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Gibberellic Acid and Cytokinin Affect *Phalaenopsis* Flower Morphology at High Temperature

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Abstract. **Gibberellin A_3 (GA_3: 1, 3, or 5 μg/shoot), ^{6}N-benzyladenine (BA: 1, 3, or 5 μg/shoot), or both were applied to the flowering shoots of a white hybrid *Phalaenopsis* orchid (Leda) when they were 2 to 3 cm (stage 1, no flower primordia) long at high temperature (30 °C day/25 °C night). When flowering shoots were treated with GA_3 alone, deformed flowers were more frequent with increasing GA_3 concentrations. The occurrence of GA_3-induced deformed flowers was prevented by BA at the same dose as GA_3 when applied 4 days after GA_3 treatment. BA (1, 3, or 5 μg/shoot) was also applied 4 days before (time 1) or 4 days after (time 2) GA_3 (1 μg/shoot) treatment for regulating plant characteristics. The application of BA at 1 or 5 μg/shoot to stage 1 flowering shoots at time 2 resulted in short internodes between florets, whereas BA application at time 1 had no effect. Simultaneously, BA at 1 or 5 μg/shoot applied at time 1 or time 2 to stage 2 (5 to 6 cm long, two- to three-flower primordia) flowering shoots also shortened internode length between florets as compared to GA_3 alone. When a stage 1 flowering shoot was given BA (3 or 5, but not 1 μg/shoot) and then treated with GA_3 4 days later, flower count was slightly reduced as compared to treating with GA_3 alone. However, a high dose of BA applied at time 1 or time 2 on stage 2 flowering shoots had no effect on flower count. Chemical names used: *N*-(phenylmethyl)-1*H*-purine-6-amine [benzyladenine (BA)], gibberellic acid (GA_3).**

The transition from a vegetative growth to flowering in *Phalaenopsis* requires a period of exposure to relatively cool air (Lee and Lin, 1984; Nishimura and Kosugi, 1972). The elongation of flowering shoots and initiation of flower primordia do not occur if plants are exposed to air above 28 °C (Sakanishi et al., 1980). Chen et al. (1994) showed that *Phalaenopsis amabilis* (cv. P. Pafang's Full Moon), with 8-cm-long flowering shoots, treated with GA_3 at 40 μg/shoot, resulted in flower development under noninductive high temperatures (30 °C day/25 °C night). However, flowers were deformed, with narrow sepals and petals as well as long internodes between florets.

Cytokinin is well known for regulating meristematic activity of the shoot apex (Fosket and Short, 1973; Seidlova and Krekule, 1977). Also, cytokinin promotes expansion of light-grown excised radish (*Raphanus sativus* L. cv. Crimson Giant) cotyledons (Howard and Witham, 1983). We hypothesized that cytokinin may be effective in promoting the lateral expansion of *Phalaenopsis* sepals and petals. The objective of this study was to determine the effect of BA in restoring normal flower morphology and on internode length between florets in *Phalaenopsis* before and after GA_3 treatment at high temperature.

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Materials and Methods

Plant materials. Mature hybrid *Phalaenopsis* seedling plants (Leda, bred by Dept. of Horticulture, Taiwan Sugar Research Institute) having 2- to 3-cm- (stage 1, no flower primordium) or 5- to 6-cm- (stage 2, two- to three-flower primordia) long flowering shoots were placed in growth chambers with a 9-h photoperiod and 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux. The warm chambers were kept at 30 °C day/25 °C night, and the control chambers at 25 °C day/20 °C night, which is the ideal condition for flowering (Lee and Lin, 1984). Plant management was similar to that described previously (Chen et al., 1994).

Frequency of GA_3 application and flower count (Expt. 1). GA_3 (Sigma, St. Louis) was dissolved in 10% (v/v) aqueous ethanol and 1 μL of a solution (1 μg of GA_3) was injected into the cavity of the second visible bud scale below the flowering shoot apex once, twice, or three times at 7-d intervals at stage 1. The experiment was conducted at 30 °C day/25 °C night. The design was a randomized complete block with five single plant replications. Analysis of variance (ANOVA) was performed and Duncan's multiple range test was used for comparing the means.

