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Influence of $CuSO_4$ Spectral Filters, Daminozide, and Exogenous Gibberellic Acid on Growth of *Dendranthema* X *grandiflorum* (Ramat.) Kitamura 'Bright Golden Anne'*

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Abstract. The response of chrysanthemum plants to gibberellic acid (GA_3) and daminozide, grown under 6% $CuSO_4$ and water (control) spectral filters, was evaluated to determine the involvement of gibberellins in regulation of plant height under $CuSO_4$ filters. The $CuSO_4$ filter increased the red (R)/far-red (FR), and blue (B)/R ratio (R = 600–700 nm; FR = 700–800 nm; B = 400–500 nm) of transmitted light. PPF under 6% $CuSO_4$ filter was reduced by about 34% compared to PPF under water filter which averaged about 750 $\mu M \cdot m^{-2} \cdot s^{-1}$. Control plants were shaded with Saran Wrap to ensure equal PPF as in the $CuSO_4$ chamber. GA_3 application increased plant height under both the control and $CuSO_4$ filter, but the height increase under the $CuSO_4$ filter was about 20% greater than that under the control filter. Daminozide treatment reduced plant height under the control and $CuSO_4$ filter, but the height reduction in control plants was slightly greater than under the $CuSO_4$ filter. The height reduction caused by daminozide was prevented by GA_3 application in plants grown under the control or $CuSO_4$ filter. The results suggest that GA_3 may be partially involved in height reduction under $CuSO_4$ filters.

Manipulation of environmental factors, such as temperature and irradiance, has been investigated as nonchemical means for controlling plant growth due to recent restrictions on use of some chemical growth regulators (Heins and Erwin 1990, Mortensen and Stromme 1987). Light intensity and quality, specifically higher red (R) irradiance relative to far-red (FR) irradiance, have been shown to reduce plant height of pea (Noguchi and Hashimoto 1990) and maize (Vanderhoef et al. 1979), and to promote lateral bud outbreak of tomato (Tucker 1975). Although there is a growing demand for artificial lighting for plant growth, lamps with the best spectral quality for plant growth have not been developed. Artificial lighting sources may lead to irregular plant growth due to uneven spectral distribution (spectral gaps) of the lighting source (Protasova et al. 1990). Spectral filters can be used to alter the quality of natural light received by plants. Liquid spectral filters containing a $CuSO_4$ solution have been shown to reduce height of chrysanthemum, tomato, lettuce (Mortensen and Stromme 1987), and potted roses (McMahon and Kelly 1990).

Endogenous gibberellins (GA) play an important role in the control of stem elongation and internode length of many plant species (Dijkstra and Kuiper 1989, Murfet 1990, Ross et al. 1990). It has been suggested that the stem elongation in response to changes in light quality may be mediated by change in GA level (Morgan et al. 1980) or GA sensitivity (Reid and Ross 1988). Campell and Bonner (1986) concluded that 3β-hydroxylation of GA_{20} to GA_1 in dwarf pea seedlings is prevented by R irradiance and controlled by phytochrome. Our preliminary results indicated that plant responses to irradiance transmitted through $CuSO_4$ spectral filters are similar to some of the responses to chemical growth regulator ancymidol (Starman et al. 1989). Most of the chemical growth regulators exert their effects via regulation of GA biosynthesis or action (Graebe 1987). Because of similarities between the effects of chemical growth regulators and $CuSO_4$ spectral filters, we hypothesized that GA biosynthesis or action may be suppressed under $CuSO_4$ spectral filters. If plants grown under $CuSO_4$ filters respond to exogenous GA application, the irradiance passing through $CuSO_4$ filters may have altered GA metab-

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olism so that plants produce less GA than control plants. However, if plants do not respond to exogenous GA, irradiance passing through $CuSO_4$ filters may have altered the sensitivity to GA or GA is not involved in this process. In a previous paper we reported that single GA_3 application, prior to placement under $CuSO_4$ spectral filters, partially overcame height reduction and some other effects of $CuSO_4$ filters, and speculated that the GA_3 effect may have diminished with time so it could not completely overcome the $CuSO_4$ effect (Rajapakse and Kelly 1990). The present experiments were conducted to investigate the involvement of gibberellins in the regulation of plant growth under $CuSO_4$ spectral filters.

