Plant Physiol. (1987) 84, 1126–1131
0032-0889/87/84/1126/06/$01.00/0

# Gibberellins in Relation to Growth and Flowering in *Pharbitis nil* Chois[1]

Received for publication September 9, 1986 and in revised form March 3, 1987

RODERICK W. KING, RICHARD P. PHARIS*[2], LEWIS N. MANDER
*CSIRO Division of Plant Industry, GPO Box 1600, Canberra ACT, 2601, Australia* (R.W.K., R.P.P.); *and Research School of Chemistry, Australian National University, P. O. Box 4, Canberra, ACT, 2601, Australia* (L.N.M.)

## ABSTRACT

**Flowering can be modified by gibberellins (GAs) in *Pharbitis nil* Chois. in a complex fashion depending on GA type, dosage, and the timing of treatment relative to a single inductive dark period. Promotion of flowering occurs when GAs are applied 11 to 17 hours before a single inductive dark period. When applied 24 hours later the same GA dosage is inhibitory. Thus, depending on their activity and the timing of application there is an optimum dose for promotion of flowering by any GA, with an excessive dose resulting in inhibition. Those GAs highly promotory for flowering at low doses are also most effective for stem elongation (2,2-dimethyl $GA_4 \gg GA_{32} > GA_3 > GA_5 > GA_7 > GA_4$). However, the effect of GAs on stem elongation contrasts markedly with that on flowering. A 10- to 50-fold greater dose is required for maximum promotion of stem elongation, and the response is not influenced by time of application relative to the inductive dark period. These differing responses of flowering and stem elongation raise questions about the use of relatively stable, highly bioactive GAs such as $GA_3$ to probe the flowering response. It is proposed that the 'ideal' GAs for promoting flowering may be highly bioactive but with only a short lifetime in the plant and, hence, will have little or no effect on stem elongation.**

There are many reports of both promotive and inhibitory effects of applied GA[3] on flowering of herbaceous higher plants and for woody species (20, 21, 30 and references therein). Even for a single woody species, apple, both inhibition and promotion of flowering have now been reported (9 and references therein). Depending on the species, the site(s) and mode(s) of GA action could differ, and this may account for the contradictory responses observed between and within a species. The complexity of response has been much discussed (7, 26). As a further illustration, Warm (24) concluded that $GA_3$ acted at two sites, in either or both the leaf and the shoot apex, in promoting the flowering of *Hyoscyamus niger*.

Although some of the contrasts noted in the responses to GAs may reflect differences in the site and timing of treatment, the GA used and its uptake and metabolism in the plant could also be important. To examine the importance of these various factors on the response of flowering to GAs, we have used the SD plant *Pharbitis nil*. Its flowering can be promoted by $GA_3$ both for the dwarf strain Kidachi (16, 17), which is naturally low in bioactive GAs (1) and for the tall strain, Violet, after its treatment with CCC (26). Flowering of both these strains can be triggered by a single exposure to a dark period of about 12 h in duration (5), and this responsiveness has allowed us to examine with precision the effects of various GAs on early processes of floral induction. Simultaneously, the effectiveness of various GAs on stem elongation has been examined.

## MATERIALS AND METHODS

**Growing Conditions and Plant Material.** Seeds of *Pharbitis nil* Chois., the dwarf strain Kidachi (obtained from Y. Ogawa, Mie Univ., Tsu City, Japan), and the tall strain Violet (obtained from Muratane Seed Co. Kyoto, Japan) were treated with concentrated $H_2SO_4$ for 35 min and then washed in running water overnight at 30°C. The seeds were sown into a mixture of equal parts of perlite plus vermiculite in 12-cm diameter pots. The seedlings were raised in continuous light (200 $\mu$mol $m^{-2}$ $s^{-1}$ PAR) first at 30°C for 2 d, then at 25°C for a further 2 d before a dark period of about 12 h at 27°C. After darkness the seedlings were moved to continuous light at 21°C until dissected for flowering response 10 to 14 d later. Seedlings were watered twice daily, once with water and once with Hoagland nutrient solution.

Dwarfing of strain Kidachi reflects its inability to produce high levels of GAs (1). Therefore, GA response was also examined in one experiment using near-isogenic lines derived from a cross between strains Violet and Kidachi (RW King, unpublished data). This use of near-isogenic lines provided a comparison of the tall/dwarf character in an otherwise common genetic background.

The dwarf strain Kidachi was used because of the known history of $GA_3$ promoting its flowering (16, 17). A marginally inductive photoperiod was chosen to provide us with the possibility of seeing both promotive and inhibitory effects of the growth regulators. Initially, we applied less-polar, monohydroxylated GAs. This allowed us to 'pulse' the GA by using the plant's own capability of metabolism to remove excessive levels of the GA (or its bioactive metabolites) which might have a negative effect on flowering (*e.g.* by promoting stem elongation). We thought that this technique might allow the applied GA per se or one of its several metabolites, to yield a positive morphogenic effect on flowering without significantly affecting vegetative growth. The use of a broad range of GA doses for the less polar GAs further increased the likelihood of finding a dosage that might be optimal for flowering, with minimal effects on (or from) other growth processes. Finally, the use of varied times of application (relative to the inductive photoperiod) allowed us to

[1] This research was supported in part by a Natural Sciences and Engineering Research Council of Canada International Collaborative Grant IC-0211, and Operating Grant, No. A-2585 to R. P. P.

