0.1                |
| 10.2 ± 0.3    | 25.3 ± 0.2                  | 25.3 ± 0.1                | 25.3 ± 0.1                  | 25.3 ± 0.1                |
| 20.1 ± 0.2    | 25.8 ± 0.2                  | 27.3 ± 0.1                | 27.3 ± 0.1                  | 27.3 ± 0.1                |

**Materials and Methods**
Therefore, PTR_intercept was chosen as an independent variable in the analysis. Measured PTR was further refined into three expressions; i.e., PTRarea, PTRplant, and PTRintercept (Liu and Heins, 1998). The PTRarea was the amount of incident light on a unit area, PTRplant was the amount of light available for a plant (mol/degree-day per plant), and PTRintercept was the amount of light intercepted by a plant (mol/degree-day per plant). Lateral shoots were numbered from the top of the plant.

Table 2. The coefficient of determination ($r^2$) of the linear regression between the ratio of radiant energy (moles of photosynthetic (400 to 700 nm) photons/m$^2$) to thermal energy (degree-day) termed photothermal ratio (PTR) plants received during the vegetative (PTRv) or reproductive stage (PTRr), and plant characteristics at anthesis. Measured PTR was further refined into three expressions; i.e., PTRarea, PTRplant, and PTRintercept (Liu and Heins, 1998). The PTRarea, PTRplant, or PTRintercept (Liu and Heins, 1998). The PTRarea (moles of photosynthetic (400 to 700 nm) photons/m$^2$ per degree-day) was the amount of incident light on a unit area, PTRplant was the amount of light available for a plant (moles of photosynthetic (400 to 700 nm) photons/degree-day per plant), and PTRintercept was the amount of light intercepted by a plant (moles of photosynthetic (400 to 700 nm) photons/degree-day per plant). Lateral shoots were numbered from the top of the plant.

| Parameter shoot | Lateral | PTR' (Expt. 1) | PTR' (Expt. 2) |
|-----------------|---------|---------------|---------------|
|                 | PTRarea | PTR_plant | PTR_intercept | PTRarea | PTR_plant | PTR_intercept |
| Total DW        | 0.35**  | 0.46***     | 0.59***       | 0.61'   | 0.94***   | 0.94***       |
| Stem DW         | 0.29**  | 0.29**      | 0.41***       | 0.78**  | 0.82***   | 0.89***       |
| Green-leaf DW   | 0.35**  | 0.52***     | 0.63***       | 0.56**  | 0.94***   | 0.93***       |
| Bract DW        | 0.31**  | 0.39***     | 0.47***       | 0.55**  | 0.95***   | 0.93***       |
| Stem diameter   |         |             |               |         |           |               |
| Lateral shoot breakage force | 0.39**  | 0.48***     | 0.59***       | 0.59    | 0.77**    | 0.75**        |
| Cyathia diameter | 0.03**  | 0.13**     | 0.14**        | 0.23**  | 0.19**    | 0.23**        |
| Inflorrescence diameter | 0.09*** | 0.15      | 0.18         | 0.00    | 0.06**    | 0.03**        |
| Bract area      | 0.10**  | 0.09**     | 0.13**        | 0.00**  | 0.15**    | 0.11**        |
| Plant height    | 0.01**  | 0.24**     | 0.28**        | 0.05**  | 0.06**    | 0.05**        |
| Lateral shoot length | 0.20**  | 0.66**     | 0.63***       | 0.19**  | 0.04**    | 0.05**        |
| Internode length | 0.07**  | 0.05**     | 0.08**        | 0.50**  | 0.90***   | 0.82***       |
| Plant diameter  | 0.09**  | 0.08**     | 0.15         | 0.66**  | 0.78**    | 0.82**        |

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Results

The relationships between the three expressions of PTR (i.e., PTRarea, PTRplant, or PTRintercept) and plant characteristics measured in the two experiments were analyzed using linear regression (Table 2). Among the three expressions of PTR, PTR_intercept correlated more closely with the data than PTR_plant or PTR_area. Therefore, PTR_intercept was chosen as an independent variable in the following analysis.

The PTR_intercept and PTR'intercept had different effects on final plant DW (Fig. 1). In Expt. 1, DW at the end of SDs increased linearly as PTR_intercept increased (Fig. 1A–D, open circles). All final DW components responded to PTR_intercept quadratically (Fig. 1A–D, solid symbols). Final plant DW increased as PTR_intercept increased up to ±0.04 mol/degree-day per plant, but further increases in PTR_intercept did not improve final plant DW accumulation.

