Effectiveness of Plant Growth Regulators under Photoselective Greenhouse Covers

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ABSTRACT. Responses to selected chemical growth retardants (daminozide, paclobutrazol, and prohexadione-Ca) and GA₁ and GA₃ under photoselective greenhouse covers with various phytochrome photoequilibrium estimates (ϕ_e) were evaluated using 'Bright Golden Anne' chrysanthemum [*Dendranthema ×grandiflora* Kitam. (syn. *Chrysanthemum ×morifolium* Ramat.)] as the model plant to better understand the height control mechanism by far red (FR) light depleted environments. Plant height linearly decreased as ϕ_e increased from 0.72 to 0.83. The rate of height decrease of daminozide treated plants was less than that of water (control) or GA₃-treated plants. The rate of height reduction was not different between control and GA₃-treated plants among chambers with various ϕ_e . Both paclobutrazol and prohexadione-Ca reduced plant height regardless of ϕ_e , but the height reduction by paclobutrazol was more than that by prohexadione-Ca. The combination of paclobutrazol and prohexadione-Ca reduced plant height more than either alone. GA₁ reversed the height reduction caused by paclobutrazol and prohexadione-Ca regardless of ϕ_e , but the height increase by GA₁ was more when it was applied with prohexadione-Ca than when applied alone. Results show that photoselective covers with high ϕ_e were effective in controlling height of chrysanthemums without chemical growth retardants. The linear relationship between plant height and ϕ_e suggests that effectiveness of photoselective covers increased as ϕ_e increased. The photosynthetic photon flux (PPF) transmission of photoselective covers decreased as the ϕ_e increased because of the increasing dye concentration. Identifying photoselective covers that effectively filter out FR light from sunlight and reduce plant height while minimizing the PPF reduction is critical for commercial success of photoselective covers. Gibberellins are, at least partially, involved in height control by photoselective covers. Photoselective greenhouse covers did not reduce responsiveness to gibberellins, and it appears that the mechanism may be to suppress gibberellin biosynthesis. Results also suggest that increased metabolism of GA₁ to GA₈ was not the mechanism of height control by photoselective covers. Chemical names used: butanedioic acid mono (2,2-dimethylhydrazide) [daminozide]; (±)-(R*,R*)-b-((4-chlorophenyl)methyl)-a-(1,1-dimethylethyl)-1H-1,2,4-triazole-1-ethanol [paclobutrazol]; 3,5-dioxo-4-(1-oxopropyl)cyclohexanecarboxylic acid [prohexadione-Ca]; gibberellic acid [GA].

In the greenhouse industry, growers often place plants at close spacing on benches and produce hanging baskets in the space above benches to maximize space utilization. In addition to a reduction in photosynthetic photon flux (PPF), close spacing and overhead crops can increase the proportion of far-red (FR) light in the lower canopy due to the absorption of red (R) light by the upper canopy. This relative increase in FR light can result in tall and spindly plants. In commercial operations, undesirable extension growth is controlled by application of chemical growth retardants. Because of potential health risks to workers and consumers, use of growth regulating chemicals has been restricted on certain crops. For example, use of daminozide (Alar; Uniroyal Chemical Co., Middlebury, Conn.) has been banned in the United States for use in controlling vegetable transplant height. As a result, no chemical growth regulators are currently labeled for height control of vegetable transplants. Although chemical growth regulators are not banned, the ornamentals industry is also faced with strict regulatory measures regarding chemical usage. Therefore, both the vegetable and ornamentals

industries could benefit from nonchemical alternatives for height control.

Plants are capable of detecting subtle changes in relative amounts of R and FR light in their environment and make morphological changes through phytochrome regulation. Upon prolonged exposure to a given environment, a photoequilibrium (ϕ) develops between the active phytochrome (Pfr) and the total phytochrome (Ptotal) [$\phi = \text{Pfr}:\text{Ptotal}$ ratio]. Morgan and Smith (1976, 1979) reported that stem elongation rate and height of a range of herbaceous plants were inversely proportional to the established ϕ in vivo. By creating an environment that promotes establishment of high ϕ in vivo, height of greenhouse crops can be controlled with no or minimal use of chemical growth retardants (Rajapakse and Kelly, 1992).

