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Thermomorphogenic and Photomorphogenic Control of Stem Elongation in *Fuchsia* Is Not Mediated by Changes in Responsiveness to Gibberellins

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Abstract. Stem elongation in *Fuchsia* × *hybrida* was influenced by cultivation at different day and night temperatures or in different light qualities. Internode elongation of plants grown at a day (25°C) to night (15°C) temperature difference (DIF+10) in white light was almost twofold that of plants grown at the opposite temperature regime (DIF−10). Orange light resulted in a threefold stimulation of internode elongation compared with white light DIF−10. Surprisingly, internode elongation in orange light was similar for plants grown at DIF−10 and DIF+10. Flower development was accelerated at DIF−10 compared with DIF+10 in both white and orange light. To examine whether the effects of DIF and light quality on shoot elongation were related to changes in gibberellin metabolism or plant sensitivity to gibberellins (GAs), the stem elongation responses of paclobutrazol-treated plants to applied gibberellins were determined. In the absence of applied gibberellins paclobutrazol (>0.32 μmol plant^{-1}) strongly retarded shoot elongation. This inhibition was nullified by the application of about 10–32 nmol of GA_1, GA_4, GA_9, GA_{15}, GA_{19}, GA_{20}, GA_{24}, or GA_{44}. The results are discussed in relation to possible effects of DIF and light quality on endogenous gibberellin levels and gibberellin sensitivity of fuchsia and their effects on stem elongation.

Key Words. Stem elongation—*Fuchsia*—DIF—Light quality—Gibberellin responsiveness—Photomorphogenesis—Thermomorphogenesis

Stem length and the extent of lateral branching are important morphogenic characteristics contributing to the ornamental value of pot and bedding plants. To control stem elongation and to acquire the desired plant stature, the use of chemical growth regulators (e.g. paclobutrazol, chloromequat, daminozide) is common practice in horticulture. However, in many countries the use of chemical growth retardants in horticulture is or will soon be restricted by legislation. Therefore, more environment-friendly alternatives for chemical growth regulation such as temperature and light quality are being studied (Erwin and Heins 1995, Mortensen and Strømme 1987) and have been the major topic of several symposia organized by the International Society for Horticultural Science (Blacquière and Bakker 1992, Cockshull et al. 1997, Hendriks and Ueber 1995, Moe and Mortensen 1992). It has been shown for many plant species that stem elongation can be reduced by growing the plant at a lower day than night temperature (for reviews, see Erwin and Heins 1995, Myster and Moe 1995). With respect to light quality, the amount of blue light and the ratio of red to far-red light perceived by the plants may have a profound effect on stem elongation and lateral branching (Smith 1994). Generally, lower amounts of blue and lower ratios of red to far-red light increase plant height by enhancing internode elongation. Wavelength-selective screens (Mortensen and Strømme 1987, Rajapakse and Kelly 1992) or supplementary lighting with specific wavelengths (Roberts et al. 1993) may be used to control plant development. Although it has been shown that both DIF (difference between day and night temperature) and light quality can be used to control plant stature satisfactorily in some plant species, in most horticultural species their effect is not enough to substitute for chemical growth regulation fully, and their use is limited to certain periods of the year.

Understanding the biochemical mechanism by which DIF and light quality control stem elongation could be

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Abbreviations: DIF, difference between day and night temperature; GA, gibberellin; DMF, *N*,*N*-dimethylformamide

helpful in developing alternatives for the chemical retardation of stem growth. In a few plant species phytochrome-mediated effects of red and far-red light on stem elongation have been shown to involve changes in gibberellin (GA) biosynthesis (Martínez-Garciá and Garciá-Martínez 1992, Reid et al. 1990). The chemicals used in horticulture to reduce stem elongation are inhibitors of GA biosynthesis, and their inhibiting effect is restored by the application of GAs. Therefore, GAs are assumed to be involved in the regulation of stem elongation by both DIF and light quality (Erwin and Heins 1995, Myster and Moe 1995). On the basis of data obtained for a number of plant species, GA metabolism in higher plants is assumed to proceed through two major biosynthetic pathways: the early 13-hydroxylation pathway ($GA_{53}\rightarrow GA_{44}\rightarrow GA_{19}\rightarrow GA_{20}\rightarrow GA_1$) and the non-13-hydroxylation pathway ($GA_{12}\rightarrow GA_{15}\rightarrow GA_{24}\rightarrow GA_9\rightarrow GA_4$) (Sponsel 1995). Depending on the plant species either GA_1 or GA_4 has been demonstrated to control stem elongation.

