J Plant Growth Regul (2000) 19:437–444
DOI: 10.1007/s003440000015

J P G R
Journal of Plant Growth Regulation

Response to Gibberellin Structural Variants Shows that Ability to Inhibit Flowering Correlates with Effectiveness for Promoting Stem Elongation of Some Plant Species

R. W. King,[1]* H. Seto,[2] and R. M. Sachs[3]

[1]CSIRO Plant Industry, GPO Box 1600, Canberra, ACT 2601, Australia ; [2]Institute of Physical and Chemical Research (RIKEN), Wako-shi, Saitama 351-0198, Japan ; [3]Environmental Horticulture, University of California Davis, Davis, CA 95616-8587, USA

Abstract

The flowering response of three plant species *Fuchsia hybrida, Pharbitis nil,* and *Spathiphyllum* 'Petite' has been examined after treatment with synthetic and natural gibberellins (GAs) including GA_1, GA_3, GA_5, 2,2-dimethyl GA_4, various of their 3α-hydroxyl epimers, the methyl ester of GA_3, a 15β-hydroxyl GA_3, and some 16,17-dihydro derivatives. Of necessity, application techniques differed between species and dose responses cannot be compared. However, comparisons across species were possible on the basis of their differential responses to the various GAs. Flowering was inhibited and, in an inverse way, stem elongation promoted when GA_3 or GA_5 was applied to *Fuchsia* or, at high doses, to *Pharbitis.* The increased stem growth was apparently responsible for inhibition of flowering because epimerization of the hydroxyl at C-3 of GA_3 or modification of GA_5 to 16,17-dihydro GA_5 created compounds that were growth inactive and that no longer inhibited flowering. However, the response of *Pharbitis* was more complex because both these GAs and their derivatives promoted flowering at doses subthreshold for growth. For *Spathiphyllum,* only promotion of flowering was evident with any GA, and the structural variants were slightly active or inactive. Thus, there are at least two antagonistic actions of GA on flowering and for *Pharbitis* either inhibition or promotion can be shown. The possibility is discussed that the inhibitory action of GA on flowering involves diversion of assimilate away from the shoot apex and into the elongating stem.

Key words: Elongation; Flowering; Gibberellin; *Fuchsia*; *Pharbitis*; *Spathiphyllum*

Introduction

Although applied gibberellin (GA) promotes flowering of some plants, including the grass *Lolium temulentum* (Evans 1964), for other species it may be inhibitory, as for *Fuchsia* (Sachs and Bretz 1961) and citrus (see Monselise and Goldschmidt 1982). A mixed response is found with *Pharbitis nil,* where GA promotes flowering when applied before a photoinductive short day, but it inhibits if applied 24 h later (King and others 1987; Ogawa 1981). Aside from providing a documentation of species differences,

Received 28 October 1999; accepted 9 May 2000; online publication 15 December 2000
*Corresponding author; e-mail: r.king@pi.csiro.au

such contrasts offer an opportunity to examine a possible inhibitory effect of GA, whereby enhanced growth of vegetative tissues would indirectly block flowering.

The responses of *Bougainvillea* illustrate how an indirect action of GA_3 could lead to inhibition of flowering. Applied GA inhibits flower development of intact plants but has no effect on isolated inflorescence meristems lacking a stem (Steffen and others 1988). Apparently, GA by promoting stem elongation of intact *Bougainvillea* plants causes a diversion of essential photosynthetic assimilate away from the shoot apex, and this leads to inhibition of flowering.

In this study, natural and synthetic gibberellins have been used in an examination of the possible antagonism between flower initiation and stem elongation. These GAs should provide some distinction between stem elongation and floral activity, especially because, with the grass *Lolium temulentum,* they variously: (i) stimulate elongation but not flowering; (ii) stimulate flowering but not elongation; (iii) stimulate both elongation and flowering; or (iv) inhibit elongation but promote flowering (see Evans and others 1990; 1994a, b). Three plant species have been examined: *Fuchsia hybrida* because gibberellins inhibit its long day flowering response (Sachs and Bretz 1961); *Pharbitis nil,* a short day plant that shows both inhibition and promotion of flowering by GAs (King and others 1987; Ogawa 1981) and *Spathiphyllum* because it is not daylength responsive, but GA_3 induces its flowering (Henny 1981).