Environments rich in R relative to FR light are favorable for establishing a high ϕ in plants and methods to estimate the ϕ (ϕ_e) from radiation measurements have been described (Hayward, 1984; Sager et al., 1988). In collaboration with Mitsui Chemicals Inc. (Tokyo, Japan) we have developed experimental photoselective greenhouse covers with a dye that absorbs FR light. Light transmitted through these covers has a higher R:FR ratio and ϕ_e than sunlight or the light transmitted through clear covers. The FR light absorption by photoselective covers increases as the dye concentration increases. By changing the dye concentration, we are able to generate photoselective covers with a range of ϕ_e . Preliminary trials indicate that these covers are effective in controlling height of a wide range of herbaceous plants without using chemical growth retardants and that height reduction increases as the ϕ_e increases (Rajapakse et al., 1998). With the commercial development of photoselective greenhouse

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Fig. 1. Photon flux distribution of light transmitted through nonshaded photosensitive panels containing various concentrations of FR light absorbing dye. Control is clear plastic panels without dye. Number following by YBM-1 indicates the percentage transmission of photosynthetic photon flux. Control, YBM-1 no. 85, no. 75, no. 65, and no. 55 are chambers with ϕ_e of 0.72, 0.75, 0.78, 0.81, and 0.83, respectively.

covers or shade materials in the future, the greenhouse industry could reduce use of growth regulating chemicals, reduce health risks to their workers and consumers, and reduce potential environmental pollution. Although photosensitive films are effective in regulating plant height, the mechanisms by which these films control stem elongation is not known. Understanding the mechanisms by which photosensitive covers regulate stem elongation could be helpful in developing management strategies. The objectives of this research were to determine the response of plants grown under photosensitive greenhouse covers with various ϕ_e to GA₁ and GA₃ and gibberellin inhibitors to better understand height control mechanisms by photosensitive covers.

Materials and Methods

PLANT MATERIAL. Rooted stem cuttings of 'Bright Golden Anne' chrysanthemum, (Yoder Bros. Inc., Pendleton, S.C.) were planted individually in 0.4-L square plastic pots containing a commercial growing medium (Scotts Metro Mix-360, Scotts-Sierra Horticultural Products Co., Marysville, Ohio). Plants were grown inside a glass greenhouse for 1 week before initiation of treatments.

PHOTOSELECTIVE COVERS. Polymethyl methacrylate (PMMA) panels (2.5 mm thick) with various concentrations of a FR absorbing dye were produced by Mitsui Chemicals, Inc. These PMMA panels are identified as control, YBM-1 no. 85, YBM-1 no. 75, YBM-1 no. 65, and YBM-1 no. 55. The percentages of PPF transmission by control, YBM-1 no. 85, no. 75, no. 65, and no. 55 were $\approx$ 92%, 85%, 75%, 65%, and 55%, respectively. Five growth chambers (1 m long $\times$ 0.8 m wide $\times$ 0.8 m high) framed with polyvinyl chloride pipes were covered (all sides except the bottom which was white plastic) with each of the

above PMMA panels. Each growth chamber had two fans on opposite sides, airflow oriented in the same direction, for ventilation. All growth chambers were inside a glass greenhouse.

PPF inside all chambers was adjusted to be the same by covering the chambers with higher PPF transmission with neutral density filters (shade cloth or cheesecloth), which did not alter light quality inside the chambers. Daily PPF integral inside the glass-house was recorded with a data logger (LI-1000) fitted with a quantum sensor (LI-190SB) (both LI-COR, Lincoln, Nebr.).

