THE EFFECTS OF LIGHT QUALITY AND TEMPERATURE ON THE GROWTH AND DEVELOPMENT OF GERANIUMS

ABDUL MATEEN KHATTAK[1], SIMON PEARSON[2], KHALID NAWAB[3], MUHAMMAD AZIM KHAN[4] AND KHAN BAHADAR MARWAT[4]

[1]*Department of Horticulture, KP Agricultural University Peshawar, Pakistan*
[2]*Winchester Growers Limited Herdgate Lane, Pinchbeck, Spalding, Lincs PE11 3UP, UK*
[3]*Department of Extension Education, KP Agricultural University Peshawar, Pakistan*
[4]*Department of Weed Science, KP Agricultural University Peshawar, Pakistan*

Abstract

The effect of light quality on the growth and development of geranium (cv. Century Rose) was examined in three different glasshouse temperatures i.e., 16ºC, 21ºC or 24ºC under natural light conditions. To alter light quality, five different colour filters i.e. blue and red absorbing (088), blue absorbing (101), two partially blue absorbing (109 and 110) and red absorbing (117) were used, with clear polythene as a control. Spectral filters as well as temperature considerably affected different growth parameters. Plant height, internode length, leaf area and flowering were significantly affected by the spectral filters as well as the temperature. In terms of the effects of the presumed photoreceptors, the data analysis indicated that plant height and internode length in geranium was regulated by the action of cryptochrome (blue acting photoreceptor) and not the phytochrome. However, time to flowering was affected by a combined action of phytochrome and cryptochrome, since the filters with high blue transmission and high phytochrome photoequilibrium resulted in early flowering. Simple models were created, through applying multiple regression technique, to predict the influence of spectral quality and temperature on plant height, internode length and time to flowering in geranium. The models could be applied to simulate the potential benefits of spectral quality and temperature in manipulation of growth and flowering in geranium. These will help in designing greenhouse cladding materials for regulation of plant growth in an environment friendly manner.

Introduction

Plants have the ability to respond to their surrounding environment and plan their growth and development according to the quality of perceived radiation. These plant responses are mainly comprehended by two groups of photoreceptors (phytochromes and cryptochromes), which regulate plant growth and development according the quality (wavelength) of prevailing radiation (Chen *et al*., 2004; Casal & Yanovsky, 2005; Franklin *et al*., 2005; Kim *et al*., 2004a,b). Phytochromes mainly perceive the red and far-red wavelengths of the ambient radiation (Smith, 1982, 1995), whereas, cryptochromes sense the ultraviolet (UV-A) and blue wavelengths of the spectrum (Meijer, 1968; Thomas & Dickinson, 1979, Ahmad & Cashmore, 1996). Research done during the present and past decades has shown that these two receptors (phytochrome and cryptochrome) organize different functions and mechanisms in plants (Smith & Whitelam, 1997; Franklin *et al*., 2003; 2005; Devlin *et al*., 2003; Chen *et al*., 2004; Valverde *et al*., 2004; Ausin *et al*., 2005; Casal & Yanovsky, 2005; Spalding & Folta, 2005).

Phytochrome is present in plants in two inter-convertible forms (Pr and Pfr), dependent upon the absorption of red or far-red radiation. Pr is the physiologically inactive form that absorbs red (R) light and Pfr is the far-red (FR) absorbing active form.

When Pr receives R light, it converts to Pfr and when Pfr receives FR, it reverts back to Pr form. Upon absorption of R or FR radiation, an equilibrium is set up between these two forms (Smith & Holmes, 1977; Attridge, 1990; Devlin *et al.*, 2003). This is known as phytochrome photoequilibrium (φ), which determines plants responses and is expressed as the ratio of Pfr (active) to total phytochrome (i.e. $\varphi = P_{fr} : P_{tot}$). So manipulating light quality could alter plant growth responses such as height and flowering.

