

Role of Gibberellins in Chrysanthemum Growth under Far Red Light-deficient Greenhouse Environments

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ABSTRACT. Plants grown in far red (FR) light deficient environments are typically shorter because of short internodes, resembling plants treated with GA biosynthesis inhibitors. The role of GAs in the reduction of stem elongation of ‘Bright Golden Anne’ chrysanthemum [*Dendranthema ×grandiflora* (Ramat.) Kitam. (syn. *Chrysanthemum ×morifolium* Ramat.)] grown in FR light deficient (–FR) environment was investigated by following the response of chrysanthemums grown in –FR environment to exogenous application of GA₁, GA₁₉, or GA₂₀, and the metabolism of GA₁₂ and GA₁₉ in –FR or +FR environment. FR light deficient environment resulted in 25% to 30% shorter plants than in +FR environment. Final height of GA₁- and GA₂₀-treated plants followed a quadratic pattern while that of GA₁₉ treated plants followed a linear pattern as the dosage increased from 0 to 50 µg/apex. The response to GA₁ was the greatest followed by GA₂₀ and GA₁₉, regardless of the light environment. Application of GA₁ (50 µg/apex) increased final height by 65% compared with no GA (0 µg/apex) application under either +FR or –FR light environment, suggesting the response to GA₁, which is the active form, remained the same. Responses to GA₁₉ and GA₂₀ declined under –FR light. [¹⁴C]GA₁₂ and [¹⁴C]GA₁₉ metabolized slowly in the –FR environment suggesting that the turnover of GAs may have caused in part the lower response to GA₁₉. Although metabolism of GA₁ under –FR environments was not investigated, observations with GA₁ application experiments support that –FR environment may have enhanced inactivation of GA₁. Chemical name used: gibberellic acid (GA).

Eliminating far red (FR) light from the greenhouse environment with liquid CuSO₄ spectral filters has been shown to effectively reduce height in a wide range of plant species (Mortensen and Stromme, 1987; Rajapakse and Kelly, 1992). Although liquid CuSO₄ filters have limited value to a commercial grower because of handling difficulties, development of photoselective plastic greenhouse covers with FR light removing properties could facilitate commercial applications of spectral filter technology. Plastic materials with FR light removing properties are not commercially available, but several plastic and pigment manufacturers are working together to develop such materials (Murakami et al., 1996; Oi et al., 1998; van Haeringen et al., 1998). Preliminary results indicate that plastic films and rigid plastic material with FR light absorbing dyes are effective in producing short, compact plants similar to those plants produced by chemical growth regulators or under liquid CuSO₄ filters (Cerny et al., 1999; Li et al., 2000; Rajapakse et al., 1998).

Understanding the physiological mechanisms by which light quality (spectral composition) manipulates stem elongation could provide invaluable information for commercial development of photoselective greenhouse covers. Plants grown in a FR light deficient (–FR) environment are phenotypically similar to plants treated with chemical growth retardants that inhibit GA biosynthesis (Rajapakse and Kelly, 1992). In chrysanthemum [*Dendranthema ×grandiflora* (syn. *Chrysanthemum ×morifolium*)], –FR environment induced reduction of stem elongation can be reversed by GA₃ application or by exposure to end-of-the-day FR

light, indicating that both GAs and phytochromes are involved in mediating the response (Rajapakse and Kelly, 1991; Rajapakse et al., 1993).

The role of GAs in the inhibition of hypocotyl growth of de-etiolating seedlings (dark grown seedlings exposed to light) has been investigated for decades. Two main theories have been proposed to explain the inhibition: exposure to light 1) alters active GA levels, resulting in inhibition of stem elongation and 2) reduces sensitivity of seedlings to active GAs. Evidence exists to support both of these theories. Campell and Bonner (1986) reported that conversion of GA₂₀ to GA₁ in pea (*Pisum sativum* L.) occurred readily in dark-grown plants but that this conversion was blocked by R light. Martinez-Garcia and Garcia-Martinez (1992) reported that FR light increased stem elongation rate of cowpea [*Vigna unguiculata* (L.) Walp. ssp. *unguiculata*] seedlings that was related to increased levels of GA₁. Toyomasu et al. (1992) reported that dark-grown lettuce (*Lactuca sativa* L.) seedlings contained higher levels of GA₁ than seedlings exposed to white light. In contrast, Reid and Ross (1988) and Reid et al. (1991) provided evidence to support that the stem elongation response to changes in light was mediated by a change in sensitivity to GAs. Weller et al. (1994) reported that dark-grown pea seedlings were about three times taller than light-grown seedlings, but there were no substantial differences in GA₁ levels in the apical regions. Recently, O'Neill et al. (2000) suggested that control of stem elongation of pea seedlings by light involves an initial inhibition of elongation by a light-induced decrease in GA₁ levels, with continued inhibition mediated by a light-induced reduction of sensitivity to endogenous active GAs.