Materials and Methods

Plant Material and Culture

Uniformly rooted "Bright Golden Anne" chrysanthemum shoot cuttings with 3–4 leaves (Yoder Bros., Pendleton, SC) were planted (April and May 1990) in 600 cm^3 (11-cm) square plastic pots containing a commercial potting mix (Mix 3B, Fafard Inc., Anderson, SC). Plants were allowed to establish, as single stem plants, in a greenhouse for 1 week before being subjected to the treatments. All plants were fertilized with 18N-3.5P-5K mM from Peter's 20-20-20 fertilizer (W.R. Grace Co., Fogelsville, PA) once daily through irrigation.

Effect of Exogenous GA_3 on Chrysanthemum Growth Under $CuSO_4$ Spectral Filters

Plants were sprayed to run-off with 0 or 0.14 mM (50 ppm) GA_3 (Pro-Gibb Plus, Abbott Laboratories, Chicago, IL) containing 0.1% Tween 20 (Fisher Scientific, NJ) as a surfactant on the day of transfer (day = 0) to growth chambers (180 × 120 cm) with 6% $CuSO_4$ or water (control) "fluid roofs." GA_3 spray was repeated on day 7, 14, and 21 in the chambers. GA_3 at 0.14 mM was selected for this experiment because our preliminary results indicated that increasing the concentration from 0.7–0.14 mM did not significantly alter the response of chrysanthemum plants in either light treatment. The chambers were placed inside a glass greenhouse to receive natural irradiance and photoperiod (average 13 h light and 11 h dark). Side walls of each chamber were covered with inside white and outside black polyethylene to prevent transmission of unfiltered natural irradiance into the chambers. Two fans at opposite sides of each chamber circulated air through a chamber and prevented temperature build-up.

Light Quality and Intensity

The spectral energy flux (350–850 nm in 5 nm increments) inside each chamber 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, Lincoln, NE). Photosynthetic photon flux (PPF) was determined as photon flux (PF) integral between 400 and 700 nm. All irradiance measurements were made between 12:00 and 14:00 h on clear days. Irradiance measurements at the beginning and end of the experiment indicated that spectral quality inside chambers did not change. The $CuSO_4$ solution used in the "fluid roof" increased the ratios of PF between wavelengths 600–700 nm (R irradiance) and 700–800 nm (FR irradiance) [R/FR], and of PF between wavelengths 400–500 nm (blue irradiance) and 600–700) [B/R], of irradiance compared to control (Fig. 1). Phytochrome photoequilibrium ($\phi = P_{fr}/P_{tot}$) under control and $CuSO_4$ filter was estimated as described by Sager et al. (1988). Estimated ϕ values for $CuSO_4$ and control filters were 0.82 and 0.72, respectively. Percentage shading (in the 400–700 nm range) by $CuSO_4$ solution was calculated using irradiance in control chamber. PPF under $CuSO_4$ filter was reduced by about 34% that of control chamber, which averaged about 750 $\mu m \cdot m^{-2} \cdot s^{-1}$. A neutral shading material (Saran Wrap) was placed over the control filter to ensure the same PPF level as in $CuSO_4$ chamber. Plants were watered and fertilized daily as described above. Average daily maximum temperatures inside $CuSO_4$ and control chambers were 29 ± 4°C and 32 ± 2°C, and minimum temperatures were 22 ± 1°C and 21 ± 1°C, respectively.

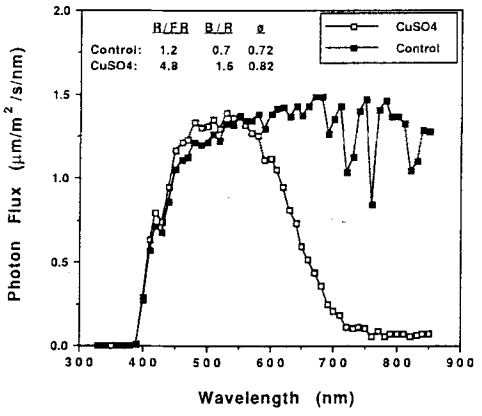

Fig. 1. Influence of 6% $CuSO_4$ or water (control) filter on photon flux distribution, ratios of photon flux between 600–700 nm and 700–800 nm (R/FR) and of photon flux between 400–500 nm and 600–700 nm (B/R), and estimated phytochrome photoequilibrium (ϕ) of transmitted light.