In controlled environment production, this could be achieved through the use of spectral filters as cladding materials. The action of phytochrome could be manipulated to reduce plant height by developing filters, which remove far-red light, thereby increasing the proportion of the phytochrome pool in the Pfr (high φ) state (Van Haeringen *et al.*, 1998). Similarly, the effect of cryptochrome could be enhanced by increasing blue light in the prevailing natural radiation (Runkle & Heins, 2001). This can be achieved by fluorescing the UVA wavelength band of the incoming solar radiation to blue wavelengths using fluorescent cladding materials or using blue LEDs (Kim *et al.*, 2004a,b).

Plant growth control through altering light quality offers a better option over the chemical control, as it is environmentally friendly. Studies on chrysanthemum (a short day plant) showed prominent effects of φ and cryptochrome (McMahon *et al.*, 1991; Rajapakse *et al.*, 1992, 1993; Rajapakse & Kelly 1991, 1992, 1995; Khattak & Pearson, 1997, 2006; Khattak *et al.*, 1999, 2004). However, with antirrhinum (a long day plant), φ showed no effect on plant height but cryptochrome had strong effects, as the plant height decreased with the increase in blue transmission (Khattak & Pearson, 2005). This triggered the quest for further investigation to test the efficacy of spectral quality for a broader range of plants, including day neutral plants, as responses of these plants have been studied rarely. For this purpose, Geranium (*Pelargonium × hortorum*) was selected for the present study, which is a day neutral, as well as, an important ornamental plant. They were studied under similar conditions like chrysanthemums (Khattak & Pearson, 2006) and antirrhinums (Khattak & Pearson, 2005), so that their growth and development could be compared.

Material and Methods

Plant Material and treatments: The experiment was conducted in the greenhouses of the School of Biological Sciences, University of Reading UK. Geranium (*Pelargonium × hortorum*) cv. Century Rose (F1 Hybrid) seeds were purchased from Colegrave Seeds, Banbury, UK., and were sown into module trays with SHL (Sinclair Horticulture Ltd., Lincoln, UK) seed compost. The seeds were covered with a thin layer of vermiculite, watered and put in a growth room set at 15ºC and lit at 100 µmol m^{-2} s^{-1} with white fluorescent tubes for 16 hd^{-1}. The trays were kept moist until germination. The seed germinated six days from sowing and the seedlings were watered at three days intervals thereafter. Fifteen days after germination, the seedlings were moved from the growth room to glasshouse, kept for two days and then potted to 9cm pots containing a mixture of 75% potting compost and 25% perlite. Two days later, the plants were shifted to one of the three identical glasshouse compartments set at three different temperatures i.e., 15ºC, 20ºC and 25ºC. In each compartment there were six different spectral filters replicated twice. The filters were wrapped on wooden frames making chambers of 30cm width, 60cm length and 60cm height. Four plants were placed in each filter-covered chamber on capillary matting, and kept until flowering.

Spectral filters: Six different solid spectral filters were used, 5 obtained from Lee Filters Ltd., Andover, UK (filters 088, 101, 109, 110, 117), and 150μm clear low density polyethylene (LDPE) was used as a control. The filters were selected so that the analysis could test for independent effects of a blue acting receptor (cryptochrome), such that they would provide the same overall Photosynthetically Active Radiation (PAR) transmission and φ, but have different 'blue' transmissions. Other claddings were chosen that gave different φ. The actual spectral transmissions between 300 to 800nm for each of the materials was measured and then R:FR, B:R, B:FR ratios and φ were calculated (see Khattak & Pearson, 2006).

Data collection and analysis: The average temperatures recorded over the duration of the experiment were 16ºC, 21ºC, 24ºC (although the temperatures for the compartments were set at 15ºC, 20ºC and 25ºC respectively). The daily light integral received outside the greenhouse (measured with a Kipp solarimeter) averaged over the duration of the experiment was 6.7 $MJm^{-2}d^{-1}$. Different plant growth and development parameters were measured including plant height, internode length, leaf number, area and weight, stem weight and flowering. The data were analysed using two-factor analyses of variance technique. Multiple linear regression techniques were also applied to parameters like plant height, internode length and days to flowering to develop simple growth models. MSTATC software (Michigan State University, USA) was used for computing analysis of variance and least significant difference (LSD) tests, and MS Excel for regression analysis.