Effect of GA_3 and BA applications. BA was dissolved in 0.2 M H_2SO_4, diluted successively with distilled water, so that 1 μL of a solution applied to each flowering shoot contained 1, 3, or 5 μg BA. BA was applied to the same site as GA_3 either 4 d before (time 1) or 4 d after (time 2) GA_3 (1 μg/shoot) had been applied at both stages of flowering shoot development.

Stage and time of BA and GA_3 application effects on flowering shoot apex dimension (Expt. 2). BA (1, 3, or 5 μg) was applied at time 1 or time 2 to the stage 1 and stage 2 flowering shoots, respectively. All experiments were conducted at 30 °C day/25 °C night. Warm control plants were kept at 30 °C day/25 °C night with or without GA_3 treatment at stage 1. In addition, plants with flowering shoots and kept at 25 °C day/20 °C night are referred to as standard plants. Apex dimensions were measured by a vernier caliper when flowering shoots were ≈20 cm long. The experiment consisted of a factorial combination of three BA concentrations, two application stages (stages 1 and 2), and two application timings (times 1 and 2) with five replications. Data were subjected to a three-way ANOVA and main effects of BA dose, stage, and time interactions were tested. A one-way ANOVA was used for all data analysis. Based on significant F values, treatment means were separated by Tukey's multiple comparison test.

Stage and time of BA and GA_3 application effects on flower count and internode length between florets (Expt. 3). BA (1, 3, or 5 μg) was applied at time 1 or time 2 to both stages of flowering shoots. All experiments were conducted at 30 °C day/25 °C night. Warm control plants with flowering shoots were grown at 30 °C day/25 °C night and treated with or without GA_3 at stage 1. Standard plants were kept at 25 °C day/20 °C night. The design for flower count and internode length between florets were randomized complete blocks with five replications. The experiment of flower count consisted a 3 × 2 × 2 factorial with BA concentrations, application stages, and application timing. Data for BA dose, stage, and time interactions were tested by a three-way ANOVA. The experiment of average internodes between florets consisted of a factorial combination of two BA doses and two BA application times. Data were statistically examined by a two-way ANOVA.

Scanning electron microscopy (Expt. 4). Sequential replications of single flower primordia were conducted using the techniques of Green and Linstead (1990) and Hernandez et al. (1991). Flowering shoots 5 to 6 cm long were used at the beginning. Molds of individual flowering shoot apices were made before chemical treatment began. Individual molds were also made from flowering shoot apices of plants on day 10 after GA_3 (5 μg/shoot) treatment (GA_3 only). Similarly, molds were made on day 5 after flowering shoots were treated with BA at 5 μg/shoot on the 5th d, followed by GA_3 (5 μg/shoot) treatment. Plants that did not receive any chemical treat-