Materials and Methods

Fuchsia Cultivation and Treatment

Plants of *Fuchsia hybrida* (cv. Lord Byron), grown from cuttings, were maintained at a temperature of 24/19°C day/night in natural daylight of 10 h/d in shuttered cabinets in the Canberra phytotron (Morse and Evans 1962). The 8-cm diameter cylindrical plastic pots were filled with a 1:1 mixture of perlite and vermiculite and irrigated twice daily with a modified Hoagland's nutrient solution in the morning and water in the afternoon. At 3–4 weeks the growing point was pinched to induce branching, and when 10–12 cm in height the 3–4 branched plants were moved to an artificially illuminated cabinet at 24/19°C and a 10-h photoperiod (PFD of 200 μmol m^{-2} s^{-1}) from a combination of metal halide and quartz halide lamps. After a further 3 weeks, when the plants were about 25 cm high, floral induction and GA treatments began. A total of four florally inductive, continuous-light long days were given, each involving the 10-h short day extended with a 14-h exposure to a low irradiance from incandescent lamps (15 μmol m^{-2} s^{-1}). Stem length, recorded daily, was measured from a marked, partially expanded leaf. Sometimes there were chance differences in the starting stem lengths, and these could be removed by presenting stem elongation as an increment. Flowering was recorded after 21 d. Gibberellins were applied to the shoot tip in a 10-μL drop of 10% (v/v) ethanol in water. Control plants were treated with 10% ethanol alone. There were 10 to 16 plants per treatment, and values are presented as averages ± SEM.

Spathiphyllum Cultivation and Treatment

Plants of *Spathiphyllum* cv. 'Petite' were supplied as plug stock by Newports Nursery (Winmallee, NSW). After 6 leaves had formed, they were transplanted into 12-cm diameter pots filled with perlite vermiculite (50:50) and fertilized daily with a modified Hoagland's nutrient solution followed by watering each evening. The plants were grown in a glasshouse of the Canberra phytotron at a temperature of 24/19 (avg, 20.7°C) in a 16-h photoperiod. Natural sunlight intensities were reduced by 60% using a layer of shade cloth. Humidity was maintained under these enclosures using a misting period of 30 s every 10 min during the day. At the time of chemical treatment, the plants were 6–8 weeks from transplantation and had formed an average of 11.0 ± 1.4 leaves on the main shoot. Lateral shoots appeared later. Gibberellins were applied in 95% ethanol as a single spray of about 5 mL per plant. Control plants were treated with 95% ethanol alone. Flower opening was recorded at weekly intervals. There were 6–8 plants per treatment, and values are presented as averages ± SEM.

Pharbitis Cultivation and Treatment

Experiments were conducted with *Pharbitis nil,* Choisy, strain Violet, a normal height line, and Kidachi, a gibberellin-responsive dwarf line. Germination and growing conditions were as described before (King and others 1987). The seedlings were grown in continuous light, and when 5 d old were exposed to a single florally inductive short-day dark period of 13 h. Hypocotyl and petiole lengths were recorded daily after the short day, and stem elongation and flowering response were recorded after 10 d. Gibberellins were applied once to the cotyledonary petioles in 5 μL of 95% (v/v) ethanol in water

(that is, a total of 10 µL/plant). Control plants were treated with 95% ethanol alone. There were up to 14 and sometimes more plants per treatment. Values are presented as averages ± SEM or the value of the least significant difference is shown.

Chemicals

Most of the gibberellins were provided by L.N. Mander (RSC, ANU) and included GA_1, GA_3, GA_5, 2,2-dimethyl GA_4, *exo* 16,17-dihydro GA_3, *exo* 16,17-dihydro GA_5, and *exo* 13-*O*-acetyl-16,17-dihydro GA_5. Synthesis of the C-16,17 modified gibberellins is described in Evans and others (1994a). The 3α-OH epimer of active gibberellins can be synthesized simply but may be contaminated with up to 1% of the 3β-OH epimer. Therefore, some treatments involved pure 3α-epimer synthesized directly by the procedures described in Seto and others (1998). Synthesis of C-3 methoxy GAs was by Seto.

Results

Gibberellins, Flowering and Stem Elongation of *Fuchsia*

Our preliminary studies of flowering of *Fuchsia,* cv. Lord Byron, confirmed earlier findings of Sachs and Bretz (1961). All plants flowered after exposure to a minimum of 2 long day (LD) photoperiods. Four LD of 24 h light each day consistently led to the formation of 4 to 5 flowers per plant. For flowering the photoperiod had to exceed 14 h, and plants in short days remained vegetative for many months.

Gibberellin (GA_3) applied at the time of LD exposure inhibited flowering of *Fuchsia* (Figure 1; as also reported by Sachs and Bretz 1961; Sachs and others 1967). A GA_3 dose of 30–100 ng/plant approached saturation for inhibition of flowering (Figures 1, 2). These findings with GA_3 were confirmed in six further experiments. In one data set shown in Figure 2 the response to a 1-ng dose has been disregarded because it did not fit with the other data in that experiment nor with the trends found in the other six experiments. The higher GA_3 doses increased stem elongation by up to 25 to 30% (Figures 1, 2).

The synthetic gibberellin, 2,2-dimethyl GA_4 inhibited flowering better than GA_3 (Table 1, Exp. II). Of the three GAs used in Table 1, 2,2-dimethyl GA_4 gave the greatest stimulation of stem elongation (data not shown), and it was the most effective for inhibition of flowering. However, epimerization of the C-3 hydroxyl group led to inactivity of this GA.