Effect of Daminozide and GA_3 on Chrysanthemum Growth Under $CuSO_4$ Spectral Filters

At the end of the establishment period, plants were sprayed to runoff with 22 mM (3500 ppm, commercially recommended concentration) daminozide or 22 mM daminozide followed by 0.14 mM GA_3 prior to transfer to chambers. Leaves were allowed to dry for 30 min before GA_3 application. Control plants were sprayed with water and Tween 20 (0.1%). Spray treatments were repeated after 14 days in the growth chambers. Average daily maximum temperatures inside $CuSO_4$ and control chambers were 33 ± 1°C and 34 ± 1°C, and minimum temperatures were 22 ± 1°C and 24 ± 2°C, respectively.

Data Collection and Analysis

Plant height (height from soil level to apical bud) and number of

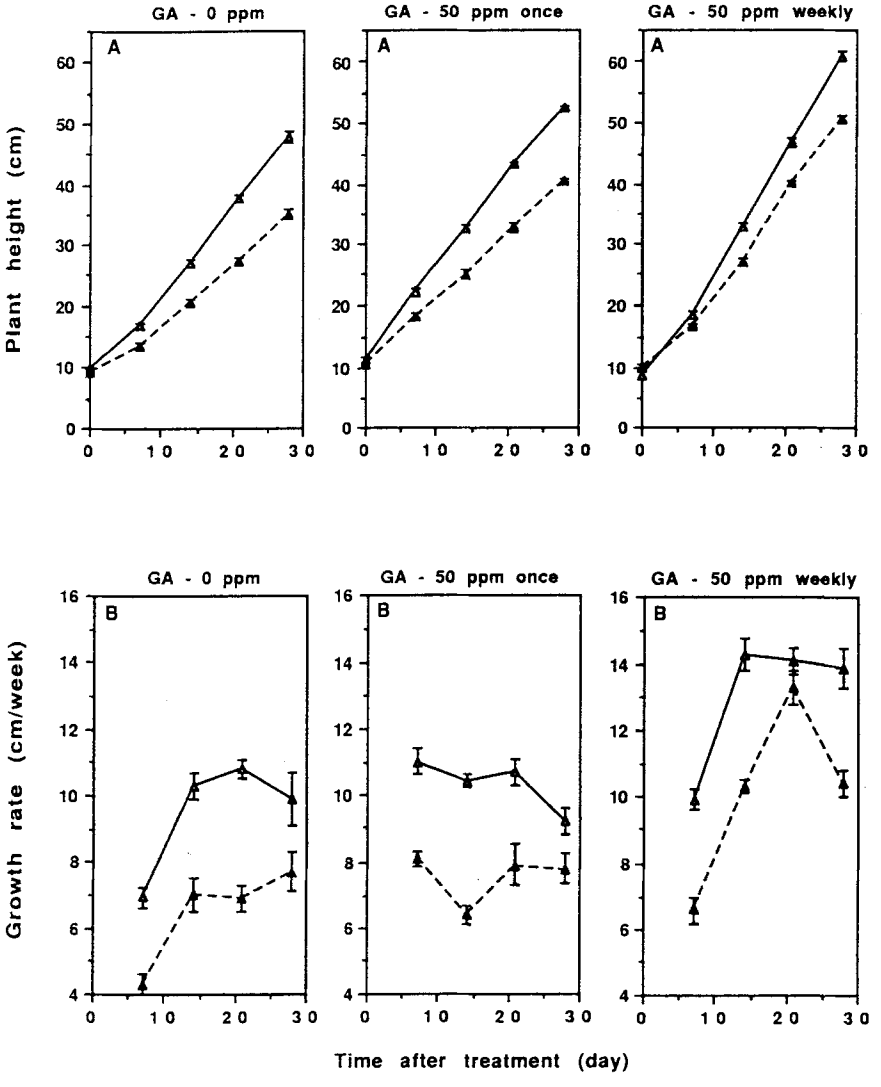

Fig. 2. Plant height (A) and growth rate (B) of "Bright Golden Anne" chrysanthemum plants treated with GA_3 (50 ppm) and grown under control (——) or $CuSO_4$ (– – – –) spectral filter.

fully expanded leaves were recorded weekly for 4 weeks. Growth rate (GR) was calculated from height increase data. Average internode length was calculated as plant height/number of leaves. Leaf area (LI-3100 area meter, LI-COR, Lincoln, NE) and dry weights of stems and leaves were measured at the end (28 days) of both experiments. For dry weight measurements, tissue was oven-dried at 85°C for 48 h.