In the present study, fuchsia, a bedding plant in which stem elongation has been shown to respond to both DIF (Erwin et al. 1991, Tangerås 1979) and light (Erwin et al. 1991, Vince-Prue 1977), was used as a model plant. The aim of our investigations was to examine whether changes in stem elongation of pot and bedding plants by differences in light quality and DIF are mediated by changes in GA metabolism and thus by endogenous GA levels or by changes in plant responsiveness toward GAs.

Materials and Methods

Plant Material and Growth Conditions

Rooted cuttings of *Fuchsia hybrida* Dollarprinzessin were planted in 0.08-liter plastic pots in a 60% peat soil, 30% peat, 10% river sand mixture supplied with 0.75 kg m^{-3} NPK mix (14:16:18) and 3 kg m^{-3} lime. The experiment was started by pruning the cutting above the most basal pair of leaves and transferring the plants into climate-controlled growth chambers. The day/night temperature difference was set to 25/15°C (DIF+10, i.e. day-night temperature difference = 10°C) or 15/25°C (DIF−10). Photosynthetic photon flux at the plant level was 120 μmol m^{-2} s^{-1} for 12 h day^{-1} (Philips TL58HF/84 cool white fluorescent lamps). Blue-deficient, orange-colored light was obtained by filtering the light of the white fluorescent lamps through one layer of an orange acetate filter that transmitted only wavelengths above 500 nm (for spectral characteristics, see Maas et al. 1995). Air humidity in the growth chambers was kept at 75 ± 0.5% at 25°C and at 54 ± 0.5% at 15°C to maintain a constant vapor pressure deficit of 0.79 kPa. The soil in the pots was kept moist by applying tap water regularly to the irrigation mat on which the pots were placed.

Application of Growth Regulators

At the start of each experiment plants were given a single application of 0 (control plants) or 1.0 μmol of paclobutrazol (Bonzi, ICI Holland BV, Rotterdam) as a 10-mL drench to the soil at the base of the plant. Preliminary experiments (Maas and van Hattum 1997) showed that this amount of paclobutrazol resulted in maximum inhibition of stem elongation of the newly formed lateral shoots without causing necrosis of the subtending leaves from the original cutting.

GAs (pure preparations purchased from Prof. L. N. Mander, Research School of Chemistry, Canberra, Australia) were dissolved in 50% (v/v) ethanol and were applied as a single 5-μL droplet to the fresh cut surface of the stem above the basal pair of leaves. Control plants received only 5 μL of 50% ethanol.

Growth Measurements

Plants were harvested 4 weeks after the start of the treatments. At harvest both lateral shoots were divided into leaves and stems. The length of the stems and the fresh and dry weights (after 24 h at 80°C) of stems and leaves were determined. Specific leaf area was calculated from the area and fresh weight of discs punched out of the leaves.

Chlorophyll Content

The chlorophyll of about 20 mg of fully expanded leaves was extracted in 5 mL of *N,N*-dimethylformamide (DMF) for 24 h at 4°C in the dark. Chloropyll *a* and *b* content was calculated from the extinction value of the extract at 647 and 664.5 nm according to the formulas given by Inskeep and Bloom (1985).

