Role of Gibberellin A₄ and Gibberellin Biosynthesis Inhibitors on Flowering and Stem Elongation in *Petunia* under Modified Light Environments

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Abstract. In our previous experiments, greenhouse films that selectively remove far-red (FR) light from the growing environment reduced the stem elongation but delayed anthesis of long day plants. In the present research we investigated if the application of gibberellin A₄ and gibberellin (GA) biosynthesis inhibitors could overcome the delay in anthesis of *petunia* (*Petunia ×hybrida* Vilm.-Andr.), a quantitative long-day plant, under a FR light deficient environment. The GA biosynthesis inhibitors prohexadione-Ca and *exo*-C-16,17-dihydro GA₅ (GA₅) were used because of their ability to prevent catabolism of active GAs. Anthesis and stem elongation were investigated under control, red (R; 600 to 700 nm) and FR (700 to 800 nm) light-absorbing (A_R and A_{FR}) films. The R:FR ratios of control, A_R, and A_{FR} films were 1.03, 0.71, and 1.51, respectively. Air temperatures among treatment chambers were not different. A_R film did not affect anthesis or stem elongation, but A_{FR} film reduced stem elongation and delayed anthesis by 12 days. Exogenous application of GA₄ had no effect on stem elongation, shoot dry weight or days to anthesis at any concentration (0 to 100 mg·L⁻¹) tested under control, A_R, or A_{FR} films. Anthesis was delayed with increasing concentration (0 to 200 mg·L⁻¹) of prohexadione-Ca under all treatments. Prohexadione-Ca at 200 mg·L⁻¹ delayed anthesis by 11 and 7 days under the control and A_{FR} film, respectively, suggesting an interaction between light quality and prohexadione-Ca treatment. Exogenous GA₄ accelerated anthesis under both films but the promotion was greater under the A_{FR} films. However, GA₄ treatment increased stem elongation and the increase in stem elongation was greater under the A_{FR} film. Addition of GA₅ to GA₄ had no added effect on flowering and failed to reduce stem elongation. Therefore, GA or GA inhibitors are not suitable for flower promotion under A_{FR} films.

Greenhouse covers that selectively remove far-red (FR; 700 to 800 nm) light from the greenhouse have been used to produce short, compact bedding plants without chemical growth regulators (Rajapakse et al., 1999). However, FR light has been shown to play a role in flower production in certain plant species. For example, in chrysanthemum [*Dendranthema ×grandiflora* Ramat Kitam. (syn. *Chrysanthemum ×morifolium*), R light delayed and FR light promoted flower initiation (Cathey and Borthwick, 1957). Supplementing the growing environment with incandescent light rich in FR light accelerated flowering in *Arabidopsis* mutants (Bagnall, 1993) and snapdragon [*Antirrhinum majus* L.] (Cremer et al., 1998). In our previous studies, flowering of snapdragon

and *petunia* (*Petunia ×hybrida* Vilm.-Andr.), long-day (LD; short night) plants, was delayed up to 13 d under FR light deficient environments during weakly inductive photoperiods but no delay in flowering of these species was observed under strongly inductive conditions (Cerny et al., 2003). The delay in flowering was attributed to the delay in floral primordia initiation and overall development of the floral meristem under the FR deficient environment. Flowering of zinnia, cosmos (short-day plants),

and miniature rose (day neutral plant) was not influenced by the FR deficient conditions. Therefore, greenhouse covers that selectively filter out FR light could have adverse effects on growers' production schedules depending on the crop and the growing season. Understanding the mechanisms by which FR light affects flowering could help develop practices to overcome adverse effects.

Gibberellins (GAs) play a key role in the transition from the vegetative to the reproductive stage in LD and cold requiring plants. The rate of GA biosynthesis in some LD plants increased under LD conditions when stem elongation and flower formation took place (Zeevaert and Gage, 1993). Applied gibberellins induced flowering of many LD or cold requiring plants under noninductive conditions (Zeevaert, 1983). However, in some short-day and day-neutral plants, applied GAs did not affect flowering.