Results

Effects of spectral filters and temperature: A detailed comparison of the effects of spectral filters and temperature on the growth and development of geranium is given in Table 1.

Significant differences (p≤0.001) in plant height were found. Measurements of plant height (PH; table 1) at flowering show that the shortest (17.8cm) plants were found in the 117 (highest blue) treatment, while 101 (lowest blue) produced the tallest (24.2 cm) plants. The data suggested an evidence for the action of cryptochrome, since materials with the same PAR transmission and φ, but with different blue transmissions had significantly different (p≤0.001) plant heights. Furthermore, plant height decreased as the amount of blue increased in the cladding material. The control, 110, 109, and 088 materials (blue transmissions of 21.9, 18.3, 13.7 and 7.6% respectively) led to respective plant heights of 19.4, 20.0, 21.7 and 22.7cm. In order to see whether the plant height in geranium was only affected by blue transmission or the PAR also had a role, the data were plotted against the blue as well as the PAR transmission of the materials. In the case of blue (Fig. 1), there was a strong effect (r^2=0.9698; p≤0.001), as described above, where the height decreased linearly with the increase in blue transmission. However, in the case of PAR (Fig. 2), there was no significant (r^2=0.0024; p≤0.93) effect on PH. Thus the data from the experiment show that there was a strong effect of blue light on PH, suggesting a role of cryptochrome. However, φ did not appear to have any effect on PH in geranium. Plant height was significantly affected (p≤0.01) by temperature too. PH was greatest (23.4 cm) at 21ºC, while 16ºC and 24ºC led to shorter plants (18.9 and 20.7cm respectively).

Table 1. Effect of light quality and temperature on geranium growth and development.

	Plant height (cm)	Internode length (cm)	Number of leaves	Leaf area (cm²)	Leaf fresh weight (g)	Leaf dry weight (g)	Specific leaf weight (mg.cm⁻²)	Stem fresh weight (g)	Stem dry weight (g)	Days to flowering	Number of flowers
Filter											
Control	19.4	1.23	22.9	1443.5	51.59	4.65	3.23	20.35	2.12	108.7	45.2
088	22.7	1.64	18.4	1282.4	44.10	3.74	2.90	20.58	1.97	137.4	33.8
101	24.2	1.68	19.5	1403.2	50.79	4.39	3.18	23.17	2.08	132.9	28.3
109	21.7	1.41	21.4	1551.8	56.27	4.76	3.09	20.78	2.01	109.2	37.3
110	20.0	1.31	22.5	1434.2	53.18	4.56	3.18	19.60	2.00	113.2	36.2
117	17.8	1.25	19.4	1220.7	44.91	3.76	3.09	15.71	1.55	122.2	31.8
Significance	***	***	**	*	*	*	NS	*	*	**	***
LSD values	3.64	0.15	3.19	215.3	7.97	0.74		4.25	0.42	20.56	8.71
Temperature											
16°C	18.9	1.36	22.0	1316.4	52.31	4.49	3.42	21.84	2.28	127.7	46.7
21°C	23.4	1.53	20.6	1644.3	58.05	4.83	2.93	22.09	2.13	118.9	34.8
24°C	20.7	1.37	19.4	1207.2	40.05	3.61	2.99	16.16	1.45	115.1	24.8
Significance	**	***	*	***	***	***	**	***	***	*	***
LSD values	2.58	0.11	1.64	209.1	7.75	0.72	0.32	4.13	0.41	10.58	6.16
Interaction											
Filter × temperature	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	**