[2] Permanent address: Plant Physiology Research Group, Biology Department, University of Calgary, Calgary, Alta. T2N 1N4 Canada.

[3] Abbreviations: GA/GAs, gibberellins as a class; CCC, 2-chloroethyltrimethylammonium chloride.

determine whether there were periods of increased sensitivity (with regard to either positive or negative effects) and, when combined with a broad range of dosages, further increased the likelihood of finding an optimal dosage.

**Application of Gibberellins.** The GAs were dissolved in 80, 90, or 95% ethanol/water (v/v) and applied as a 1 $\mu$l drop to the underside of the petiole of each cotyledon. Control plants were treated with solvent alone. Sources or methods of synthesis of GAs were: $GA_1$ and 2,2-dimethyl $GA_4$ (2, 12 and references therein); $GA_3$ (Sigma Chemical Co.); $GA_4$ (>97% $A_4$) and $GA_7$ (>95% $A_7$) (Abbott Laboratories, North Chicago, IL); $GA_5$ (14); $GA_{32}$ was purified from immature fruit of *Prunus persica* (25).

The choice of $GA_4$ and $GA_5$ was based on their known rapid metabolism in several plant systems, including *Pharbitis* (6) and apple (10), as well as being active in the promotion of flowering (19, 20). The use of $GA_3$ constituted a 'control' of sorts (*e.g.* it was used by Ogawa [16, 17]), and it is known to be relatively long-lived (11). Once activity was evident from the use of $GA_4$, the use of the highly biologically active C-2 dimethyl derivative of $GA_4$ (see Refs. cited in [12]) seemed logical. Gibberellin $A_7$ was chosen because of its high efficacy on conebud differentiation in Pinaceae conifers (21), and $GA_1$ was chosen because of its known role as the 'effector' GA in vegetative stem elongation of both a monocot and a dicot (23). Gibberellin $A_{32}$ was chosen because a compound(s) of similar chromatographic polarity appeared immediately following the inductive photoperiod in *Lolium* (22), and Lona (8) had earlier noted a significant flowering effect on *Perilla* of extracts of immature peach seeds, which are known to be especially rich in $GA_{32}$ (25).

There were three or four pots per treatment with six or seven seedlings per pot. For any one treatment the variance between pots was less than that between plants, so variance between pots within treatments was neglected for statistical analysis. Values given are means, ±1 SE of the mean, except where otherwise noted.

## RESULTS AND DISCUSSION

**Gibberellin Dosage and Stem Elongation.** Stem elongation increased with GA dosage up to at least 20 $\mu$g per plant (Fig. 1). In one experiment (not shown) $GA_7$ at various doses was included along with 2,2-dimethyl $GA_4$, $GA_3$, and $GA_4$. Final stem length depended on the harvest date. However, it is clear that effectiveness of the various GAs was: 2,2-dimethyl $GA_4 \gg GA_{32} > GA_3 > GA_5 > GA_7 > GA_4$. Thus, greater activity of 2,2-dimethyl $GA_4$ than for $GA_4$ (50–100 times) holds not only for monocotyledonous plants as has been noted (12), but also for at least one dicotyledonous plant. This ranking was maintained in the tall and dwarf strains and for GAs dissolved in 80, 90, or 95% ethanol. In an earlier study Ogawa (16) reported a somewhat similar ranking of effectiveness for GAs dissolved in water and applied to strain Kidachi ($GA_3 > GA_7 = GA_1 > GA_5 > GA_4$).

An approximately 10-fold greater dose of any GA was required to trigger elongation of the dwarf strain, Kidachi, compared with the tall strain, Violet (Fig. 1). A comparable difference for $GA_3$ is also evident for an isogenic tall/dwarf line (see later). These differences in response could be related to the earlier finding of Barendse and Lang (1) of an approximately 3-fold lower level of bioactive GA in Kidachi than in Violet. Their data relating to responsiveness to exogenous $GA_3$ are ambiguous but also point to greater doses being required for Kidachi. It is clear that the relative ineffectiveness in promotion of elongation by $GA_1$ or $GA_4$ is not an indication of a late biosynthetic block as both these GAs were equally ineffective in the GA-sufficient tall, or the GA-limited dwarf strains. Rather, their low activity in stem elongation probably reflects a reduced uptake or transport (12), enhanced metabolism (catabolism/conjugation), and/or whether or not the GA is active per se or must first be converted to an active form (23). Differences in metabolism are probably the most likely explanation for activity differences (*e.g.* $GA_{32}$ and $GA_3$ *versus* $GA_5$, $GA_7$, $GA_4$, or $GA_1$). The dramatically enhanced effectiveness of 2,2-dimethyl $GA_4$ for stem elongation (Fig. 1) may result primarily from increased uptake and transport (12) rather than from any hindrance of 2$\beta$-hydroxylation (12).

