

Spectral Filters and Growing Season Influence Growth and Carbohydrate Status of Chrysanthemum

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Abstract. The interactions of light quality and growing season on growth and carbohydrate content of chrysanthemum [*Dendranthema × grandiflorum* (Ramat.) Kitamura] plants were evaluated using 6% CuSO₄ and water (control) as spectral filters. Light transmitted through the CuSO₄ filter significantly reduced plant height and internode length compared to control plants regardless of the season. However, the degree of response varied with growing season. Light transmitted through CuSO₄ filters delayed flowering. Total number of flowers was not affected by spectral filter, but plants grown under CuSO₄ filter had smaller flowers than those grown under the control filter. Light transmitted through CuSO₄ filter resulted in reduced leaf and stem soluble sugar (sucrose, glucose, and fructose) and starch concentrations regardless of the growing season. However, the magnitude of reduction was greater in spring- than in fall-grown plants. Stems of fall-grown plants had more starch deposition than spring-grown plants under both filters. Filters with specific spectral characteristics can be used as alternative means of producing compact plants in the greenhouses, however, the delay in flowering and smaller flowers could limit their use for growth control of plants intended for flower production.

A wide range of nonchemical methods for growth regulation of ornamental crops has received much attention in recent years (Heins and Erwin, 1990; Latimer et al., 1991; McMahan and Kelly, 1990; Mortensen and Stromme, 1987). Our research focusing on manipulation of greenhouse light quality as a nonchemical alternative indicated that light transmitted through CuSO₄ filters reduced plant height similar to chemical growth regulators and produced compact plants in a range of horticultural crops (McMahan and Kelly, 1990; Rajapakse and Kelly, 1992). Our results with miniature roses indicated that light transmitted through CuSO₄ filters interacted with growing season and altered flower development (Rajapakse and Kelly, 1994). Alteration of light quality in the greenhouse for plant growth regulation may be feasible with the use of electric light sources with various spectral qualities, by appropriate fluid roof greenhouses, and/or by developing greenhouse construction material with specific spectral properties. However, further research is needed to enhance our knowledge of light quality as a nonchemical alternative.

Although the light transmitted through CuSO₄ filters reduced plant height and internode length, the mechanism of height control by CuSO₄ filters is not well understood. In our previous experiments, we observed that the reduction of plant height and internode length by light transmitted through CuSO₄ spectral filters could be reversed by weekly application of gibberellic acid (GA₃) or by exposure to end-of-day far-red (FR) light, suggesting that GA and phytochrome may be involved in the growth regulation under CuSO₄ filters (Rajapakse and Kelly, 1991; Rajapakse et al., 1993). Gibberellic acid increases soluble sugar and starch content in soybean (*Glycine max* L.) and *Phalaenopsis amabilis* leaves and promotes sink activity in the apical meristem (Cheikh and Brenner, 1992; Chen et al., 1994). Gibberellic acid also increases the activity of two key enzymes in sucrose metabolism, sucrose phosphate synthase activity (SPS) of soybean

and spinach (*Spinacia oleracea* L.) leaves (Cheikh et al., 1992) and cell wall invertase activity of dwarf pea seedlings (Wu et al., 1993), while paclobutrazol, a GA inhibitor, decreases the activity of SPS (Cheikh et al., 1992). Morns and Arthur (1985) reported that the rapid cell expansion and internode elongation of bean (*Phaseolus vulgaris* L.) stems were positively associated with high levels of hexose sugars and low levels of sucrose. Based on these observations, we hypothesized that the light quality under CuSO₄ filters may reduce the carbohydrate status of plants, which may contribute to the reduction of internode length under CuSO₄ filters. The primary objective of the present investigation was to examine carbohydrate status of plants grown under CuSO₄ filters in attempts to understand the physiological basis of growth control by spectral filters. The experiments were repeated over three seasons to examine possible interaction between growing season and spectral filters on growth and carbohydrate status of chrysanthemum.

