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Effects of GA_3 and NAA on Leaf Lamina Unfolding and Flowering of *Cyclamen persicum*

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Abstract. **Treatments with gibberellic acid (GA_3), naphthaleneacetic acid (NAA), or their combination to *Cyclamen persicum* Mill. 'Swan Lake' plants resulted in separate, antagonistic, or cooperative effects on leaf lamina unfolding, days to flowering, number of leaves at first flower, and length of the first flower's peduncle. Generally, GA_3 accelerated plant growth nonspecifically, resulting in plants which flowered earlier than untreated plants, but with a similar number of leaves at first bud flowering. The combination of GA_3 plus NAA specifically accelerated flowering, but this effect diminished as the treatment frequency or quantity of the NAA application increased.**

Many plant species may be placed into flowering categories according to their specific photoperiodic and temperature responses (26). Recently, these responses have been associated with subsequent endogenous hormone changes (5, 25), but the identification of actual flowering factor(s) remains largely unresolved.

Day-neutral plants usually attain a specific vegetative state prior to flower initiation and in one such plant, *Helianthus annuus*, growth-regulator treatments accelerated shoot elongation and indirectly hastened flowering (9). *Cyclamen persicum* is also a day-neutral plant (24) but, unlike *Helianthus*, its floral buds arise within the leaf axils on a very compressed stem while the terminal apex remains vegetative. Based on the existing knowledge of correlative inhibition, the growth of these axillary floral buds may be influenced by the terminal vegetative meristem. Axillary floral bud development in cyclamen commences only after the 6th or 7th true leaf primordium has differentiated (23, 24) and each subsequent leaf subtends a flower bud.

Several gymnosperms (17, 18) and day-neutral angiosperms with axillary flowers (3, 4, 13, 28) flowered sooner than their untreated counterparts in response to GA applications. Although never proven, the direct effect of GA in these angiosperms may be to stimulate floral initiation, diminish an inhibition system, or accelerate development and/or elongation of the peduncle and finally the flower bud. With the latter, applied GA has enhanced tissue differentiation and development, even when not associated with flower initiation (14, 15, 16, 21). This response may be very important for day-neutral plants. Studies with *Cosmos* (15), *Limonium* (29), and *Lycopersicon* (1) demonstrated that tissue receptivity to GA changed with plant age. Information is lacking with respect to the response of cyclamen to GA_3 applied prior to 180 days after seeding, although Kohl & Kofranek (8) have described some effects of repeated GA applications to older cyclamen.

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Auxins also have been implicated in the correlative inhibition of lateral vegetative buds by the terminal apex (10), as well as the enhancement of floral scape elongation (2, 6, 20). The objectives of this study were to determine the influence of GA_3 and NAA on vegetative and reproductive development of cyclamen.

Materials and Methods

Seeds for 2 separate experiments were sown on December 5, 1979, in 5 × 5-cm plastic pots. 'Beautiful Helena' and the F_1 hybrid, 'Swan Lake', were used in expt. 1; 'Swan Lake' was used in expt. 2. Cultural procedures were as described by Widmer et al. (27). Plants were selected for uniformity and placed in the greenhouse 40 days after seeding; at 90 days, the plants were shifted into 8.8 × 8.8-cm pots.

In each experiment, applications of GA_3 and NAA were made 150 days after seed sowing, and in some cases repeated at 7-day intervals for a total of 5 or 10 applications (Table 1). At the 150-day stage, all plants had an average of 10–12 unfolded leaves. The selection of this stage, however, was based on the certainty that all plants were reproductive since the first 3 flower buds per plant were macroscopically visible (about 1 mm). All treatments of GA_3, NAA, or GA_3 + NAA were applied to the apical meristem as 0.5-ml aliquots using a micropipette. Solutions were prepared on the day of treatment; the GA_3 and NAA combination treatments were applied as a single solution and controls received double-distilled water. The experimental design for both experiments was a randomized complete block with 7 replications.

Table 1. Treatments as 0.5-ml aliquots to the crown of the cyclamen plants starting 150 days after seeding.