Results

Effects of DIF and Light Quality on Shoot Morphogenesis

Various morphogenic characteristics of fuchsia were affected by light quality and DIF (Table 1). In white light, shoots grown at DIF−10 were about 45% shorter than at DIF+10. Shoots grown in orange light were 2.5 and 1.5 times longer at DIF−10 and DIF+10, respectively, than in white light, and there was no significant difference in length between the temperature treatments. Increases in shoot length were paralleled by increases in stem dry weight. Leaf dry weight was higher in plants grown at DIF+10 than at DIF−10, but it was not affected significantly by light quality. Consequently, dry weight distribution within the shoots, expressed as the dry weight ratio of leaves to stem, was influenced strongly by DIF in white light but not in orange light. The highest ratio was found for shoots grown in white light at DIF−10 and the lowest for shoots grown in orange light. Specific stem dry weight was similar for shoots grown in white light at both DIF treatments and for shoots grown in orange light at DIF−10, but it was about 30% higher in plants grown at DIF+10 in orange light. Finally, no effect of DIF and light quality was observed for the dry matter content of leaves and stems and for specific leaf area.

In one experiment plants were grown for an additional 4 weeks at DIF−10 or DIF+10 in white or orange light. In both white and orange light plants grown for 8 weeks at DIF−10 showed fully developed flower buds, whereas those grown at DIF+10 did not yet show any sign of

Table 1. Effects of a day-night temperature difference of +10°C (DIF+10) or −10°C (DIF−10) on the length, dry weight (DW), dry matter content (DMC), specific stem weight, specific leaf area (SLA), and leaf chlorophyll content of shoots of *Fuchsia* × *hybrida* grown for 4 weeks in 120 μmol m^{-2} s^{-1} white or orange light. Data represent the averages of six (length), four (chlorophyll), or three measurements ± S.D.

	White light		Orange light	
	DIF−10	DIF+10	DIF−10	DIF+10
Shoot length (mm)	82 ± 8	149 ± 26	208 ± 13	232 ± 25
Stem DW (mg)	42 ± 5	81 ± 24	108 ± 14	159 ± 6
Leaf DW (mg)	236 ± 39	304 ± 70	234 ± 19	349 ± 11
Shoot DW (mg)	278 ± 43	385 ± 94	341 ± 32	508 ± 10
Leaf: stem DW ratio	5.6 ± 0.6	3.8 ± 0.3	2.2 ± 0.1	2.2 ± 0.1
Specific stem DW (mg mm^{-1})	0.51 ± 0.02	0.54 ± 0.08	0.52 ± 0.05	0.69 ± 0.08
Stem DMC (%)	6.7 ± 0.2	6.9 ± 0.1	6.8 ± 0.7	6.9 ± 0.2
Leaf DMC (%)	9.7 ± 0.6	9.4 ± 0.1	9.1 ± 0.5	9.9 ± 0.3
SLA (cm^2 g^{-1} FW)	50 ± 2	53 ± 4	57 ± 3	54 ± 2
Chlorophyll *a* (mg g^{-1} FW)	1.29 ± 0.07	1.89 ± 0.03	1.33 ± 0.06	1.85 ± 0.08
Chlorophyll *b* (mg g^{-1} FW)	0.33 ± 0.02	0.59 ± 0.01	0.37 ± 0.03	0.61 ± 0.02

flower development (Fig. 1). Plants treated with paclobutrazol also frequently showed young flower buds (<3 mm) after 4 weeks of growth, whereas no sign of flower bud development was observed for plants given no paclobutrazol or plants given paclobutrazol followed by GA (data not shown).

The levels of chlorophyll *a* and *b* in the leaves of fuchsia were affected significantly by the day/night temperature regime at which the plants were grown (Table 1). At DIF−10 the levels of chlorophyll *a* and *b* were, respectively, about 30 and 40% lower than those at DIF +10. Chlorophyll levels were not affected by the quality of the light in which the plants were grown (Table 1).