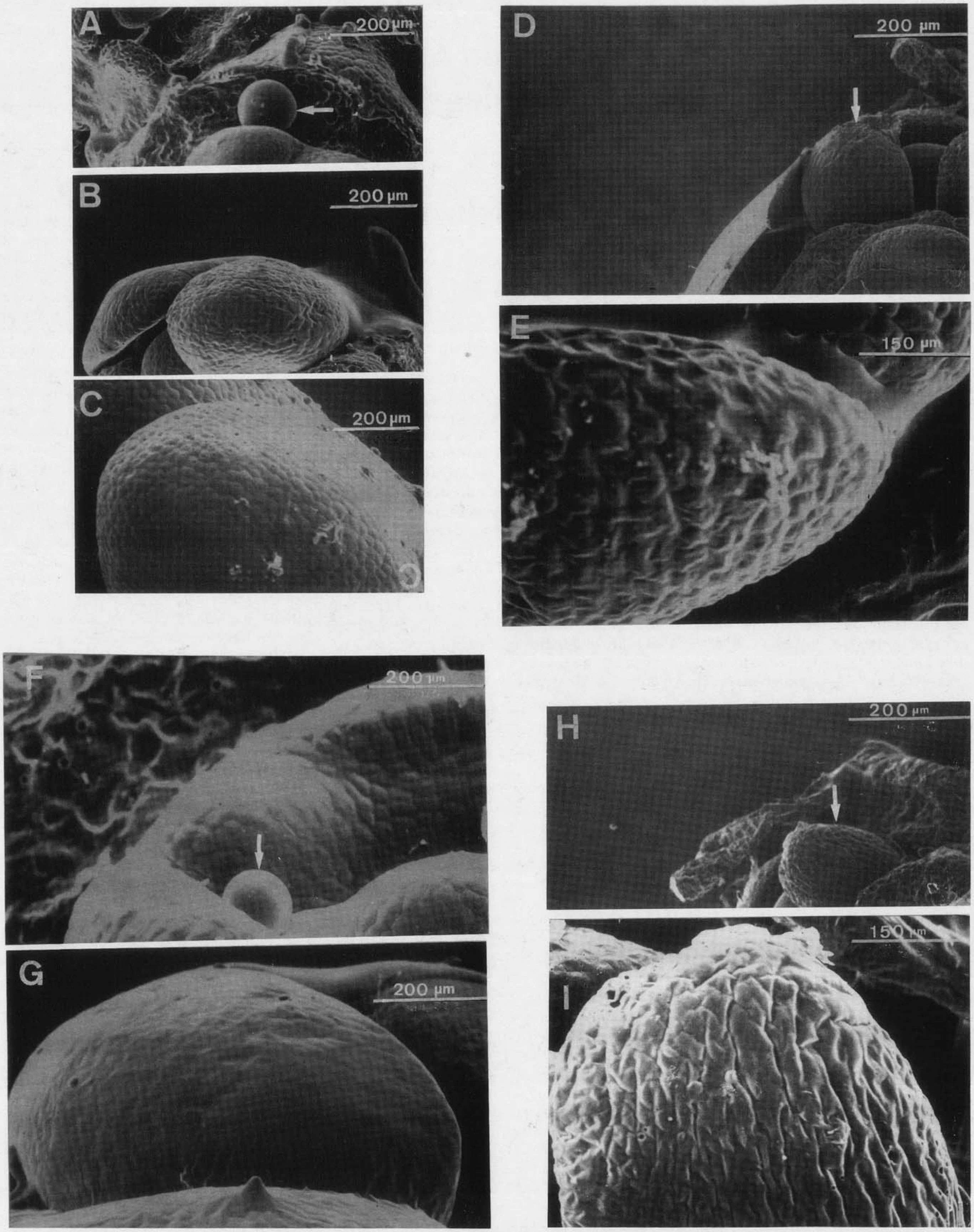

Fig. 1. Effect of GA_3 and BA on morphology of flower primordia in *Phalaenopsis*. Plants with 5- to 6-cm-long flowering shoots at the beginning were used and grown at high temperature (30 °C day/25 °C night). (**A**) Flower primordium before chemical treatment, arrow indicates flower primordium; (**B**) 5 d after GA_3 treatment at 5 µg/shoot; (**C**) 5 d after GA_3 treatment, followed by BA application at 5 µg/shoot, and photographed on the 5th d after BA was applied; (**D**) flower primordium (arrow) before chemical treatment; (**E**) the same flower primordium as **D**, 10 d after GA_3 (5 µg/shoot) treatment; (**F**) flower primordium (arrow) before chemical treatment; (**G**) the same flower primordium as **F** after 10 d of growth at standard conditions (25 °C day/20 °C night); (**H**) flower primordium at the beginning of high temperature (30 °C day/25 °C night). Arrow indicates flower primordium; (**I**) flower primordium 10 d after high temperature.