Spectral photon flux distribution was determined at the beginning and end of the experiment in 10 nm increments from 330 to 1100 nm using a spectroradiometer (LI-1800) fitted with a remote cosine sensor (LI-1800-10) (both LI-COR) between 1200 and 1300 HR on clear days. Spectral distribution curves of light transmitted through nonshaded photosensitive covers are illustrated in Fig. 1. The dye in YBM-1

photosensitive covers intercepted FR wavelengths of sunlight (maximum interception at 760 nm). The interception of FR wavelengths increased as the dye concentration increased. Multiple light scan readings indicated that light quality was uniform within a chamber and did not change during the course of the experiment. The R:FR ratios (R = 600 to 700 nm; FR = 700 to 800 nm) under the control, YBM-1 no. 85, no. 75, no. 65, and no. 55 chambers were 1.1, 1.5, 2.7, 4.3, and 6.1, respectively, and ϕ_e [estimated as described by Sagar et al. (1988)] was 0.72, 0.75, 0.78, 0.80, and 0.83, respectively (Table 1).

EXPERIMENT 1: PLANT RESPONSE TO DAMINOZIDE AND GA₃ UNDER PHOTOSELECTIVE COVERS WITH VARIOUS ϕ_e . After a 1-week establishment period, 24 plants were placed in each of the five chamber having various ϕ_e . Six plants each received a spray of one of the following treatments to run off on the day of transfer to the chambers and, again, 2 weeks later: 1) GA₃ at 50 mg·L⁻¹ (Pro-Gibb Plus, Abbott Laboratories, Chicago, Ill.), 2) daminozide at 3500 mg·L⁻¹ (Uniroyal Chem. Co), 3) daminozide at 3500 mg·L⁻¹ + GA₃ at 50 mg·L⁻¹, and 4) water only (control). Daminozide is a late stage gibberellin (GA) biosynthesis inhibitor that blocks the 3B-hydroxylation of GA₂₀ to GA₁ (Brown et al., 1997). Therefore, the combination of daminozide and GA₃ was used to

Table 1. Transmission of photosynthetic photon flux (PPF), R:FR ratios, and estimated phytochrome photoequilibrium (ϕ_e) of the photosensitive covers.

Treatment ^z	PPF ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	ϕ_e^y	R:FR ^x
Control	1252	0.72	1.1
YBM-1 no. 85	1090	0.75	1.6
YBM-1 no. 75	980	0.78	2.7
YBM-1 no. 65	832	0.81	4.3
YBM-1 no. 55	748	0.83	6.1

^zNumber following YBM-1 indicates the percentage transmission of PPF.

^yEstimated as described by Sagar et al. (1988).

^xR = 600 to 700 nm; FR = 700 to 800 nm.

Fig. 2. Effect of daminozide and GA₃ on plant height of 'Bright Golden Anne' chrysanthemums grown under photoselective greenhouse covers with various phytochrome photoequilibrium estimates (ϕ_e). Vertical bars indicate $\pm$ SE ($n = 12$). If the vertical bars are not seen, SE was smaller than the symbol. Lines were fitted to $y = \beta_0 + \beta_1 x$, where y is height and x is ($\phi_e - 0.72$). Intercept (β_0) represents plant ht. inside the control chamber (ϕ_e of 0.72). Predicted regression equations are: water, height = $34.3^b - 96.1^a x$, $r^2 = 0.99$; daminozide, height = $19.5^c - 36.8^b x$, $r^2 = 0.99$; GA₃, height = $44.5^a - 76.6^a x$, $r^2 = 0.90$; daminozide + GA₃, height = $43.6^a - 97.4^a x$, $r^2 = 0.97$. Intercepts (β_0) and slopes (β_1) with same superscripted letter (lowercase and uppercase, respectively) are not significantly different at $P = 0.05$.

determine the responsiveness to GA₃ when endogenous GA supply was blocked.

