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Regulating Vegetative Growth and Flowering with Gibberellic Acid in Intact Plants and Cultured Phylloclades of 'Crimson Giant' Easter Cactus

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Abstract. **Investigations were performed to determine the influence of gibberellic acid (GA_3) on intact plants and cultured phylloclades of 'Crimson Giant' Easter cactus *[Rhipsalidopsis gaertneri* (Regel) Moran]. Responses of intact plants depended on GA_3 concentration, number of spray applications, and application time. Single GA_3 applications delayed flowering and reduced the percentage of apical phylloclades flowering and number of flower buds per plant when applied before floral primordia formation [from 20 days before to the start of long days (LDs)], but hastened flowering and did not affect the percentage of apical phylloclades flowering or number of flower buds per plant when applied during floral bud development (20 days after the start of LDs). When sprays were applied at or before the start of LDs, increasing the GA, concentration resulted in fewer plants flowering, longer flowering delays, and further decreases in the number of flower buds per plant. Multiple GA_3 applications were more inhibitory to flowering than single applications. Whole plants and cultured phylloclades exhibited similar reactions to GA_3, but cultured phylloclades were more responsive to GA_3 than intact plants. Intact plants and cultured phylloclades generally produced more new phylloclades as GA_3 concentration increased. Spine growth also increased when phylloclades were cultured in a GA_3-containing medium. Flowering was accelerated by ≈5 days when GA, was applied to intact plants with 1- to 2-mm-long flower buds. GA, may be horticulturally useful for Easter cactus crop scheduling.**

Easter cactus-currently *Rhipsalidopsis gaertneri* (Regel) Moran (Liberty Hyde Bailey Hortorium, 1976), but proposed by Barthlott (1987) as *Hatiora gaertneri* (Regel) Barthlott-is an epiphytic shrub with a determinate growth pattern that produces a series of flattened, two-ribbed joints (phylloclades). Areoles (modified axillary buds) are restricted to the margins and apexes of phylloclades (Liberty Hyde Bailey Hortorium, 1976). Areoles that develop below the phylloclade apex are solitary, whereas, at the apex, areoles are crowded together to form a composite areole (Barthlott, 1987). Flowers and new phylloclades develop almost invariably from composite areoles on apical phylloclades and infrequently from subapical areoles or subapical phylloclades (Boyle, 1992; Liberty Hyde Bailey Hortorium, 1976).

Areoles area prominent anatomical feature of cacti, and each areole contains several spine primordia and an areolar meristem (Boke, 1944). Vegetative shoots (phylloclades), leaves, spines, flowers, and roots arise through the activity of the areolar meristem (Gibson and Nobel, 1986). Mauseth and Halperin (1975) were able to regulate the developmental pattern in cultured areoles of *Opuntia polyacantha* Haw. by varying the proportions of GA_3, cytokinin, and auxin in the medium. These results demonstrate that exogenously applied GA_3 may strongly influence the developmental fate of the areolar meristem.

Exogenously applied GA has modified growth and development in a wide range of plants. Growth of stems and other organs is promoted by GA and results from enhanced cell division, increased carbohydrate hydrolysis, and increased cell-wall plasticity (Sachs, 1961; Salisbury and Ross, 1978). GA also regulates or promotes flowering in several species. GA induces many long-day (LD) plants to flower under noninductive short days (SDS) (Lang and Reinhard, 1961; Wittwer and Bukovac, 1958) and substitutes for the LD phase in several dual-photoperiod species, including long–short-day plants (LSDPs) (Bünsow and Harder, 1956) and short-long-day plants (SLDPs) (Chouard, 1960; Ketellapper and Barbaro, 1966). In short-day plants (SDPs), GA applied during inductive photoperiods generally inhibits or delays floral initiation (Vince-Prue, 1975), but GA may accelerate floral development if applied after floral initiation (Greulach and Haesloop, 1958; Stuart and Cathey, 1962). In the SDP *Schlumbergera truncata* (Haw.) Moran (Cactaceae), GA_3 inhibits flower bud formation and delays flowering when applied before or at the beginning of SDS, accelerates flowering by up to 2 weeks when applied at the visible bud stage (buds 1 to 3 mm long), and has no or little influence when applied in the late flower development stage (buds 6 to 8 mm long) (Fujihara, 1959; Halevy and Rudich, 1968; Ho et al., 1985; Runger, 1984). In a few SDPs, GA has promoted floral initiation when applied to plants under noninductive LDs (Nanda et al., 1967; Wittwer and Bukovac, 1958), but GA cannot substitute for the SD requirement in most SDPs. Further, GA_3 cannot replace the SD phase in several dual-photoperiod species (Ketellapper and Barbaro, 1966; Penner, 1960; Wellensiek, 1960).