Table 1. Benzyladenine (BA) application and apex size in the flowering shoots of *Phalaenopsis*. BA and GA_3 (1 µg/shoot) were applied to flowering shoots. All treated plants were grown at 30 °C day/25 °C night. N = 5 for all experiments.

BA (µg/shoot)	Time of BA application[z]	Apex dimension (mm) (means ±SD) Length (L)	Width (W)	L/W
		Stage 1[y]		
1	1	2.6 ± 0.1[x]	1.5 ± 0.1	1.7
	2	2.4 ± 0.2	2.2 ± 0.2	1.1
3	1	2.4 ± 0.1	1.6 ± 0.1	1.5
	2	2.4 ± 0.2	2.2 ± 0.1	1.1
5	1	2.4 ± 0.1	1.8 ± 0.2	1.3
	2	2.4 ± 0.2	2.4 ± 0.2	1.0
		Stage 2[w]		
1	1	2.6 ± 0.1	2.0 ± 0.2	1.3
	2	2.5 ± 0.1	2.0 ± 0.3	1.3
3	1	2.6 ± 0.2	2.2 ± 0.2	1.2
	2	2.6 ± 0.2	2.4 ± 0.1	1.1
5	1	2.6 ± 0.1	2.5 ± 0.1	1.0
	2	2.6 ± 0.1	2.5 ± 0.1	1.0
Warm control[v]				
$+GA_3$		3.2	1.9	1.7
$-GA_3$		1.7	1.3	1.3
Standard plant (25 °C day/20 °C night)		2.7	2.6	1.0

[z]1 = BA applied 4 d before GA_3; 2 = BA applied 4 d after GA_3.
[y]Stage 1 indicates flowering shoot with no flower primordia.
[x]Data obtained when flowering shoot length had reached 20 cm.
[w]Stage 2 denotes flowering shoot with two- to three-flower primordia.
[v]The warm control plants were grown at 30 °C day/25 °C night with or without GA_3 treatment at stage 1.

ment were kept at 25 °C day/20 °C night (standard plants) or 30 °C day/25 °C night (warm controls), respectively, and molds of the shoot apices were made at the beginning and again 10 d later. All experiments were repeated three times.

Bud scales at the tips of flowering shoots were removed with two to three inner bud scales remaining. The molding procedure involved covering the buds with Mirror-Wash 3 polyvinylsiloxane impression material (Kerr's Manufacturing Co., Romulus, Mich.). Once hardened, the mold was removed with a pair of tweezers, inverted, and affixed to a slide by the use of Reflect dental-impression polymer (Kerr's Manufacturing Co.). The depression in the mold was filled with a mixture of Master Mend Epoxy (Duro Loctite Co., Automotive Consumer Group, Cleveland). The hardened casts were removed, mounted on scanning electron microscope stubs, and sputter-coated with gold–platinum. The casts were examined with a Hitachi 2400 scanning electron microscope (Tokyo) at 12 kV and photographed.

Effect of GA_3 and BA on flower characteristics (Expt. 5). GA_3 (1, 3, or 5 µg/shoot) was injected into stage 1 flowering shoot apices as described for Expt. 1. Additionally, GA_3 (1, 3, or 5 µg/shoot) was applied to stage 1 flowering shoot apices and the same doses of BA were applied to those at stage 2. All the above plants were kept at 30 °C day/25 °C night. Standard plants were kept at 25 °C day/20 °C night. Flower morphology was recorded by photography 2 d after flowers had opened. All experiments were repeated four times.

Results

Plants that were treated with GA_3 at 1 µg/shoot twice and three times produced more flowers (7.3) than those treated only once (6.9), but the difference is not commercially significant. The untreated plants did not produce flowers under the warm conditions.