Plants were fertilized three times a week at irrigation with 1 g·L⁻¹ of a 20N-4.4P-16.7K water soluble fertilizer (Peters 20-10-20 Peat-Lite Special, Scotts-Sierra Horticultural Products Co., Marysville, Ohio). Plants in all chambers received an average daily PPF integral of 15.5 ± 0.3 mol·m⁻² on a clear day. Daily maximum and minimum air temperatures inside chambers were recorded during the experiment. Average daily maximum ($30 \pm 2^\circ\text{C}$) or minimum ($20 \pm 1^\circ\text{C}$) temperatures during the experimental period were not different among chambers.

EXPERIMENT 2: PLANT RESPONSE TO EARLY AND LATE GA INHIBITORS UNDER HIGH ϕ_e . Plant response to paclobutrazol [early inhibitor of GA biosynthesis, Coolbaugh and Hamilton, 1976] and prohexadione-Ca [late inhibitor of GA biosynthesis (Brown et al., 1997)] was evaluated inside control ($\phi = 0.72$) and YBM-1 no. 55 ($\phi = 0.83$) chambers. Chrysanthemums were grown as described previously. After a 1-week establishment period, 48 plants were transferred to each chamber. A set of six plants in each chamber was treated with one of the following eight treatments: 1) GA₁ at 50 μg per apex (Sigma Chem. Co., St. Louis, Mo.) as a 10 μL drop to the apex, 2) paclobutrazol (PA) at 0.73 mg active ingredient (a.i.) per pot as a 10-mL soil drench (Bonzi, Uniroyal Chem. Co), 3) prohexadione-Ca (PR) at 200 mg·L⁻¹ a.i. as foliar

spray (BAS 125 10W, BASF Corp., Research Triangle Park, N.C.), 4) combination of paclobutrazol at 0.73 mg a.i. and prohexadione-Ca at 200 mg·L⁻¹ a.i. (PA + PR), 5) combination of paclobutrazol at 0.73 mg a.i. and GA₁ at 50 μg (PA + GA₁), 6) combination of prohexadione-Ca at 200 mg·L⁻¹ a.i. and GA₁ at 50 μg (PR + GA₁), 7) combination of paclobutrazol at 0.73 mg a.i., prohexadione-Ca at 200 mg·L⁻¹ a.i., and GA₁ at 50 μg (PA + PR + GA₁), and 8) water only (control). Plants were treated on the day of transfer to the growth chambers and, again, after 2 weeks in the chambers. GA₁ was dissolved in 95% ethanol, diluted with water to 50% ethanol and was applied as a 10- μL drop to the apex using a syringe. For the combination treatments, plants were pre-treated with the respective growth retardant as described before GA₁ application. A separate set of six control plants was treated with 50% ethanol and the height of controls did not differ. Plants in experimental chambers received an average daily PPF integral of 14.1 ± 0.5 mol·m⁻² on a clear day.

EXPERIMENTAL DESIGN AND ANALYSIS. Experimental chambers were randomly positioned inside a glass greenhouse. Because of the limited number of chambers, experiments were repeated once to replicate. The experimental design was a randomized complete block design with a split-plot arrangement of the treatments. The light treatment (ϕ_e) was the main plot factor and the growth regulator treatments were the subplots. The blocking factor for the experiment was the replicate. Sets of six plants were the experimental units for the subplot factor and groups of growth regulator treatment (four for expt. 1 and eight for expt. 2) were the experimental units for the whole plot factor.

Plant height (distance from the medium surface to shoot apex) was measured for 4 weeks at weekly intervals. The number of fully expanded leaves was counted, and leaf and stem dry weights (DWs) were taken at termination. Average internode length was determined as height/number of leaves. For DW measurements, shoots were oven-dried for 5 d at 85°C .

