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) on intact plants and cultured phylloclades of ‘Crimson Giant’ Easter cactus [Rhipsalidopsis gaertneri (Regel) Moran]. Responses of intact plants depended on GA concentration, number of spray applications, and application time. Single GA applications delayed flowering and reduced the percentage of apical phylloclades flowering and number of flower buds per plant when applied before floral primordium 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 applications were more inhibitory to flowering than single applications. Whole plants and cultured phylloclades exhibited similar reactions to GA, but cultured phylloclades were more responsive to GA than intact plants. Intact plants and cultured phylloclades generally produced more new phylloclades as GA concentration increased. Spine growth also increased when phylloclades were cultured in a GA-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.

Eastern 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 are 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, cytokinin, and auxin in the medium. These results demonstrate that exogenously applied GA 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; Kettlelapper 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 Haasloop, 1958; Stuart and Cathey, 1962). In the SDP Schlumbergera truncata (Haw.) Moran (Cactaceae), GA 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; Haley 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 cannot replace the SD phase in several dual-photoperiod species (Kettlelapper 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. 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.

Materials and Methods

General procedures. Plants were propagated and grown in glasshouses at the Univ. of Massachusetts, Amherst (lat. 42°22.5'N).
Plants were fertilized weekly with 20N-4.3P-16.6K (12% NO₃-N, 8% NH₄-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 to 200 mg/N per liter every 2 weeks until the experiments ended.

Thermostat setpoints were 18/20°C (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-1000-16; LI-COR, Lincoln, Neb.). The datalogger was configured with a sampling interval of 60 sec and recorded mean PPFs and temperatures at 1-h intervals. GA₃ was applied to intact plants (Expts. 1 and 2) near midday (1200 hr); temperature, PPF, and natural photoperiod on GA₃ application dates are provided in Table 1.

**Multiple GA₃ applications on intact plants (Expt. 1).** Whole phylloclades were propagated on 28 Apr. 1987 in 72-cell plastic trays using one phylloclade per 35-cm² 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-cm³ (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 µmol·m⁻²·s⁻¹ (400 to 700 nm) from 1600 to 2200 h. Actual glasshouse temperatures were 18 ± 1.5°C nights/21 ± 2°C days and ranged from 16 to 28°C. Treatments included GA₃ (Pro-Gibb; Abbott Labs, North Chicago) at 25 or 50 mg-liter⁻¹ in one, two, three, or four applications. GA₃ solutions contained Tween 20 (polyoxyethylene sorbitan monolaureate) at 1 ml-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 abscission application 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 new apical phylloclades 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 \[\log_3(X + 1)\] 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 GA₃ 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-cm³ 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 ± 1.5°C nights/21 ± 2°C days and ranged from 16 to 28°C. Treatments included GA₃ (Pro-Gibb) at 5.50, and 500 mg-liter⁻¹ and an unsprayed control. GA₃ solutions contained Tween 20 at 1 ml-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 GA₃ 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 GA₃-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 h) 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 GA₃ application dates.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>GA₃ application date</th>
<th>Air temp (°C)</th>
<th>Photosynthetic photon flux (µmol·m⁻²·s⁻¹)</th>
<th>Natural photoperiod (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>10 Jan. 1988</td>
<td>21.5 ± 0.1</td>
<td>442 ± 44</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>17 Jan. 1988</td>
<td>20.1 ± 0.1</td>
<td>389 ± 24</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>24 Jan. 1988</td>
<td>21.6 ± 0.1</td>
<td>136 ± 26</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>31 Jan. 1988</td>
<td>21.4 ± 0.3</td>
<td>607 ± 66</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>11 Jan. 1989</td>
<td>18.9 ± 0.5</td>
<td>153 ± 20</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>21 Jan. 1989</td>
<td>17.8 ± 1.3</td>
<td>422 ± 107</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>31 Jan. 1989</td>
<td>18.5 ± 0.7</td>
<td>259 ± 30</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>10 Feb. 1989</td>
<td>18.4 ± 0.7</td>
<td>373 ± 79</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>20 Feb. 1989</td>
<td>19.0 ± 0.1</td>
<td>292 ± 71</td>
<td>10</td>
</tr>
</tbody>
</table>

*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 (±1σ) for 1000 to 1359 h.*

*Duration of daylight (interval between sunrise and sunset) at lat. 42°N. Data are from List (1951).*
immersing 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 oriented vertically in 55-cm (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, at 0, 0.1, 1, 10, or 100 mg·liter⁻¹. Crystaline GA₃ (Grade III; Sigma, St. Louis) was dissolved in ethanol, and, to preserve GA₃ 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 ± 1.5°C. 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, 1991). 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 GA₃ 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 GA₃ (Table 2). Increasing the number of GA₃ 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 GA₃ 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 GA₃ 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 GA₃ 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 GA₃, depending on concentration and application time (Table 3). Flowering was inhibited when GA₃ at 50 or 500 mg·liter⁻¹ was applied at or before the start of LDs. Generally, one application of GA₃ at 500 mg·liter⁻¹ resulted in fewer plants flowering, greater delays in flowering, and fewer flower buds compared to a single application of GA₃ at 50 mg·liter⁻¹. Applying GA₃ 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 GA₃ was applied 20 days after the start of LDs, flowering was hastened but the percentage of apical phylloclades flowering and number of flower buds per plant was decreased in plants sprayed with GA₃.