GA_3 at 5 µg/shoot significantly changed the morphology of flower primordia. Flower primordia were elongated significantly rather than spherical 10 d after GA_3 treatment when compared with those in warm control or in standard plants (Fig. 1 E, G, and I). When flowering shoots were treated with a single application of GA_3 at 5 µg, and with the same dose of BA 5 d later, the appearance of flower primordia after five more days was the same as if it had not been treated with GA_3 (Fig. 1 B, C, G, and I). Flower primordium morphology in warm controls was identical to that of standard plants (Fig. 1 G and I).

Desirable flowering shoot apex characteristics (length and width of flowering shoot apex almost equal) was obtained when GA_3 (1 µg/shoot) was followed by BA (time 2) at 1, 3, or 5 µg/shoot at stage 1 flowering shoots, and also when stage 2 flowering shoots were treated with BA at any of the three doses at either time 1 or time 2 (Table 1). In contrast, when flowering shoots were treated with GA_3 only, the apex length was greatly enhanced, whereas the widths were reduced significantly (Table 1). Interactions of stage on length, and stage, BA dose, BA timing, and stage × BA timing on width of flowering shoot apices were significant (Table 2).

Stage 1 flowering shoots treated with BA (3 or 5 µg, but not 1 µg/shoot) at time 1 resulted in a lower flower count than treated with GA_3 alone. However, the flower count was higher as compared to GA_3 alone or to standard plants when BA (1, 3 or 5 µg/shoot) was applied at time 2 (Table 3). When stage 1 flowering shoots were treated with BA (3 or 5 µg/shoot) at time 1 or time 2, the GA_3-modified flower morphology was prevented, even when the flower size was smaller when BA was applied at time 1 (data not shown). Similarly, when stage 2 flowering shoots were treated with BA (1, 3, or 5 µg/shoot) at either time 1 or time 2, flower count was not affected . There were significant stage, BA timing, and stage × BA timing interactions for flower count (Table 4).

When a stage 1 flowering shoot was treated with BA at 1 or 5 µg/shoot at time 1, it did not shorten internode length between florets, whereas BA treatment at time 2 caused a dramatic decrease as compared to GA_3 alone (Table 5). BA application to stage 2 flowering shoots at either time 1 or time 2 also shortened the internode length between florets as compared to GA_3 alone. However, the internodes (average values: 1.9 cm) were longer than when BA was applied to stage 1 flowering shoots at time 2. Internode length between florets was affected significantly by BA timing interactions (Table 6).

The petals were longer when GA_3 doses were high (3 or 5 µg/shoot), whereas petals were wider with GA_3 (1, 3, or 5 µg/shoot) followed by the same dose of BA as GA_3 than for the GA_3 treatment alone. GA_3 treatment (1,

Table 2. Three-way fixed model analysis of variance for the apex size of *Phalaenopsis* in response to treatment with benzyladenine (BA) before (time 1) or after (time 2) GA_3 application.

Source of variation	Length df	Length Mean square	Length F	Width df	Width Mean square	Width F
Stage	1	0.270	12.30*	1	1.268	48.29***
BA dose	2	0.004	0.18	2	0.621	23.67***
BA timing (time 1 and time 2)	1	0.041	1.86	1	1.470	56.00***
Stage × BA dose	2	0.012	0.54	2	0.068	2.60[NS]
Stage × BA timing	1	0.001	0.04	1	0.963	36.70***
BA dose × BA timing	2	0.019	0.86	2	0.012	0.45[NS]
Stage × BA dose × BA timing	2	0.003	0.12	2	0.015	0.58[NS]
Error	36	0.022		36	0.026	

[NS, *, ***]Nonsignificant or significant at $P = 0.05$ and 0.001, respectively.

Table 3. Benzyladenine (BA) application and flower count in *Phalaenopsis*. BA and GA_3 (1 μg/shoot) were applied to flowering shoots. All treated plants were grown at 30 °C day/25 °C night. N = 5 for all experiments.