Data from the experiment were analyzed using analysis of variance procedures of the PROC MIXED of SAS (SAS Inst., Inc., Cary, N.C.). The ϕ_e factor was evaluated by linear, quadratic, cubic, and quadratic contrasts. Polynomial regression models were fit to the data using contrasts. Powers of ($\phi_e - 0.72$) were used so that the intercept term would represent the mean for the control light treatment value of ϕ_e (0.72). Comparisons of polynomial coefficients for the different growth regulator treatments were done using pairwise t tests.

Results

RESPONSE TO DAMINOZIDE AND GA₃ UNDER PHOTOSELECTIVE COVERS WITH VARIOUS ϕ_e . Plant height decreased linearly ($P < 0.05$) as the ϕ_e increased, regardless of the growth regulator treatment (Fig. 2). The degree of height control by daminozide as ϕ_e increased was less than that for water or GA₃-treated plants. The rate of height decrease for the treatment with GA₃ at increasing ϕ_e was not significantly different from the water treated plants.

Number of leaves was not affected by ϕ_e or the growth regulator treatment (data not presented). Internode length responded to

increasing ϕ_e in a similar pattern to that of height and growth regulator treatments (data not presented).

Dry matter accumulation was influenced by the photosensitive covers and the growth regulator treatment (Fig. 3). Table 2 represents the regression coefficients of fitted lines in Fig. 3 and the significance of slopes at $P < 0.05$. Leaf dry matter accumulation decreased as ϕ_e increased, except for GA₃-treated plants which had similar leaf DW at all ϕ_e . Leaf DW of water and daminozide + GA₃-treated plants decreased linearly as the ϕ_e increased while that of daminozide treatment followed a quadratic pattern. Stem DW of control (water) and daminozide treated plants decreased linearly as the ϕ_e increased. The rate of decrease was greater in control plants (greater β_1 , Table 2) than in daminozide treated plants. Total shoot DW of water and GA₃-treated plants decreased linearly while in daminozide treated plants it followed a quadratic trend. Overall, plants that received GA₃ or daminozide + GA₃ had greater DW. Specific stem DW (stem DW per unit length) or specific leaf DW (leaf DW per unit area) was not affected (data not presented), indicating that the decreased DW was mainly a result of smaller plants (data not presented).

EFFECTIVENESS OF EARLY AND LATE GA BIOSYNTHESIS INHIBITORS. Both paclobutrazol and prohexadione-Ca resulted in shorter plants in control ($\phi_e = 0.72$) and YBM-1 no. 55 ($\phi_e = 0.83$) chambers (Fig. 4), but the height reduction by paclobutrazol was more than that of prohexadione-Ca. The combination of paclobutrazol and prohexadione-Ca reduced plant height more than either of them alone. Exogenous GA₁ increased plant height over the water-treated control in both light environments. GA₁ treatment reversed height reduction caused by paclobutrazol and prohexadione-Ca in plants grown in control and YBM-1 chambers. The height increase by GA₁ was greater when it was applied with prohexadione-Ca than when it was applied with paclobutrazol or alone. There was no significant interaction between the plant growth regulator and ϕ_e treatments.

Discussion

Photosensitive covers with high ϕ_e reduced height of 'Bright Golden Anne' chrysanthemums without use of chemical growth retardants. In separate studies, the height of several vegetable and ornamental crops was also reduced by photosensitive greenhouse covers, indicating that photosensitive covers are effective for a wide range of crops (Rajapakse et al., 1999). The linear relationship between plant height and ϕ_e (Fig. 2) in this study suggests that effectiveness of photosensitive covers increases as ϕ_e is increased. The PPF transmission of photosensitive covers decreases as the ϕ_e increases because of the increasing dye concentration. Identifying photosensitive covers that effectively filter out FR light from sunlight and reduce plant height while minimizing the PPF reduction is critical for commercial success of photosensitive covers. Our data indicate that photosensitive covers with ϕ_e of 0.78 (which corresponds to $\approx 25\%$ PPF reduction) was effective in achieving a 20% to 30% height reduction of chrysanthemum (Oi et al., 1998; Rajapakse et al., 1998; Rajapakse et al., 1999).