This research investigated the role of GAs in stem elongation of chrysanthemum in –FR environments. Specific objectives were to 1) determine the response of chrysanthemums grown in –FR environment to exogenous application of GA₁, GA₁₉, or GA₂₀, and 2) determine whether metabolism of GA₁₂ and GA₁₉ differs in –FR and +FR environments. Chrysanthemum was selected because of its known response to light quality and its endogenous GAs have been identified (Nishijima et al., 1997).

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Materials and Methods

PLANT MATERIAL AND CULTURE. Uniform rooted stem cuttings of 'Bright Golden Anne' chrysanthemum with three to four leaves (Yoder Brothers, Pendleton, S.C.) were planted in 600-mL plastic pots containing a commercial potting medium (Fafard Mix 3B, Fafard, Anderson, S.C.). Plants were allowed to establish for 1 week in a glasshouse before treatment implementation. 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) during the experiment.

LIGHT ENVIRONMENT. The +FR and -FR treatments were randomly assigned to six constructed chambers (each 1.2 × 1.2 × 1.2 m; three +FR and three -FR) inside a glass greenhouse. Top (roof) of the -FR chambers were covered with 8 mm thick polycarbonate panels filled with 4% CuSO₄·5H₂O (w/v). Top of the +FR chambers were covered with water filled panels. In each chamber, two fans (one attached to the lower left corner and the other attached to the upper right corner of the opposite side) were oriented in the same direction for airflow and to prevent heat buildup. The chamber sidewalls were covered with polyethylene (black on the outside and white on the inside) to prevent the transmission of nonfiltered natural light into the chambers. Average daily maximum (28 ± 2 °C) and minimum (19 ± 1 °C) temperatures inside -FR and +FR chambers were not different during the experimental period.

Photosynthetic photon flux (*PPF*) inside each chamber was measured at the beginning and at the end of the experiment (between 1200 and 1300 HR) with a LI-250 quantum meter fitted with a LI-190SA sensor (LI-COR, Inc., Lincoln, Nebr.). The *PPF* was adjusted to be equal inside all chambers by covering the control chambers with cheesecloth. Average midday *PPF* inside chambers on a clear day was 700 ± 112 μmol·m⁻²·s⁻¹.