BA (μg/shoot)	Time of BA application[z]	Flowers/flowering shoot (no.) (Means ±SD)
	Stage 1[y]	
1	1	7.3 ± 0.8[x]
	2	7.5 ± 0.8
3	1	6.5 ± 0.6
	2	7.5 ± 0.8
5	1	6.2 ± 0.4
	2	7.5 ± 0.8
	Stage 2[w]	
1	1	7.3 ± 0.8
	2	7.5 ± 0.8
3	1	7.5 ± 0.4
	2	7.6 ± 0.9
5	1	7.5 ± 0.8
	2	7.5 ± 0.8
Warm control[v]		
+GA_3		7.0
–GA_3		0
Standard plant (25 day °C/20 °C night)		7.0

[z]1 = BA applied 4 d before GA_3; 2 = BA applied 4 d after GA_3.
[y]Stage 1 indicates flowering shoot with no flower primordia.
[x]Data obtained 2 d after flowers had opened.
[w]Stage 2 denotes flowering shoot with two- to three-flower primordia.
[v]The warm control plants were grown at 30 °C day/25 °C night with or without GA_3 treatment at stage 1.

Table 4. Three-way fixed model analysis of variance for the flower count of *Phalaenopsis* in response to treatment with benzyladenine (BA) before (time 1) or after (time 2) GA_3 application.

Source of variation	df	Mean square	F
Stage	1	2.722	4.41*
BA dose	2	0.389	0.63[NS]
BA timing (time 1 and time 2)	1	3.556	5.57*
Stage × BA dose	2	0.722	1.17[NS]
Stage × BA timing	1	2.722	4.41*
BA dose × BA timing	2	0.389	0.63[NS]
Stage × BA dose × BA timing	2	0.722	1.17[NS]
Error	60	0.617	

[NS],*Nonsignificant or significant at $P = 0.05$, respectively.

Table 5. Benzyladenine (BA) application on average length of internode between florets in the flowering shoots of *Phalaenopsis*. GA_3 at 1 μg/shoot was applied to flowering shoot, and all plants were grown at 30 °C day/25 °C night. N = 5 for all experiments.

BA (μg/shoot)	Time of BA application[z]	Internode length (cm) (Means ±SD)
	Stage 1[y]	
1	1	2.5 ± 0.2[x]
	2	1.8 ± 0.2
5	1	2.5 ± 0.2
	2	1.5 ± 0.2
Warm control[w]		
+GA_3		2.8
–GA_3		No flower
Standard plant (25 day °C/20 °C night)		1.4

[z]1 = BA applied 4 d before GA_3; 2 = BA applied 4 d after GA_3.
[y]Stage one indicates flowering shoot with no flower primordia.
[x]Data obtained 2 d after flowers had opened.
[w]The warm control plants were grown at 30 °C day/25 °C night with or without GA_3 treatment.

Table 6. Two-way fixed model analysis of variance for the average internode length of *Phalaenopsis* in response to treatment with benzyladenine (BA) before (time 1) or after (time 2) GA_3 application.

Source of variation	df	Mean square	F
BA dose	1	0.106	3.04[NS]
BA timing (times 1 and 2)	1	2.641	75.9***
BA dose × BA timing	2	0.076	2.71[NS]
Error	12	0.035	

[NS],***Nonsignificant or significant at $P = 0.001$, respectively.

3, or 5 μg/shoot) led to a wide space between the upper three small petals, while BA at the same dose as GA_3 counteracted this effect (Fig. 2). In these experiments, normal flower morphology was clearly associated with a balance between gibberellin and cytokinin dose.

Discussion

As reported in our previous paper (Chen et al., 1994), GA_3 at 40 μg/flowering shoot induced flower development of *Phalaenopsis* at high temperature. In that experiment, a pure white species was selected as the plant material. However, in this work, a GA_3-sensitive white hybrid with a mixture of red and yellow spots in the basal three petals was used. For this hybrid, GA_3 at 1 to 5 μg/flowering shoot can be recommended to the growers (W.S. Chen, unpublished). Also, since there is only a slight difference in flower counts in response to the number of GA_3 applications, we suggest a single application.