Gibberellins are known to stimulate stem elongation of many plant species. The change in stem elongation in response to changes in R and FR light in the environment has been reported to be mediated by changes in gibberellin levels due to reduced synthesis (Morgan et al., 1980) or increased destruction (Lockhart, 1959), or by reduced responsiveness of plants to gibberellins

Fig. 3. Effect of daminozide and GA₃ on (A) leaf, (B) stem, and (C) total dry weight of 'Bright Golden Anne' chrysanthemums grown under greenhouse covers with various phytochrome photoequilibrium estimates (ϕ_e).

Table 2. Regression coefficients of fitted lines for the relationship between leaf, stem or total DWs of ‘Bright Golden Anne’ chrysanthemums and phytochrome photoequilibrium estimates (ϕ_e). $Y = \beta_0 + \beta_1 (\phi_e - 0.72) + \beta_2 (\phi_e - 0.72)^2$.

Treatment	Estimated regression coefficients		
	β_0	β_1	β_2
Leaf			
Water	2.0 a ^z	-3.60 b	0
Daminozide	2.1 a	-13.2 a	85.3
GA ₃	1.9 a	0	0
Daminozide + GA ₃	2.0 a	-3.3 b	0
Stem			
Water	1.4 b	-5.0 b	0
Daminozide	0.8 c	-2.5 c	0
GA ₃	1.8 a	-4.2 b	
Daminozide + GA ₃	2.0 a	-14.5 a	75.5
Total			
Water	3.5 bc	-8.8 b	0
Daminozide	3.0 c	-19.0 a	112.6 a
GA ₃	3.8 ab	-5.42 b	0
Daminozide + GA ₃	4.1 a	-24.6 a	134.6 a

^zMean separation within columns for a tissue factor by pairwise *t* test at *P* = 0.05.

(Reid and Ross, 1988). It is possible, therefore, that photosensitive covers reduce plant height by altering the gibberellin metabolism or the responsiveness. In the current experiments, both exogenous GA₁ and GA₃ reversed the height reduction caused by the photosensitive covers with high ϕ_e . Our results with exogenous GA₃ or GA₁ application indicate that responsiveness to gibberellins was not reduced in plants grown under photosensitive panels with high ϕ_e . It is possible that gibberellin levels may have been reduced in plants grown under high ϕ_e environments. Our quantification studies (unpublished data) indicated that GA₁₉ levels were higher and GA₁ levels were lower in chrysanthemum plants grown under CuSO₄ filters which had a ϕ_e of 0.81. In addition, metabolism of radiolabelled GA₁₉ was slower in CuSO₄-filter-grown plants than in control plants (unpublished data). These observations suggest that suppression of gibberellin biosynthesis may be the cause for reduced height under FR light depleted environments. Martinez-Garcia and Garcia-Martinez (1992) reported that FR light-induced stem elongation of cowpea [*Vigna sinensis* (L.)] was related to increased levels of GA₁. Campbell and Bonner (1986) reported that conversion of GA₂₀ (inactive) to GA₁ (active), occurs readily in dark-grown dwarf pea (*Pisum sativum* L.) seedlings and this conversion is prevented by R light.

Most chemical growth retardants, including the ones tested herein, reduce stem elongation by blocking gibberellin biosynthesis (Brown et al., 1997; Coolbaugh and Hamilton, 1976). If the mode of action of photosensitive films were to block GA biosynthesis, plants treated with daminozide would not have responded under the high ϕ environment. In the present experiment,

daminozide treatment further reduced the height of plants grown under photosensitive covers indicating that the covers were not as effective as daminozide in blocking GA biosynthesis. The mag-

Fig. 4. Weekly height increase of ‘Bright Golden Anne’ chrysanthemums grown in (A) control or (B) YBM-1 no. 55 chambers in response to prohexadione-Ca (PR), paclobutrazole (PA), and GA₁ application. Vertical bars indicate $\pm$ SE (n = 12). If the vertical bars are not seen, SE was smaller than the symbol.

nitude of height reduction caused by daminozide decreased as ϕ_e of the growing environment increased (Fig. 2), suggesting that GA biosynthesis may be progressively reduced as ϕ_e increases.