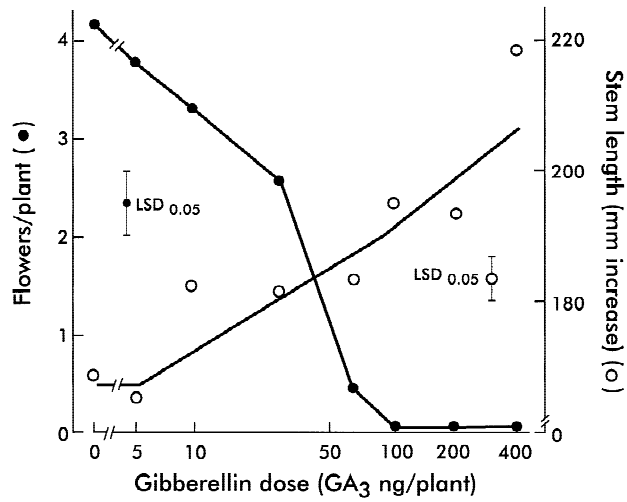

Figure 1. Stimulation of stem elongation and inhibition of flowering of *Fuchsia* after a single application of different doses of GA_3 to the shoot tip on the day of commencing exposure to 4 long days. Twenty-one days after treatment, the number of flowers per plant and stem length were measured. Over this period stem length of the untreated control plants increased from ~25 to 170. The GA treatment only enhancing this by about 30%. There were 12–14 replicates. Bars show least significant differences (LSD $p = 0.05$). Lines fitted by eye or to the data points.

Stem elongation was weaker with GA_3, and it was also marginally less active as an inhibitor of flowering than 2,2-dimethyl GA_4. GA_1 showed no inhibition of flowering at 30 ng/plant (Table 1), and this dose did not lead to significant promotion of stem elongation (data not shown). In another experiment, GA_1 was slightly inhibitory to flowering at 100 ng/plant (2.4 ± 0.4 vs. 4.3 ± 0.4 flowers per plant).

The inhibitory effect of GA_3 on flowering was lost with methylation of the carboxyl group (Table 1) or with epimerization of the 3-hydroxy from the β to the α configuration, both for GA_3 (Figure 2) as also for 2,2-dimethyl GA_4 (Table 1). When analyzed by GC-MS the sample of 3-*epi* GA_3 contained about 1% of GA_3. Such contamination would account for the onset of inhibition by 3-*epi* GA_3 applied at a dose 100- to 1000-fold greater than the threshold value for GA_3 of about 1–5 ng per plant. Experiments reported later used high-purity samples of 3-*epi* GA_3.

Over a wide dose range, 16,17-dihydro GA_5 did not inhibit flowering, although GA_5 was inhibitory (Figure 2), nor did it affect stem elongation (data not shown). These findings contrast dramatically with those for the long-day grass *Lolium* (Evans and others 1994b), where the 16,17-dihydro form of GA_5

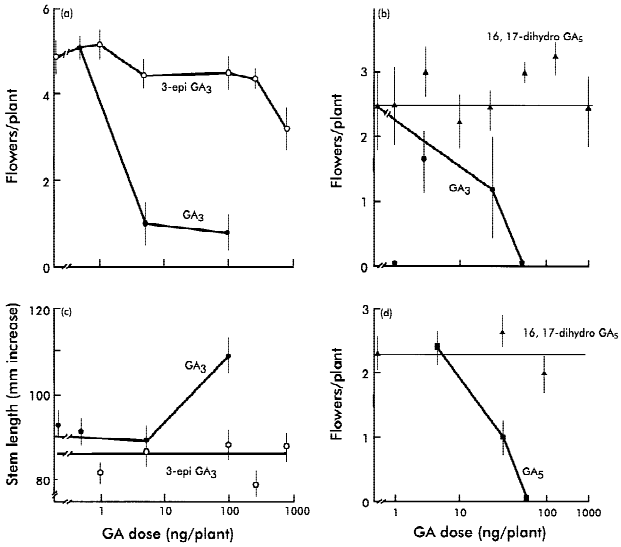

Figure 2. Gibberellin dose response for inhibition of flowering and promotion of stem elongation of *Fuchsia:* (a, c) effects of GA_3 or 3-*epi*-GA_3 on stem elongation and flowering; (b, d) inhibition of flowering by GA_3 and GA_5 compared with 16,17-dihydro GA_5. Values are means ± SEM. Where no SE bars are evident, they were smaller than the symbol (n = 10–14).

Table 1. Inhibition of long day-induced flowering of *Fuchsia* cv. Lord Byron by natural and synthetic gibberellins in three experiments.