The role of light quality in GA biosynthesis and the sensitivity of plants to GAs has been investigated for decades. Campell and Bonner (1986) found that the conversion of GA₂₀ (inactive) to GA₁ (active) in pea (*Pisum sativum* L.) occurred readily in dark-grown plants but this conversion was blocked by R light. Martinez-Garcia and Garcia-Martinez (1992) reported that FR light increased GA₁ levels in cowpea seedlings [*Vigna unguiculata* (L.) Walp. ssp. *unguiculata*]. In contrast, Reid et al. (1991) and Weller et al. (1994) provided evidence to support that the stem elongation response to changes in light was mediated by a change in sensitivity to GAs. O'Neill et al. (2000) reported that the initial exposure of etiolated pea seedlings to light decreased GA₁ levels and continued exposure decreased seedling sensitivity to endogenous GAs. Maki et al. (2002) reported that the response of chrysanthemums to GA₁ was not affected by the absence of FR light in the growing environment but the response to GA₁₉ and GA₂₀ decreased when FR light was not present. The reduced response to GA₁₉ was attributed to decreased turnover of active GAs because GA₁₂

Fig. 1. Spectral transmission pattern of control, red (A_R) and far-red light absorbing (A_{FR}) films.

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Table 1. Influence of dosage of *exo*-C-16,17-dihydro GA₃ on main stem length, shoot dry weight, and days to anthesis of 'Countdown Burgundy' petunia plants grown in photoselective film chambers.

Filter	Dihydro GA ₃ concn (mg·L ⁻¹)	Stem length (cm)	Shoot dry wt (g)	Days to anthesis
Control ^z	0.0	19.0 ^y	10.4	58
	1.0	19.6	10.1	54
	3.3	20.7	9.5	57
	10.0	18.9	9.9	56
	33.0	19.6	9.9	57
	100.0	19.9	9.8	58
A _{FR}	0.0	19.9	8.5	70
	1.0	20.1	8.2	72
	3.3	20.5	8.2	72
	10.0	19.4	8.3	70
	33.0	20.0	8.3	73
	100.0	19.0	7.9	72
A _R	0.0	19.8	9.7	61
	1.0	19.8	9.1	63
	3.3	21.8	9.3	62
	10.0	22.0	9.4	63
	33.0	21.9	8.8	62
	100.0	19.3	9.0	63
ANOVA				
Filter		NS	NS	*
Concentration		NS	NS	NS
Filter × concentration		NS	NS	NS

^zControl is the clear film, A_{FR} is the far-red light absorbing film and A_R is the red light absorbing film.

^yEach number is the mean of 10 plants.

^{ns,*}Non-significant or significant at *P* = 0.05.

Fig. 2. Effect of prohexadione-Ca on stem length, days to anthesis, and shoot dry weight of 'Countdown Burgundy' petunia grown in control and far-red light absorbing (A_{FR}) chambers.

and GA₁₉ metabolized slowly in the absence of FR light. Recent work indicated that both GA biosynthesis and catabolism are important in growth regulation by GAs. Martinez-Garcia et al. (2000) reported that exposure to FR light increased GA₁ levels in cowpea apices due to reduced inactivation of GA₁. Based on these observations, we hypothesized that reduced GA level, due to reduced biosynthesis or increased catabolism, may be causing the delay in flowering under FR light deficient environments.

If decreased GA levels cause a delay in flowering under FR light absorbing photoselective covers, exogenous application of GAs and/or inhibitors of GA catabolism could reverse the effect. The application of GAs however, caused an increase in stem elongation under FR light deficient environments (Rajapakse and Kelly, 1991). Hisamatsu et al. (2000) reported that prohexadione-Ca, a GA biosynthetic inhibitor that also prevents catabolism of GA₁ (Brown et al., 1997) promoted flowering in stock (*Matthiola incana* L.). King et al. (2000) reported that, in some species, flower-promoting (or inhibiting) activity of GAs is inversely related to their effectiveness in promoting stem elongation. Several synthetic GAs with structural variations have recently been synthesized and their flower promoting ability has been investigated. For example, Evans et al. (1994)

reported that C-16,17-dihydro GA₃ was as effective as GA₃ in inducing flowering in *Lolium temulentum* L., but it reduced stem elongation by 40%. GA₃, like its dihydro derivatives, is an inhibitor of GA metabolism (Junttila et al., 1997; Rademacher, 2000) and increased flowering is, most likely, a result of delaying degradation of endogenous GAs. Ben-Tal and Belausov (2000) reported that endo-16,17-dihydro GA₃ was effective in flower promotion of aster (*Aster novi-belgii* L.), phlox (*Phlox* spp. L.), and limonium (*Limonium* spp. Mill.) but not effective in enhancing flowering of solidago (*Solidago* spp. L.) and hypericum (*Hypericum calycinum* L.).

In this research we investigated the effects of C-16,17-dihydro GA₃ and prohexadione-Ca on flowering and height of petunia under R and FR absorbing films. If these chemicals could overcome flowering delay without causing excessive stem elongation, growers could use this technique to overcome potential adverse effects of photoselective films on flowering.