Both experiments were repeated. The experimental design was completely randomized with five single-plants per treatment combination. Data were subjected to analysis of variance. Differences among treatment means were tested using single degree of freedom contrasts or Duncan's multiple-range test.

Results

Influence of Exogenous GA_3 on Chrysanthemum Growth Under $CuSO_4$ Spectral Filter

Plants grown under $CuSO_4$ filter (without GA_3) were 27% shorter than the plants grown under control filter at the end of the experiment (Fig. 2A). The reduction in plant height under $CuSO_4$ filter was evident within 1 week after light treatment. Exogenous GA_3 application increased plant height in both control and $CuSO_4$ treatments. However, the height increase by GA_3 under $CuSO_4$ filter was significantly greater (45%) than that under control filter (27%), indicating that plant sensitivity to exogenous GA_3 was greater under $CuSO_4$ filter. Plants treated with single GA_3 spray (one spray on day = 0) were significantly taller than the non-GA_3-treated plants under both control and $CuSO_4$ filters, but they were significantly shorter than the plants which received weekly GA_3 application. Final height of weekly GA_3-treated plants grown under $CuSO_4$ filter was similar to the height of non-GA_3-treated plants under control filter, indicating that weekly exogenous GA_3 applications could overcome the height reduction caused by light quality under $CuSO_4$ filter.

Table 1. Effect of light treatment and weekly exogenous gibberellic acid (GA_3) application on average internode length, dry weight (dry wt) and dry weight distribution of "Bright Golden Anne" chrysanthemum plants 4 weeks after treatment. Numbers in parentheses indicate the percentage dry matter accumulated.

Treatment[a]	GA_3 (mM)	Internode length (cm)	Total dry wt (g)	Leaf dry wt (g)	Stem dry wt (g)
Control	0	2.2	6.2	3.8 (61)	2.4 (39)
	0.14	2.7	6.5	3.6 (55)	2.9 (45)
$CuSO_4$	0	1.5	4.1	2.9 (71)	1.2 (29)
	0.14	2.2	5.1	3.3 (65)	1.8 (35)
ANOVA[b]					
Treatment		—***	—***	—**	—***
GA_3		—***	—***	—*	—**
Treatment × GA_3		NS	NS	—*	NS

[a] Control and $CuSO_4$ treatments received same irradiance. R/FR inside control and $CuSO_4$ chambers were 1.2 and 4.8, respectively.
[b] NS, *, **, ***: Nonsignificant or significant at P = 0.05, P = 0.01, or P = 0.001, respectively.

Number of leaves per plant was not affected by irradiance or GA_3 application (data not shown). Light passing through $CuSO_4$ filter reduced internode length of non-GA_3-treated plants by 32% compared to same plants grown under control filter (Table 1). Weekly GA_3 applications increased internode length in both light treatments, but response was greater under $CuSO_4$ filter. Plants treated with single application of GA_3 had longer internodes 1 week after the treatment under both filters but at the end of the experiment the difference was not significant from non-GA_3-treated plants (data not shown). Weekly GA_3-treated plants grown under $CuSO_4$ filter and non-GA_3-treated plants in control chamber had similar internode length (Table 1).

Growth rate of non-GA_3-treated plants was reduced by light passing through $CuSO_4$ filter (Fig. 2B). GA_3 increased GR in both light treatments with a greater response under $CuSO_4$ filter. Weekly GA_3 application increased GR of plants grown under $CuSO_4$ filter to a level comparable to non-GA_3-treated plants in control chamber.