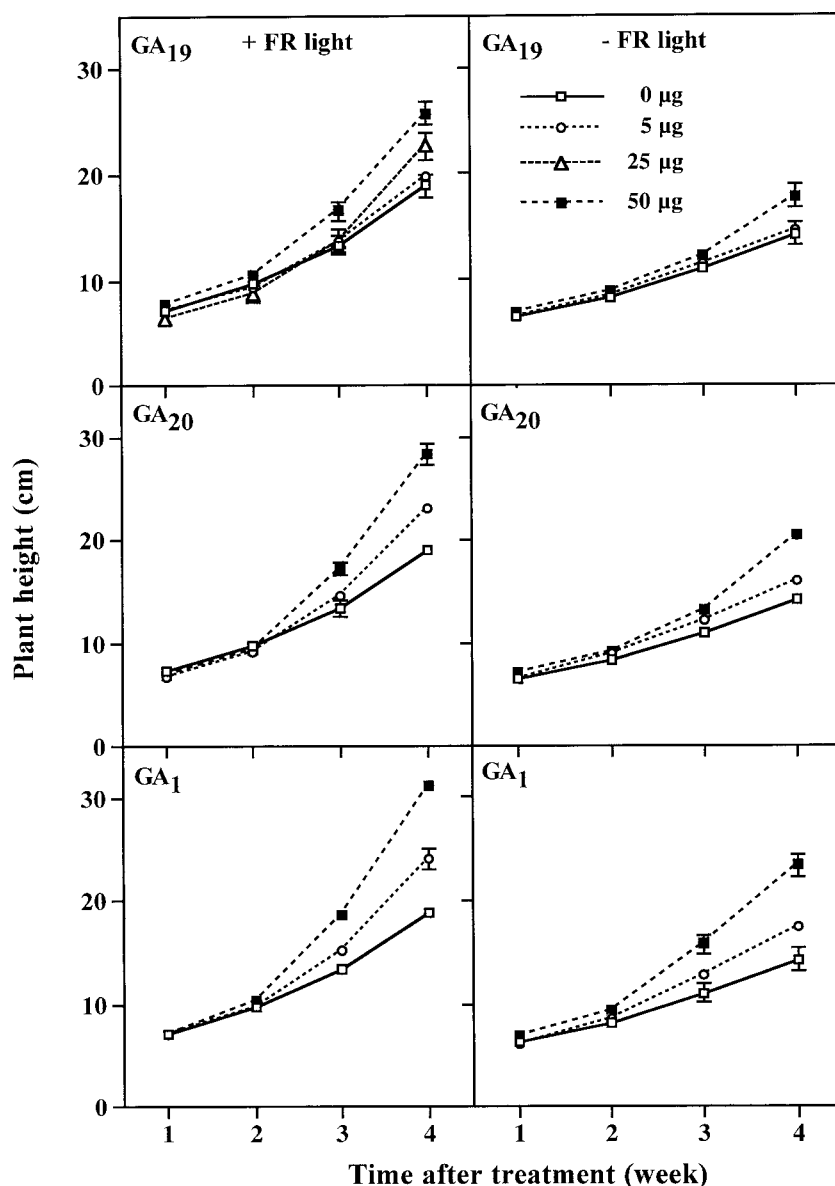
Spectral photon distribution was measured at the beginning and at the end of the experiment with a LI-1800 spectroradiometer fitted with a LI-1800-10 remote cosine sensor (LI-COR). The photon flux distribution (350 to 1100 nm at 10-nm intervals) under CuSO₄ filters has been reported previously (Rajapakse and Kelly, 1992). The R/FR ratios (R = 600 to 700 nm; FR = 700 to 800 nm) were 1.1 in water and 3.1 in CuSO₄ chambers. The phytochrome photoequilibrium (P_{fr}/P_{total}) estimates of transmitted light were 0.72 in water and 0.80 in CuSO₄ chambers (estimated as described by Sager et al., 1988).

PLANT RESPONSE TO SELECTED CONCENTRATIONS OF GA₁, GA₁₉, AND GA₂₀. GAs (GA₁, GA₁₉, and GA₂₀, purchased from Lew Mander, Australian National University, Canberra, Australia) were dissolved in 95% ethanol, then diluted with distilled water to 50% ethanol. A group of five plants in each chamber was treated with 0 (control), 0.5, 5, 25, or 50 μg/apex of each GA solution in a 10 μL micro-drop on day 0, 7, 14, and 21. Two control treatments were used: one set of control plants was treated with 10 μL of 50% ethanol and the other set with 10 μL of distilled water. GAs were applied along the midrib of the first

fully opened leaf below the apex (Tatineni et al., 2000). Treated plants were placed randomly within each chamber. Plant height was recorded weekly.

METABOLISM OF GA₁₂ AND GA₁₉. [¹⁴C]GA₁₂ and [¹⁴C]GA₁₉ (1.85 × 10⁹ Bq/mmol) were purchased from Lew Mander. Chrysanthemum plants were grown in +FR and -FR chambers for 2 weeks before treating them with radiolabeled GAs. Expanding leaves of 24 plants in each chamber were treated with 6 × 10⁶ Bq of [¹⁴C]GA₁₂ or [¹⁴C]GA₁₉ in a 10-μL drop of 95% ethanol per plant. Application was made along the midrib of the newly expanded leaf. Following a 24, 48, 72, or 96 h incubation period for GA₁₂ and a 48, 72, 96, or 120 h incubation period for GA₁₉, apices including the treated leaf were harvested around 1200 HR (six plants per incubation period for each GA) directly into liquid nitrogen, ground to a powder, and extracted