Materials and Methods

Photoselective filters. Photoselective greenhouse films containing R or FR light absorbing dyes that corresponded to 75% PPF transmission were used in the experiment. The photoselective films are identified as control (clear), FR light absorbing (A_{FR}) and R light absorbing (A_R). Light transmission characteristics of the photoselective films are shown in Fig. 1. The A_{FR} and A_R films intercepted FR and R wavelengths with maximum absorption at 730 nm and 690 nm, respectively. Growth chambers (1.2 × 1.2 × 1.2 m) made of PVC pipe frames were covered with the above films. Two replicate chambers were used for each treatment, each randomly placed inside a clear double-layer polyethylene greenhouse (Klerk's Plastic Products Manufacturing, Inc., Richburg, S.C.).

The PPF inside each chamber was measured at three locations within each chamber at the beginning and at the end of the experiment (between 1200 and 1400 HR) with a quantum meter (LI-185S; LI-COR, Inc., Lincoln, Nebr.) fitted with a quantum sensor (LI-190SA). The PPF was adjusted to be equal inside all chambers by covering the control chambers with cheesecloth. Two fans, one located at the top of the chamber and the other located on the opposite lower side provided ventilation for the chambers. Greenhouse cooling/heating setpoints were 27/20 °C, respectively.

Spectral photon distribution was measured on clear days between 1200 and 1400 HR at the beginning and at the end of the experiment with a spectroradiometer (LI-1800) fitted with a remote cosine sensor (LI-1800-10). The phytochrome photoequilibrium (P_{fr}/P_{total}) estimates of transmitted light for the control, A_{FR}, and A_R films were 0.71, 0.77, and 0.67, respectively (estimated as described by Sager et al., 1988). The broad-band R/FR ratios (R = 600 to 700 nm; FR = 700 to 800 nm) for the control, A_{FR}, and A_R films were 1.05, 1.51, and 0.67, respectively.

Daily minimum and maximum air tem-

Table 2. Influence of GA₄ and *exo*-C-16,17-dihydro GA₅ (GA₅) (10 mg·L⁻¹ concentration of each) on stem length, days to anthesis, number of flowers, number of laterals, and number of flower buds of 'Countdown Burgundy' petunia grown under photosensitive films.

Filter	Growth regulator	Stem length (cm)	Days to anthesis	Flowers (no.)	Laterals (no.)	Flower buds (no.)
Control ^a	Water	10.0 ^b	48	7.0	6.5	11
	GA ₄	15.6	45	7.0	5.1	9
	GA ₄ + GA ₅	18.4	44	9.0	5.5	12
A _{FR}	Water	8.1	63	5.0	7.9	18
	GA ₄	15.9	53	6.0	5.9	14
	GA ₄ + GA ₅	15.4	53	8.0	5.9	12
ANOVA						
Filter		*	*	NS	NS	NS
Growth regulator		***	***	NS	***	***
Control: water vs. GA ₄		***	NS	NS	**	NS
Control: water vs. GA ₄ + GA ₅		***	NS	NS	*	NS
A _{FR} : water vs. GA ₄		***	*	NS	***	**
A _{FR} : water vs. GA ₄ + GA ₅		***	*	NS	***	***
Filter × growth regulator		NS	NS	NS	NS	*

^aControl and A_{FR} are clear and the far red light absorbing films, respectively.

^bEach number is the mean of 16 plants.

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

peratures were monitored using minimum/maximum thermometers. Daily light integral (DLI) inside the photosensitive chambers were recorded with a data logger (LI-1000) fitted with quantum sensors (LI-190SB; programmed to collect readings every 5 min) during each set of experiments. Experiment 1 was conducted from November through February. Experiment 2 was conducted from February through April. The average daily photoperiod during Expt. 1 and Expt. 2 ranged from 10 to 11 h·d⁻¹ and 11 to 13 h·d⁻¹, respectively. The photoperiod was determined based on the U.S. Naval Observatory Sunrise and Sunset Table for Greenville, S.C. Average daily maximum/minimum air temperatures inside the chambers were the same among treatments; 33 ± 2°C/15 ± 2°C for Expt. 1 and 35 ± 2°C/16 ± 2°C for Expt. 2, respectively. Plants received an average daily light integral of 9.5 ± 0.5 mol·m⁻²·d⁻¹ and 11.5 ± 0.5 mol·m⁻²·d⁻¹ in all treatments for Expts. 1 and 2, respectively.