NS = Non significant

* = Significant at p≤0.05

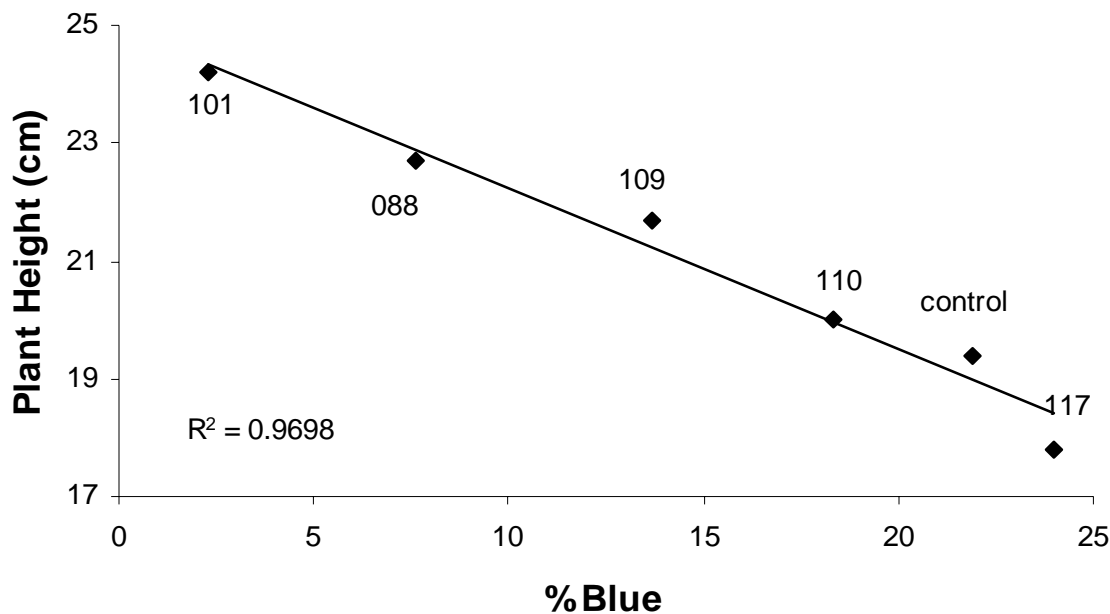** = Significant at p≤0.01

*** = Significant at p≤0.001

Fig. 1. The effect of blue (400-500nm) transmission on geranium plant height at flowering stage.
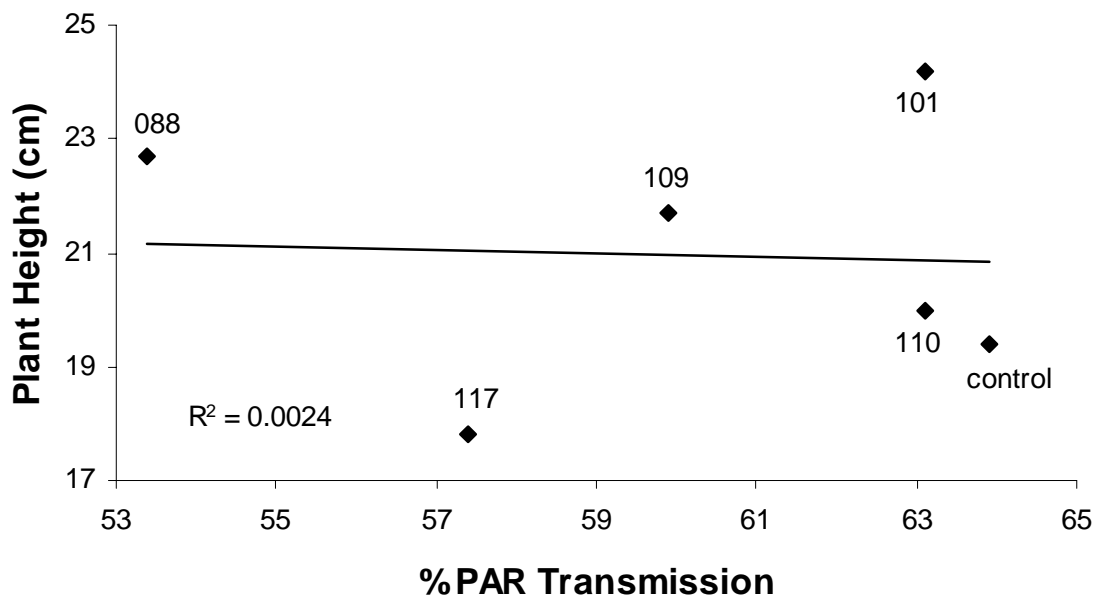

Fig. 2. The effect of PAR (photosynthetically active radiation; 400-700nm) transmission on geranium plant height at flowering stage.