Limited information has been published on the responses of *R. gaertneri* to growth regulators (Boyle, 1992; Boyle et al., 1988; Kaukovirta, 1979), and we are unaware of any published reports on the responses of *R. gaertneri* to GA_3. The purpose of this research was to determine the morphological responses of intact plants and cultured phylloclades of the SLDP *R. gaertneri* 'Crimson Giant' to application time, number of applications, and concentration of exogenously applied GA_3.

Materials and Methods

General procedures. Plants were propagated and grown in glasshouses at the Univ. of Massachusetts, Amherst (lat. 42°22.5'N).

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Plants were fertilized weekly with 20N-4.3P-16.6K (12% NO_3-N, 8% NH_4-N) at 200 mg N/liter. Fertilization began after phylloclades were rooted and was discontinued 4 weeks before the start of LDs to hasten apical phylloclade maturation. Four weeks after start of LDs, fertilization was resumed and applied at 200 mg/N per liter every 2 weeks until the experiments ended

Thermostat setpoints were 18/20C (heat–vent) during all experiments. Photosynthetic photon flux (PPF) and air temperatures were monitored with a datalogger (model LI- 1000) equipped with a quantum sensor (model LI- 190SA) and an aspirated thermistor (model LI-1OOO- 16; LI-COR, Lincoln, Neb.). The datalogger was configured with a sampling interval of 60 sec and recorded mean PPFs and temperatures at l-h intervals. GA_3 was applied to intact plants (Expts. 1 and 2) near midday (1200 HR); temperature, PPF, and natural photoperiod on GA_3 application dates are provided in Table 1.

Multiple GA_3 applications on intact plants (Expt. 1). Whole phylloclades were propagated on 28 Apr. 1987 in 72-cell plastic trays using one phylloclade per 35-cm^3 cell. The propagation medium was a commercial soilless mix composed of sphagnum peat, perlite, and vermiculite (Fafard Mix no. 2, Conrad Fafard, Springfield, Mass.). Rooted phylloclades were transplanted singly into 520-cm^3 (10-cm-diameter) plastic pots containing Fafard Mix no. 2. Plants received natural daylengths (NDs) from propagation until 10 Jan. 1988. LDs were provided from 10 Jan. until the experiment ended by supplementing ND with incandescent irradiation at 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (400 to 700 nm) from 1600 to 2200 HR. Actual glasshouse temperatures were 18 ±1.5C nights/20 ± 2C days and ranged from 16 to 26C.

Treatments included an unsprayed control and GA_3 (Pro-Gibb; Abbott Labs, North Chicago) at 25 or 50 $mg \cdot liter^{-1}$ in one, two, three, or four applications. GA_3 solutions contained Tween 20 (polyoxyethylene sorbitan monolaurate) at 1 $ml \cdot liter^{-1}$ as a surfactant and were applied to plants with a hand sprayer at ≈ 15 ml/plant. The initial treatment was applied on 10 Jan.; the other abdication dates were 17, 24, and 31 Jan. The experiment was a completely randomized design with eight pots per treatment.