Fig. 1. Weekly height of 'Bright Golden Anne' chrysanthemums grown in +FR and -FR light environments in response to GA₁, GA₁₉, or GA₂₀ treatment. Except for GA₁₉ treatment in +FR environment, heights of plants treated with 25 or 50 μg/apex were not different. Therefore, the response for 25 μg/apex is not shown in the graphs. Vertical bars indicate SE (n = 15). If the vertical bars are not seen, SE was smaller than the symbol.



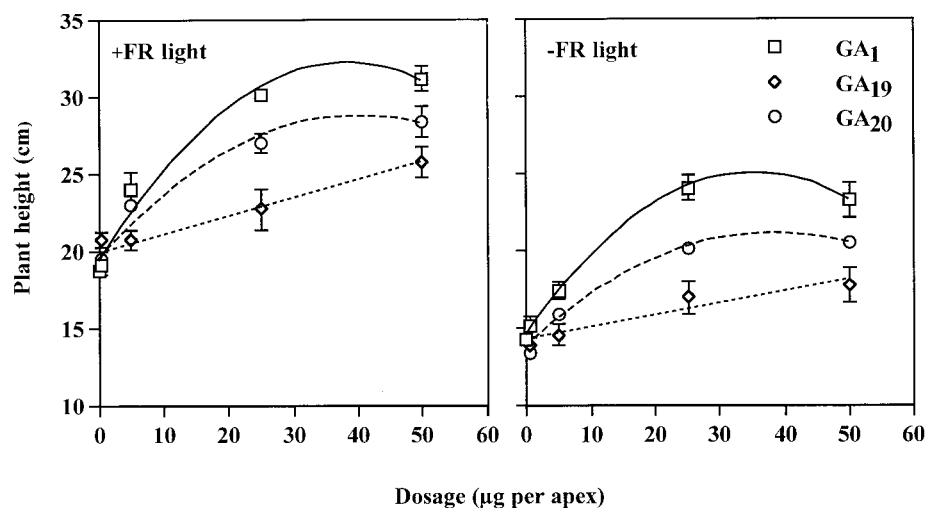


Fig. 2. Influence of exogenous GA₁, GA₁₉, or GA₂₀ application and their dosage on final height of 'Bright Golden Anne' chrysanthemums grown with (+FR) or without (–FR) far red light. Vertical bars indicate SE (n = 15). If the vertical bars are not seen, the SE was smaller than the symbol. Lines were fitted to $y = b_0 + b_1x$ or $b_0 + b_1x + b_2x^2$ where y is height (Ht) and x is dosage. Predicted regression equations are: For +FR GA₁, $Ht = 19.6 + 0.66^a x - 0.009^a x^2$, $r^2 = 0.98$; GA₁₉, $Ht = 19.6 + 0.12^a x$, $r^2 = 0.93$; and GA₂₀, $Ht = 19.6 + 0.46^b x - 0.006^b x^2$, $r^2 = 0.96$. For –FR GA₁, $Ht = 14.1 + 0.62^a x - 0.009^a x^2$, $r^2 = 0.99$; GA₁₉, $Ht = 14.1 + 0.15^c x$, $r^2 = 0.92$; and GA₂₀, $Ht = 14.1 + 0.35^b x - 0.005^b x^2$, $r^2 = 0.98$. Regression coefficients, b_1 or b_2 , with same superscripted letter (lowercase and uppercase, respectively) were not significantly different at $P = 0.05$. Predicted saturation dosages for GA₁ and GA₂₀ were 38.5 and 40.5 µg/apex for +FR, and 35.5 and 39.3 µg/apex for –FR light treatments, respectively.