Treatment	Dose	Flowers per plant	
		Exp. I	Exp. II
Control (4 LD)		4.3 ± 0.4	3.6 ± 0.2
GA_3	30 ng/plant	0.7 ± 0.4	2.0 ± 0.8
2,2-dimethyl GA_4	30 ng/plant	0	0.3 ± 0.3
2,2-dimethyl-3-*epi* GA_4	30 ng/plant	3.5 ± 0.5	3.0 ± 0.3
16,17-dihydro-2, 2-dimethyl-3-*epi* GA_4	30 ng/plant	—	3.0 ± 0.4
GA_1	30 ng/plant	5.2 ± 0.7	—
		Exp. III	
Control (4 LD)		4.9 ± 0.4	
GA_3	100 ng/plant	0.8 ± 0.4	
GA_3 methyl ester	100 ng/plant	4.5 ± 0.5	

All plants were exposed to 4 LD beginning at the time of a single application of 10 µL of various gibberellins to the shoot tip. The control was treated with the same aqueous:ethanol (90:10, v/v) solution. Values are means ± SEM (n = *10–14)*

both promotes flowering and inhibits growth. With *Fuchsia,* this same GA_5 derivative was apparently inactive (Figure 2).

Table 2. Effect of GAs on flowering of *Spathiphyllum* "Petite."

Treatment	Flowers/ plant	Weeks to flowering
a		
Control (ethanol)	0	>18 (0/8)
GA_3 (400 mg L^{-1})	6.8 ± 1.1	11 (8/8)
GA_5 (400 mg L^{-1})	4.4 ± 0.9	14 (8/8)
exo 16,17–dihydro GA_5 (400 mg L^{-1})	0.4 ± 0.2	>18 (3/8)
b		
Control (ethanol)	0.3 ± 0.3	>18 (1/6)
GA_3 (500 mg L^{-1})	9.3 ± 0.6	12 (6/6)
exo 16,17–dihydro GA_5 (500 mg L^{-1})	0.3 ± 0.3	>18 (1/6)
15β–OH GA_3 (500 mg L^{-1})	5.5 ± 0.9	11 (6/6)
exo 13–*0*–acetyl–16,17–dihydro GA_5 (500 mg L^{-1})	0	>18 (0/6)
c		
Control (ethanol)	0	>18 (0/5)
GA_3 (500 mg L^{-1})	10.5 ± 0.4	11 (5/5)
GA_1 (500 mg L^{-1})	0.8 ± 0.3	18 (3/5)
GA_1 (1000 mg L^{-1})	8.2 ± 1.0	13 (5/5)

GA was applied once to leaves in ethanol (95%) using an atomizer. Three experiments (a, b, c) are shown. Final assessment of flowering was made after 18 weeks. Values are means ± SEM and the number of plants flowering is shown in parentheses.

Gibberellins and Flowering of *Spathiphyllum*

After a single spray (~5 mL/plant) of GA_3 at 400 mg L^{-1} in 95% ethanol, the first flowers appeared at 11 weeks (Table 2). Plants aged anywhere from 4 to 16 weeks old at the time of GA_3 treatment always flowered 11 to 12 weeks after treatment, despite large differences in their size (data not shown). Control plants sprayed with 95% ethanol alone had not flowered by 18 weeks; first flowers were evident at 26 weeks (Table 2). Flower induction must have been rapid (within 3–5 weeks) because we found only a small further production of leaves (up to 3) by the time of conversion of the apex to flower formation. Ogawa (1993) reported a similar timing of floral initiation after GA_3 treatment.

Both GA_3 and GA_5 were effective for flowering of *Spathiphyllum* (Table 2), and GA_3 was at least twice as active as GA_1. Of the various derivatives tested, addition of a hydroxyl group to C-15 had little effect despite the enhanced floral activity of this compound relative to GA_3 when it was applied to the grass *Lolium temulentum* (Evans and others 1990). The 16,17-dihydro derivative of GA_5 was essentially inactive, and its 13-*0*-acetyl derivative had no effect.

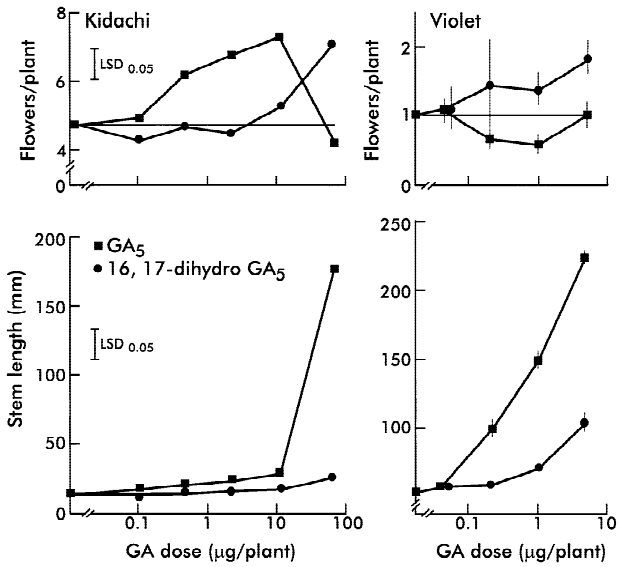

Figure 3. Effect on stem length and flowering of *Pharbitis nil* of various doses of GA_5 or 16,17-dihydro GA_5 applied once to the cotyledonary petioles 14 h before a 13-h short day. Two strains were examined, the dwarf, Kidachi, and the tall, Violet. Values of the least significant difference (LSD) shown at $p = 0.05$. Where no SE bars are evident, they were smaller than the symbol (n = 10–14).