Material and Methods

Plant material. 'Bright Golden Anne' chrysanthemum was used in all experiments. Uniformly rooted chrysanthemum shoot cuttings with three to four leaves (Yoder Bros., Pendleton, S.C.) were planted in 600-cm² square plastic pots containing a commercial potting mix (Mix 3B, Fafard, Anderson, S.C.). Plants were grown as single-stem plants in the greenhouse for 10 days before being subjected to the light treatments. All plants were fertilized once daily at irrigation, with 18N-3.5P-5K mm from Peter's 20-20-20 fertilizer (W.R. Grace Co., Fogelsville, Pa.).

Spectral filter treatment. After the 10-day establishment period, plants were transferred to growth chambers with 6% CuSO₄·5H₂O (w/v) or water (control) fluid roofs (spectral filters). The design of spectral filter growth chambers was described by Rajapakse and Kelly (1992). All chambers were placed inside a nonshaded greenhouse. The experiment was first conducted in spring (March to May 1991) and repeated in summer (June to August 1991) and fall (September to November 1991). Average day temperatures inside the CuSO₄ or control chambers in spring, summer and fall were 24 ± 4C, 30 ± 3C and 25 ± 4C and nights were 20 ± 2c, 22 ± 1c, and 18 ± 4C, respectively. Average photoperiods

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for spring, summer, and fall experiments were ≈ 12.5 , 14, and 10 h, respectively.

Spectral quality. The spectral photon flux (350 to 850 nm in 5-nm increments) of light transmitted through CuSO_4 and unshaded control filters was measured between 1200 and 1400 HR at the beginning and end of each experiment with a LI-1800 spectroradiometer fitted with a LI-1800-10 remote cosine sensor (LI-COR, Lincoln, Neb.). The photon flux distribution, ratios of photon flux between 600 to 700 nm and 700 to 800 nm (R: FR) and of photon flux between 400 to 500 nm and 600 to 700 nm [blue (B) : R] and phytochrome photoequilibrium (ϕ , estimated as described by Sager et al., 1988) of light transmitted through CuSO_4 and unshaded control filter, are presented in Fig. 1. Light measurements made at the beginning and end of the experiments indicated that neither the spectral quality nor the relative transmission changed significantly during the experimental period. Photosynthetic photon flux (PPF) of light transmitted through CuSO_4 and control filters was determined with a LI-185 quantum meter fitted with a LI-190SA quantum sensor. The 6% CuSO_4 filter reduced PPF by $\approx 34\%$ compared to that in the greenhouse. A neutral shading material (cheese cloth), was placed over the control filter to ensure the same PPF level as in the corresponding CuSO_4 chamber. Average PPF inside CuSO_4 or control chamber was ≈ 970 , 1072, and 840 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in spring, summer, and fall, respectively.

Data collection. Plants were grown inside the spectral filter chambers for 4 weeks. At the end of four weeks, plant height (height from soil level to apex), number of fully expanded leaves, leaf and stem dry weight, and carbohydrate concentrations were measured. Average internode length (plant height/number of leaves), dry weight per unit leaf area, and dry weight per unit length of stem were calculated. For dry weight measurements, plants were oven dried at $\approx 85\text{C}$ for 48 h.

Flower development was evaluated in 10 representative plants in the fall experiment (September 1991) and the experiment was repeated in December 1991. Days to flower (number of days from placing in chamber to first petal opening), number of flowers and flower buds, diameter of flowers (when flowers had four to six layers of petals open) and flower fresh and dry weights were recorded.