Total dry weight and leaf and stem dry weight of non-GA_3-treated plants grown under $CuSO_4$ filter were reduced by 34%, 24%, and 50%, respectively, compared to control plants (Table 1). GA_3 application increased the total dry weight of plants grown under $CuSO_4$ filter by 24% and 5% in control plants. GA_3 application had no effect on leaf dry weight under control filter, but under $CuSO_4$ filter it was increased by 14%. Stem dry weight of both control and $CuSO_4$ plants was increased by GA_3 application but the increase was greater in plants grown under $CuSO_4$ filter. Irradiance passing through $CuSO_4$ filter increased dry matter partitioning into leaves, while in stems it was decreased in non-GA_3-treated plants (Table 1). GA_3 application reduced dry matter partitioning into leaves and increased dry matter partitioning into stems under both control and $CuSO_4$ filters.

Effect of Daminozide and GA_3 on Chrysanthemum Growth Under $CuSO_4$ Spectral Filter

The involvement of GA in stem elongation reduction under $CuSO_4$ filter was further investigated by treating plants with daminozide, a compound known to inhibit GA biosynthesis. Daminozide treatment reduced plant height under both control and $CuSO_4$ filters, but the height reduction under control filter (32%) was slightly greater than that under $CuSO_4$ filter (27%) (Fig. 3A). Average internode length and GR were also reduced by daminozide in both light treatments (Table 2, Fig. 3B). The height reduction caused by daminozide was fully prevented by the application of GA_3 under control filter (Fig. 3A). However, under $CuSO_4$ filter, plants treated with daminozide followed by GA_3 were taller than nondaminozide-treated plants. Plants receiving daminozide and GA_3 in control chamber were taller (23%) than the plants receiving the same treatment in $CuSO_4$ chamber. Average internode length and GR responded in a similar manner.

Treatment with daminozide reduced total leaf area and leaf size in plants grown under control and $CuSO_4$ filters (Table 2). The reduction of leaf area caused by daminozide could be alleviated by GA_3 application.

Daminozide reduced total dry weight by 27% and 12% over nontreated plants grown under control and $CuSO_4$ filters, respectively (Table 3). Treatment with daminozide reduced leaf and stem dry weight of plants grown under $CuSO_4$ and control filters but the dry weight reduction caused by daminozide was greater under control filters than that of the plants grown under $CuSO_4$ filter. GA_3 application increased leaf and stem dry weight of plants grown under control and $CuSO_4$ filters. Treatment with daminozide increased dry matter accumulation into leaves (64%) and decreased stem dry matter accumulation (23%) under control filter; however, in plants grown under $CuSO_4$ filter, dry matter distribution pattern was not affected by daminozide treatment (Table 3). GA_3 application prevented the effect of daminozide on dry matter distribution pattern in both control and $CuSO_4$ plants.