Plant Responsiveness to Gibberellins

Different amounts of various types of GAs were applied to fuchsia plants treated with or without the GA biosynthesis inhibitor paclobutrazol. Four weeks later the length of both lateral shoots was measured. Application of paclobutrazol reduced the elongation of the shoots by more than 85% at both light qualities and DIF treatments compared with their accompanying control plants (Fig. 2*A*). Shoot elongation of paclobutrazol-treated plants could be restored by applying GA_1, GA_4, GA_9, GA_{15}, GA_{19}, GA_{20}, GA_{24}, or GA_{44}. A linear relationship was observed between shoot length and the logarithm of the amount of applied GAs between 0 and 100 nmol (Fig. 3). The average regression coefficients for this relationship were 0.76 (GA_1), 0.89 (GA_4), 0.85 (GA_9), 0.81 (GA_{15}), 0.91 (GA_{19}), 0.93 (GA_{20}), 0.91 (GA_{24}), and 0.94 (GA_{44}), and for each type of GA the regression coefficient was not affected significantly by either DIF or light quality. Application of GA_1 to plants not treated with paclobutrazol had no or only a small stimulating effect on stem elongation of plants grown in orange light and abolished the differences in shoot length between plants grown at DIF−10 and DIF+10 in white light as well as those between white and orange light at amounts ⩾32 nmol $plant^{-1}$ (Fig. 2*B*).

For most of the tested GAs, plant responsiveness, defined as the slope of the linear regression line fitted to these dose-response data, was not affected significantly by light quality or DIF treatment (Fig. 4). On average, responsiveness was slightly lower for the non-13-hydroxylated GAs (15, 24, 9, and 4) than for the 13-hydroxylated GAs (44, 19, 20, and 1). Of the latter group of GAs the highest responsiveness was noted for GA_{19}, especially when the plants were grown in orange light (Fig. 4). Application of up to 100 nmol of GA_8 did not increase the shoot length of paclobutrazol-treated plants significantly (data not shown).

Discussion

Excessive stem elongation in plants grown in orange light or in white light at positive DIF did not simply result from longer but thinner internodes. The specific stem weight, that is, the dry weight per unit stem length, was similar for plants grown in white light at DIF−10 or DIF+10 and grown in orange light at DIF−10. Orange lighting at DIF+10 even resulted in longer and thicker stems as specific stem dry weight was about 30% higher than that of plants grown under the other conditions. The relative amount of total shoot dry weight allocated to the stem increased with the extent of stem elongation, resulting in a decrease in leaf to stem dry weight ratio. Similar effects of orange light on internode elongation and dry weight distribution between leaves and stem were observed in *Rosa* × *hybrida* (Maas and Bakx 1995)

Fig. 1. *F. hybrida* Dollarprinzessin after an 8-week cultivation in orange or white light at DIF−10 or DIF+10.

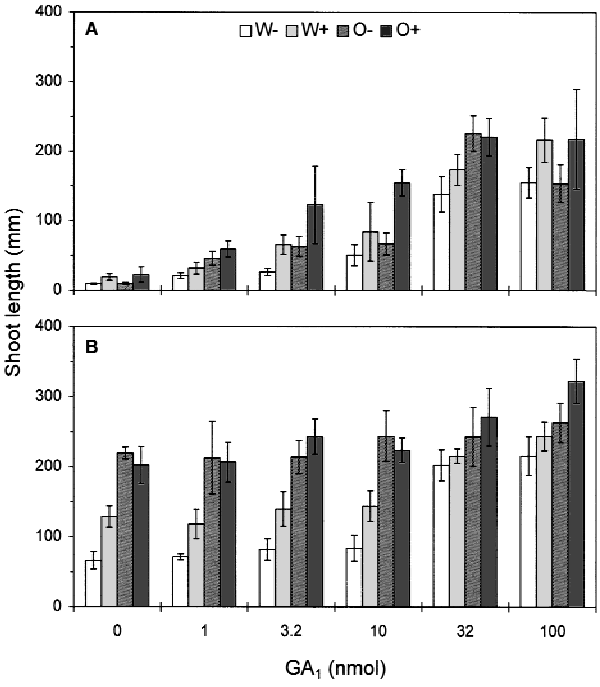

Fig. 2. Effects of GA_1 application on the length of lateral shoots of *F. hybrida* Dollarprinzessin grown for 4 weeks in white (*W*) or orange light (*O*) at DIF−10 (−) or DIF+10 (+). At the start of the experiments plants were given 1 μmol (*A*) or 0 (*B*) μmol of paclobutrazol to the roots. Shoot lengths represent the averages of three measurements with three plants each ± S.D.