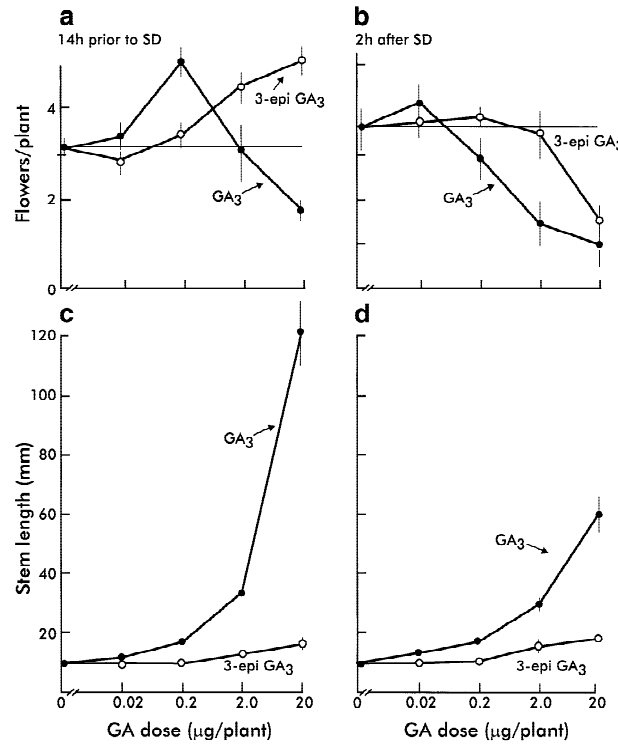

Figure 4. Effect on flowering and stem elongation of *Pharbitis nil,* strain Kidachi, of various doses of GA_3 or 3-*epi* GA_3. Application was (a,c) 14 h before or (b, d) 2 h after exposure to a 13-h inductive short day. Values are means ± SEM for at least 14 replicate seedlings. Where no SE bars are evident, they were smaller than the symbol.

Although GA_3 was active at 150 mg L^{-1}, in the same experiment the pure 3α-epimer of GA_3 was inactive at a 2000 mg L^{-1} dose (data not shown).

Gibberellins, Flowering and Stem Elongation of *Pharbitis nil*

Flowering of *Pharbitis nil,* strain Kidachi, is promoted by low doses of GA_3 and GA_5 but inhibited at high doses (Figures 3, 4) as we have reported previously (King and others 1987). Relative to the response to GA_3, a higher dose was required for promotion of flowering by GA_5, a less growth-active GA (Figure 3 compare Figure 4). Furthermore, for promotion of flowering there was increased tolerance to high GA_5 doses before it became inhibitory.

The later the time of GA application relative to the time of exposure to a single inductive short day, the greater the inhibition (for example, 14 h before vs. 2 h after the short day, Figure 4). Thus, a gibberellin could show considerable promotion of flowering over a wide dose range with an early application (Figures 3, 4) but a much-restricted promotion at the later application time. Likewise, at either time, the more growth active a gibberellin (for instance, GA_3 vs. GA_5) the narrower its dose tolerance (Figures 3, 4).

The threshold GA dose was similar for onset of inhibition of flowering of *Pharbitis* and for stimulation of stem elongation. Compelling evidence of this relationship is seen for both GA_3 (Figure 4) and GA_5 (Figure 3). The findings with 3-*epi* GA_3 point in the same direction, but this derivative was so weakly active on growth that when applied before the photoinductive treatment a sufficient dose for inhibition was not reached even at the highest dose used (Figure 4). The epimer therefore promoted flowering at substantially higher doses than were tolerated for GA_3. Overall, with the onset of elongation, there was a clear switch from promotion to inhibition of flowering.

Both the 16,17-dihydro GA_5 derivatives tested here promoted flowering of the dwarf strain Kidachi (Figure 2, Table 3) but, at the doses used, there was little or no effect on stem elongation and we could not establish whether there was an inverse relationship between flowering and enhanced stem elongation. However, the tall strain, Violet, is more sensitive to gibberellin (King and others 1987; Ogawa 1981), and it did show stimulation of stem elongation by high doses of 16,17-dihydro GA_5 (Figure 3).

Table 3. Effect of the 16,17-dihydro functional group on the action of various gibberellins on stem elongation and flowering of *Pharbitis nil* cv. Kidachi.

Treatment	Stem length (mm)	Flowers/ plant
Control	10 ± 3	5.1 ± 0.2
GA_3	231 ± 35	4.0 ± 0.3
GA_5	128 ± 34	4.6 ± 0.3
16,17-dihydro GA_5	27 ± 2	6.2 ± 0.2
15β-OH GA_5	521 ± 22	3.6 ± 0.2
exo 15β-OH-16,17-dihydro GA_5	13 ± 1	6.6 ± 0.2

*GA treatments were given 12 h before a 13-h inductive dark period interrupting continuous light. GA dose was 5 µg/plant to the cotyledonary petioles. Values are means ± SEM (*n = 15*).*

Thus, we imagine that in Kidachi it would be possible to inhibit flowering and promote stem elongation at very high doses of 16,17-dihydro GA_5. The 100-fold difference between the dwarf and tall strain, Kidachi and Violet in their threshold GA_5 dose for elongation (Figure 3) may be due to changes in either or both GA sensitivity and biosynthesis. However, not all of this difference is specific to the dwarf phenotype. Dwarf/tall near-isogenic lines showed a less than fivefold difference in the threshold for GA_3 promotion of elongation (King and others 1987). Also, here, with application of GA_3 rather than GA_5 there was little evidence of a differential response between dwarf and tall lines (Figure 4 compare Figure 3).