Treatment			Total growth regulator applied per plant	
GA_3 (ppm)	NAA (ppm)	Application frequency	GA_3 (μg)	NAA (μg)
		Expt. 1		
0	0	Control	0.0	0.0
25	0	1×	12.5	0.0
25	0	5×[z]	62.5	0.0
25	0	10×	125.0	0.0
0	10	1×	0.0	5.0
0	10	5×	0.0	25.0
0	10	10×	0.0	50.0
25	10	1×	12.5	5.0
25	10	5×	62.5	25.0
25	10	10×	125.0	50.0
5	10	1×	2.5	5.0
5	10	5×	12.5	25.0
5	10	10×	25.0	50.0
		Expt. 2		
0	0	Control	0.0	0.0
125	0	1×	62.5	0.0
250	0	1×	125.0	0.0
0	50	1×	0.0	25.0
0	100	1×	0.0	50.0
125	50	1×	62.5	25.0
250	100	1×	12.5	50.0
25	50	1×	12.5	25.0
50	100	1×	25.0	50.0

[z]Multiple treatments at 7-day intervals.

The number of unfolded leaves/plant was determined every 7 days from 81 to 220 days after seed sowing. Other data collected included the number of days to first, 2nd, and 3rd open flower, the number of leaves at first flower, length of the first flower's peduncle, and the length of the same peduncle 2 weeks after flower opening. Data on days to 2nd and 3rd flower were included to see if any effect on the first flower would continue. The criterion for individual treatment effect "significance" was the single degree of freedom F-test evaluated at the 5% level or less.

Results

Results of expt. 1 indicated cultivar differences, but no cultivar × treatment interaction. Only the significant 'Swan Lake' responses are presented here, but data for 'Beautiful Helena' and nonsignificant 'Swan Lake' responses are available (11). All comparisons are with the control, unless stated otherwise.

In expt. 1, NAA alone had no effect on leaf unfolding. The significant effects of GA_3 alone and combined with NAA are shown in Table 2. Control plants unfolded an average of 3 leaves/week from days 197–220, while twice as many unfolded after 10 GA_3 applications. Plants given one or 5 GA_3 applications also unfolded leaves faster, but only plants given 5 or 10 applications eventually produced significantly more leaves (11 and 16.8, respectively, on day 220) than the control. The GA_3 + NAA combination treatment results depended upon the specific ratios of the growth regulators and the number of consecutive treatments administered to the plant. When treated with 25 ppm GA_3 + 10 ppm NAA, plants which received 10 consecutive applications had 7.2 more unfolded leaves than the control on day 197, and 20.4 more on day 220. With 5 consecutive applications of 25 ppm GA_3 + 10 ppm NAA, the first significant increase in leaf number (10.6) occurred on day 220. One 25 ppm GA_3 + 10 ppm NAA application showed a consistent, but insignificant trend to more unfolded leaves/plant.

In expt. 2, treatment with NAA alone had no effect on leaf unfolding. Table 3 shows the significant effects of 125 or 250 ppm GA_3, 125 ppm GA_3 + 50 ppm NAA, and 250 ppm GA_3 + 100 ppm NAA treatments on leaf unfolding. Plants treated with either GA_3 level alone had significantly greater leaf counts from day 190. By day 220, control plants averaged 34.5 unfolded leaves and plants treated with 125 and 250 ppm GA_3 had 26.8 and 21.2 more unfolded leaves, respectively. Similarly, plants treated with both GA_3-NAA combinations had 14.9 and 22.1 more unfolded leaves.

Table 2. Mean differences (n = 7) from the control in the number of unfolded leaves/cyclamen plant.

Treatment[z]			No. of days after seeding			
GA_3 (ppm)	NAA (ppm)	No. times applied	197	204	213	220
0	0	Control	24.9	27.1	30.2	33.9
25	0	5	+ 4.2	+ 5.3	+ 8.4	+11.0*
25	0	10	+ 8.7*	+10.9*	+15.4*	+16.8*
25	10	5	+ 2.3	+ 3.5	+ 6.1	+10.6*
25	10	10	+ 7.2*	+10.3	+15.2*	+20.4*

[z]Initiated 150 days after seeding.
*Significant difference from control, determined by the single degree-of-freedom F-test, 5% level.

Table 3. Mean differences (n = 7) from the control in the number of unfolded leaves/cyclamen plant.