Data were collected on days to flowering from the start of LDs (10 Jan.) to full expansion of the first flower, number of flower buds per flowering apical phylloclade, number of flower buds per plant, and percentage of apical phylloclades flowering. The experiment ended on 20 Apr. 1988. Before statistical analysis, the numbers of flower buds per flowering apical phylloclade and new apical phylloclades per plant were log-transformed [$\log_{10}(X + 1)$] and percentage values were arcsin-transformed. All variables were analyzed by SAS's (1985) General Linear Model (GLM) procedure. Single degree-of-freedom contrasts were used to test for treatment differences.

Single GA_3 applications on intact plants (Expt. 2). Whole phylloclades were propagated on 27 Mar. 1988 using procedures and materials described in Expt. 1. Rooted phylloclades were transplanted singly into 520-cm^3 plastic pots containing Fafard Mix no. 2. Plants were grown under ND from propagation until 31 Jan. 1989, and were then given LDs (as described in Expt. 1) until the experiment ended. Actual glasshouse temperatures were 18 ± 1.5C nights/21 ± 2C days and ranged from 16 to 28C. Treatments included GA_3 (Pro-Gibb) at 5,50, and 500 $mg \cdot liter^{-1}$ and an unsprayed control. GA_3 solutions contained Tween 20 at 1 $ml \cdot liter^{-1}$ and were applied with a hand sprayer at ≈15 ml/plant. Treatments were applied on 11 Jan. (20 days before the start of LDs), 21 Jan. (10 days before the start of LDs), 31 Jan. (start of LDs), 10 Feb. (10 days after start of LDs), and 20 Feb. (20 days after the start of LDs). The experiment was a completely randomized design with eight pots per treatment.

At the start of LDs, 24 mature apical phylloclades were removed from eight supplementary plants (three phylloclades per plant) that were the same age and maintained under the same conditions as the controls. Apexes were dissected under a stereomicroscope at ×50 magnification to determine the developmental stage of the areolar meristems in the composite areole. Data were also collected on the presence of visible flower buds at each application date, flower bud length, days to flowering from the start of LDs (31 Jan.) to full expansion of the first flower, number of flower buds per plant, number of new apical phylloclades per plant, percentage of apical phylloclades flowering, and percentage of apical phylloclades with new phylloclades. The experiment ended on 1 May 1989. Chi-square tests were used to test for differences in percentage of flowering plants between GA_3 treatments and controls. Other variables were analyzed by SAS's (1985) GLM procedure. Percentage variables were arcsin-transformed and numbers of flower buds and new apical phylloclades per plant were log-transformed before analysis. Single degree-of-freedom contrasts were used to test for treatment differences.

In vitro responses of phylloclades cultured on GA_3-containing media (Expt. 3). Mature apical phylloclades were harvested on 21 Feb. 1990 from glasshouse-grown stock plants. Before harvest, stock plants were exposed to 8 weeks of 8-h SDs (0800 to 1600 HR) to satisfy the SD phase for flowering (Boyle, 1991). Surface contamination was reduced by pruning the bristly spines on the composite areole with scissors. Phylloclades were surface-disinfected by im-

Table 1. Glasshouse environmental conditions recorded on GA_3 application dates.

Experiment	GA_3 application date	Air temp (°C)[z]	Photosynthetic photon flux ($\mu mol \cdot m^{-2} \cdot s^{-1}$)[z]	Natural photoperiod[y] h	min
1	10 Jan. 1988	21.5 ± 0.1	442 ± 44	9	20
	17 Jan. 1988	20.1 ± 0.1	389 ± 24	9	31
	24 Jan. 1988	21.6 ± 0.1	136 ± 26	9	44
	31 Jan. 1988	21.4 ± 0.3	607 ± 66	10	0
2	11 Jan. 1989	18.9 ± 0.5	153 ± 20	9	21
	21 Jan. 1989	17.8 ± 1.3	422 ± 107	9	39
	31 Jan. 1989	18.5 ± 0.7	259 ± 30	10	0
	10 Feb. 1989	18.4 ± 0.7	373 ± 79	10	23
	20 Feb. 1989	19.0 ± 0.1	292 ± 71	10	50