Carbohydrate analysis. Plants were cut at soil level between 1100 and 1200 HR and immediately frozen in liquid N and stored at -70C until freeze drying. Leaf and stem tissues were separated after freeze drying and ground in a Wiley mill to pass through a 40-mesh screen. Soluble sugars from 50 mg of ground tissue were extracted with 12 methanol :5 chloroform :3 water (by volume) as described by Miller and Langhans (1989). The extract was evaporated to dryness under a vacuum and the residue was dissolved in 2 ml high-performance liquid chromatography (HPLC)-grade water. Soluble sugars were separated and detected using a HPLC system (Waters 600E system controller, 700 WISP autosampler, 410 refractive index detector and 810 baseline workstation, Waters Associates, Milford, Mass.) with a Bio-Rad HPX-87C column maintained at 85C . Quantification of individual sugars was based on the internal standard, mannitol (1 mg). Starch was determined using enzymatic hydrolysis of dried residue following soluble sugar extraction as described by Haissig and Dickson (1979). After drying the residue, 4 ml of acetate buffer (100 mM pH 4.5) was added to the residue and placed in a boiling water bath for 30 min. Samples were then cooled to room temperature and incubated at 55C for 2 days with 1 ml of amyloglucosidase (50 units) (Sigma Chemical Co., St. Louis). After 2 days of incubation, a 100- μl aliquot was removed and glucose concentra-

tion determined in a 5-ml assay mixture containing 5 units peroxidase, 25 units glucose oxidase, and 0.2 mg *o*-dianisidine (Sigma Chemical Co.). After incubating 30 min at 30C , the reaction was stopped by adding 1 ml of 2.2 N HCl to each sample and absorbance was measured at 450 nm. Quantification was based on known glucose standards.

Experimental design and data analysis. Control and CuSO_4 filters were randomly assigned to four growth chambers in two replicates. Ten single stem plants were used in each treatment in replicate for growth analysis (total of twenty plants per treatment per season). For carbohydrate analysis, five single plants were used in each treatment in replicate (total of ten plants per treatment per season). Carbohydrate analysis was made in spring and fall experiments only. Data were subjected to analysis of variance.

Results

Growth parameters. Plants grown in summer were taller than the plants grown in spring or fall under both light filters (Table 1). However, internode length was similar within a filter treatment regardless of the growing season indicating that the plants grown in summer produced more nodes than in spring and fall. Light transmitted through the CuSO_4 filter reduced plant height and internode length compared to respective control plants, regardless of the growing season. However, the percentage reduction in plant height under CuSO_4 filters was greater in spring- and fall-grown ($\approx 30\%$) compared to summer-grown ($\approx 20\%$) plants.

Light transmitted through the CuSO_4 filter reduced leaf and stem dry weights compared to those of control plants, but the magnitude of dry weight reductions varied with the season resulting in an interaction between growing season and spectral filters (Table 1). The percentage reduction of stem dry weight by CuSO_4 filters was much greater than the reduction of leaf dry weight (average of $\approx 54\%$ reduction of stem dry weight vs. average of $\approx 27\%$ leaf dry weight reduction). The dry weight per unit leaf area (LDA) was significantly reduced by light transmitted through the CuSO_4 filter except in fall grown plants. The dry weight per unit length of stem (SDL) was reduced considerably by the light transmitted through the CuSO_4 filter with greatest reduction in summer ($\approx 40\%$ reduction in SDL in summer vs. $\approx 33\%$ in spring or fall).

Flower development on early (September) and late (December) fall-grown plants was delayed by 13 and 7 days, respectively, by the light transmitted through CuSO_4 filters (Table 2). Total number of flowers (open and unopen) was not affected by the light quality under CuSO_4 filters. Flower diameter of plants grown under the control filter was greater than that of plants grown under CuSO_4 filter. Fresh and dry weights per flower were also reduced by the spectral quality under CuSO_4 filters.

Carbohydrate status. Spring-grown plants had more carbohydrates than fall-grown plants under the respective spectral filter, probably due to the higher PPF during spring than in fall. The soluble sugar fraction of leaves was mainly comprised of sucrose and fructose (Table 3). Glucose was present in small quantity in spring but was not detectable in fall-grown plants. In the stems, sucrose, glucose, and fructose were present in approximately equal concentrations in spring. Stems of fall-grown plants contained a very small quantity of glucose ($<2\text{ mg}\cdot\text{g}^{-1}$ dry weight). An unidentified substance (eluted ≈ 7.05 min after injection), was present in stems, but not in leaves, of control plants in relatively large amounts ($\approx 20\text{ mg}\cdot\text{g}^{-1}$ dry weight in spring). The unidentified substance was not detected in stems of plants grown under CuSO_4 filter.