Treatment[z]		No. of days after seeding			
GA_3 (ppm)	NAA (ppm)	174	190	204	220
0	0	15.3	20.6	26.2	34.5
125	0	+ 4.0*	+14.0*	+19.5*	+26.8*
250	0	− 1.0	+ 6.3*	+15.4*	+21.2*
125	50	+ 1.3	+ 7.7*	+ 8.1*	+14.9*
250	100	+ 3.7*	+11.1*	+14.5*	+22.1*

[z]Applied 150 days after seeding.
*Significant difference from control by the single degree-of-freedom F-test, 5% level.

Number of leaves at first flower. In expt. 1, control plants had the most unfolded leaves (62.5) when the first flower opened (Table 4). The number of unfolded leaves increased as the number of applications of 25 ppm GA_3 + 10 ppm NAA increased from one to 10.

In expt. 2, control plants had 56.5 unfolded leaves when the first flower opened (Table 4). No treated plants flowered with a significantly lower leaf number. Plants treated with 250 ppm GA_3 + 100 ppm NAA had 14.4 more unfolded leaves at first flower than did controls.

Number of days to first, 2nd, and 3rd flower. In expt. 1, control plants required 262, 265, and 267 days to reach first, 2nd, and 3rd open flower, respectively (Table 5). No treatment inhibited flowering. First flowering was advanced significantly by one, 5, or 10 applications of 25 ppm GA_3 or 25 ppm GA_3 + 10 ppm NAA, and one or 5 applications of 5 ppm GA_3 + 10 ppm NAA. The 2nd bud flowered significantly earlier on plants in all treatments except one application of 25 ppm GA_3 or one application of 5 ppm GA_3 and 10 ppm NAA. Only multiple applications from among these same treatments significantly accelerated 3rd bud flowering.

In expt. 2, control plants required 263, 266, and 267 days to reach first, 2nd, and 3rd open flower, respectively (Table 5). Plants treated with 125 and 250 ppm GA_3, 125 ppm GA_3 + 50 ppm NAA, 25 ppm GA_3 + 50 ppm NAA, and 50 ppm GA_3 + 100 ppm NAA flowered significantly earlier than the control. Only the first 3 of these treatments hastened 2nd bud flowering, and none accelerated 3rd bud flowering.

Table 4. Mean difference (n = 7) from the control in the number of leaves/cyclamen plant recorded at first flower.

	Treatment[z]			Response
Experiment	GA_3 (ppm)	NAA (ppm)	No. times applied	No. of leaves
1 (Control)	0	0	0	62.5
	25	10	1	−22.3*
	25	10	5	−14.6*
	25	10	10	− 1.9
2 (Control)	0	0	0	56.5
	250	100	1	+14.4*

[z]Initiated 150 days after seeding.
*Significant difference from the controls for expt. 1 and 2, respectively, determined by the single degree-of-freedom F-test, 5% level.

Table 5. Mean differences (n = 7) from the control in the number of days to 1st, 2nd, and 3rd flower of cyclamen plants.

	Treatment[z]			Response		
Experiment	GA_3 (ppm)	NAA (ppm)	No. times applied	1st flower	2nd flower	3rd flower
1 (Control)	0	0	0	261.8	265.2	266.6
	25	0	1	−18.2*	−14.9	−13.5
	25	0	5	−31.1*	−30.8*	−22.6*
	25	0	10	−27.5*	−26.4*	−21.9*
	25	10	1	−25.3*	−23.2*	−12.4
	25	10	5	−36.4*	−39.8*	−39.8*
	25	10	10	−34.1*	−34.8*	−30.7*
	5	10	1	−19.1*	−16.5	−13.3
	5	10	5	−30.0*	−31.6*	−23.3*
2 (Control)	0	0	0	263.0	266.0	267.0
	125	0	1	−26.9*	−23.9*	−20.1
	250	0	1	−24.6*	−23.2*	−18.1
	125	50	1	−30.8*	−27.3*	−20.4
	25	50	1	−15.6*	−12.3	− 7.1
	50	100	1	−21.8*	−20.8	−13.6

[z]Initiated 150 days after seeding.
*Significant difference from the controls for expt. 1 and 2, respectively, determined by the single degree-of-freedom F-test, 5% level.