[z]Actual glasshouse air temperatures and photosynthetic photon flux were collected by a datalogger configured with a sampling interval of 60 sec and recording mean values at 1-h intervals. Data are averages of hourly means (±SE) for 1000 to 1359 HR.
[y]Duration of daylight (interval between sunrise and sunset) at lat. 42°N. Data are from List (1951).

mersing them for 25 min in a 20% (by volume) bleach solution (1.05% NaOCl) containing 0.8% Tween 20 as a surfactant, followed by three rinses in sterile distilled water. Explants were obtained by excising a ≈1.5-cm-long, wedge-shaped piece from the phylloclade apex, which included the entire composite areole. Explants were oriented vertically in 55-cm^3 (25-mm-diameter) vials containing 10 ml of sterile Murashige and Skoog (1962) medium that was solidified with 7 g Difco Bacto-agar/liter and supplemented with GA_3 at 0, 0.1, 1, 10, or 100 mg·$liter^{-1}$. Crystalline GA_3 (Grade III; Sigma, St. Louis) was dissolved in ethanol, and, to preserve GA_3 activity, stock solutions were filter-sterilized and added after autoclaving the medium (van Bragt and Pierik, 1971). The experiment was a completely randomized design with 10 replications (vials) per treatment.

Cultures were maintained in a growth room maintained at 25 ± 1.5C. Irradiance was provided by cool-white fluorescent lamps (≈35 µmol·m^{-2}·s^{-1} PPF), and a 16-h (LD) photoperiod was maintained to induce flowering in the cultured phylloclades (Boyle, 199 1). After 35 days in vitro, data were collected on the numbers of flower buds and secondary (2°) phylloclades (those developing from the composite areole), and the presence of spine growth on the composite areole. The experiment was repeated on 12 Mar. 1990 using mature apical phylloclades collected from the stock plants previously described.

Percentage data were analyzed by single degree-of-freedom chi-square tests. Two variables (flower buds per explant and 2° phylloclades per explant) were log-transformed and analyzed by SAS's (1985) GLM procedure using data combined from both experiments. Homogeneity of error variances was previously verified using a two-tailed F test (Gomez and Gomez, 1984).

Results and Discussion

Experiment 1. All plants produced flowers, regardless of GA_3 concentration or number of applications. Compared to unsprayed plants, flowering was delayed and the percentage of apical phylloclades flowering and number of flower buds per plant was decreased in plants sprayed with GA_3 (Table 2). Increasing the number of GA_3 applications resulted in a linear increase in the number of days to flowering and linear decreases in the percentage of apical phylloclades flowering and number of flower buds per plant. With GA_3 at 25 mg·$liter^{-1}$, the number of flower buds per flowering apical phylloclade was not affected by number of applications, but at 50 mg·$liter^{-1}$, the number of flower buds per flowering apical phylloclade decreased linearly as the number of applications increased. Generally, plants treated with GA_3 at 50 mg·$liter^{-1}$ produced fewer flowers and flowered later than plants treated with 25 mg·$liter^{-1}$.

Experiment 2. At the start of LDs, dome-shaped areolar meristems (150 to 175 µm in diameter) and a few immature phylloclades (<800µm long) were observed in the composite areoles of apical phylloclades collected from the supplementary plants. None of the composite areoles that were examined contained floral primordia. No flower buds were visible on plants when GA_3 was applied from 20 days before to 10 days after start of LDs. At 20 days after start of LDs, flower buds were clearly visible on untreated plants and were a maximum of 1 to 2 mm long.