overnight in 50 mL of 80% methanol in distilled water. Following filtration through Whatman 3 filter paper, the residue was extracted twice with 15 mL of 100% methanol. The combined filtrates were reduced to the aqueous phase in vacuo at 35 °C and purified as described by van Huizen et al. (1995) to obtain an acidic ethyl acetate fraction containing free GAs. Residue was first dissolved in 100 mL of methanol, followed by 900 mL of 0.01% trifluoroacetic acid (TFA). Radiolabeled products of the GA₁₂ and GA₁₉ were resolved by high-performance liquid chromatography (HPLC) on a reversed-phase Nova-Pak 5 mm Radial Pak column (1.5 × 8 cm) (Waters Corp., Milford, Mass.), which performed the following gradient. The samples were eluted at a flow rate of 1.5 mL·min^{–1} using a programmed gradient of 0.01% TFA in 10% methanol solution (solvent A) and pure methanol (solvent B): 100% solvent A for 10 min, 30 min linear ramp to 70% solvent B, 15 min linear ramp to 75% solvent B, and 2 min ramp to 100% solvent B. Fractions were collected (ISCO Foxy Jr., Lincoln, Nebr.) according to the retention times of radiolabeled standards, and detected by an on-line radioactivity monitor (INUS, Inc., Tampa, Fla.).

EXPERIMENTAL DESIGN, DATA COLLECTION, AND ANALYSIS. The experimental design was a randomized complete block design with a split-plot arrangement of the treatments. The light treatment was the whole plot factor. GAs and dosages were the subplot factors. A factorial treatment arrangement was used for the subplot factors. The experiment was repeated once to replicate. Plant height (distance from the growing medium to the apex) was measured weekly. Data were subjected to analysis of variance and linear and quadratic effects were tested using RSREG procedure of SAS (SAS Institute, Inc., Cary, N.C.). Since there were no significant differences between 50% ethanol and distilled water controls in the application experiment, only the water control was used in data analysis.

Results and Discussion

PLANT RESPONSE TO GA₁, GA₁₉, AND GA₂₀. Far red light deficient environment resulted in ≈25% to 30% shorter plants than in the +FR environment (Fig. 1). The reduction in stem elongation under –FR environment was evident within 2 weeks after treatment. Exogenous GA₁, GA₁₉, and GA₂₀ promoted stem elongation but the magnitude of the increase varied with the type of GA, dosage, and the light environment. Plants treated with GA₁, GA₁₉, or GA₂₀ at 0.5 µg/apex were not significantly taller than the water treated (0 µg/apex) plants under both light environments (data not presented). GA₁ and GA₂₀ at 5 µg/apex increased height of plants grown in both light environments, but GA₁₉ at 5 µg/apex did not increase height under either light environment.

Application of GA₁, GA₂₀, or GA₁₉ at 50 µg/apex increased final height by 64%, 49%, and 36%, respectively, compared with no GA (0 µg/apex) application under +FR light. Under –FR light, GA₁, GA₂₀, or GA₁₉ at 50 µg/apex increased final height by 65%, 44%, and 25%, respectively. Data suggest that the response to GA₁, which is an active form, remained the same (64% vs. 65%) between the two light environments, whereas responses to GA₁₉ (36% vs. 25%) and GA₂₀ (49% vs. 44%) decreased under –FR light. This could have been due to reduced metabolism of GA₁₉ and GA₂₀ to the active form under –FR light. The height increase by GA₁₉ was less than that of GA₂₀ as it encompasses inhibition of metabolism one additional step (GA₁₉ to GA₂₀) in the pathway compared to metabolism of GA₂₀ to GA₁. In a previous paper, Tatineni et al. (2000) reported that exogenous GA₁ increased height of nonpaclobutrazol-treated and paclobutrazol-treated plants in a –FR light deficient environment created by photosensitive greenhouse covers. This supports results herein that the –FR light environment did not reduce the response of plants to active GAs. Maas and van Hattum (1998) reported that differences in shoot elongation under various light and temperature conditions did not result from light quality or temperature mediated changes in plant response to GA₁.