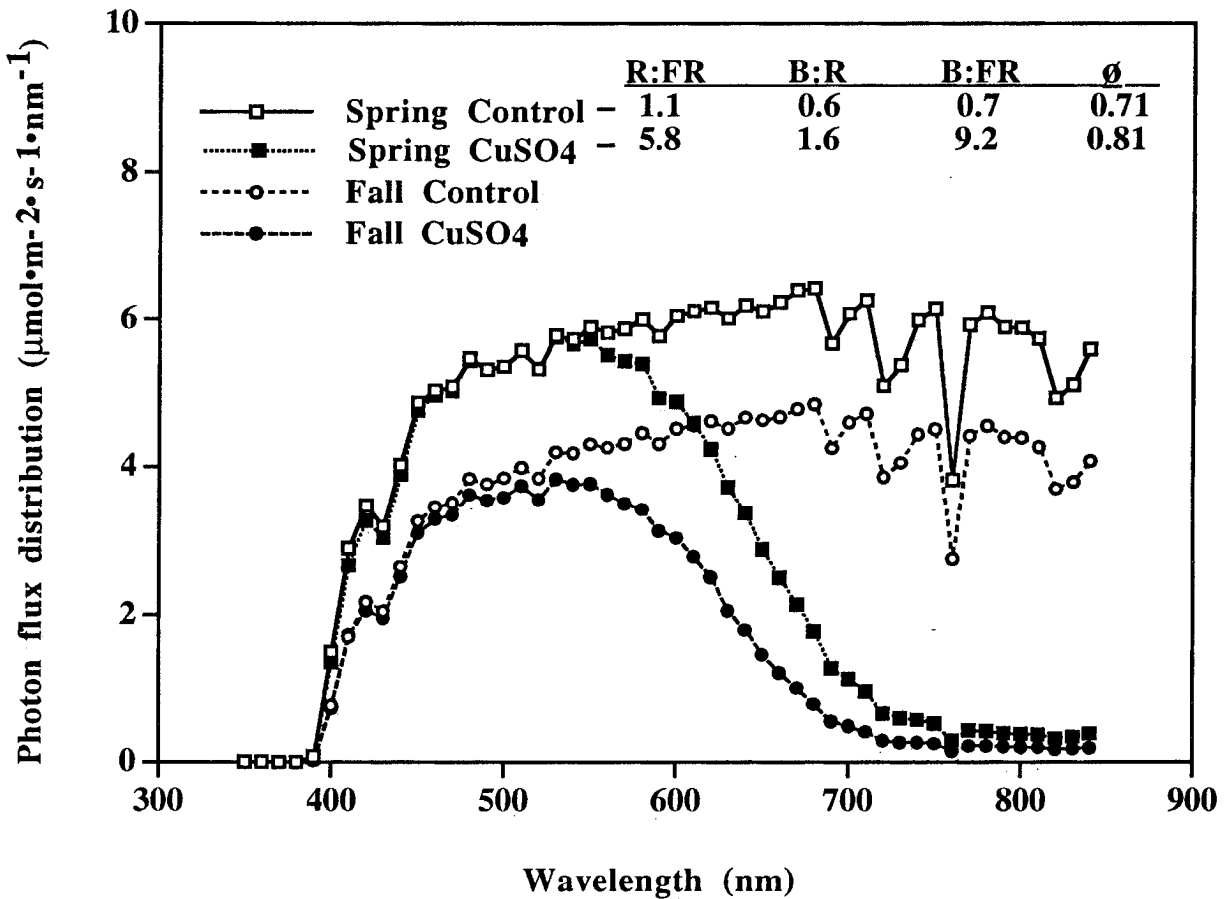


Fig. 1. Photon flux distribution, ratios of photon flux between 600–700 nm and 700–800 nm (R : FR) and of photon flux between 400–500 nm and 600–700 nm (B : R), and phytochrome photoequilibrium (ϕ) of light transmitted through 6% CuSO₄·5H₂O or unshaded control filter in fall and spring.