Flowering was either inhibited, unaffected, or accelerated by GA_3, depending on concentration and application time (Table 3). Flowering was inhibited when GA_3 at 50 or 500 mg·$liter^{-1}$ was applied at or before the start of LDs. Generally, one application of GA_3 at 500 mg·$liter^{-1}$ resulted in fewer plants flowering, greater delays in flowering, and fewer flower buds compared to a single application of GA_3 at 50 mg·$liter^{-1}$. Applying GA_3 10 days after the start of LDs did not affect days to flowering, but reduced the percentage of apical phylloclades flowering and number of flower buds per plant. When GA_3 was applied 20 days after the start of LDs, flowering was hastened but the percentage of apical phyllo-

Table 2. Influence of GA_3 concentration and number of applications on flowering of 'Crimson Giant' Easter cactus (Expt. 1).

GA_3 concn (mg·$liter^{-1}$)	No. of applications	Days to flowering[z]	Apical phylloclades flowering (%)	Flower buds/ flowering apical phylloclade (no.)	Flower buds/ plant (no.)
0 (control)	---	57	67	1.7	25.3
25	1	62	54	1.5	19.9
	2	69	49	1.6	21.9
	3	69	42	1.4	16.9
	4	80	28	1.5	11.5
50	1	64	56	1.6	25.1
	2	73	35	1.9	17.8
	3	86	31	1.3	10.6
	4	86	10	1.2	4.0
Contrasts					
Control vs. GA_3		***	***	NS	**
Control vs. 25 mg·$liter^{-1}$		***	***	NS	**
Control vs. 50 mg·$liter^{-1}$		***	***	NS	**
25 mg·$liter^{-1}$ vs. 50 mg·$liter^{-1}$		***	***	NS	***
25 mg·$liter^{-1}$, no. applications linear		**	***	NS	*
25 mg·$liter^{-1}$, no. applications quadratic		NS	NS	NS	NS
50 mg·$liter^{-1}$, no. applications linear		***	***	*	***
50 mg·$liter^{-1}$, no. applications quadratic		NS	NS	NS	NS

[z]Days to flowering from start of long days (10 Jan. 1988) for all treatments.
[NS,*,**,***]Nonsignificant or significant at $0.05 \geq \alpha > 0.01$, $0.01 \geq \alpha > 0.001$, or $\alpha \leq 0.001$, respectively, according to F test of contrast between treatments.

Table 3. Influence of GA_3 concentration and application time on flowering and vegetative growth of 'Crimson Giant' Easter cactus (Expt. 2).

GA_3 concn (mg·liter^{-1})	Application time[z]	Plants flowering (%)	Days to flowering[y]	Apical phylloclades flowering (%)	Flower buds/ plant (no.)	Apical phylloclades with new phylloclades (%)	New apical phylloclades/ plant (no.)
0 (control)	---	100	60	82	25.3	4	0.6
5	–20	100	61	75	16.4	2	0.3
	–10	100	64	76	24.5	0	0
	0	100	62	63	17.0	9	1.8
	10	100	58	75	20.4	5	1.4
	20	100	55	82	24.8	1	0.3
50	–20	100	73	31	6.6	10	2.5
	–10	100	83	25	7.0	22	6.5
	0	50[x]	85	6	1.5	22	7.0
	10	100	56	42	11.1	5	1.0
	20	100	56	68	19.4	3	0.6
500	–20	13[x]	92	1	0.1	32	10.5
	–10	0[x]	---	0	0	33	10.4
	0	13[x]	77	1	0.3	22	5.6
	10	100	58	42	7.9	4	0.6
	20	100	55	75	22.8	2	0.5
Contrasts							
Control vs. GA_3, day –20			***	***	***	*	*
Control vs. GA_3, day –10			***	***	***	**	***
Control vs. GA_3, day 0			***	***	***	**	**
Control vs. GA_3, day 10			NS	***	***	NS	NS
Control vs. GA_3, day 20			*	NS	NS	NS	NS
Control vs. 5 mg·liter^{-1}			NS	NS	NS	NS	NS
Control vs. 50 mg·liter^{-1}			***	***	***	NS	***
Control vs. 500 mg·liter^{-1}			w	***	***	**	***
50 mg·liter^{-1} vs. 500 mg·liter^{-1}			w	***	***	*	*
5 mg·liter^{-1}, date linear			***	NS	NS	NS	NS
5 mg·liter^{-1}, date quadratic			*	*	NS	NS	NS
50 mg·liter^{-1}, date linear			***	***	***	*	**
50 mg·liter^{-1}, date quadratic			***	***	***	**	**
500 mg·liter^{-1}, date linear			w	***	***	***	***
500 mg·liter^{-1}, date quadratic			w	***	***	NS	NS