Significant differences ($p \leq 0.001$) in internode lengths (IL; table 1) were found for different spectral filters. The responses followed a similar pattern as those of the plant height. This again shows the involvement of a cryptochrome, since the IL varied with the amount of blue transmitted regardless of φ. The effect of temperature on IL was almost identical to that of plant height. Longest internodes (1.53cm) were recorded at 21ºC and 16ºC and 24ºC exhibited shorter internodes, i.e., 1.36 and 1.37cm respectively.

The number of leaves (NL; table 1) was significantly ($p \leq 0.01$), affected by spectral quality. The measurements showed that maximum leaves (22.9) were obtained from the control, while filter 088 produced minimum leaves (18.4). It appears that there was an interaction between blue and φ. This was because the filters with high φ, as well as high blue (control, 109 and 110) produced more leaves than those with either low blue or low φ (i.e. 088, 101 and 117).

Temperature also affected the number of leaves significantly (p≤0.05). The lowest temperature (16ºC) produced maximum leaves (22.0), followed by 21ºC (20.6 leaves), while the highest temperature resulted in minimum (19.4) leaves. This was perhaps due to the earlier switch between vegetative to reproductive growth at the higher temperatures. It is also supported by the time to flowering data, which show that plants at higher temperatures flowered significantly earlier than those at the low temperatures.

In terms of leaf area (LA; table 1), there was no evidence for an effect of a blue photoreceptor (cryptochrome), since the control, 110, 109 and 101 filters (same φ but different levels of blue) had statistically similar leaf areas (1403.2 to 1551.8cm^2). There was a suggestion that low φ led to a reduced leaf area, since the 088 and 117 filters (both low φ) led to significantly (p≤0.001) lower leaf areas (1282.4 and 1220.7cm^2 respectively). Variations in temperature also affected the leaf area significantly (p≤0.001). The intermediate temperature (21ºC) resulted in plants with maximum leaf areas (1644.3cm^2). The other two temperatures i.e. the highest (24ºC) and lowest (16ºC) gave similar results, producing 26.58 and 19.94% smaller leaf areas respectively.

The spectral filters significantly (p≤0.001) affected both the leaf fresh and dry weights (LFW and LDW; table 1). The data followed a similar trend as those for leaf area. In all cases, the 088 and 117 filters (low φ) led to significantly (p≤0.05) lower weights than the other spectral materials. There may be a possible interaction between cryptochrome and φ, because the materials with either low φ (088 and 117) or low blue (101) led to 13.19 and 14.94% lesser leaf fresh and dry weights. On the other hand the materials with high φ and a proportionally high blue produced higher fresh and dry weights. Temperature also had an enormous effect on leaf weights. In both cases (i.e., leaf fresh and dry weights), the intermediate temperature (21ºC) produced the highest (p≤0.001) weights (58.05g LFW and 4.83g LDW) followed closely by the lowest temperature (16ºC) with 52.31g fresh and 4.49g dry weights. The highest temperature (24ºC) produced the lowest weights. Specific leaf weight represents the thickness of the leaf, as it is the leaf dry weight per unit leaf area. It is surprising that spectral filters had no effect on specific leaf weight (SLW; table 1). Variation in temperature, on the other hand, led to significantly different (p≤0.01) SLW. The SLW was highest at the lowest (16ºC) temperature and decreased with the increase in temperature. The warmest (24ºC) and intermediate (21ºC) temperatures produced 12.57% and 14.33% lower SLW respectively.

Stem fresh and dry weights (SFW and SDW; table 1) were significantly (p≤0.05) affected by spectral filters. In both cases, the 117 (high blue) material produced the lowest SFW (15.71g) and SDW (1.55g). The rest of the filters behaved similarly with the 101(low blue) producing the highest (23.17g) stem fresh weight. Temperature variation also affected both the SFW and SDW significantly (p≤0.001). The highest temperature (24ºC) produced the lowest, while the other two (16ºC) and (21ºC) gave similar SFW and SDW. At the highest temperature (24ºC), the SFW was 26% and SDW was 31% lower than the other two temperatures.