Not only was plumule/stem elongation enhanced by GAs, but the petiole and hypocotyl elongated and the area of the cotyledons almost doubled. These latter changes were first evident 2 d after treatment and had gone to completion within 9 d (results not shown).

**Effect on Stem Elongation of Time of Gibberellin Treatment.** For both Kidachi and Violet sensitivity of stem elongation to $GA_3$ or $GA_4$ did not change dramatically with time (Fig. 2). Effects of GAs on elongation were no different whether seedlings

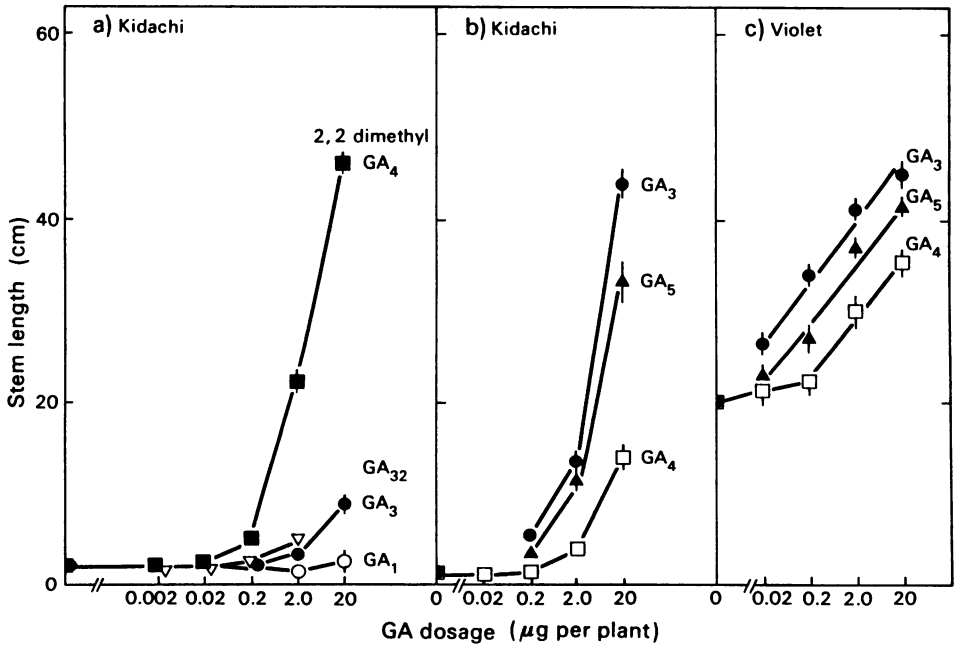


FIG. 1. Effect on stem length of varying amounts of different GAs applied once to the petiole of *Pharbitis*, at 16 h (a) or 5 h (b, c) before induction for the dwarf strain, Kidachi (a, b) or the tall strain, Violet (c). Flowering data for Kidachi are given in Figure 3. All GAs were applied in 95% ethanol unless otherwise indicated. The inductive dark period of 13.25 h began about 130 h after seed sowing. Means are for at least 16 replicate seedlings. Bars are 2 × the SE of the mean.

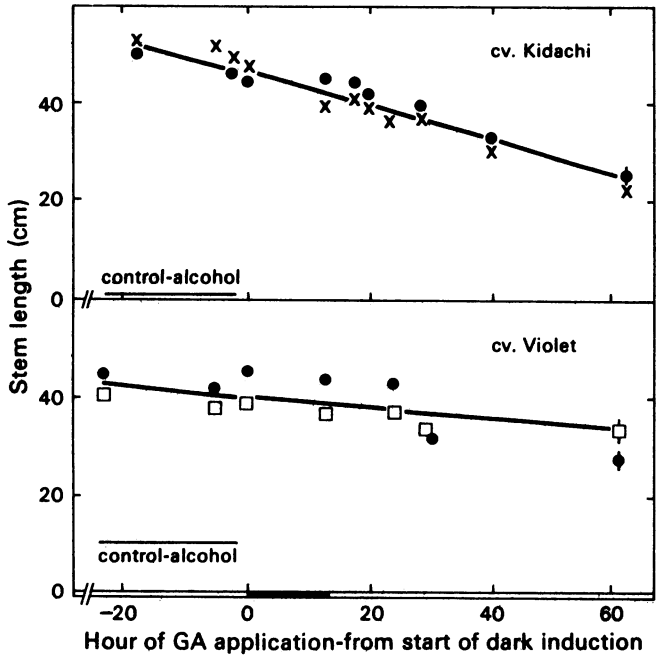


FIG. 2. Effect on stem length of the time of a single petiole application of 20 μg of $GA_3$ (●, ×) or $GA_4$ (□), or of untreated control plants. Seedlings were exposed to a 13.25 h inductive dark period (●, □), or held in continuous light (×). Stem lengths were measured 14 d after the inductive treatment (0 h). Other conditions as in Figure 1. Flowering response of Kidachi to $GA_3$ in this experiment is given in Figure 4b.

had been kept in continuous light or induced to flower by exposure to a single dark period. The reduced stem elongation following later applications possibly reflects the fact that stem length was measured at a fixed real time and not at a fixed time from treatment. In addition, older seedlings may not have been as responsive. Over a 24-h period Ogawa (17) also found no effect of time of application on shoot elongation, although in his data the response to $GA_3$ was limited (*e.g.* stem lengths of 20 mm without $GA_3$ *versus* 50 mm after $GA_3$ application).