That 16,17-dihydro GA_5 promoted stem growth of *Pharbitis* was unexpected as in our earlier studies with the grass *Lolium,* it inhibited stem elongation (Evans and others 1994b). No impurities caused by either GA_5 or GA_3, the logical contaminants, could be detected by GC-MS at a limit 1000-fold greater than that for detecting 16,17-dihydro GA_5. Thus, this sample of 16,17-dihydro GA_5 was pure, and it is clearly active for growth but at a 50- to 100-fold higher dose than for GA_5 (Figure 3).

As for the studies with *Fuchsia,* the 3-*epi* GA_3 contained a low level of GA_3 as a contaminant. However, by using an alternative synthetic approach (Seto and others 1998), pure 3-*epi* GA_3 was produced and differential flowering and stem growth responses were confirmed (Figure 5). Additional variants of the functional group at C-3 were also synthesized (Seto unpublished), and, as shown in Figure 5, these compounds were often more growth promoting than GA_3 and, conversely, did not promote flowering but were more inhibitory. At the dose used (2 µg/plant), GA_3 gave a flowering response no different from control when applied 14 h before darkness, but this dose was probably on the threshold of being inhibitory given the tradeoffs between dose and timing of application (Figure 4).

Discussion

In general, gibberellins promote flowering of long day plants (see Pharis and King 1985), but for the long day plant *Fuchsia* they are very potent inhibitors (Sachs and Bretz 1961) as we have confirmed here (Figures 1, 2 and Table 1). This inhibition of flowering by GA is apparently linked to promotion of stem elongation (Figures 1, 2). Most cogent is the comparison between growth-inactive GAs and their growth-active counterparts. For example, over a wide range of doses, the 3α-hydroxy epimers of gibberellins do not inhibit flowering (Figure 2, Table 1), and they are essentially growth inactive (Figure 2, compare to Evans and others 1994a and ref. therein). Likewise, 16,17-dihydro GA_5, a potential growth retardant, had no effect on stem elongation of *Fuchsia* (data not shown) and showed none of the floral inhibition observed for its natural counterpart, GA_5 (Figure 2).

The use of a set of GAs, which, for growth, are variously active (for instance, GA_1, GA_3, GA_5, 2,2-dimethyl GA_4), inactive (e.g., GA epimers) or growth retardants on grasses (for example, 16,17-dihydro GA_5; Evans and others 1994b), has provided a focus for comparing the different species used in this study. Such a comparison of growth and flowering responses across GAs but within a species provides a valid way to analyze species distinctions despite the very much greater (1000-fold) threshold dose required for response of *Spathiphyllum* compared with the other two species. As an aside, we have no explanation for the dose differences between species but consider it likely that for *Spathiphyllum* in particular there are limitations on GA uptake and delivery to the shoot apex.

With *Pharbitis,* inhibition of flowering at high GA doses was associated with enhanced stem elongation, as with *Fuchsia,* but, with either species, inhibition was lost (Figures 2–5 and Table 3) on treatment with GA derivatives that we had found previously to be growth inactive or growth retardive for a monocotyledonous species (for example, see Evans and others 1994a, b). In fact, our evidence that 16,17-dihydro GA_5 can promote growth of *Pharbitis* (Figure 3) but inhibit that of *Lolium* indicates that this GA derivative may act not only to block GA biosynthesis (Junttila and others 1997) but may also