Length of peduncle. In expt. 1, plants in only one treatment, a single application of 25 ppm GA_3 and 10 ppm NAA at 150 days, had shorter peduncles (Table 6). Plants given multiple applications of 25 ppm GA_3 or 25 ppm GA_3 + 10 ppm NAA had significantly longer (3.1–4.5 cm) peduncles. There was no linear relationship between the degree of additional elongation and the number of GA_3 or GA_3 + NAA applications. Peduncles in all treatments elongated an additional 2 cm in the 2 weeks after flowering.

In expt. 2, plants treated with 125 and 250 ppm GA_3 had respective peduncle lengths of 14.2 and 15.2 cm. Only the former was significantly shorter than the control's length of 17.7 cm (Table 6). No treatment caused a significant increase in peduncle length. All peduncles elongated an additional 2 cm in the 2 weeks after flowering, regardless of treatment.

Table 6. Mean cyclamen peduncle length differences (n = 7) from the control.

	Treatment[z]			
Experiment	GA_3 (ppm)	NAA (ppm)	No. times applied	Peduncle response (cms)
1 (Control)	0	0	0	18.2
	25	0	5	+ 3.4*
	25	0	10	+ 3.8*
	25	10	1	− 4.6*
	25	10	5	+ 3.1*
	25	10	10	+ 4.6*
2 (Control)	0	0	0	17.7
	125	0	1	− 3.5*
	250	0	1	− 2.5

[z]Initiated 150 days after seeding.
*Significant by difference from the controls for expt. 1 and 2, respectively, determined the single degree-of-freedom F-test, 5% level.

Discussion

Cyclamen treated with GA_3 and NAA 150 days after seeding exhibited changes in reproductive and vegetative development. The observed effects are summarized in Table 7, but since NAA alone had no effect, it has been omitted.

Plants which received only GA_3 always flowered earlier with a normal complement of leaves at first flower. Although this conflicts with the response of *Impatiens balsamina* (22), a long-night plant, it illustrates the complexity of the GA_3 effect on different flowering mechanisms. A role for GA_3 in peduncle elongation enhancement is more universal, having previously been reported in *Cosmos* (15), *Silene* (25), *Streptocarpus* (12), and even earlier cyclamen (28) studies. Yet, for cyclamen, this response may not have been due to GA_3 alone since repeated treatments stimulated peduncle elongation, while single, high concentrations caused either inhibition or no effect.

A role for endogeneous auxin in this process is likely. When combined with GA_3, NAA significantly altered, and often directed, the effect of GA_3 on reproductive and vegetative development. The balance and magnitude of both growth regulators were critical to the subsequent response. When the amount of GA_3 exceeded NAA, floral acceleration was the culmination of either of 2 different effects: 1) a specificity for peduncle growth and bud maturation; or 2) a nonspecific enhancement of vegetative and reproductive development. Based on the response to GA_3 alone, the 2nd effect is likely to be the dominant effect of GA_3 masking any influence of the accompanying NAA.

When the amount of NAA exceeded GA_3 in the combination treatments, the effects lacked the specificity previously described. NAA was simply an antagonist of the GA_3-enhanced leaf unfolding and peduncle elongation. Again, NAA had no effect on any of the measurements when applied alone.

In an anatomical sense, the cyclamen peduncle is analogous to a vegetative shoot (19). Therefore, the roles of applied IAA and GA_2 in *Phaseolus* internode elongation (7) are important to interpretation of our data. Auxin stimulates only radial cell growth of the *Phaseolus* internode. The observed inability of NAA alone to alter peduncle length would be expected, should such a response exist in cyclamen. Gibberellin stimulates transverse cell divisions in *Phaseolus* internodes, an effect which conceivably could lead to excessive peduncle elongation, as observed in response to repeated GA_3 treatments. Finally, Kigel (7) stated that the effects of IAA and GA_3 together caused enhanced cell elongation, while the IAA simultaneously inhibited the transverse cell divisions attributed to the GA_3 component. Earlier flowering on shorter peduncles, in response to a single application of 25 ppm GA_3 plus 10 ppm NAA, is a strong indication that this combined effect also operates in cyclamen. Since multiple applications of this same combination affect peduncles excessively, GA_3 apparently can overcome the auxin effect.