Final height of GA₁ and GA₂₀ treated plants followed a quadratic pattern while that of GA₁₉ treated plants followed a linear pattern as the dosage per plant increased from 0 to 50 µg (Fig. 2). Based on the regression analysis, the predicted saturation dosages for GA₁ was 38.5 and 35.5 µg/apex under the +FR and –FR environments, respectively. If the reduction of stem elongation under –FR environment was mediated by reduced GA₁ levels (due to reduced metabolism of GA₁₉ or GA₂₀), then the height of plants treated with a saturating level of GA₁ (50 µg/apex) in + and –FR environments should not be different. However, in the present investigation, final height of plants treated with GA₁ at 50 µg/apex and grown under +FR light was about 33% greater (31.2 cm vs. 23.4 cm) than plants receiving the same dosage under –FR light (Fig. 1). O'Neill et al. (2000) suggested that light inhibition of stem elongation of pea seedlings involves an initial inhibition by a light-induced decrease in GA₁ levels, with continued inhibition mediated by a light-induced reduction of sensitivity to endogenous active GAs. Recent research has shown that exposure to light enhances catabolism of active GAs to their inactive counterparts (Ait-Ali et al., 1999; Gil and Garcia-Martinez, 2000). A possible explanation for our observation is that GA₁ was catabolized faster under –FR light. It could also be possible that –FR light environment resulted in production of endogenous

Table 1. Metabolism, as analyzed by HPLC-radiocounting, of [^{14}C]GA $_{12}$ or [^{14}C]GA $_{19}$ applied to 'Bright Golden Anne' chrysanthemum apices grown with (+FR) or without (–FR) far red light. Data are percentages of total radioactivity in the HPLC fraction corresponding to GA $_{12}$, GA $_9$ /GA $_{15}$, and GA $_{19}$ or GA $_{19}$, GA $_{20}$, and GA $_1$. Each value is the mean of 24 plants.

Time after application	Light environment		<i>P</i>	Time after application	Light environment		<i>P</i>
(h)	+FR	−FR		(h)	+FR	−FR	
GA ₁₂				GA ₁₉			
0	100.0	100.0		0	100.0	100.0	
24	35.8	47.7	0.06	24	74.2	79.4	>0.10
48	37.4	50.5	0.04	48	76.6	81.8	>0.10
72	18.9	21.5	>0.10	96	49.8	73.7	0.01
96	19.8	25.8	>0.10	120	56.2	75.9	0.02
GA ₉ /GA ₁₅ -like fraction				GA ₂₀ -like fraction			
0	0	0		0	0	0	
24	44.4	32.3	0.05	24	8.9	6.6	>0.10
48	45.0	32.1	0.04	48	9.2	6.9	>0.10
72	51.9	40.8	>0.10	96	15.9	8.5	0.01
96	53.7	41.9	>0.10	120	13.4	8.0	0.04
GA ₁₉ -like fraction				GA ₁ -like fraction			
0	0	0		0	0	0	
24	19.8	20.0	>0.10	24	6.9	6.8	>0.10
48	17.6	17.3	>0.10	48	5.4	4.2	>0.10
72	29.2	38.5	0.09	96	19.0	8.1	0.01
96	26.4	32.3	>0.10	120	14.7	6.5	0.05

growth inhibitors. Noguchi and Hashimoto (1990) reported that exposure to R light produced unidentified endogenous growth inhibitors in pea plants that are controlled by phytochrome.

GIBBERELLIN METABOLISM. The data collected from HPLC-radiocounting suggest that changes in light quality had an effect on metabolism of GA $_{12}$ and GA $_{19}$ (Table 1). [^{14}C]GA $_{12}$ was metabolized to similar products in both environments. Radiolabeled peaks eluting at the retention times of GA $_{19}$ -, GA $_{15}$ -, and GA $_9$ -like substances were the major radiolabeled products present in the acidic ethyl acetate fraction. Radiolabeled products eluting in the GA $_9$ /GA $_{15}$ -like fraction were greater than the GA $_{19}$ -like fraction, indicating preference for the non-13-hydroxylation pathway for the applied GA $_{12}$. The finding that [^{14}C]GA $_{12}$ was metabolized to GA $_9$ and GA $_{15}$ -like substances is not surprising. GA $_9$ and trace levels of GA $_{15}$, both non-13-hydroxylated GAs, have been identified in chrysanthemum (Nishijima et al., 1997), indicating that the non-13-hydroxylation pathway is also present in chrysanthemum. In vegetative pea plants, where both the 13-hydroxylation and non-13-hydroxylation pathways exist, GA 20-oxidase prefers nonhydroxylated substrates, even though 13-hydroxylated GAs predominate (Hedden, 1997). The percentage of [^{14}C]GA $_{12}$ recovered during 48 h from plants grown in +FR environment was less than that recovered from plants grown in –FR environment, indicating that metabolism of [^{14}C]GA $_{12}$ was slower in –FR environment. The percentage of GA $_9$ /GA $_{15}$ -like fraction recovered from +FR grown plants following 48 h incubation was greater than –FR grown plants but recovery of labeled GA $_{19}$ -like fraction was not different between light environments.