Light transmitted through CuSO₄ filters reduced leaf and stem total soluble sugar and starch concentrations. However, the magnitude of reduction was greater in spring than in fall (Table 3). For example, light transmitted through the CuSO₄ filter reduced leaf soluble sugar and starch concentration by ≈54% and ≈7170, respectively in spring-grown plants but only 29% and 24% in fall-grown plants. A similar trend was observed for stem soluble sugars in plants grown under CuSO₄ filters. The reduction of individual sugars also varied considerably under CuSO₄ filters (Table 3). In

leaves of spring grown plants, the reduction of glucose concentration (74%) was the greatest followed by sucrose (54%) and fructose (42%). In stems, however, reduction of unknown compound was the greatest (100%) followed by glucose (46%), sucrose (30%) and fructose (20%). A similar trend has lesser amounts of individual sugars was observed in fall but the magnitude was lower than that in spring. Stems of fall-grown plants had more starch deposition than spring-grown plants under both spectral filters. However, CuSO₄ filter did not significantly alter stem

Table 1. Influence of spectral filters and growing season on height (HT), internode length (INL), and leaf and stem dry weight (LDW and SDW) of 'Bright Golden Anne' chrysanthemum plants. Numbers in parentheses indicate the percentage of total leaf and stem dry matter.

Season [†]	Filter	HT (cm)	INL (cm)	LDW (g)	SDW (g)	LDA [‡] (g·cm ⁻²)	SDL [‡] (g·cm ⁻¹)
Spring	Control	37.0	1.8	3.8 (60)	2.5 (40)	0.0048	0.068
	CuSO ₄	26.7	1.4	2.9 (71)	1.2 (29)	0.0038	0.045
Summer	Control	44.8	1.9	4.8 (61)	3.1 (39)	0.0038	0.069
	CuSO ₄	35.5	1.4	3.3 (69)	1.5 (31)	0.0026	0.042
Fall	Control	33.5	1.7	2.3 (68)	1.1 (32)	0.0027	0.033
	CuSO ₄	23.0	1.2	1.7 (77)	0.5 (23)	0.0025	0.022
Season		***	NS	***	***	***	***
Filter		***	***	***	***	**	***
Season x filter		NS	NS	**	***	**	***

[†]Spring, summer, and fall plants were grown in March to May, June to August, and September to November 1991, respectively.

[‡]LDA = leaf dry weight/leaf area; SDL = stem dry weight/height.

*, **, *** Nonsignificant or significant at P = 0.05, 0.01, or 0.001, respectively.

starch concentration of fall-grown plants compared to that of control plants.

When expressed as total sugar content (concentration of sugar \times leaf or stem dry weight), the reduction of leaf and stem soluble sugar and starch contents by the CuSO₄ filter was greater than that of concentration (Table 4). Total leaf soluble sugar content of plants grown under the CuSO₄ filter was reduced by 65% and 47% in spring and fall-grown plants, respectively, compared to control plants. Stem total soluble sugars were reduced by 68% and 61% by the CuSO₄ filter in spring and fall-grown plants, respectively. Leaf and stem starch contents were reduced \approx 80% by CuSO₄ filter in spring-grown plants. Although, CuSO₄ filter did not significantly alter stem starch concentration of fall-grown plants compared to that of control plants, total starch content was reduced by 50%.