**GA Dosage and Flowering.** Flowering of strain Kidachi (but not Violet) could readily be promoted by a single application of GA prior to an inductive dark period (Fig. 3). However, there was a clear optimum, and both the minimum effective dose and the optimum dose were higher the less the activity of the GA in promoting stem elongation (see above). $GA_3$ was equally effective in these two experiments when applied in 95 or 80% ethanol. The highly water-soluble $GA_{32}$, however, appeared to be less effective in 95% than in 80% ethanol (data not shown). Ogawa (17) found only stimulation of flowering up to a dose of 0.1 μg $GA_3$ per plant and clearly from our data this was at or below the optimum. His applications were to the plumule and the $GA_3$ was dissolved in water. However, these differences in technique are unimportant. As shown in Table I, flowering was inhibited by high doses of $GA_3$ (10 μg/plant) whether application was in ethanol or water, or to the plumule or petiole. Clearly, had Ogawa (17) examined higher dosages of $GA_3$, then inhibitory effects of $GA_3$ would also have been evident.

**Flowering and the Time of Gibberellin Application.** The inhibition of flowering at high GA dosage correlated with considerable stimulation of stem elongation (Fig. 1 *versus* Fig. 3), and its action was consistent at all times of GA application before and after the inductive dark period (Fig. 2). However, for flowering, both promotive and inhibitory responses were evident depending on the timing of treatment. Low GA dosages prior to the inductive dark period were generally promotory as illustrated for $GA_3$ and $GA_4$ (Fig. 4). The two separate experiments with $GA_3$, and

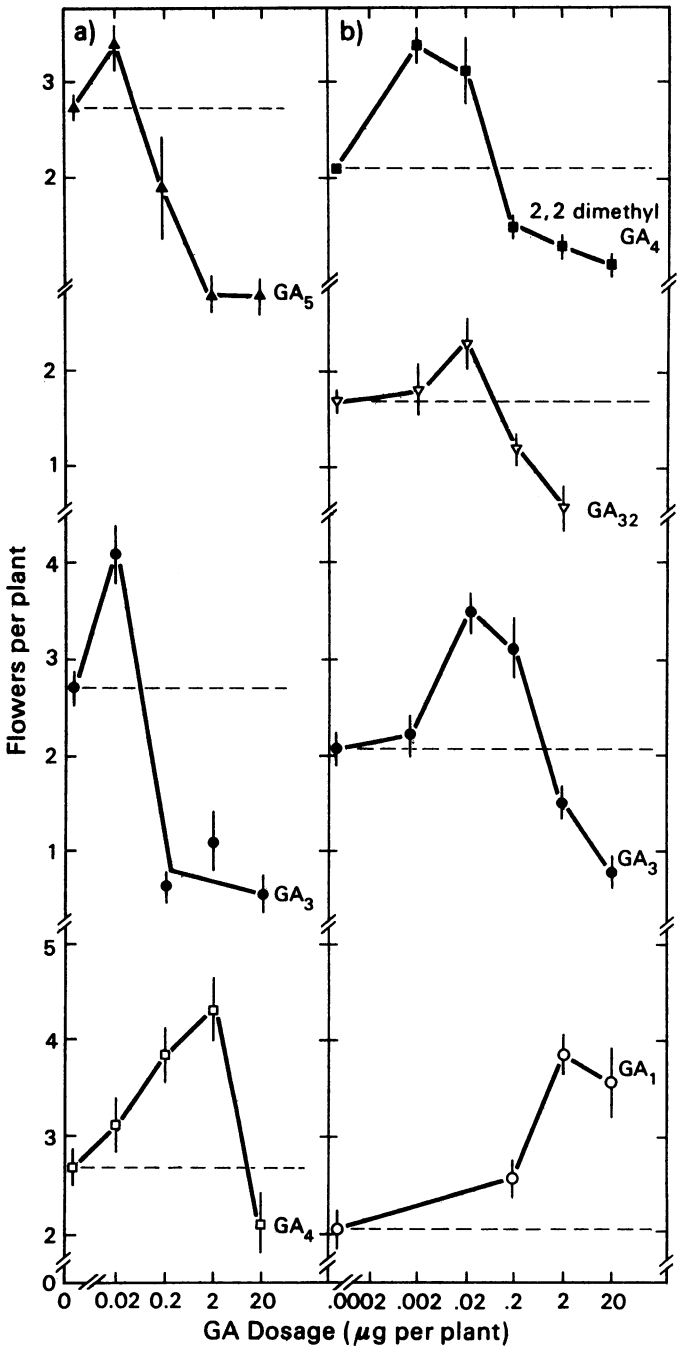


FIG. 3. Effect on flowering of varying amounts of GAs applied once to the petiole either 5 h (a) or 16 h (b) before starting an inductive 13.25 h dark period. Ethanol concentration was 95% for (a) and 80% for (b).

the one with $GA_5$ (Fig. 4) highlight the phase of inhibition that occurs after the inductive dark period. Promotion before darkness was, however, not always evident. This we attribute to difficulties in applying an optimal GA dose at just the right time before darkness, yet one which is not so high that it remains active in the plant until the inhibitory phase occurs, some 24 h later.