In terms of flowering (DF; table 1), the materials with high φ and proportionally high blue (control, 110 and 109; % blue transmission of 21.9, 18.3 and 13.7 respectively) led to early flowering. Whilst the material with the same φ but lowest blue transmission (101; 2.3% blue) flowered significantly (p≤0.001; 20 to 24 days) later than the other high

φ materials, suggesting a role of cryptochrome in flowering. The 088 and 117 (both having low φ) took maximum days to flowering (29 and 14 days respectively compared to control), which suggest that a decrease in φ can also result in delayed flowering. Temperature also affected the time to flowering in geraniums. Plants at the lowest temperature (16ºC) took significantly (p≤0.05) longer to flower (127.7 days) followed by the intermediate temperature (21ºC), while the highest temperature (24ºC) led to the earliest flowering in geranium (115 days).

Spectral filters also significantly (p≤0.001) affected the number of flowers (NF; table 1). Maximum flowers (45.2) were observed under control (high φ; high blue) and the flowers were minimum (28.3) under 101 (high φ; lowest blue) filter, suggesting a role of cryptochrome. The effect of temperature was also enormous (p≤0.001), with the lowest (16ºC) temperature producing maximum (46.7) flowers. The number decreased (to 34.8 and 24.8) with the increase in temperature (to 21ºC and 24ºC respectively).

Simulation of the effects of spectral filters and temperature: The data were also analysed using multiple regression analysis to develop simple quantitative relationships, which could be used to model and forecast plant height, internode length and time to flowering for geranium plants grown under any spectral quality.

Plant height (PH) was found to be a function of the amount of blue light (B) and temperature (T); and the phytochrome photoequilibrium state (φ) having no significant effect, thus;

$$PH = 8.31\pm2.92 - 13.28\pm1.98 \ \textbf{B} + 0.90\pm0.16 \ \textbf{T} \qquad (r^2 = 0.84, \ 15 \ \text{d.f.})$$

The high r^2 (0.84) indicates that the model provided an excellent fit to the data.

For internode length (IL), the amount of blue (B) and temperature (T) had significant effects, but the phytochrome photoequilibrium (φ) showed no effect;

$$IL = 0.82\pm0.29 - 1.07\pm0.15 \ \textbf{B} + 0.05\pm0.018 \ \textbf{T} \qquad (r^2 = 0.80, \ 15 \ \text{d.f.})$$

The high r^2 in both cases shows that the model represents a good fit to the data.

Time to flowering (DF) was found to be a function of the amount of blue (B) present, the phytochrome photoequilibrium (φ) and temperature (T), Thus,

$$DF = 314.3\pm30.8 - 70.6\pm11.4 \ \textbf{B} - 202.3\pm39.4 \ \varphi - 1.59\pm0.48 \ \textbf{T} \qquad (r^2 = 0.80, \ 14 \ \text{d.f.})$$

The high r^2 in this case as well indicates that the model provides a good fit.

Discussion

The data presented here show clearly that spectral quality has substantial effect on the growth and development of geranium. There was a strong effect of blue light on geranium plant height confirming the presence of cryptochrome (photoreceptor acting in the blue region of the spectrum). Significant reductions were found in the height of geranium with the increase in blue transmission confirming previous studies on other species (Mortensen & Stromme, 1987; Thomas & Dickinson, 1979; Young, 1981; Mortensen, 1990; Runkle & Heins, 2001). However, it was surprising that phytochrome

photoequilibrium (φ) did not appear to have any effect on the plant height of geranium. Similar results were found for antirrhinum (Khattak & Pearson, 2005) where plat height was strongly affected by blue transmission but φ had no effect. Nevertheless, these results are in contrast to (Khattak & Pearson, 1997; 2006) who observed that chrysanthemum plant height was strongly affected by φ as well as blue light. This might be due to species sensitivity because, some plants are more sensitive to blue, some to φ, while for some there is an interaction between blue and φ (Casal, 1994).