Discussion

Plant height was reduced by the light transmitted through CuSO₄ filter regardless of the growing season, suggesting that

alteration of greenhouse light quality may be used year-round provided that irradiance is sufficient to maintain photosynthesis. The height reduction under the CuSO₄ filters was mainly caused by decreased internode length, as the number of nodes was not significantly different between plants grown under control and CuSO₄ filters. Flowering was delayed by 1 to 2 weeks under the CuSO₄ filter depending on the season. The long delay in flowering of early fall plants could be attributed to the longer days in early fall compared to late fall plants. In addition to the delay in flowering, light transmitted through the CuSO₄ filter resulted in smaller flowers compared to those grown under the control filter. However, the number of flowers was not affected by light quality. A similar delay in flowering and smaller flowers was observed in miniature roses grown under CuSO₄ filters (Rajakpase and Kelly, 1994). The delay in flowering and smaller flowers could limit the use of greenhouse light quality for height control of plants intended for flower production.

Our results indicate that CuSO₄ filters reduced percentage dry matter accumulation into stems (on the average from 37% under

Table 2. Influence of spectral filters on flower development of 'Bright Golden Anne' chrysanthemum plants in early and late fall.

Season ^z	Filter	Time to flower ^y (days)	No. of flowers	Flower diam ^x (cm)	Flower fresh wt ^w (g)	Flower dry wt ^v (g)
Early fall	Control	59	14	7.8	3.5	0.36
	CuSO ₄	72	12	6.8	2.6	0.28
Significance		**	NS	*	*	*
Late fall	Control	54	9	10.2	4.6	0.45
	CuSO ₄	60	8	8.8	3.6	0.38
Significance		**	NS	**	**	**

^zEarly fall and late fall plants were grown in September and December 1991.

^yTime taken from beginning of treatment to first petal opening.

^xFlower diameter was recorded when a flower had four to six layers of open petals.

^wFresh and dry weight per flower.

^v***, **, * Nonsignificant or significant at $P = 0.05, 0.01$, or 0.001, respectively.

Table 3. Influence of spectral filters and growing season on leaf and stem carbohydrate concentration of 'Bright Golden Anne' chrysanthemum plants.

Season ^z	Filter	Sucrose	Glucose	Fructose	Unknown	TSS ^y	Starch
<i>Leaf</i>							
Spring	Control	17.1	6.5	11.9	--- ^x	35.5	49.9
	CuSO ₄	7.9	1.7	6.9	---	16.5	14.3
Fall	Control	7.9	---	7.3	---	15.2	45.0
	CuSO ₄	5.4	---	5.4	---	10.8	34.4
Season		***	***	***	---	***	***
Filter		***	***	***	---	***	***
Season x filter		***	***	**	---	***	***
<i>Stem</i>							
Spring	Control	23.4	25.3	18.1	20.4	66.8	6.2
	CuSO ₄	16.5	13.5	14.5	0	44.5	2.3
Fall	Control	15.5	1.9	8.5	2.3	25.9	23.3
	CuSO ₄	14.2	1.2	6.7	0.9	22.1	23.5
Season		***	***	***	***	***	***
Filter		**	***	**	***	**	**
Season x filter		*	***	NS	***	***	***

^zSpring and fall plants were grown in March to May and September to November 1991, respectively.

^yTSS = total soluble sugars; sum of sucrose, glucose, and fructose.

^xNot detectable.

^v***, **, * Nonsignificant or significant at $P = 0.05, 0.01$, or 0.001, respectively.

Table 4. Influence of spectral filters and growing season on total carbohydrate content in leaves and stems of 'Bright Golden Anne' chrysanthemum plants^a.

Season ^b	Filter	Sucrose	Glucose	Fructose	Unknown	TSS ^c	Starch
<i>Leaf</i>							
Spring	Control	65.0	24.7	45.2	---	134.9	189.6
	CuSO ₄	22.9	4.9	20.0	...	47.9	41.5
Fall	Control	18.2	---	16.8	...	35.0	103.5
	CUSO ₄ Z	9.2	...	9.2	---	18.4	58.5
Season		***	***	***		***	***
Filter		***	***	***		***	***
Season x filter		**	***	**		***	***
<i>Stem</i>							
Spring	Control	58.5	63.3	45.3	51.0	167.0	15.5
	CuSO ₄	19.8	16.2	17.4	0	53.4	2.8
Fall	Control	17.1	2.1	9.4	2.5	28.5	25.6
	CuSO ₄	7.1	0.6	3.4	0.5	11.1	11.8
Season		***	***	***	***	***	***
Filter		**	***	**	***	**	**
Season x filter		*	**	NS	***	***	***

^aTotal carbohydrate content = concentration × dry weight (of leaves or stems).