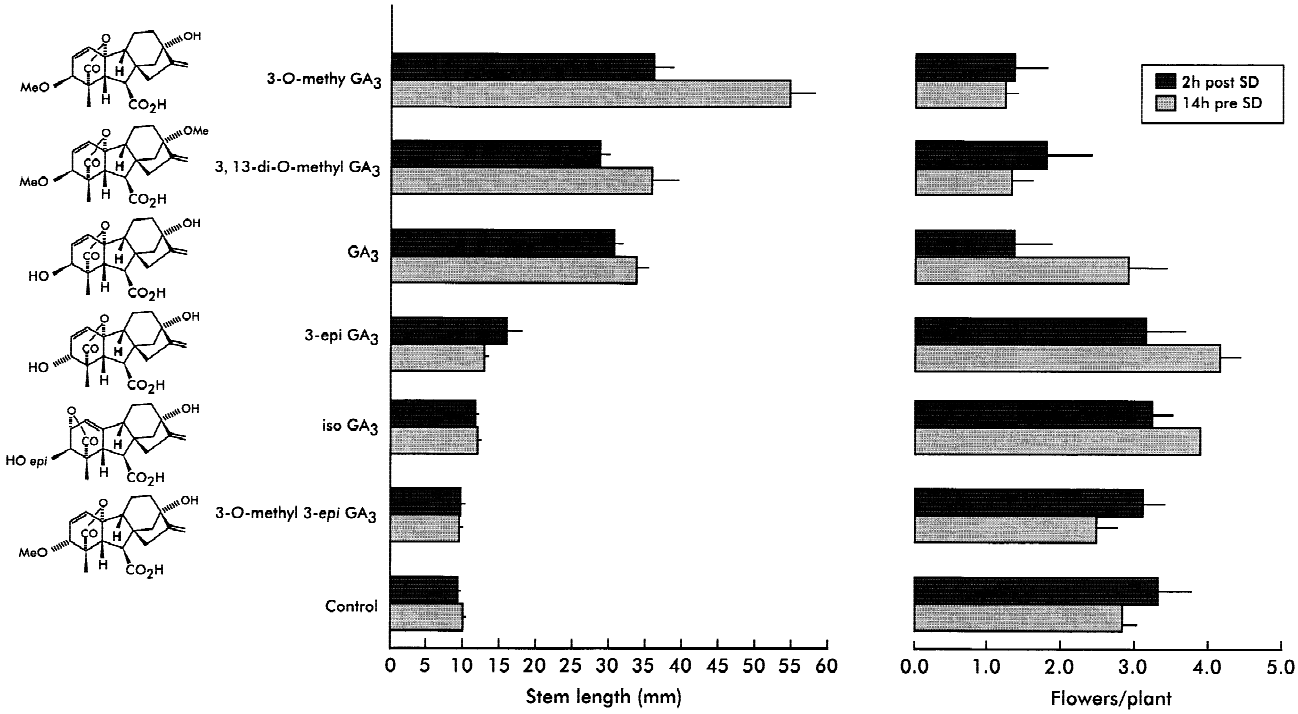

Figure 5. Effect on flowering and stem elongation of *Pharbitis nil,* strain Kidachi, of a single application of 2-μg per plant of various structural variants of GA_3. Values are means ± SE for at least 14 replicate seedlings.

act directly on growth, albiet in an attenuated fashion relative to GA_5. Overall these findings with *Pharbitis* and *Fuchsia* indicate that GA-enhanced growth is involved in the GA-induced inhibition of flowering.

The contrary observation, that flowering of *Pharbitis* was promoted at a low dose of a growth active GA or with a high dose of a less active GA, agrees with our previous findings (King and others 1987 and see Ogawa 1981). However, such promotion occurred at GA doses that did not stimulate stem elongation (Figures 3–5). Hence we suggest this argues for a second and positive or florigenic role for GA in regulating flowering of *Pharbitis,* a florigenic role also seen with *Spathiphyllum,* where GAs promoted flowering (Table 2). A florigenic action was also evident in our previous studies with the long-day plant, *Lolium temulentum,* where these various GAs showed only promotion of flowering, and, moreover, stem growth was not part of this flowering response (Evans and others 1994a, b).

How gibberellins could inhibit flowering of one plant species (for instance, *Fuchsia*), be promotory for others (for example, *Lolium* and *Spathiphyllum*), and show both promotion and inhibition (for instance, *Pharbitis*) highlights a complex control of floral initiation and development. Promotory responses to GAs, at least for *Lolium,* could indicate a distinctive response perhaps involving increased activity at the shoot apex of transcriptional regulators including the *GAMYB* gene (Gocal and others 1999). On the other hand, for inhibition of flowering, our evidence of an inverse relationship with stem growth indicates a mechanism related to competition in the allocation of photosynthetic assimilate. Certainly with *Fuchsia,* there is a parallel between inhibition of its flowering by GA and reduction in apex sucrose content after GA treatment (King and Ben-Tal, in press). This same response would explain why GA inhibits flowering of the long-day plant *Pisum* (Barber and others 1958) and particularly because assimilate is considered important in its flowering responses (Weller and others 1997). Even promotion of flowering of *Pharbitis* by low GA doses could be explained in terms of apex sucrose levels were GA able to enhance import in the absence of potential competition by stem growth.

As an aside, it is interesting that the 16,17-dihydro GA_5 inhibits stem elongation of *Lolium* (Evans and others 1994b) but is inactive with *Fuchsia* or promotory at high doses with *Pharbitis.* We have shown that in *Lolium,* 16,17-dihydro GA_5 acts as a growth retardant by blocking at least one enzymatic step in the biosynthesis of native growth-active GA (Junttila and others 1997). However, it is also clear that 16,17-dihydro GA_5 does retain some

ability to stimulate elongation (Figure 3), so that its action on both GA perception and on GA biosynthesis needs to be examined in the future if we are to provide a complete understanding of the growth-retardant action of this novel GA derivative. The consequences for flowering and growth caused by changes at C-3 of GA_3 (Figure 5) are also interesting and require further analysis.