**Genotype and Gibberellin Response.** Strain Violet has a high content of bioactive GAs (1), and its stem elongation in response to GAs is more sensitive than for the dwarf strain Kidachi (see above). Any effect of GAs on flowering of strain Violet could, however, be demonstrated only with great difficulty. Only in one

Table I. *Inhibition of Flowering by $GA_3$*

$GA_3$ was applied in ethanol (95%) or water to the petiole or plumule 15 h after the start of a 13.25 h inductive dark period. Control plants were treated with ethanol (95%). The minimum number of replicates was 21.

| Site of $GA_3$ Application (20 μg/plant) | Control | Ethanol as Solvent | Water as Solvent |
|---|---|---|---|
| | *mean flowering response ± 1 SE of the mean* | | |
| Petiole | 2.85 ± 0.10 | 1.55 ± 0.10 | 2.09 ± 0.23 |
| Plumule | 2.85 ± 0.10 | 1.81 ± 0.10 | 1.62 ± 0.15 |

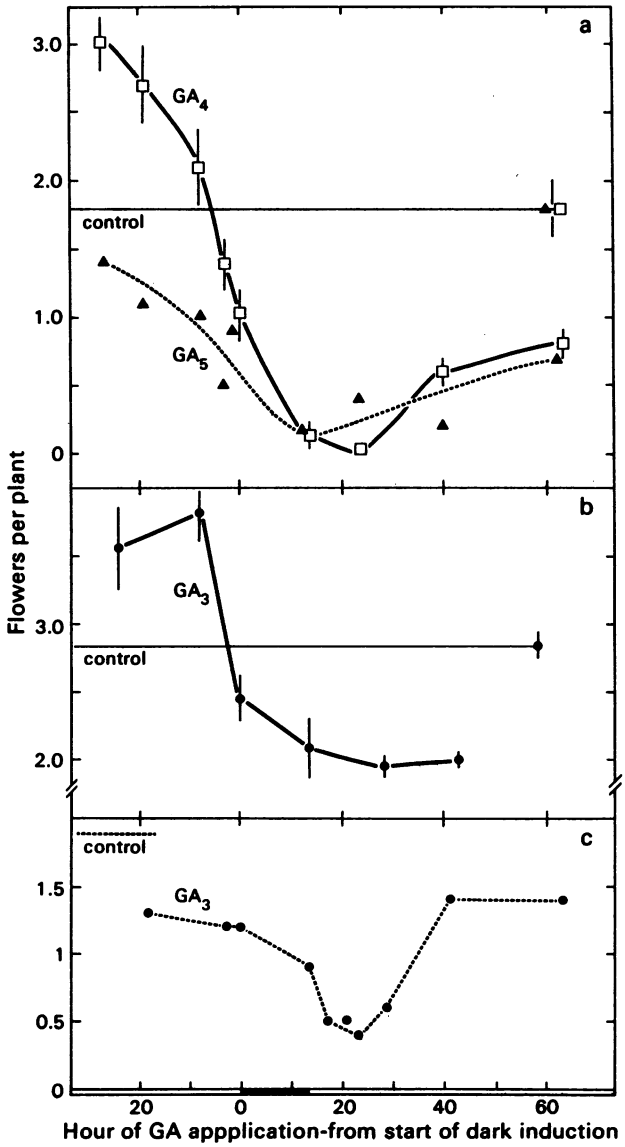


FIG. 4. Effect of time (relative to the start of the inductive dark period) of a single petiole application of GAs (20 μg/plant) on flowering of *Pharbitis* strain Kidachi. Controls (dosage 0) treated once only with 95% ethanol. Three separate experiments are shown (a, b, c).

experiment was there any significant promotion of flowering for $GA_3$ applied before the inductive dark period (Fig. 5). Clear evidence of later inhibition was also hard to obtain (Fig. 5) and, because of these difficulties, we also examined isogenic tall/dwarf lines developed from a cross between Violet and Kidachi (RW