Metabolism of [^{14}C]GA $_{19}$ was slower than that of [^{14}C]GA $_{12}$ (Table 1). After 120 h of incubation, plants grown under the +FR environment had \approx 56% recovery of [^{14}C]GA $_{19}$ fraction compared to 75% recovery from those plants in –FR environment. Percentage recovery of GA $_{20}$ - and GA $_1$ -like fractions increased as the incubation period increased. The percentage of labeled GA $_{20}$ - and GA $_1$ -like fractions were greater in the +FR than –FR environment. These results suggest that metabolism of both [^{14}C]GA $_{12}$ and [^{14}C]GA $_{19}$ in –FR environment was reduced and that the reduced level of bioactive

GAs may have caused in part reduction of stem elongation under –FR light. In the present application studies we found that final height of plants treated with GA $_{19}$ at 50 μg /apex under +FR light was 45% greater (25.8 cm vs. 17.8 cm) than under –FR light. Final height of plants treated with GA $_{20}$ at 50 μg /apex was 39% greater (28.4 vs. 20.5 cm) than the corresponding plants grown under –FR light. Juntilla (1993) observed that while GA $_{20}$ and GA $_1$ counteracted the short day induced cessation of elongation growth in birch (*Betula pubescens* Ehrh.), GA $_{19}$ was inactive. Beall et al. (1996) reported that turnover of GA $_{19}$ in bean (*Phaseolus vulgaris* L.) seedlings increased when FR light was added to the growing environment.

One limitation of the present study is that the inactive catabolic products of active GAs were not determined. 2 β -hydroxylase is a key enzyme that catabolizes active GAs, such as GA $_1$ and GA $_4$, to their inactive catabolites, GA $_8$ and GA $_{34}$, respectively. Recent work has shown that GA $_1$ levels decreased rapidly and GA $_8$ levels increased during de-etiolation of pea seedlings (Ait-Ali et al., 1999; Gil and Garcia-Martinez, 2000). However, the transcript levels coding for GA 20-oxidase and 3 β -hydroxylase enzymes (that catalyzes the conversion of GA $_{19}$ to GA $_{20}$ and GA $_{20}$ to GA $_1$, respectively) increased during de-etiolation indicating that reduced metabolism of GA $_{19}$ or GA $_{20}$ did not contribute to the decrease in GA $_1$ levels. Martinez-Garcia et al. (2000) reported that end-of-day exposure to FR light increased GA $_1$ levels in cowpea apices due to reduced inactivation of GA $_1$. Although metabolism of GA $_1$ under –FR environments was not investigated, present observations with GA $_1$ application experiments support that –FR environment may have enhanced inactivation of GA $_1$. Exposure of plants to –DIF (higher night than day temperature) is another alternative that has been investigated widely to reduce stem elongation of greenhouse plants. Physiological basis of stem growth control by –DIF is not well understood but we believe that both light and temperature manipulation have similar mechanisms. Grindal et al. (1998) reported that exposure of pea plants to –DIF increased the ratio of GA $_8$:GA $_1$ suggesting that height reduction by –DIF was mediated through reduced GA $_1$ levels via inactivation process.

Data herein indicate that the response of chrysanthemum to exogenous GA₁ was not reduced but the response to GA₁₉ and GA₂₀ was reduced under –FR light environment. The reduced response to GA₁₉ and GA₂₀ was probably mediated by reduction of GA metabolism. Although metabolism of GA₁ under –FR environments was not investigated, observations with GA₁ application experiments support that the –FR environment may have enhanced inactivation of GA₁.

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