[z]Days relative to before (–) or after the start of long days.
[y]Days to flowering from start of long days (31 Jan. 1989) for all treatments.
[x]Treatment significantly different from control by chi-square test, $P \leq 0.05$; chi-square = 3.841 for 1 df.
[w]Contrast not estimable due to missing values or treatments.
[NS,*,**,***]Nonsignificant or significant at $0.05 \geq \alpha > 0.01$, $0.01 \geq \alpha > 0.001$, or $\alpha \leq 0.001$, respectively, according to F test of contrast between treatments.

clades flowering and number of flower buds per plant were not affected. GA_3 at 5 mg·liter^{-1} generally did not affect vegetative growth or flowering, regardless of application time, but was as effective as 50 or 500 mg·liter^{-1} in accelerating flowering when applied 20 days after the start of LDs.

GA_3-treated plants generally produced more new phylloclades than the controls (Table 3). There was a highly significant negative correlation between the number of flower buds per plant and new apical phylloclades per plant (r =-0.83), P<0.001 under H_o: rho = 0 (n=14)]. There was also a highly significant negative correlation between the percentage of apical phylloclades flowering and the percentage of apical phylloclades with new phylloclades (r = -0.91), $P < 0.001$ under H_o: rho = 0 (n = 14)]. The number of new phylloclades depended on GA_3 concentration and application time. Applying GA_3 from 20 days before to the start of LDs resulted in a higher percentage of apical phylloclades with new phylloclades and more new apical phylloclades per plant compared with the controls (Table 3). There were no differences between controls and plants treated with GA_3 at 5 mg·liter^{-1} in the percentage of apical phylloclades with new phylloclades or the number of new apical phylloclades per plant. However, increasing GA_3 from 50 to 500 mg·liter^{-1} resulted in a higher percentage of apical phylloclades with new phylloclades and more new apical phylloclades per plant.

The morphology of flowers and phylloclades was altered by GA_3. Relative to the controls, new phylloclades and flowers on plants treated with GA_3 at 50 or 500 mg·liter^{-1} were thinner and elongated (data not presented). GA_3 at 5 mg·liter^{-1} did not affect the morphology of new phylloclades, but some flowers were elongated slightly when GA_3 at 5 mg·liter^{-1} was applied 20 days after starting LDs.

Flowering responses of intact plants depended on GA_3 concentration, application time, and number of applications. A single GA_3 application delayed flowering and reduced the percentage of apical phylloclades flowering and number of flower buds per plant when applied to plants before the formation of floral primordia,

i.e., from 20 days before to the start of LDs, but hastened flowering and did not affect the percentage of apical phylloclades flowering or number of flower buds per plant when applied to plants during floral bud development, i.e., 20 days after starting LDs (Table 3). Increasing the concentration always resulted in longer flowering delays and fewer flowers when GA_3 was applied at or before starting LDs. In addition, multiple GA_3 applications were more inhibitory than single applications and resulted in fewer flowers and longer flowering delays (Table 2). Similar results were obtained with the SDP *S. truncata* (Fujihara, 1959; Halevy and Rudich, 1968; Ho et al., 1985; Runger, 1984). *Rhipsalidopsis gaertneri* and *S. truncata* are remarkably similar in their responses to GA_3, even though *R. gaertneri* is a SLDP at 18 to 22C (Boyle et al., 1988; Boyle, 1991) whereas *S. truncata* is a SDP at 15 to 21C (Runger and Poole, 1985). The results of the current experiments and those with *S. truncata* demonstrate that GA_3 may inhibit or promote flowering, depending on the stage of plant development when applied.