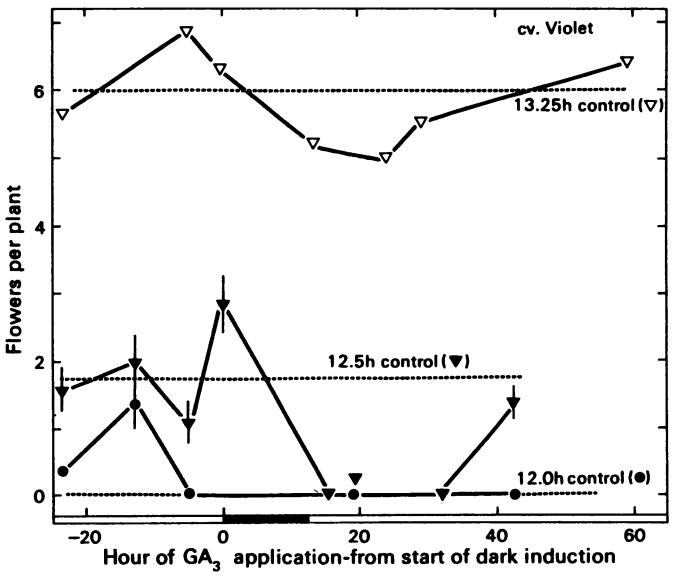


FIG. 5. Effect of time (relative to the start of the inductive dark period) of application of $GA_3$ (20 μg/plant) on flowering of *Pharbitis* strain Violet. Data is for three separate experiments with inductive dark periods of: 12.0 (●); 12.5 (▼); 13.25 h (▽). Bars are 2 × the SE of the mean. Values are significantly different from control ($P \leq 0.05$) for promotion by $GA_3$ (12 h dark) and for inhibition by $GA_3$ (12.5 h dark).

King, unpublished data). As for the parent strains, a lower GA dose was required in the tall than in the dwarf line for stimulation of stem elongation (Fig. 6). Again, as for dwarf Kidachi (Fig. 3), in the isogenic dwarf, for applications prior to the inductive treatment, promotion of flowering was found at low doses, and at higher doses inhibition was observed. Flowering of the tall isogenic line, however, was not influenced by any dose of $GA_3$. In a further experiment even lower $GA_3$ doses (<2 ng/plant) were tested but, again, there was no response. Possibly for this tall isogenic line endogenous levels of GAs are saturating for flowering, and in strain Violet the level may be close to saturating.

## CONCLUSIONS

Promotion of flowering of dwarf lines of *Pharbitis nil* is possible but only with careful choice of GA dosage, type, and the timing of treatment relative to an inductive dark period.

Although GAs appear to be nonlimiting for flowering in normal height, high-GA lines of *Pharbitis* (*e.g.* Figs. 5 and 6), they were limiting in dwarf lines (*e.g.* Fig. 3) and in tall seedlings treated with CCC (26). Use of B-955 (*N,N*-dimethylamino-succinamic acid) not only retarded stem growth of *P. nil* (cv Violet), it also inhibited flowering, implying a GA requirement for both processes (27). In noninductive conditions GAs have no effects on flowering of *Pharbitis* (18), but this lack of activity could equally well reflect the inhibition of flowering resulting from too much GA or from a GA that may have been more readily taken up and/or transported to a site of action (*e.g.* 2,2-dimethyl $GA_4$ *versus* $GA_4$, Figs. 1 and 3), or, after a SD exposure, from applications made after the inductive treatment. In the present study, this inhibition of flowering was correlated with excessive stem elongation and, as summarized in Figure 7, an 'effective' GA for flowering may be relatively ineffective for stem elongation, as is also evident for $GA_4$ on apple (9) and $GA_{32}$ on *Lolium temulentum* (22). Distinctions between GA type and vegetative *versus* flowering responses may also explain the effectiveness for flowering of $GA_5$ on *Chrysanthemum* (19) and of $GA_{13}$ on another SD plant, *Impatiens* (15).

One explanation for our finding of an optimum in the response

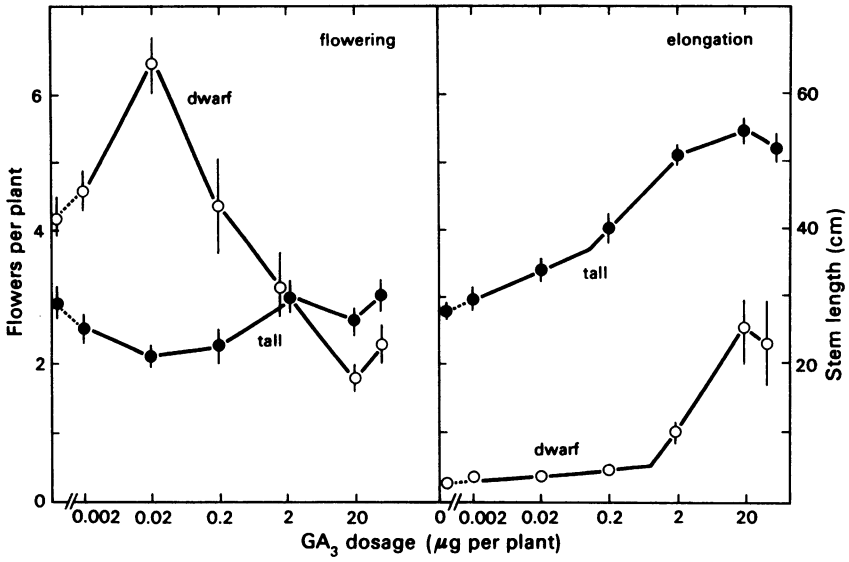


FIG. 6. Effect of the dosage of $GA_3$ on flowering and stem elongation (measured after 10 d) of near-isogenic tall/dwarf lines of *Pharbitis*. Curves fitted by eye. Other conditions as in Figure 1.