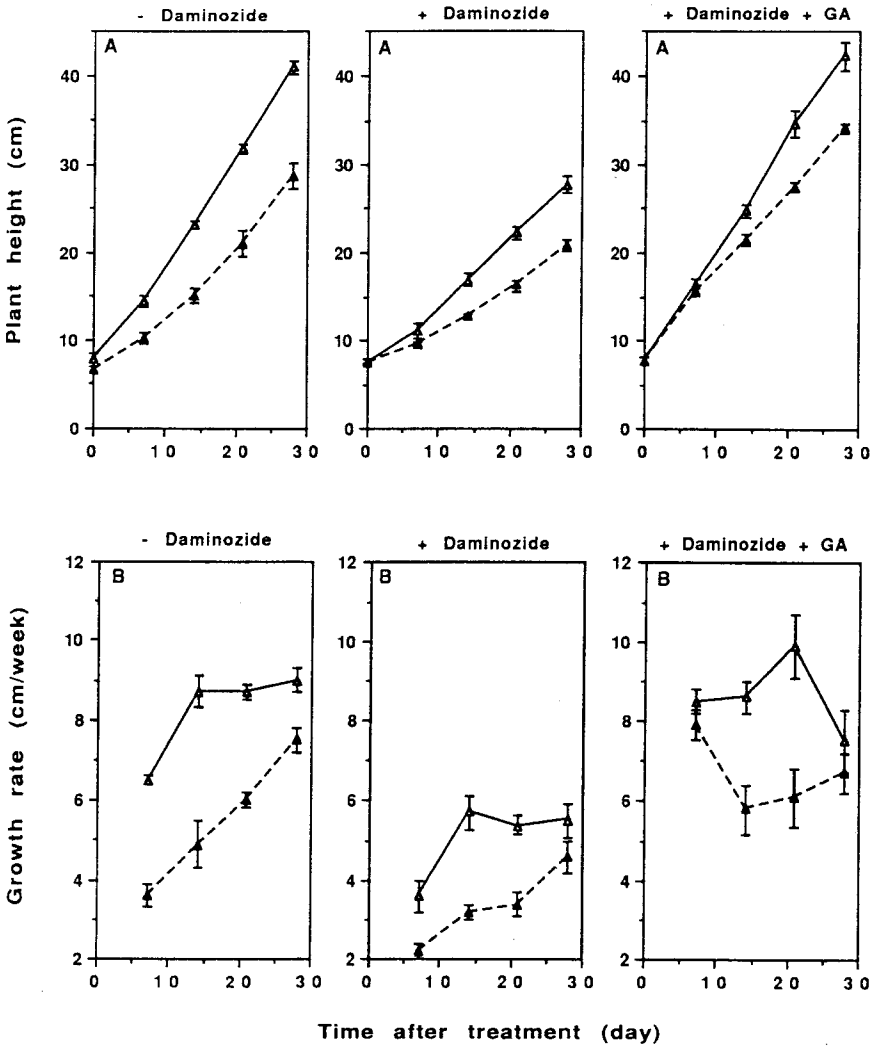

Fig. 3. Plant height (A) and growth rate (B) of "Bright Golden Anne" chrysanthemum plants treated with daminozide (3500 ppm) or daminozide plus GA_3 (3500 ppm + 50 ppm) and grown under control (——) or $CuSO_4$ (– – – –) spectral filter.

Discussion

Growth of chrysanthemum plants was affected by the irradiance passing through $CuSO_4$ filter which contains a higher proportion of R/FR, B/R, and estimated phytochrome photoequilibrium. Height reduction of plants under $CuSO_4$ filter was mainly caused by the decrease in average internode length and the reduced GR because number of nodes was not different between plants grown under control or $CuSO_4$ filters. In previous experiments, $CuSO_4$ filters have been shown to reduce height of chrysanthemum (Mortensen and Stromme 1987, Rajapakse and Kelly 1990), tomato and lettuce (Mortensen and Stromme 1990), petunia and geranium (Benson and Kelly 1990), and potted roses (McMahon and Kelly 1990). Irradiance high in red wavelengths has been reported to inhibit stem elongation of maize seedlings (Vanderhoef et al. 1979) and pea (Noguchi and Hashimoto 1990). Recent work by Britz and Sager (1990) with soybean and sorghum has shown that irradiance deficient in blue wavelengths produced taller plants similar to irradiance high in FR wavelengths. However, McMahon et al. (1991) found no difference in chrysanthemum growth between plants grown under blue-light-deficient and natural irradiance filters. Light-quality-induced growth inhibition has been studied in order to understand the mechanism by which R irradiance inhibits stem elongation (Metzger 1988, Murfet 1990). Despite the extensive studies, the actual mechanism of stem-elongation reduction has yet to be found. It has been suggested that the stem-elongation response to change in light quality may be mediated by a change in GA level (Morgan et al. 1980) or GA sensitivity (Murfet 1990, Reid and Ross 1988). GA applications have been shown to reverse the light inhibition of stem growth

Table 2. Effect of light treatment, daminozide (22 mM), and GA_3 (0.14 mM) application on average internode length, leaf area, and leaf size of "Bright Golden Anne" chrysanthemum plants 4 weeks after treatment.

Treatment[a]	Growth regulator	Internode length (cm)	Leaf area (cm^2)	Leaf size (cm^2)
Control	None	1.7	939.4	40.5
	Daminozide	1.3	755.0	37.7
	Daminozide + GA_3	1.7	1033.1	42.0
$CuSO_4$	None	1.2	882.0	38.3
	Daminozide	0.9	745.8	33.9
	Daminozide + GA_3	1.3	1013.6	40.7
Anova and contrasts[b]				
Treatment		—***,[c]	NS	—**
Growth regulator		—***	—***	—***
Control: None vs. Dam.		—***	—**	NS
None vs. Dam. + GA_3		NS	NS	NS
Dam. vs. Dam. + GA_3		—***	—***	—**
$CuSO_4$: None vs. Dam.		—***	—*	—**
None vs. Dam. + GA_3		NS	—*	NS
Dam. vs. Dam. + GA_3		—***	—**	—***
Treatment × growth regulator		NS	NS	NS

[a] Control and $CuSO_4$ treatments received same irradiance intensity. R/FR inside control and $CuSO_4$ chambers were 1.2 and 4.8, respectively.
[b] Single degree of freedom contrasts.
[c] NS, *, **, ***: Nonsignificant or significant at P = 0.05, P = 0.01, or P = 0.001, respectively.