and *Phaseolus vulgaris* (Maas et al. 1995). However, the enhanced internode elongation and decreased leaf to stem dry weight ratio of fuchsia grown in white light at DIF+10 compared with DIF−10 was accompanied by increases in both leaf and stem dry weights, whereas in *Phaseolus* it occurred almost completely at the expense of leaf dry weight. Contrary to light quality, DIF not only affects plant height significantly but also total shoot growth. After 4 weeks at DIF−10, the total shoot biomass of fuchsia was about 30% less than at DIF+10, which was most likely the result of both a lower rate of photosynthesis, caused by the lower chlorophyll levels and day temperatures and a higher rate of respiration during the night, caused by the higher night temperature.

Erwin et al. (1994) demonstrated that the effect of DIF on stem elongation of *Lillium longiflorum* resulted from changes in cell elongation but not cell division. Darkness-induced enhancement of internode elongation in *P. vulgaris* was also attributed solely to an increased cell expansion rather than cell number (Morris and Arthur 1984). However, GA-induced stem elongation in rosette plants and the elongation response of some monocots were also partly caused by increases in cell division rates (see Métraux 1987).

The biochemical mechanisms by which DIF and light quality affect stem elongation are not known. The endogenous plant growth regulator GA_1 has been shown to

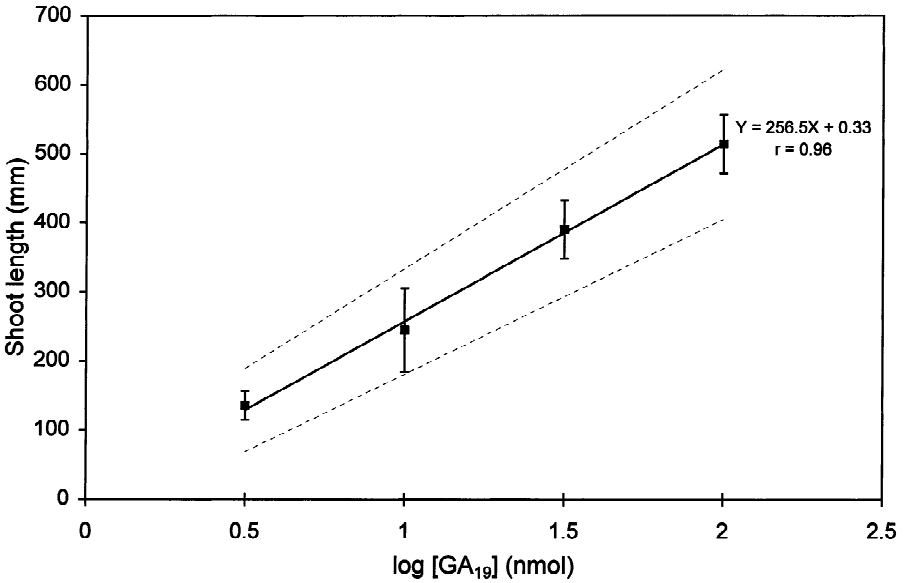

Fig. 3. Shoot length of *F. hybrida* Dollarprinzessin supplied with 1 μmol of paclobutrazol and with different amounts of GA_{19} determined after a growth period of 4 weeks in orange light at DIF−10. Shoot lengths represent the averages of three measurements with three plants each ± SD. The linear regression line fitted through the individual shoot length data and its 95% confidence interval are shown as the *solid* and *dotted lines*, respectively.