In Expt. 2, all components of DW increased linearly as PTR_intercept increased (Fig. 1E–H, solid symbols). The slope of the linear regressions in Fig. 1E–H can be interpreted as the rate of DW increase per mole of photons for each degree-day. Of the different organs, bract DW increased at the greatest rate: 63 g per mol/degree-day per plant (Fig. 1H). Stem and green leaf DW increased at 22 and 50 g per mol/degree-day per plant (Fig. 1F–G), respectively.

Analysis of the relationship between PTR_intercept and final plant DW in Expt. 1 is complicated by the fact that plants were under different conditions before and after the start of SDs. At the onset of SDs, plants had accumulated different DW (total, stem, and leaf) following growth under different PTR treatments for 5 weeks (Fig. 1A–C, open symbols). The net gain in plant DW during the subsequent SD flowering period was plotted against PTR_intercept and the relationships showed a quadratic relationship within each temperature regime (Fig. 2A–C). The aftereffect of PTR_intercept on net plant DW gain during reproductive development was obvious. The most DW net gain during reproductive development was achieved when PTR_intercept was $\approx 0.05$ mol/degree-day per plant at 22°C, 0.055 at 23°C, and 0.035 at 27°C. In Expt. 2, net DW gain during reproductive development (Fig. 2D–F) increased linearly as PTR_intercept increased, as did total DW gain (Fig. 1E–G).

Both vegetative and reproductive PTR_intercept were correlated.
positively with stem diameter at anthesis (Fig. 3A and C, solid symbols). However, the PTR\textsubscript{v intercept} had a significantly greater effect on stem diameter than the PTR\textsubscript{r intercept}. The slope of the linear regressions in Fig. 3A and C represents the rate of stem diameter increase per mole of photons for each degree-day, and the rate was about twice as great with a PTR\textsubscript{v intercept} increase as with a PTR\textsubscript{r intercept} increase (32.8 vs. 17.0 mm per mol/degree-day). An increase in PTR\textsubscript{v intercept} from 0.02 to 0.06 mol/degree-day per plant during vegetative development (Expt. 1) resulted in an increase in stem diameter of ≈1.3 mm, but a similar increase during reproductive development (Expt. 2) resulted in an increase of only 0.7 mm.

Fig. 1. Effects of the ratio of radiant energy [moles of photosynthetic (400 to 700 nm) photons/m²] to thermal energy (degree-day) termed photothermal ratio (PTR) intercepted by poinsettia plants during the vegetative stage (PTR\textsubscript{v intercept}) or the reproductive stage (PTR\textsubscript{r intercept}) on plant dry weight (DW) accumulation at the onset of short-day induction (open symbols) and at anthesis (solid symbols). ***Significant at \(P = 0.001\).

The PTR\textsubscript{v intercept} had more influence on stem strength than the PTR\textsubscript{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 (basal) lateral shoot and PTR\textsubscript{v intercept} (Fig. 3B) but not PTR\textsubscript{r intercept} (Fig. 3D). When PTR\textsubscript{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.

Inflorescence and cyathia diameter were affected by PTR\textsubscript{r intercept}, not PTR\textsubscript{v intercept} (Fig. 4). Plants developed larger bracts and cyathia as PTR\textsubscript{r intercept} increased. Plants grown under a PTR\textsubscript{r intercept} of 0.09 mol/degree-day per plant produced a 39-cm-diameter inflorescence and 17-mm-diameter cyathia. These diameters were ≈10 cm and 8 mm larger, respectively, than those for plants grown at a PTR\textsubscript{v intercept} of 0.02 mol/degree-day per plant. There was a similar tendency in total bract area (Fig. 5), which was 0.32 m² in the highest PTR\textsubscript{v intercept} treatment and 0.16 m² in the lowest PTR\textsubscript{v intercept} treatment. Plant diameter, lateral shoot and internode length, and plant height were not affected by either PTR\textsubscript{v} or PTR\textsubscript{r} (Table 2).

**Discussion**

The PTR concept describes light energy available for photosynthesis per growing degree-day. Since plant developmental rate is a linear function of temperature, i.e., number of degree-days above the base temperature, then PTR also describes light energy available for photosynthesis per fraction of plant development, e.g., unfolding of one leaf, development of a flower, etc. Plant photosynthesis and dry-matter accumulation increase as intercepted light increases, while plant developmental rate increases as temperature increases from the base to the optimum temperature. Plant biomass accumulation per fraction of plant development, therefore, depends on PTR. A large PTR\textsubscript{v intercept} means that plants intercept more photons, thus accumulating more biomass, during the current fraction of development. This relationship has been quantified in our previous (Liu and Heins, 1997, 1998) and present experiments (e.g., Fig. 1A–C, open symbols; Fig. 1E–H, solid symbols).