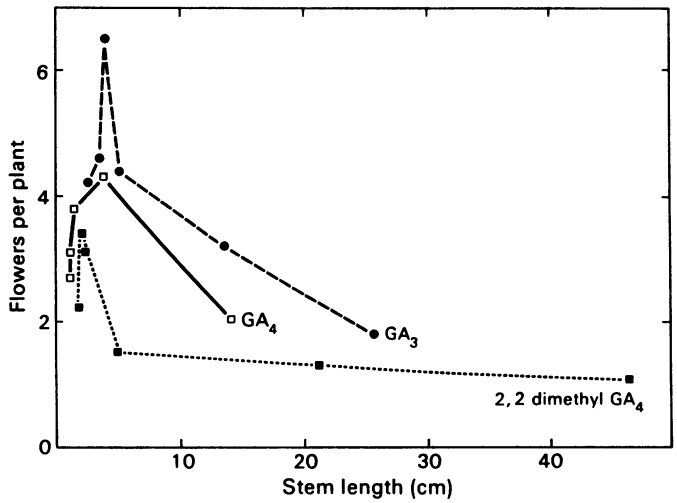


FIG. 7. Relationship between degree of stem elongation after 10 d and flowering response for dwarf lines of *Pharbitis* following treatments before induction with various GAs. The line joining the plot points follows the sequence of increasing GA dosage.

of flowering to GAs is that they play a dual role. A single site of response appears probable, and there is compelling evidence that action is at the shoot apex in *Pharbitis* (17, 18, 26; Table I). Perhaps this action involves a change in the plastochron at the shoot apex. Such a change, for example, is known to be associated with the $GA_3$-promoted flowering in *Xanthium* (3). The switch from promotion to inhibition could relate to enhancement of stem elongation in too close an association with the progression of events of flower initiation and early differentiation. At higher doses of GA (prior to induction), however, a potentially massive promotion of flowering may be counteracted by too long a retention of the GA, which then leads to inhibition of flowering.

An implication of these findings is that the role of GAs in flowering may need reexamination. The reports with other species (20) of GAs either inhibiting or promoting flowering might reflect extremes of a dual response that would only be evident from applications of the appropriate GA at the right dose and timing. One such case is seen in apple in which inhibition of flowering has generally been reported for treatments with $GA_3$, a $GA_{4/7}$ mixture, or $GA_7$, whereas promotion results with $GA_4$ or 3-epi-$GA_4$ applied at the appropriate time (9). Attention to timing and GA type has also allowed, routinely, the promotion of flowering by $GA_{4/7}$ and other less-polar GAs applied to Pinaceae family conifers (see literature cited in Refs. 20 and 21).

If the more effective GAs for flowering are essentially 'pulsed,' that is, remain active for only a short period before metabolism renders them ineffective, then it is intriguing that change in the photoperiod causes a brief switch in availability of endogenous GAs. Work by Zeevaart and colleagues (4, 13, 28, 29) indicates that conversion of the $C_{20}$ $GA_{19}$ to the $C_{19}$ $GA_{20}$ is under photoperiodic control. Our further studies of GA changes at the shoot apex of the LD plant *Lolium temulentum* (22) also support such a scenario. The availability of GA precursors to deliver such a pulse of GA at the apex on receipt of a flowering stimulus also fits with our findings herein of a brief 'time window' and narrow 'optimum dose range' for GAs to promote flowering.

*Acknowledgments*—Many long discussions with and valuable comments by L. T. Evans are gratefully acknowledged. V. Pharis and H. Chadim are thanked for their assistance with GA treatments and Bruce Twitchin for synthesis of 2,2 dimethyl $GA_4$. We also gratefully acknowledge the gift of $GA_{32}$ from Dr. I. Yamaguchi, Department of Agricultural Chemistry, University of Tokyo.