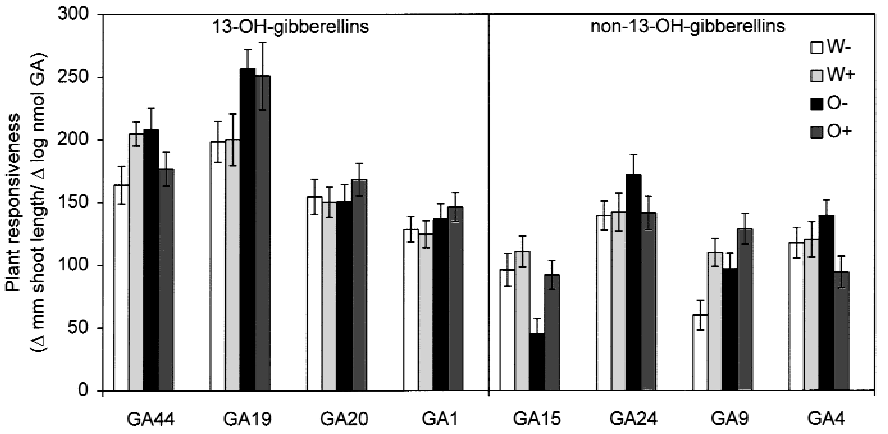

Fig. 4. Plant responsiveness of paclobutrazol-treated *F. hybrida* Dollarprinzessin grown at DIF−10 (−) or DIF (+) in white (*W*) or orange light (*O*) to a number of GAs of the early 13-hydroxylation and the non-13-hydroxylation pathways. Responsiveness was calculated as the slope of the linear regression line fitted through the data of shoot length plotted against the logarithm of the amount of gibberellins applied (see Fig. 3). The *error bars* represent the 95% confidence interval of the calculated regression lines.

be of great importance for stem elongation, and its synthesis has been found to be influenced by both temperature (Hazebroek et al. 1993), light quality (Martínez-Garciá and Garciá-Martínez 1992), irradiance level (Gawronska et al. 1995), and photoperiod (Olsen et al. 1995, Zeevaart and Gage 1993). The reduced internode elongation of the dwarf *le* mutant of pea was shown to result from a reduced GA_1 synthesis caused by an inhibition of the 3-β-hydroxylation of GA_{20} into GA_1 (Ross et al. 1992). Far-red light-induced stimulation of shoot elongation in *Vigna sinensis* was found to be related to increased levels of GA_1 caused by stimulation of the 3-ß-hydroxylation GA_{20} to GA_1 (Martínez-Garciá and Garciá-Martínez 1992). Stimulation of shoot elongation in *Thlaspi arvense* as a response to a cold period was found to be related to an increased hydroxylation of the GA precursor kaurenoic acid into 7-OH kaurenoic acid (Hazebroek et al. 1993). Photoperiodic control of stem elongation in *Silene armeria* (Talon and Zeevaart 1992), *Spinacia oleracea* L., and *Agrostemma githago* L. (Zeevaart and Gage 1993), and *Salix pentandra* (Olsen et al. 1995) was related to the synthesis and levels of GA_1. However, the increased elongation of dark-grown and *Iv* mutants of pea (Weller et al. 1994) and the phytochrome-mediated differences in shoot elongation between wild type tomato plants and transgenic tomato plants overexpressing the gene encoding for type II phytochrome (López-Juez et al. 1995) appeared to result from increased responsiveness of the plant to its endogenous levels of GA_1 and not to differences in GA_1 levels.

Our observation that paclobutrazol-treated fuchsia plants showed the same stem elongation responses to exogenously applied GAs at DIF−10 and DIF+10 and in white and orange light indicates that the observed differences in shoot elongation of plants grown at these various conditions in the absence of paclobutrazol did not