^bSpring and fall plants were grown in March to May and September to November 1991, respectively.

^cTSS = total soluble sugars; sum of sucrose, glucose, and fructose.

^WNot detectable.

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

control to 27% under CuSO₄filter) and increased dry matter accumulation into leaves (on the average from 63% under control to 72% under CuSO₄filter) suggesting that the translocation of photosynthates may be affected by light quality under CuSO₄ filters (Table 1). Changes in R: FR and ϕ cause redistribution of dry matter within a plant (Morgan and Smith, 1978). Kasperbauer (1987) reported that lowering R : FR increased photosynthate partitioning into shoots and developing seeds of soybean. Warrington and Mitchell (1976) reported that blue light sources increased the leaf: shoot ratio compared to red or balanced light sources.

The results of the present study showed that the light transmitted through CuSO₄filters resulted in reduced soluble sugars (sucrose, glucose, and fructose) and starch concentrations compared to control plants. Due to restricted growth of leaves and stems under CuSO₄filters, the percentage reduction of total carbohydrate content was greater than that of concentration. Similar to the present findings, light transmitted through CuSO₄filters resulted in a 40% and 65% reduction of leaf sucrose and starch concentration, respectively, in miniature roses (Rajapakse and Kelly, 1994). The reduction of carbohydrate pools under CuSO₄filters may be a result of reduced photosynthesis or increased respiration of plants grown under CuSO₄filters compared to control plants. It is also possible that more carbohydrates were partitioned into roots under the CuSO₄filter but this was not investigated. However, in a previous report, we have shown that light transmitted through CuSO₄filters reduced root dry weight by $\approx 30\%$ (Rajapakse and Kelly, 1992). In the present study, no attempts were made to examine the rates of photosynthesis or dark respiration. Our previous work with tomato transplants indicated that the rate of photosynthesis was not significantly different between plants grown under control and CuSO₄filters on a leaf area basis but the photosynthesis was lower in plants grown under CuSO₄filters than control filters when expressed on per unit chlorophyll basis (Benson, 1992). In support of our observation, Kasperbauer (1988) reported that tobacco plants exposed to high FR : R light had higher

photosynthetic rates per unit of chlorophyll or per mass of leaf, but photosynthetic rates were not different on leaf area basis.

Szasz and Barsi (1971) reported that red light stimulated sugar accumulation while blue light decreased sucrose and fructose content. Warrington and Mitchell (1976) also reported that red light increased leaf carbohydrate concentration of soybean and sorghum compared to blue or white light. The reduced carbohydrate status of plants grown under CuSO₄filters maybe explained by alteration of R : FR, B : R or ϕ values of transmitted light. However, with the filters used in the current research, it is difficult to determine which portion of the spectrum caused the effect under CuSO₄filter. Further work is required to test this hypothesis.

We conclude that filters with specific spectral characteristics can be used as alternative means of controlling height and producing compact plants in the greenhouses. However, the response of plants may vary with the growing season. Flowering should be evaluated with individual flower crops as flowering response may interact with the quality of light and the growing season. We have previously shown that CuSO₄filters slightly accelerated flowering in early spring-grown miniature rose plants but slightly delayed flowering in late spring and summer (Rajapakse and Kelly, 1994). The reduced carbohydrate levels of plants grown under CuSO₄filters could lead to adverse effects on postharvest quality following shipping or storage and the effect could be more pronounced if plants are exposed to high temperatures during shipping and storage. We have previously reported that miniature rose plants grown under CuSO₄filters had slightly higher percentage of yellow leaves after shipping at 4 or 1 SC than control plants (Rajapakse and Kelly, 1994).

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