## LITERATURE CITED

1. BARENDSE GWM, A LANG 1972 Comparison of endogenous gibberellins and of the fate of applied radioactive gibberellin $A_1$ in a normal and dwarf strain of Japanese morning glory. Plant Physiol 49: 836–841
2. BEALE MH, J MACMILLAN 1981 Preparation of 2- and 3-substituted gibberellins $A_9$, and $A_4$ for bioassay. Phytochemistry 20: 693–701
3. ERICKSON RO, RD MEICENHEIMER 1977 Photoperiod induced change in phyllotaxis in *Xanthium*. Am J Bot 64: 981–988
4. GIANFAGNA T, JAD ZEEVAART, WJ LUSK 1983 Effect of photoperiod on the metabolism of deuterium-labelled gibberellin $A_{53}$ in spinach. Plant Physiol 72: 86–89
5. Imamura S, M Maramatsu, SI Kitajo, A Takimoto 1966 Varietal differences in photoperiodic behaviour of *Pharbitis nil* Chois. Bot Mag Tokyo 79: 714–721
6. KOSHIOKA M, RP, PHARIS, RW KING, N MUROFUSHI, RC DURLEY 1985 Metabolism of [$^3$H]gibberellin $A_5$ in developing *Pharbitis nil* seeds. Phytochemistry 24: 663–671
7. LANG A 1965 Physiology of flower initiation. *In* W Ruhland, ed, Encyclopedia of Plant Physiology, Vol XV/1. Berlin, Springer-Verlag, pp 1380–1536
8. LONA F 1972 Morphogenins in growth and development of plants. *In* H Kaldewy, Y Vardar, eds, Hormonal Regulation of Plant Growth and Development. Verlag Chemie, Weinheim, pp 423–429
9. LOONEY NE, RP PHARIS, M NOMA 1985 Promotion of flowering in apple trees with gibberellin $A_4$ and C-3 epi-gibberellin $A_4$. Planta 165: 292–294
10. LOONEY NE, A KAMIENSKA, RL LEGGE, RP PHARIS 1978 Metabolism of [$^3$H] gibberellin $A_4$ in relation to flower initiation in apple. Acta Hortic 80: 105–114
11. MCCOMB AJ 1964 The stability and movement of gibberellic acid in pea seedlings. Ann Bot 28: 669–687
12. MACMILLAN J 1985 Gibberellins: metabolism and function. *In* DD Randall,

DG Blevins, RL Larson, eds, Current Topics in Plant Biochemistry and Physiology 1985, Vol 4. University of Missouri-Columbia, pp 53–66

13. METZGER JD, JAD ZEEVAART 1980 Effect of photoperiod on the levels of endogenous gibberellins in spinach as measured by combined gas chromatography-selected ion current monitoring. Plant Physiol 66: 844–846
14. MUROFUSHI N, RC DURLEY, RP PHARIS 1974 Preparation of radioactive gibberellins $A_{20}$, $A_5$ and $A_8$. Agric Biol Chem 38: 475–476
15. NANDA KK, HN KRISHNAMOORTHY, KL TOKY, K LATA 1969 Effects of gibberellins $A_3$, $A_4$+$_7$, and $A_{13}$ and of (−)-kaurene on flowering and extension growth of *Impatiens balsamina* under different photoperiods. Planta 86: 134–142
16. OGAWA Y 1977 Differences in effectiveness of various gibberellins on shoot elongation and flower formation in *Pharbitis nil* Chois. J. Jpn Soc Hortic Sci 46: 117–122
17. 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
18. OGAWA Y, JAD ZEEVAART 1967 The relation of growth regulators to flowering. *In* SI Imamura, ed, Physiology of Flowering in *Pharbitis nil*. Jpn Soc Plant Physiol, Tokyo, pp 107–119
19. PHARIS RP 1972 Flowering of *Chrysanthemum* under non-inductive long day of gibberellins and $N^6$-benzyladenine. Planta 105: 205–212
20. PHARIS RP, RW KING 1985 Gibberellins and reproductive development in seed plants. Annu Rev Plant Physiol 36: 517–568
21. PHARIS RP, SD ROSS 1986 Hormonal promotion of flowering in Pinaceae family conifers. *In* A Halevy, ed, Handbook on Flowering, Vol 5. CRC Press, Boca Raton, FL, pp 269–286
22. PHARIS RP, LT EVANS, RW KING, LN MANDER 1987 Giberellins, endogenous and applied, in relation to flower induction in the long-day plant *Lolium lemulentum*. Plant Physiol 84: 1132–1138
23. PHINNEY BO 1984 Gibberellin $A_1$, dwarfism and the control of shoot elongation in higher plants. *In* Crozier A (ed), The Biosynthesis and Metabolism of Plant Hormones, SEB Seminar Series 23: 17–41. Cambridge University Press, New York
24. WARM E 1980 Effect of phytohormones and salicylic acid on flowering and stem elongation in the long-day plant *Hyoscyamus niger*. Z Pflanzenphysiol 99: 325–330
25. YAMAGUCHI I, T YOKOTA, N MUROFUSHI, Y OGAWA, N TAKAHASHI 1970 Isolation and structure of a new gibberellin from immature seeds of *Prunus persica*. Agric Biol Chem 34: 1439–1441
26. ZEEVAART JAD 1964 Effects of the growth retardant CCC on floral initiation and growth in *Pharbitis nil*. Plant Physiol 39: 402–408
27. ZEEVAART JAD 1966 Inhibition of stem growth and flower formation in *Pharbitis nil* with *N,N*-dimethylamino-succinamic acid (B-995). Planta 71: 68–80
28. ZEEVAART JAD 1971 Effects of photoperiod on growth rate and endogenous gibberellins in the long-day rosette plant spinach. Plant Physiol 47: 821–827
29. ZEEVAART JAD 1973 Gibberellin $A_{20}$ content of *Bryophyllum daigremontianum* under different photoperiodic conditions as determined by gas-liquid chromatography. Planta 114: 285–288
30. ZEEVAART JAD 1983 Gibberellins and flowering. *In* A Crozier, ed, The Biochemistry and Physiology of Gibberellins, Vol 2. New York, Praeger, pp 333–374