Maksymowych et al. (1976) and Wardlaw and Mitra (1958) indicated GA_3 application to *Xanthium* shoots and the fern apex, respectively, resulted in a 2-fold increase in volume of the apical dome. The increase in volume of the apical dome by gibberellin treatment can be interpreted as correlative growth due to an increased rate of leaf production. During the transition to flowering in *Phalaenopsis,* the inflorescence apex continued to form primordia on its sides. These primordia did not develop into leaves and axillary primordia but, instead, formed bracts that grew out either into flowers or a flower axis. Thus far, GA_3 treatment on *Phalaenopsis* at high temperature led to longitudinal growth of flower primordia as early as 10 d after GA_3 application, and this process can be fully prevented by BA treatment (Figs. 1 and 2). Furthermore, the size of the flowering shoot apices was almost identical to the plants under standard conditions when 5 μg BA was applied after GA_3 treatment. Also, the growth in width of shoot apices increased with increasing BA concentrations (Table 1). Kinetin-induced cell division in the shoot apex of ferns (Wardlaw and Mitra, 1958) and *Sinapis* (Bernier et al., 1975) has been observed. These results suggest radial expansion of the apical dome was at least partially due to kinetin treatment. The changes in cell division induced by cytokinin may be a response to the increased width growth, which is normally associated with the further development of flower primordia in *Phalaenopsis.* The elucidation of the regulatory mechanism of flower primordium growth by BA remains unknown.

Another interesting finding of the present study is that 3 or 5 μg of BA per flowering shoot given before the formation of flower primordia (stage 1) reduced flower counts (Table 3). When BA (3 or 5 μg/shoot) was applied just after the appearance of flower primordia (4 d after stage 1), flower counts increased. Further, BA at 1 μg/shoot had no effect on flower count, regardless of application timing (Table 3). We cannot explain this