Our data presents strong evidence that GA_3 alone is not responsible for cyclamen peduncle elongation. Apparently, a GA_3-induced auxin synthesis and/or action mechanism is responsible for this process. Although GA_3 can independently enhance peduncle growth on intact plants, Lyons (11) also showed that it could not induce a debudded peduncle to elongate without the simultaneous application of NAA. This gibberellin-auxin interaction may be an integral part of the flowering process of many plants, particularly those classified as day-neutral.

In terms of bloom advancement and plant quality, the preferred treatment is 25 ppm GA_3, applied once at 150 days after seeding (when the plant has 10–12 unfolded leaves). Previous recommendations (28) of treatment at 180 days were for 10 ppm GA_3 on F_1 hybrids (which usually are more sensitive) and 25 ppm on other cultivars. However, at 150 days, 0.5 ml of 25 ppm GA_3 [about 6% of solution volume recommended by Widmer et al. (28)] successfully hastened flowering of 2 very different cultivars—'Beautiful Helena' (nonhybrid, miniature type) and 'Swan Lake' (F-1 hybrid) without problems. If additional cultivars respond similarly to GA_3 application at 150 days, there should be no need to use 2 different concentrations. Although the application of 0.5 ml per plant is not practical on a commercial basis, there is an alternative to consider. If the total quantity of GA_3 applied to the plant elicits the response, then a larger solution volume containing lower GA_3 concentrations to provide the same total GA_3 (e.g., 5 ml of 2.5 ppm GA_3) may have a similar effect. This theory was not tested in the present study.

Table 7. Summary of the effects of GA_3 and NAA treatments applied at 150 days after seeding as 0.5-ml aliquots to the crown of cyclamen plants.

Treatment			Treatment effect		
GA_3 (ppm)	NAA (ppm)	No. times applied	No. of leaves	Days to flowering	Peduncle length
25	0	1	0[z]	−[y]	0
25	0	5	0	−	+[x]
25	0	10	0	−	+
125	0	1	0	−	−
250	0	1	0	−	0
25	10	1	−	−	−
25	10	5	−	−	+
25	10	10	0	−	+
125	50	1	0	−	0
250	100	1	+	0	0
5	10	1	0	−	0
5	10	5	0	−	0
5	10	10	0	0	0
25	50	1	0	0	0
50	100	1	0	−	0

[z]Represents no treatment effect.
[y]Represents significantly fewer leaves, earlier flowering, or shorter peduncles than the control (5% level).
[x]Represents significantly more leaves or longer peduncles than the control (5% level).

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Production Potential and Survival of Fall- and Spring-seeded Asparagus

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Abstract. **Seed of asparagus (*Asparagus officinalis* L.) germinated normally after 2 months of constant freezing (−10°C) or chilling (4°) under water-saturated conditions in laboratory germination studies. However, temperatures cycling weekly from chilling to freezing for 2 months reduced germination to less than 50%, and temperatures cycling weekly from warm (21°/16°, day/night) to chilling to freezing for 2 months reduced germination to 0. The stands of asparagus, field-seeded in November and December, were reduced 85% by winterkill in comparison to spring seeding in March and April. Seeding densities from 10 to 40 seed/m did not compensate for stand loss. The greatest contributor to winterkill apparently was seed rot. March seeding increased plant height, but not crown quality or the number of shoots initiated in comparison to conventional April seeding. High seeding densities did not reduce plant growth or crown yields in the spring plantings. Stand establishment was not different between the spring planting dates. Early March seeding at high densities is recommended.**

Nursery production of asparagus crowns by direct-seeding is complicated by slow, erratic seed germination and slow seedling growth. In comparison, self-sown or volunteer asparagus seedlings emerge earlier in spring and are more advanced than those conventionally spring-sown. Simulating this phenomenon by seeding asparagus in the fall has potential for earlier seed germination and emergence, avoidance of excessive weed competition, and higher quality crown production. Kotowski (3) reported that 73% of fall-seeded asparagus germinated the following spring, although germination under optimal conditions was 91%.

The optimum temperature for asparagus seed germination is about 25°C, with 10° the minimum germination temperature (1). Low temperature stratification after presoaking in water stimulated the rate of germination (2). Under field conditions, the benefits of cold temperature stratification may be obscured by

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