Experiment 3. Contaminated cultures (13 in total) were discarded before data collection. Statistical analysis was performed on data collected from 87 uncontaminated cultures.

For number of flower buds per explant and 2° phylloclades per explant, there were no significant differences between the two experiments (21 Feb. and 12 Mar. 1990) nor was there a significant experiment × GA_3 interaction (Table 4). Both variables, however, were significantly affected by GA_3 concentration. The number of flower buds decreased linearly as GA_3 concentration increased, and the percentage of explants with flower buds was significantly lower among explants cultured in GA_3-amended medium compared to those in GA_3-free medium (Table 5). The percentage of explants with 2° phylloclades and the percentage of explants with spine growth were significantly higher among those cultured in GA_3-amended medium than in those in GA_3-free medium. GA_3 increased the number of 2° phylloclades compared to the controls, but the response to GA_3 concentration was nonlinear. The number of 2° phylloclades increased as GA_3 concentration increased from 0 to 1 mg·liter^{-1}, and then decreased at concentrations >1 mg·liter^{-1}. The correlation between numbers of flower buds per explant and 2° phylloclades per explant was negative but not significant ($r = -0.71$, $P > 0.05$ under H_0: rho = 0 (n = 5)]. Lack of significance may have been due to the inhibition of flower and phylloclade formation when explants were cultured on medium containing GA_3 at 100 mg·liter^{-1} (Table 5).

Whole plants and cultured phylloclades exhibited similar reactions to GA_3, but cultured phylloclades were more responsive to GA_3 than intact plants (Tables 2, 3, and 5). GA_3 at 5 mg·liter^{-1} generally did not affect the vegetative or reproductive growth of intact plants (Table 3), whereas GA_3 at 0.1 mg·liter^{-1} inhibited flowering and promoted vegetative growth in cultured phylloclades (Table 5). Mauseth and Halperin (1975) also reported that GA_3 at concentrations as low as 0.01 mg·liter^{-1} elicited responses in quiescent buds of *O. polyacantha* that were cultured in vitro. In Expt. 2, the maximum number of new phylloclades was obtained when plants were treated with GA_3 at 500 mg·liter^{-1} (Table 3); in

Table 4. Analysis of variance for flower bud and phylloclade development for cultured phylloclades of 'Crimson Giant' Easter cactus (Expt. 3).

		Mean squares	
Source of variation	df	Flower buds/ explant (no.)	2° Phylloclades/ explant (no.)
Experiment (E)[z]	1	0.0132	0.0055
Replications within E	18	0.0096	0.0297
GA_3 concentration (GA_3)	4	0.5584***	0.2900***
E × GA_3	4	0.0112	0.0142
Pooled Error	59	0.0181	0.0421

[z]F test performed using replications within E as the error term.
***Significant at $P \leq 0.001$.

Table 5. Influence of GA_3 concentration on flowering and vegetative growth of cultured phylloclades of 'Crimson Giant' Easter cactus (Expt. 3).