Plant material. 'Countdown Burgundy' petunia seeds were germinated under intermittent mist. At the first true leaf stage, uniform seedlings were transplanted into 0.6-L pots containing a commercial potting medium (Fafard 3-B, Fafard Inc., Anderson, S.C.) and moved into the treatment chambers. Plants were spaced pot to pot at transplant and spacing increased to avoid contact between plants as they developed. Plants were fertilized three times a week at irrigation with 1 g·L⁻¹ of a 20N-4.4P-16.7K water soluble fertilizer (Peters 20-10-20 Peat-Lite Special, Scotts-Sierra Horticultural Products Co., Marysville, Ohio).

Experiment 1: Dose response of *exo*-C-16,17-dihydro GA₅ and prohexadione-Ca. At transplant, 45 plants were placed in each of the treatment chambers. After a 2-week establishment period (when the plants had four true leaves) a group of five plants in each chamber was sprayed to runoff once weekly for 3 weeks with one of the following treatment solutions. The treatment solutions were 1) water; 2) 1, 3.3, 10, 33, or 100 mg·L⁻¹ *exo*-C-16,17-dihydro GA₅ (Provided by W. Rademacher, BASF Agricultural Center, Limburgerhof, Germany); and 3) 50, 100, or 200 mg·L⁻¹ prohexadione-Ca

(BAS 125 10W, BASF Corp., Research Triangle Park, N.C.). All treatment solutions contained 0.1% Tween 20 as a surfactant (Fisher Scientific, NJ). Most developmental work on dihydro GA₅ has been performed on monocots. Since barley (*Hordeum vulgare* L.) is known to respond to dihydro GA₅, barley plants were treated with the *exo*-C-16,17-dihydro GA₅ solution to confirm activity of solutions. Petunia plants developed phytotoxicity to 100 mg·L⁻¹ *exo*-C-16,17-dihydro GA₅ spray; therefore, plants were treated only once. Treated plants were placed randomly within each chamber. Plants were removed briefly from chambers for chemical treatment and then placed back in their respective chambers.

Experiment 2: Plant response to GA₄ and combination of GA₄ and *exo*-C-16,17-dihydro GA₅. At transplant, 28 plants were placed inside each of the treatment chambers. After a 2-week establishment period a group of eight plants in each chamber received one of the following treatments containing 0.1% Tween 20 surfactant to run off once weekly for 3 weeks: 1) water only (control), 2) 10.0 mg·L⁻¹ GA₄, and 3) 10.0 mg·L⁻¹ GA₄ and 10 mg·L⁻¹ *exo*-C-16,17-dihydro GA₅. Treated plants were placed randomly within each chamber. Plants were removed briefly from chambers for chemical treatment and then placed back in their respective chambers.

Experimental design and data analysis. The experimental chambers were randomly placed inside the clear plastic greenhouse. Two replicate chambers were used for each film treatment. The experimental chambers were arranged in a randomized complete block design and the data analyzed as a split plot with photosensitive films (control, A_R, and A_{FR}) as the whole-plot factor. In the dose response experiment, the growth regulators (*exo*-C-16,17-dihydro GA₅ and prohexadione-Ca) were the split plot factors. In the second experiment, the *exo*-C-16,17-dihydro GA₅ and GA₄ combination was the split plot factor.

Plant height (height from the soil surface to the main shoot apex), number of lateral shoots, days to visible flower bud formation, days to anthesis, number of flowers and flower

buds per plant, and flower diameter of the first fully open flower were recorded. For shoot dry weight measurements, shoots were oven-dried for 2 d at 85 °C. Data were analyzed using analysis of variance of SAS (SAS Inst., Inc., Cary, N.C.).

Results and Discussion

The *exo*-C-16,17-dihydro GA₅ had no effect on stem elongation, shoot dry weight or days to anthesis in petunia at any concentration tested (Table 1). The synthetic GA₅ derivatives have reduced shoot elongation in certain monocots possibly by inhibiting the 3β-hydroxylation step of GA metabolism (Rademacher, 2000). Lee et al. (1998) reported that C-16,17-dihydro-GA₅ isomers hastened floral initiation and development in sorghum (*Sorghum bicolor* L.) but strongly inhibited shoot growth by reducing GA₁ levels. Dihydro GAs, thus far, has been found to reduce shoot elongation only in graminaceous species (Rademacher, 2000).