Both paclobutrazol and prohexadione-Ca were effective in controlling plant height under a photosensitive cover with high ϕ_e , but paclobutrazol was more effective than prohexadione-Ca in reducing stem elongation (Fig. 4). The difference in effectiveness between the two compounds could be due to different modes of action. Paclobutrazol blocks an early step in the gibberellin biosynthetic pathway [oxidation of ent-kaurene to GA₁₂ (Coolbaugh and Hamilton, 1976)], whereas prohexadione-Ca blocks a late step in the pathway [3 β -hydroxylation of GA₂₀ to GA₁ (Brown et al., 1997)]. Prohexadione-Ca has been also shown to prevent metabolism of GA₁ to inactive GA₈ by blocking the 2 β -hydroxylation (Brown et al., 1997).

Exogenous GA₁ promoted growth of paclobutrazol or prohexadione-Ca-treated plants regardless of the light environment. This also shows that the shorter plants under the photosensitive cover were not a result of reduced sensitivity to gibberellins. Maas and van Hattum (1998) reported that paclobutrazol-treated fuchsia (*Fuchsia x hybrida* Hort. ex Vilm.) plants showed a similar response to exogenous GA₁ when grown at higher night temperatures than day temperatures (–DIF) or at higher day temperatures than night temperatures (+DIF). They also reported that response to GA₁ was similar under white or orange light regardless of the temperature regime. Their data suggested that the differences in shoot elongation they observed under various light and temperature conditions did not result from light quality or day/night temperature mediated changes in plant sensitivity to GA₁. Assuming that these growth retardants block GA biosynthesis, the additional height reduction by growth retardants under photosensitive covers suggests that gibberellin biosynthesis may not be the only height controlling mechanism under photosensitive covers.

When applied together with prohexadione-Ca, GA₁ in the plant may be sustained for a longer period thereby increasing plant height greater than treatment with GA₁ alone (Fig. 4). Recent work by Ait-Ali et al. (1999) has shown that exposure of etiolated pea seedlings to white light decreased GA₁ levels due to increased 2 β -hydroxylase activity. Their results show that light-enhanced degradation of GA₁ plays a role in reduced stem elongation when dark grown plants are transferred to light. If photosensitive covers enhance metabolism of GA₁ to GA₈, the response to exogenous GA₁ and the combination of prohexadione-Ca and GA₁ should have been small under photosensitive covers. GA₁ increased the height of plants grown under photosensitive covers and when applied with prohexadione-Ca, height increase was greater than GA₁ alone, indicating that the increased metabolism of GA₁ to GA₈ did not cause height reduction by photosensitive covers.

In summary, our results show that photosensitive greenhouse covers with high ϕ_e controlled height of greenhouse-grown 'Bright Golden Anne' chrysanthemums without chemical growth retardants. Photosensitive covers with ϕ_e of 0.78 were effective in achieving $\approx$ 20% height reduction without chemical growth regulators. In the present work, experimental chambers were kept inside a glasshouse so that the PPF reduction was greater than if the photosensitive covers were used as the primary cover. If the photosensitive covers were used as the primary greenhouse cover, then the covers with higher ϕ_e than 0.78 may still provide sufficient

PPF to grow a satisfactory crop, especially in southern latitudes where irradiance is high. Results also suggest that gibberellins are at least partially involved in height reduction induced by photosensitive covers. Photosensitive greenhouse covers did not reduce the responsiveness to gibberellins, and it appears that the mechanism may be to suppress gibberellin biosynthesis. Photosensitive covers were not as effective as chemical growth retardants in suppressing gibberellin biosynthesis.