The 088 and 117 materials (having low φ) produced the lowest leaf areas and leaf fresh and dry weights for geranium. Same effects were found for chrysanthemum (Khattak & Pearson, 1997; 2006), confirming that the effect was due to phytochrome. Variation in temperature showed enormous effects on plant growth and flowering in geranium. The plant height and internode length increased as the temperature increased from 16ºC to 21ºC, but then decreased with increase in temperature. These results are in consistence with Mortensen & Larsen (1989), who observed a decrease in shoot length at high temperature (above 22ºC) for some plants.

The data on time to flowering showed that light quality as well as temperature had an effect on geranium flowering. The time to flowering was affected by both the blue light and phytochrome, although phytochrome did not show any effect on plant height. This suggests an interaction between phytochrome and cryptochrome activity and to achieve shorter desirable plants as well as early flowering in geranium, spectral material with high blue transmission as well as high φ should be selected. Similar effects were observed in chrysanthemum (Khattak & Pearson, 2006), where flowering was affected by both cryptochrome and φ. However, these results in contrast to antirrhinum (Khattak & Pearson, 2005), where cryptochrome and φ had no effects on flowering time. It means that further investigation is needed on other species with varying spectral environments. The interaction between light quality and temperature were largely not significant, suggesting that the spectral filters will operate effectively over a wide temperature range.

References

Ahmad, M. and A.R. Cashmore. 1996. Seeing blue: the discovery of cryptochrome. *Plant Mol. Boil.,* 30: 851-861.

Attridge, T.H. 1990. Light and plant Responses. Edward Arnold, London, UK.

Ausin, I., C.A. Blanco, J.M.M. Zapater. 2005. Environmental regulation of flowering. *Int. J. Dev. Biol.,* 49: 689-705.

Casal, J.J. 1994. Stem extension responses to blue light require Pfr in tomato seedlings but are not reduced by low phytochrome levels of the aurea mutant. *Physioligia Plantarum,* 91: 263-267.

Casal, J.J. and M.J. Yanovsky. 2005. Regulation of gene expression by light. *Int. J. Dev. Biol.,* 49: 501-511.

Chen, M., J. Chory and C. Fankhauser. 2004. Light signal transduction in higher plants. *Annu. Rev. Genet.,* 38: 87-117.

Devlin, P.F., M.J. Yanovsky and S.A. Kay. 2003. A genomic analysis of the shade avoidance response in Arabidopsis. *Plant Physiol.,* 133: 1617-1629.

Franklin, K.A., U. Preakelt, W.M. Stoddart, O.E. Billingham, K.J. Halliday and G.C. Whitelam. 2003. Phytochromes B, D and E act redundantly to control multiple physiological responses in Arabidopsis. *Plant Physiol.,* 131: 1340-1346.

Franklin, K.A., V.S. Larner and G.C. Whitelam. 2005. The signal transducing photoreceptors of plants. *Int. J. Dev. Biol.,* 49: 653-664.

Khattak, A.M. and S. Pearson. 1997. The effects of light quality and temperature on the growth and development of chrysanthemums cvs. Bright golden Ann and Snowdon. *Acta Hort.,* 435: 113-122.

Khattak, A.M. and S. Pearson. 2005. Light quality and temperature effects on Antirrhinum growth and development. *J. Zhejiang Univ. Sci.,* 6B(2): 119-124.

Khattak, A.M. and S. Pearson. 2006. Spectral filters and temperature effects on the growth and development of chrysanthemums under low light integral. *J. Plant Growth Reg.,* 49(1): 61-68.

Khattak, A.M., S. Pearson and C.B. Johnson. 2004. The effects of far red filters and plant density on the growth and development of chrysanthemums. *Scientia Hort.,* 102(3): 335-341.

Khattak, A.M., S. Pearson, and C.B. Johnson. 1999. The effects of spectral filters and nitrogen dose on the growth of chrysanthemum (*Chrysanthemum morifolium* Ramat. Cv. Snowdon). *J. Hort. Sci. and Biotech.,* 74(2): 206-212.

Kim, H.H., G.D. Goins, R.M. Wheeler and J.C. Sager. 2004a. Green-light supplementation for enhanced lettuce growth under red- and blue-light-emitting diodes. *Hort. Sci.,* 39(7): 1617-1622.