result from light quality or DIF-mediated changes in plant sensitivity to GA_1. Assuming that in fuchsia, as in most other plant species, GA_1 is the GA controlling stem elongation, the effects of DIF or light quality on the metabolic conversion of precursor GAs into GA_1 and thus on GA_1 levels could be a mechanism by which DIF and light quality control stem extension, as was observed for the temperature-controlled stem elongation in *T. arvense* (Hazebroek et al. 1993) and the phytochrome-mediated elongation in *V. sinensis* (Martínez-Garciá and Garciá-Martínez 1992). However, enzymatic restriction of GA_1 synthesis from its precursor GAs by negative DIF and white light, compared with positive DIF and orange light, cannot explain the differences in shoot elongation at these growth conditions because the response of paclobutrazol-treated fuchsias to GA_{44}, GA_{19}, and GA_{20} was not affected significantly by the temperature and light treatments. Similar observations were made for GA_4, the GA reported to control elongation in *Arabidopsis thaliana* (Talon et al. 1990) and *Cucumis sativus* (Nakayama et al. 1989), and its precursors GA_{15}, GA_{24}, and GA_9. In general, the elongation responses to these non-13-hydroxylated GAs was somewhat less than those to the 13-hydroxylated GAs (GA_{44}, GA_{19}, GA_{20}, and GA_1). Feeding labeled precursors of GA_4 and determining their metabolic turnover into other GAs would be a useful approach to see whether GA_4 itself can regulate stem elongation in fuchsia or whether it is first converted into GA_1. As expected, GA_8, which is considered to be the first biodegradation product of GA_1 as a result of 2-β-hydroxylation (Sponsel 1995), did not affect shoot elongation of fuchsia. Although 2-β-hydroxylation of GA_1 to form the inactive GA_8 is a mechanism to control the steady-state level of GA_1, it is not the mechanism that controls the response to DIF or light quality, because the responsiveness to GA_1 would have been different for plants grown at DIF−10 and DIF+10 in white light and for plants grown in white and orange light. Therefore, we conclude that if GAs control the elongation response of fuchsia to changes in DIF and light quality, they probably affect elongation by changing GA biosynthesis because GA responsiveness of paclobutrazol-treated plants was not affected. An explanation for the lack of response of orange light-grown plants to negative DIF could be that orange light results in such an increase in GA that it is saturating for elongation for plants grown at either temperature regime, thereby making the plants insensitive to negative DIF. Saturating endogenous levels of GAs would also explain why exogenous application of GAs to plants grown in orange light in the absence of paclobutrazol did not or only slightly enhance stem elongation compared with that of white light-grown plants. In *Campanula isophylla* reduction of stem elongation by negative DIF was accompanied by a reduction in GA_1 levels of the whole shoot (Jensen et al. 1996). However, as the leaves and stems of this plant were taken together for GA extraction, the question remains whether GA_1 levels in the elongating internodes were also significantly different.

In fuchsia GA levels may not only be involved in the regulation of stem elongation, but also in the control of flowering. Fuchsia is a long day plant requiring photoperiods of more than 12 h for flower initiation. GAs have been reported to prevent flower induction by long day treatments, whereas GA biosynthesis inhibitors may stimulate flower initiation of plants grown in short days (see Wilkins 1985). Induction of flowering in fuchsia by long days is therefore considered to result from a long day-induced reduction in GA biosynthesis. Assuming that both stem elongation and flower induction in fuchsia depend on the level of an active GA, our results suggest that the effects of negative DIF on stem elongation and flowering are two independent processes; the promotion of flowering by negative DIF occurred both in white and orange light, whereas a reduction in stem elongation was noted only in white light. Flower initiation and stem elongation in fuchsia may be regulated independently by GAs as has been reported for several long-day plants (see Metzger 1995). According to this concept, negative DIF would have been sufficient to reduce the level of the GA inhibiting flower induction, but not that of the GA controlling stem elongation of fuchsias grown in orange light. Only when plants were treated with paclobutrazol, which results in a general decrease of the levels of all GAs, was the induction of flower development always accompanied by a reduction in stem elongation. To test our hypothesis that both temperature regime and light quality affect stem elongation by changes in GA levels, we are currently analyzing the GA contents of internodes during their elongation growth in white and orange light at DIF−10 or DIF+10. Ultimately, the determination of the active GA and its biosynthesis pathway will also be useful to develop genetically modified fuchsias and other pot and bedding plants that show reduced stem elongation without the use chemical growth retardants.

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