The three expressions of PTR can be used in different situations. The PTR\textsubscript{v,area} which is based on the number of incident photosynthetic photons per unit area, can be 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 irradiance. When the plant canopy overlaps and becomes solid, light available for each plant depends on irradiance and plant spacing. In this situation, PTR\text{plant}, which is based on the number of photosynthetic photons available per plant, is more appropriate than PTR\text{area}. The PTR\text{intercept} is a better expression than the other two because it is related directly to the number of photosynthetic photons intercepted by a plant. However, because light interception is a dynamic factor dependent on leaf area, it is more difficult to calculate than PTR\text{area} or PTR\text{plant}.

Further examination of the effect of PTR on total DW accumulation before (Fig. 1A, open symbols) or after (Fig. 1E, solid symbols) the onset of SDs showed that total DW increased at a similar rate in both situations (between 145 and 135 g per mol/degree-day per plant). The slightly lower rate during reproductive development may be due to shading of leaves by developing bracts, although no data were collected to quantify this shading, which always occurs during poinsettia reproductive development. However, stem growth was more closely related to the PTR\text{r}. The rate of increase in stem DW during vegetative development was about twice that of the increase during reproductive development (42 vs. 22 g per mol/degree-day). Similarly, the rate of increase in stem diameter was greater during the vegetative stage than during the reproductive stage (42 vs. 17 mm per mol/degree-day, respectively; Fig. 3A, open symbols, and 3C). Moreover, the increased stem diameter at the start of short days was still present at anthesis (Fig. 3A, solid symbols). The final stem diameter of the second lateral shoot from the top increased ∼24% as PTR\text{r} increased from 0.02 to 0.06 mol/degree-day per plant, an increase in stem cross-sectional area of ∼50%.

It is clear that PTR\text{r} affected bract DW accumulation more than that of other organs (Fig. 1F–H). After flower induction, assimilate partitioning patterns change. The reproductive sink becomes strong, which may limit the assimilate partitioning to leaf, stem, and root growth (Gardner et al., 1985). Bracts are part of the reproductive organs in poinsettia, and their DW increased faster than that of other organs as PTR\text{r} increased (i.e., 63, 50, and 22 g·mol⁻¹ per degree-day per plant for bracts, green leaves, and stems, respectively).

The effect of PTR\text{r} on DW gain can persist to anthesis (Fig. 2). The aftereffect of PTR\text{r} on DW varied with temperature during the vegetative stage because plants grown at higher temperatures developed more leaf area than those at lower temperatures. Therefore, even though plants were under the same environmental and spacing conditions during the reproductive stage, those with a large initial leaf area intercepted more light and accumulated more biomass than those with a smaller initial leaf area.

Lateral stem breakage is problematic in poinsettia production, since stem breakage reduces plant marketability and economic value. Many factors, including genetics, mineral nutrition, and cultural practices, may cause lateral stem breakage (Leonard and Nell, 1998). We found that PTR was one of the factors that affect basal stem breakage (Table 2; Fig. 3B). The higher the PTR\text{r}, the stronger the lowest lateral shoot. In contrast, PTR\text{r} had little or no effect on stem breakage, probably because the lateral shoots were well developed before flower induction. Another important
The reason is that PTR strongly affected stem growth and development. Stem DW accumulation increased significantly as the PTR increased, resulting in thicker and stronger 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 stems, the effect of PTR on stem breakage might start as early as the stock-plant stage.

Although a higher PTR did not reduce stem breakage, a higher PTR improved the finished plant quality by increasing bract and cyathia size. Bract area, inflorescence diameter, and cyathia diameter increased linearly as PTR increased (Fig. 4C and D, Fig. 5). When PTR 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. Greater DW accumulation in the higher PTR 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 ≈1 °C higher under the high DLI treatment (15 mol·m⁻²·d⁻¹) than the low DLI treatment (5 mol·m⁻²·d⁻¹). Temperature differences would occur during the day when supplemental lights (high-pressure sodium lamps) were turned on in the high DLI treatment. The larger bracts may result from both high PTR and higher day temperature.

Cyathia abscission is another parameter related to poinsettia plant quality. Increasing temperature, reducing irradiance by shading, or using closer spacing promoted cyathia abscission (Miller and Heins, 1986). Therefore, it can be inferred that cyathia abscission also is related to PTR.
Increasing PTR near anthesis by reducing temperature or increasing DLI may reduce cyathia abscission.

Results presented herein 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, perhaps reducing stem breakage at anthesis. During the reproductive stage, a high PTR improves plant appearance by increasing bract area and cyathia diameter and, possibly, reducing cyathia abscission.

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