(Campell and Bonner 1986, Lockhart 1959). The involvement of certain GAs in control of stem elongation and internode length of many plant species has been well-established (Dijkstra et al. 1990, Graebe 1987, Zeevaart 1985). Our preliminary results indicated that a single application of GA_3 prior to light treatment could partially alleviate the growth inhibition caused by light passing through $CuSO_4$ filters, and speculated that the GA_3 effect may be diminished with time (Rajapakse and Kelly 1990). Weekly GA_3 application in the current experiments overcame the height reduction caused by light passing through $CuSO_4$ filter (Fig. 2A). Plants grown under $CuSO_4$ filter responded more to exogenous GA_3 application than the plants grown under control filter, suggesting that sensitivity of plants to GA_3 was not lowered by light in the $CuSO_4$ chamber. It is possible that GA became limiting in plants grown under $CuSO_4$ filter due to reduced biosynthesis or the decreased conversion from inactive (bound) to active (free) form even if plants were able to produce GA. Lockhart (1964) suggested that conversion of GA to "active form" may be prevented by R irradiance and promoted by FR irradiance. Campell and Bonner (1986) concluded that 3β-hydroxylation of GA_{20} (precursor) to GA_1 (active form) in dwarf pea seedlings is prevented by R irradiance and is controlled by phytochrome.

Although the results indicate the possible involvement of GA metabolism in height reduction under $CuSO_4$ filter, there was evidence to indicate that response was not solely mediated by alteration of GA metabolism. In a preliminary experiment, we have shown that increasing the GA_3 concentration from 0.07–0.14 mM (25–50 ppm) did not significantly alter the response of plants in either light treatment. Therefore, we could assume that 0.14 mM was a saturating level of GA_3. If the response to light transmitted through the $CuSO_4$ filter was mediated solely by an alteration of GA_3 metabolism, the plant response to a saturating level of GA_3 in control and $CuSO_4$ chamber would have been the same. However, the final height of weekly GA_3-treated plants grown under the control filter was about 20% greater than the plants receiving the same treatment under the $CuSO_4$ filter (Fig. 2A). A similar response to GA_3 was observed for internode length and GR under control and $CuSO_4$ filters. These observations indicate that something other than GA_3, such as another form of active GA or growth inhibitor, may be involved or the absorption of exogenous GA_3 was reduced due to leaf morphological and anatomical differences under the $CuSO_4$ filter. It would be interesting to investigate morphological and anatomical characteristics of plants grown under these filters. The fact that plants grown under the $CuSO_4$ filter responded more to exogenous GA_3 compared to control indicates that

Table 3. Effect of light treatment, daminozide (22 mM), and GA_3 (0.14 mM) application on dry weight (dry wt) and dry weight distribution of "Bright Golden Anne" chrysanthemum 4 weeks after treatment. Numbers in parentheses indicate the percentage of dry matter accumulated.

Treatment[a]	Growth regulator	Total dry wt (g)	Leaf dry wt (g)	Stem dry wt (g)	Root dry wt (g)
Control	None	6.0	3.6 (60)	1.7 (28)	0.7 (12)
	Daminozide	4.4	2.8 (64)	1.0 (23)	0.6 (13)
	Daminozide + GA_3	7.5	4.2 (56)	2.4 (32)	0.9 (12)
$CuSO_4$	None	3.3	2.3 (70)	0.6 (18)	0.4 (12)
	Daminozide	2.9	2.1 (72)	0.5 (17)	0.3 (11)
	Daminozide + GA_3	4.6	3.1 (67)	1.0 (22)	0.5 (11)
Anova and contrasts[b]					
Treatment		—***,[c]	—***	—***	—***
Growth regulator		—***	—***	—***	—***
Control: None vs. Dam.		—***	—**	—***	—*
None vs. Dam. + GA_3		—***	—*	—***	—**
Dam. vs. Dam. + GA_3		—***	—***	—***	—***
$CuSO_4$: None vs. Dam.		NS	NS	NS	NS
None vs. Dam. + GA_3		—***	—***	—**	NS
Dam. vs. Dam. + GA_3		—***	—***	—***	—**
Treatment × growth regulator		—*	NS	—***	—[ns]