Overall, when a gibberellin treatment promoted stem growth or was at a threshold dose for this response, flowering of *Fuchsia* and *Pharbitis* was inhibited. No such inverse relationship was found in our earlier studies with *Lolium* where use of these same gibberellins showed that flowering could be uncoupled from stem elongation. Possibly in *Lolium* GAs have a direct effect on flowering, as is evident also for *Spathiphyllum.* By contrast, with *Fuchsia* and *Pharbitis,* at high GA doses stem growth may compete for photosynthetic assimilates to the detriment of flower development at the shoot apex. The corollary for *Lolium* and, perhaps *Spathiphyllum,* is that they are less dependent on assimilate during flowering, and/or that any stem growth associated with early events of flowering is not sufficient to compete with the apex for available photosynthetic assimilates.

ACKNOWLEDGMENTS

A. Poole is thanked for GC-MS analysis, J. Johnston and C. Blundell for technical assistance, L. T. Evans and R. P. Pharis for ongoing discussions and criticism during the course of this study. L. N. Mander, ANU, Canberra, supplied most of the gibberellins. Some of this work was supported by a grant from the Australian Horticultural Research and Development Corporation to R.W.K.

REFERENCES

Barber HN, Jackson WD, Murfet IC, Sprent JI. 1958. Gibberellic acid and the physiological genetics of flowering in peas. Nature 182:1321–1322.

Evans LT. 1964. Inflorescence initiation in *Lolium temulentum* L. V The role of auxins and gibberellins. Aust J Biol Sci 22:773–786.

Evans LT, King RW, Chu A, Mander LN, Pharis RP. 1990. Gibberellin structure and florigenic activity in *Lolium temulentum,* a long-day plant. Planta 182:97–106.

Evans LT, King RW, Mander LN, Pharis RP. 1994a. The relative significance for stem elongation and flowering in *Lolium temulentum* of 3β-hydroxylation of gibberellins. Planta 192:130–136.

Evans LT, King RW, Mander LN, Pharis RP, Duncan KA. 1994b. The differential effects of C-16,17-dihydro gibberellins and related compounds on stem elongation and flowering in *Lolium temulentum.* Planta 193:107–114.

Gocal GFW, Gubler F, Poole AT, Watts RJ, Blundell C, King RW. 1999. Long day up-regulation of *Lolium* GAMyb expression during early stages of inflorescence formation. Plant Physiol 119:1271–1278.

Henny RJ. 1981. Promotion of flowering of *Spathiphyllum* Mauna Loa with gibberellic acid. Hort Sci 16:554–555.

Junttila O, King RW, Poole A, Kretschmer G, Pharis RP, Evans LT. 1997. Regulation in *Lolium temulentum* of the metabolism of gibberellin A_{20} and gibberellin A_1 by 16,17-dihydro GA_5 and by the growth retardant, LAB 198999. Aust J Plant Physiol 24:359–369.

King RW, Pharis RP, Mander LN. 1987. Gibberellins in relation to growth and flowering in *Pharbitis nil* Chois. Plant Physiol 84:126–131.

King RW, Ben-Tal Y. 2001. A florigenic effect of sucrose in *Fuschsia* is blocked by gibberellin-induced assimilate competition. Plant Physiol (in press)

Monselise SP, Goldschmidt EE. 1982. Alternate bearing in fruit trees. Hortic Rev 4:128–173.

Morse RN, Evans LT. 1962. Design and development of CERES—an Australian phytotron. J Agr Eng Res 7:128–140.

Ogawa Y. 1981. Stimulation of the flowering of *Pharbitis nil* Chois by gibberellin A_3: time dependent action at the apex. Plant Cell Physiol 22:675–681.

Ogawa Y. 1993. Flower production of *Spathiphyllum patinii* by gibberellin A_3 and miniaturization of flowering plants. Bull Fac Bioresources, Mie Univ 11:191–197.

Pharis RP, King RW. 1985. Gibberellins and reproductive development in seed plants. Ann Rev Plant Physiol 36:517–568.

Sachs RM, Bretz CF. 1961. The effect of daylength, temperature, and gibberellic acid upon flowering in *Fuchsia hybrida.* Am Soc Hort Sci 80:581–588.

Sachs RM, Kofranek AM, Show-Yin Shyr. 1967. Gibberellin-induced inhibition of floral initiation in *Fuchsia.* Am J Bot 54:921–929.

Seto H, Fujioka S, Kamiya Y, Yoshida S. 1998. Improved procedures for direct conversions of natural 3 beta-hydroxy-gibberellins to alpha-hydroxy and 3-oxo-gibberellins. Heterocycles 48:2245–2251.

Steffen JD, Sachs RM, Hackett WP. 1988. *Bougainvillea* inflorescence meristem development: comparative action of GA_3 in vivo and in vitro. Am J Bot 75:1225–1227.

Weller JL, Reid JB, Taylor SA, Murfet IC. 1997. The genetic control of flowering in pea. Trends Plant Sci 2:412–418.