Kim, H.H., G.D. Goins, R.M. Wheeler and J.C. Sager. 2004b. Stomatal conductance of lettuce grown under or exposed to different light quality. *Ann. Bot.,* 94: 691-697.

McMahon, M.J., J.W. Kelly and D.R. Decoteau. 1991. Growth of *Dendranthema × Grandiflorum* (Ramat.) Kitamura under Various Spectral Filters. *J. Amer. Soc. Hort. Sci.,* 116(6): 950-954.

Meijer, G. 1968. Rapid growth inhibition of gherkin hypocotyls in blue light. *Act. Bot. Neerl.,* 17: 9-14.

Mortensen, L.M. 1990. Effects of temperature and light quality on growth and flowering of *Begonia hiemalis* Fotsch. and *Campanula isophylla* Moratti. *Scientia Hort.,* 44: 309-314.

Mortensen, L.M. and E. Stromme. 1987. Effects of light quality on some greenhouse crops. *Scientia Hort.,* 33: 27-36.

Mortensen, L.M. and G. Larsen. 1989. Effects of temperature and light quality on growth of six foliage plants. *Scientia Hort.,* 39: 149-159.

Rajapakse, N.C. and J.W. Kelly. 1991. Influence of $CuSO_4$ filters and exogenous gibberellic acid on growth of *Dendranthema grandiflorum* (Ramat.) Kitamura 'Bright Golden Ann'. *J. Plant growth Reg.,* 10: 207-214.

Rajapakse, N.C. and J.W. Kelly. 1992. Regulation of chrysanthemum growth by spectral filters. *J. Amer. Soc. Hort. Sci.,* 117(3): 481-485.

Rajapakse, N.C., M.J. McMahon and J.W. Kelly. 1993. End of day far-red light reverses height reduction of chrysanthemum induced by $CuSO_4$ spectral filters. *Scientia Hort.,* 53: 249-259.

Rajapakse, N.C., R.K. Pollock, M.J. McMahon, J.W. Kelly and R.E. Young. 1992. Interpretation of light quality measurements and plant response in spectral filter research. *Hort. Sci.,* 27(11): 1208-1211.

Rakapakse, N.C. and J.W. Kelly. 1995. Spectral filters and growing season influence growth and carbohydrate status of chrysanthemum. *J. Amer. Soc. Hort. Sci.,* 120(1): 78-83.

Runkle, E.S. and R.D. Heins. 2001. Specific functions of red, far red, and blue light in flowering and stem extension of long-day plants. *J. Amer. Soc. Hort. Sci.,* 126(3): 275-282.

Smith, H. 1982. Light quality, photoperception, and plant strategy. *Ann. Rev. Plant. Physiol.,* 33: 481-518.

Smith, H. 1995. Physiological and ecological function with in the phytochrome family. *Ann Rev. Plant Physiol. Plant Mol. Biol.,* 46: 289-315.

Smith, H. and G.C. Whitelam. 1997. The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant Cell and Environ.,* 20: 840-844.

Smith, H. and M.G. Holmes. 1977. The function of phytochrome in the natural environment: III. Measurement and calculation of phytochrome photoequilibrium. *Photochem and Photobiol.,* 25: 547-550.

Spalding, E.P. and K.M. Folta. 2005. Illuminating topics in plant photobiology. *Plant Cell and Environ.,* 28: 39-53.

Thomas, B. and H.G. Dickenson. 1979. Evidence for two photoreceptors controlling growth in de-etiolated seedling. *Planta,* 146: 545-550.

Valverde, F., A. Mouradov, W. Soppe, D. Ravenscroft, A. Samach and G. Coupland. 2004. Photoreceptor regulation of CONSTANS protein in photoperiodic flowering. *Sci.,* 303: 1003-1006.

Van Haeringen, C.S., J.R. West, F.J. Davis, A. Gilbert, P. Hadley, S. Pearson, A.E. Wheldon and R.G.C. Henbest. 1998. The development of solid spectral filters for the regulation of plant growth. *Photochem Photobiol.,* 62: 119-128.

Young, J.E. 1981. Light quality and stem growth in *Impatiens parviflora* DC. *New Phytol.,* 89: 47-59.