Literature Cited

- Ait-Ali, T., S. Frances, J.L. Weller, J.B. Reid, R.E. Kendrick, and Y. Kamiya. 1999. Regulation of GA₂₀-oxidase and GA 3 β -hydroxylase transcript accumulation during phytochrome-mediated de-etiolation of pea seedlings. *Plant Physiol.* 121:783–791.
- Brown, R.G.S., H. Kawaide, Y. Yang, W. Rademacher, and Y. Kamiya. 1997. Daminozide and prohexadione-Ca have similar modes of action as inhibitors of the late stages of gibberellin metabolism. *Physiol. Plant.* 101:309–313.
- Campbell, B.R. and B.A. Bonner. 1986. Evidence for phytochrome regulation of gibberellin A₂₀ 3 β -hydroxylation in shoots of dwarf (lele) *Pisum sativum* L. *Plant Physiol.* 82:909–915.
- Coolbaugh, R.C. and R. Hamilton. 1976. Inhibition of ent-kaurene oxidation and growth by α -cyclopropyl- α -(p-methoxy-phenyl)-5-pyrimidine methyl alcohol. *Plant Physiol.* 57:245–248.
- Hayward, P.M. 1984. Determination of phytochrome parameters from radiation measurements, p. 159–173. In: H. Smith and M.G. Holms (eds.). *Techniques in photomorphogenesis*. Academic Press, London.
- Lockhart, J.A. 1959. Studies on the mechanism of stem growth inhibition by visible radiation. *Plant Physiol.* 34:457–460.
- Maas F.M. and J. van Hattum. 1998. Thermomorphogenic and photomorphogenic control of stem elongation in fuchsia is not mediated by changes in responsiveness to gibberellins. *J. Plant Growth Regul.* 17:39–45.
- Martinez-Garcia, J. and J.L. Garcia-Martinez. 1992. Phytochrome modulation of gibberellin metabolism in cowpea epicotyls, p. 585–590. In: C.M. Karsen, L.C. van Loon, and D. Vreugdenhil. (eds.). *Progress in plant growth regulation*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Morgan, D.C., T. O'Brien, and H. Smith. 1980. Rapid photomodulation of stem extension in light-grown *Sinapis alba* L. Studies on kinetics, site of perception and photoreceptor. *Planta* 150:95–101.
- Morgan, D.C. and H. Smith. 1976. Linear relationship between phytochrome photoequilibrium and growth in plants under simulated natural radiation. *Nature* 262:210–212.
- Morgan, D.C. and H. Smith. 1979. A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145:253–258.
- Oi, R., N. Arai, Y. Matsuzaki, K. Seino, O. Kohgo, S. Ikado, M. Iwata, and K. Murakami. 1998. Photosensitive plastics and their effects on plant growth. *Proc. Natl. Agr. Plastics Congr.* 27:35–40.
- Rajapakse, N.C. and J.W. Kelly. 1992. Regulation of chrysanthemum growth by spectral filters. *J. Amer. Soc. Hort. Sci.* 117:481–485.
- Rajapakse, N.C., R.E. Young, M.J. McMahon, and R. Oi. 1999. Plant height control by photosensitive filters: Current status and future prospects. *HortTechnology* 9:618–624.
- Rajapakse, N.C., R.E. Young, and R. Oi. 1998. Plant growth regulation by photosensitive greenhouse covers. *Proc. Natl. Agric. Plastics Congress* 27:23–29.
- Reid, J.B. and J.J. Ross. 1988. Internode length in *Pisum*. A new gene, *lv*, conferring an enhanced response to gibberellin A1. *Physiol. Plant.* 72:595–604.
- Sager, J.C., W.O. Smith, J.C. Edwards, and K.L. Cyr. 1988. Photosynthetic efficiency and phytochrome equilibria determination using spectral data. *Trans. Amer. Soc. Agr. Eng.* 31:1882–1887.