The lack of responsiveness in petunia to *exo*-C-16,17-dihydro GA₅ could be due to lack of response of dicots or the poor absorption of solution by the leaves. To eliminate the latter possibility, barley (*Hordeum vulgare* L.) plants were treated with the *exo*-C-16,17-dihydro GA₅ solution because barley is known to respond to dihydro GA₅. Growth of the barley plants was significantly retarded by the dihydro GA₅ (data not shown) suggesting that lack of absorption of the solution may not have caused the lack of response. Similar to our results with dicots, the *exo*-C-16,17-dihydro GA₅ had no effect on stem elongation or flowering of *Spathiphyllum* (Schott.) or *Fuchsia xhybrida* (L.), however, flowering of a dwarf strain of *Pharbitis nil* was promoted with little effect on stem elongation (King et al., 2000). In the tall strain of *Pharbitis nil* (L.), which is more sensitive to gibberellins, *exo*-C-16,17-dihydro GA₅ promoted stem elongation. In contrast, a similar dihydro GA₅ derivative (*endo*-C-16,17-dihydro GA₅) increased flowering in orange, olive and grapevines (Ben-Tal and Belausov, 2000).

Stem elongation slightly decreased in re-

sponse to prohexadione-Ca treatment regardless of the light environment (Fig. 2). Plants grown under the A_{FR} film showed a greater decrease in stem length than the control plants in response to prohexadione-Ca. Prohexadione-Ca did not affect shoot dry weight of control filter grown plants but shoot dry weight of plants treated with 200 mg·L⁻¹ prohexadione-Ca was 27% less than non-prohexadione-Ca treated plants under the A_{FR} film. Prohexadione-Ca and related trinexapac-ethyl promoted flowering and stem elongation of *Matthiola incana*, a cold requiring plant (Hisamatsu et al., 1998, 2000) and this was attributed to the prevention of the inactivation of endogenous GA₄.

Non-prohexadione-Ca treated plants grown under the A_{FR} films flowered 12 d later than the control film grown plants (Fig. 2). Anthesis was delayed with increasing concentration of prohexadione-Ca under both films. Anthesis was delayed by 11 d with the 200 mg·L⁻¹ prohexadione-Ca treatment application under the control film, while 200 mg·L⁻¹ prohexadione-Ca treatment delayed anthesis by 7 d of plants grown under the A_{FR} film suggesting an interaction between light quality and prohexadione-Ca treatment.

Exposure of dark-grown seedlings to light has been shown to increase the level of inactive GAs suggesting that inactivation of functional GAs is important in light regulated responses (Gil and Garcia-Martinez, 2000). Exposure to end-of-day (EOD) FR light has been reported to decrease and subsequent exposure to R light has been shown to increase the inactivation of active GAs in elongating regions of cowpea epicotyls suggesting that inactivation of GAs is under phytochrome control (Martinez-Garcia et al., 2000). Maki et al. (2002) found that FR light deficient environments may enhance inactivation of GA₁. Our study suggests that prohexadione-Ca was more effective in reducing catabolism of GAs under A_{FR} films because prohexadione-Ca treatment reduced the delay under those films.

Gibberellin A₄ is known to stimulate flowering and stem elongation of certain plants. GA₄ was tested in combination with 10 mg·L⁻¹ dihydro GA₅. As previously noted, A_{FR} film delayed anthesis by nearly 2 weeks (Table 2). GA₄ accelerated anthesis under both films but the promotion in flower initiation and development was greater under the A_{FR} films. However, GA₄ treatment increased stem elongation and the increase in stem elongation was greater under A_{FR} film. Addition of *exo*-C-16,17-dihydro GA₅ had no added effect on flowering or stem elongation. Flowering is influenced by variation in environmental conditions, such as temperature. However, all treatments in this experiment had similar environmental conditions. Although the maximum temperatures recorded in Expt. 2 may have been higher than the optimum, temperature data from a separate experiment indicated that plants were only

exposed to the extreme temperatures for a short period of time during the afternoon.

In summary, petunia plants did not respond to the *exo*-C-16,17-dihydro GA₅. Prohexadione-Ca decreased stem elongation, but delayed anthesis with increasing concentrations. However, the delay was less under the A_{FR} film. Compounds such as prohexadione-Ca and trinexapac-ethyl are critical for being used in ornamentals with red and blue flowers since they may inhibit anthocyanin formation (Rademacher, 2000). GA₄ promoted flower initiation and development but stimulated stem elongation. The *exo*-C-16,17-dihydro GA₅ used with GA₄ failed to prevent stem elongation under all light environments. Therefore, none of the GA treatments promoted floral initiation and development without also reversing the reduction in stem elongation.

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