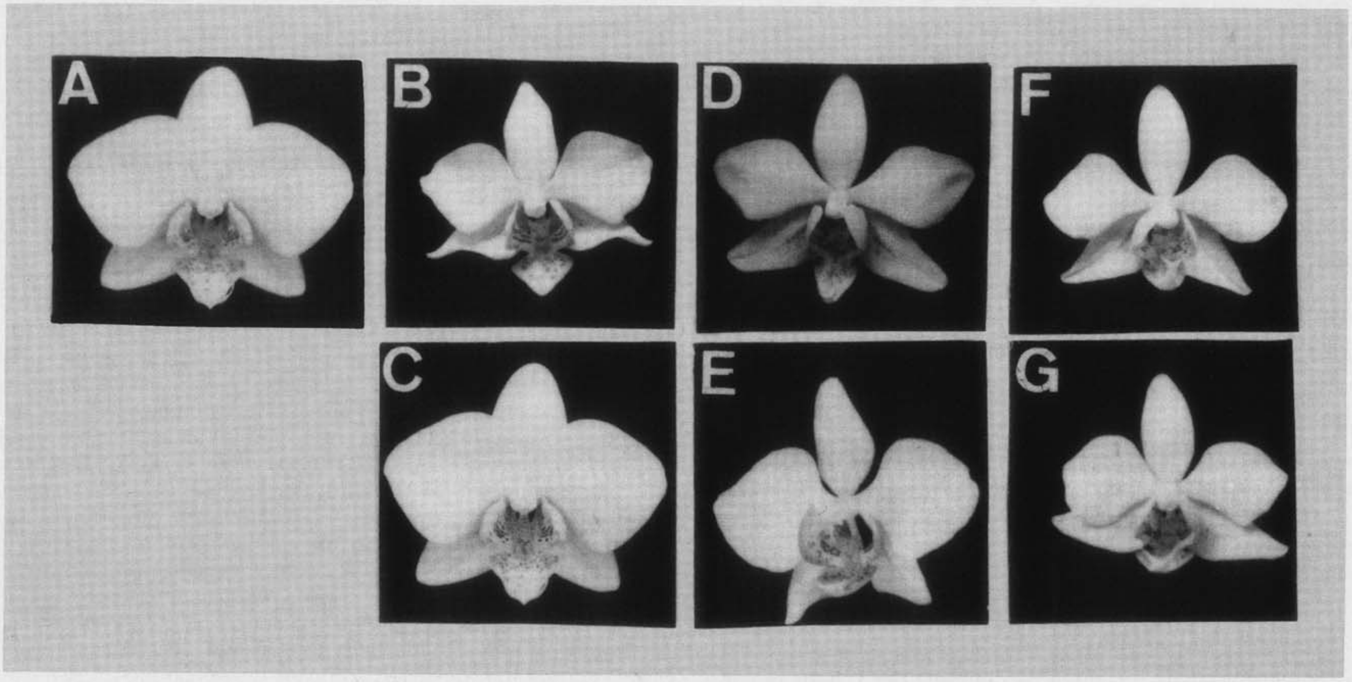

Fig. 2. Effect of GA_3 and BA on flower morphology of *Phalaenopsis*. Plants with 2- to 3-cm-long flowering shoots were used, and grown at high temperature (30 °C day/25 °C night). Flower was photographed 2 d after flowers had opened. (**A**) standard plant (25 °C day/20 °C night); (**B**) flowering shoot was treated with GA_3 at 1 µg/shoot; (**C**) flowering shoot was treated with GA_3 at 1 µg/shoot, and BA at 1 µg applied when the flowering shoot was 5 to 6 cm long; (**D**) flowering shoot was treated with GA_3 at 3 µg/shoot; (**E**) flowering shoot was treated with GA_3 at 3 µg/shoot, and BA at 3 µg applied when flowering shoot was 5 to 6 cm long; (**F**) flowering shoot was treated with GA_3 at 5 µg/shoot; (**G**) flowering shoot was treated with GA_3 at 5 µg/shoot, and BA at 5 µg applied when flowering shoot was 5 to 6 cm long.

difference, especially relative to the dynamics of floral induction by hormonal regulation at high temperature. Seidlova and Krekule (1977) reported kinetin-evoked leaf differentiation and correlatively inhibited floral transition in *Chenopodium rubrum.* In contrast, when kinetin treatment followed floral induction, some postinductive growth changes (i.e., cell division, carbohydrate content, and RNA level) are already taking place. Bud organogenesis may be stimulated leading to the induction of flower development. Miller and Lyndon (1975, 1976) also indicated the rate of cell division in the shoot apex of *Silene* increased only when the flower itself was beginning to form. Furthermore, evidence in one experiment clearly indicates that BA at 1 or 5 µg applied to the 2- to 3-cm-long inflorescence just before GA_3 treatment at 1 µg/shoot did not reduce internode length between florets. This could be fully altered when BA was applied after GA_3 treatment (two- to three-flower primordia apparent) (Table 5). These observations seem compatible with our conclusion that BA (5 µg/shoot) applied 4 d after GA_3 treatment at 1 µg/shoot (flowering shoot length ≈5 to 6 cm, stage 2) enhances flower quality in *Phalaenopsis*. Knowledge of how the timing of BA application affects the development of flower primordia and final flower shape is of paramount importance for practical culture of *Phalaenopsis.*

In conclusion, flowering in *Phalaenopsis* clearly is induced by GA_3 at 1 µg/shoot at high temperature. Our work shows that restoration of flower morphology is possible and has been successfully carried out by using BA treatment at 5 µg/shoot 4 d after GA_3 application. GA_3 and BA are useful for commercial cut flower production and/or for the flowering potted plant market of *Phalaenopsis* grown at high temperature.

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