[a] Control and $CuSO_4$ treatments received same light intensity. R/FR inside control and $CuSO_4$ chambers were 1.2 and 4.8, respectively.
[b] Single degree of freedom contrasts.
[c] NS, *, **, ***: Nonsignificant or significant at P = 0.05, P = 0.01, or P = 0.001, respectively.

irradiance passing through the $CuSO_4$ filter did not lower sensitivity to GA_3. Although GA_3 does not solely mediate the light-regulated growth, it appears that GA controlled stem elongation to a certain extent. To further support our finding, Metzger (1988) and Murfet (1990) reported that the elongation of *Thlaspi arvense* petioles and dwarf pea petiole, in response to light quality, was not solely mediated through GA. Behringer et al. (1990) also reported that stem-elongation response of pea to R irradiance is not solely mediated by either reduction in GA biosynthesis or sensitivity to GA.

Reduced dry weight under the $CuSO_4$ filter may be attributed to the reduction in plant height. Alteration of dry matter partitioning into leaves and stem suggests that translocation of photosynthates is affected by light quality. GA_3 application increased the leaf and stem dry matter accumulation under the $CuSO_4$ filter, suggesting that GAs may be involved. However, GA_3 could not completely overcome dry matter reduction caused by light transmitted through the $CuSO_4$ filter. It was interesting to note that GA_3 reduced dry matter accumulation into leaves and increased it into roots under both light treatments. It has been previously shown that GA_3 reduced dry matter accumulation into leaves (Dijkstra and Kuiper 1989).

The observations made with daminozide also indicate that GA inhibition was not the sole reason for height reduction under the $CuSO_4$ filter. If the height reduction caused by irradiance passing through $CuSO_4$ was caused by alteration of GA metabolism, response of plants grown under the $CuSO_4$ filter to daminozide (GA inhibitor) should have been small. However, in the present experiment, plants grown under control and $CuSO_4$ filters responded well to daminozide treatment by causing a 32% and 27% height reduction under control and $CuSO_4$ filters, respectively. GA_3 application completely reversed the height reduction caused by daminozide in the control chamber. However, plants receiving daminozide and GA_3 under the $CuSO_4$ filter were taller (20%) than nontreated plants, suggesting that those plants had a greater response to GA_3. A similar response was found for internode length and GR in both control and $CuSO_4$ chambers, suggesting the possible involvement of some other factor in height control under $CuSO_4$ filters.

Reduction of leaf area and leaf size by daminozide is consistent with the previous work with other growth-retarding chemicals (Starman et al. 1989). Daminozide treatment further reduced the leaf area and leaf size of plants grown under the $CuSO_4$ filter, indicating that leaf characteristics are not solely controlled by inhibition of GA.

Daminozide treatment reduced total dry weight under control and $CuSO_4$ filters with a greater re-

duction under the control filter. GA_3 application could overcome dry weight reduction caused by daminozide under both light treatments. However, GA_3 could not completely overcome the reduction in dry weight caused by light quality. Dry matter distribution into roots was not affected by light quality, daminozide, or GA_3 application.

The results suggest that exogenous GA_3 could alleviate the height reduction caused by light transmitted through the $CuSO_4$ filter, although GA_3 inhibition may not be the sole reason for growth retardation under the $CuSO_4$ filter. Beside partial involvement on GA_3 metabolism, it is possible that light quality may be affecting other factors responsible for cell wall extensibility, such as directly acting on cell walls, affecting other hormones (auxins) or another form of active GA responsible for cell elongation, or alter leaf morphological and anatomical characteristics. Light quality could also be involved in synthesis of endogenous growth inhibitors. Noguchi and Hashimoto (1990) reported that pea plants exposed to R light produced an unidentified growth inhibitor, controlled by phytochrome. Further experiments are needed and will usefully enhance our knowledge in understanding the mechanism of growth regulation by spectral filters.

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