GA_3 concn (mg·liter^{-1})	Explants with flower buds (%)	Flower buds/ explant (no.)	Explants with 2° phylloclades (%)	2° Phylloclades/ explant (no.)	Explants with spine growth (%)
0 (control)	100	1.9	0	0	0
0.1	47[z]	0.5	33[z]	0.6	60[z]
1	11[z]	0.2	68[z]	1.4	100[z]
10	22[z]	0.2	61[z]	1.1	100[z]
100	12[z]	0.1	29[z]	0.4	100[z]
Contrasts					
Control vs. GA_3		***		***	
GA_3 linear		***		NS	
GA_3 quadratic		NS		NS	

[z]Treatment significantly different from control by chi-square test, $P \leq 0.05$; chi-square = 3.841 for 1 df.
NS,*,**,***Nonsignificant or significant at $0.05 \geq \alpha > 0.01$, $0.01 \geq \alpha > 0.001$, or $\alpha \leq 0.001$, respectively, according to F test of contrast between treatments.

Expt. 3, the number of 2° phylloclades was maximal when explants were cultured on media containing GA_3 at 1 mg·liter^{-1}, and concentrations >1 mg·liter^{-1} inhibited phylloclade formation (Table 5). Differences between cultured phylloclades and intact plants in responsiveness to GA_3 may have been due to greater hormone uptake in the former, possibly due to direct contact between the GA_3-containing medium and the wounded surface of the explant.

In Expt. 3, old spines were shorter (due to trimming) and paler (due to bleaching) than new spines; as a consequence, spine growth on the composite areole was evaluated readily. Spine growth increased when phylloclades were cultured in medium containing GA_3 at >0.01 mg·liter^{-1} (Table 5). GA_3 also increased the growth of spines in *Chamaecereus silvestri* (Speg.) Britt. & Rose (Sanderson et al., 1986), *Mammillaria elongata* DC. (Sanderson et al., 1986), and *O. microdasys* (Lehm.) Pfeiff. (White et al., 1978). Exogenously applied GA_3 may have induced spine growth in 'Crimson Giant' by triggering the initiation of new spines, as reported by Mauseth and Halperin (1975) and Mauseth (1977) for *O. polyacantha.* Cactus spines are presumed to be evolutionarily derived from leaves (Boke, 1944), and since directly applying GA_3 can stimulate leaf growth (Aloni and Pressman, 1980; Gray, 1957), it is feasible that GA_3 may also promote spine growth by increasing cell division or elongation or both within existing spine primordia. Additional research is needed to discern the mechanisms responsible for GA_3-induced spine growth in 'Crimson Giant'.

Intact plants and cultured phylloclades generally produced more new phylloclades as GA_3 concentration increased, i.e., the opposite trend observed for number of flower buds (Tables 3 and 5). This inverse relationship between vegetative growth and flowering is demonstrated by the highly significant negative correlation between the numbers of flower buds per plant and new apical phylloclades per plant (r = -0.83). Phylloclade growth of 'Crimson Giant' may have been directly and indirectly affected by GA_3. Direct stimulation of stem growth via increased cell division and cell elongation has been demonstrated in several species after GA_3 was applied (Sachs, 196 1), and GA_3 would be expected to have similar effects on phylloclade growth. Also, GA_3 may have indirectly affected phylloclade growth by inhibiting flowering. Profuse flowering and a near absence of new phylloclades was the normal pattern of development, as exhibited by the controls (Tables 2 and 3). The flowering process may repress vegetative growth, and GA_3 may have reversed the repression of vegetative growth by inhibiting flowering, thus allowing phylloclades to form. GA_3 also promoted shoot growth in intact plants of C. *silvestri* (Sanderson et al., 1986), *M. elongata* (Sanderson et al., 1986), and *S. truncata* (Yonemura, 1979).

Horticultural significance. Applying GA_3 from 20 days before to 10 days after the start of LDs was either ineffective or inhibitory to flowering and, thus, would have no horticultural value for producing Easter cactus. However, a single application of GA_3 at 5 mg·liter^{-1} accelerated flowering by 5 days when applied to plants with 1-to 2-mm-long flower buds. Accelerating flowering reduces the cropping period and may aid in Easter cactus crop scheduling. GA_3 at concentrations >5 mg·liter^{-1} will also accelerate flowering, but may decrease plant quality and marketability due to deleterious effects on phylloclade and flower morphology.

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