### Table 2. Influence of GA₃ concentration and number of applications on flowering of 'Crimson Giant' Easter cactus (Expt. 1).

<table>
<thead>
<tr>
<th>GA₃ concn (mg·liter⁻¹)</th>
<th>No. of applications</th>
<th>Days to flowering</th>
<th>Apical phylloclades flowering (%)</th>
<th>Flower buds/flowering apical phylloclade (no.)</th>
<th>Flower buds/flowering plant (no.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 (control)</td>
<td>---</td>
<td>57</td>
<td>67</td>
<td>1.7</td>
<td>25.3</td>
</tr>
<tr>
<td>25</td>
<td>1</td>
<td>62</td>
<td>54</td>
<td>1.5</td>
<td>19.9</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>69</td>
<td>49</td>
<td>1.6</td>
<td>21.9</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>69</td>
<td>42</td>
<td>1.4</td>
<td>16.9</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>80</td>
<td>28</td>
<td>1.5</td>
<td>11.5</td>
</tr>
<tr>
<td>50</td>
<td>1</td>
<td>64</td>
<td>56</td>
<td>1.6</td>
<td>25.1</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>73</td>
<td>35</td>
<td>1.9</td>
<td>17.8</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>86</td>
<td>31</td>
<td>1.3</td>
<td>10.6</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>86</td>
<td>10</td>
<td>1.2</td>
<td>4.0</td>
</tr>
</tbody>
</table>

**Contrasts**

- Control vs. GA₃
- Control vs. 25 mg·liter⁻¹
- Control vs. 50 mg·liter⁻¹
- 25 mg·liter⁻¹ vs. 50 mg·liter⁻¹
- 25 mg·liter⁻¹, no. applications linear
- 25 mg·liter⁻¹, no. applications quadratic
- 50 mg·liter⁻¹, no. applications linear
- 50 mg·liter⁻¹, no. applications quadratic

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*Days to flowering from start of long days (10 Jan. 1988) for all treatments.

ns: *Nonsignificant or significant at 0.05 ≥ α > 0.01, 0.01 ≥ α > 0.001, or α ≤ 0.001, respectively, according to F test of contrast between treatments.
GA$_3$ 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 ($r = -0.83$), $P < 0.001$ (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 ($r = -0.91$), $P < 0.001$ (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 was applied at or before starting LDs. In addition, multiple GA 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, even though R. gaertneri is a SLDP at 18 to 22°C (Boyle et al., 1988; Boyle, 1991) whereas S. truncata is a SDP at 15 to 21°C (Runger and Poole, 1985). The results of the current experiments and those with S. truncata demonstrate that GA 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 interaction (Table 4). Both variables, however, were significantly affected by GA concentration. The number of flower buds decreased linearly as GA concentration increased, and the percentage of explants with flower buds was significantly lower among explants cultured in GA-amended medium compared to those in GA-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-amended medium than in those in GA-free medium. GA increased the number of 2° phylloclades compared to the controls, but the response to GA concentration was nonlinear. The number of 2° phylloclades increased as GA 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 H₀: 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 at 100 mg·liter⁻¹ (Table 5).

Whole plants and cultured phylloclades exhibited similar reactions to GA, but cultured phylloclades were more responsive to GA than intact plants (Tables 2, 3, and 5). GA at 5 mg·liter⁻¹ generally did not affect the vegetative or reproductive growth of intact plants (Table 3), whereas GA 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, 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 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).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Mean squares</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Flower buds/</td>
</tr>
<tr>
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<td></td>
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<td></td>
<td>(no.)</td>
</tr>
<tr>
<td>Experiment (E)²</td>
<td>1</td>
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<tr>
<td>Replications within E</td>
<td>18</td>
<td>0.0096</td>
</tr>
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<td>GA₂ concentration (GA₂)</td>
<td>4</td>
<td>0.5584***</td>
</tr>
<tr>
<td>E × GA₂</td>
<td>4</td>
<td>0.0112</td>
</tr>
<tr>
<td>Pooled Error</td>
<td>59</td>
<td>0.0181</td>
</tr>
</tbody>
</table>

*²F test performed using replications within E as the error term.
***Significant at P ≤ 0.001.

### Table 5. Influence of GA₂ concentration on flowering and vegetative growth of cultured phylloclades of ‘Crimson Giant’ Easter cactus (Expt. 3).

<table>
<thead>
<tr>
<th>GA₂ concn (mg·liter⁻¹)</th>
<th>Explanets with flower buds (%)</th>
<th>Flower buds/ explant (no.)</th>
<th>Explanets with 2° phylloclades (%)</th>
<th>2° Phylloclades/ explant (no.)</th>
<th>Explanets with spine growth (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 (control)</td>
<td>100</td>
<td>1.9</td>
<td>0</td>
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<tr>
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<td>Contrasts</td>
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<tr>
<td>Control vs. GA₂</td>
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<tr>
<td>GA₂ linear</td>
<td>***</td>
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<td>GA₂ quadratic</td>
<td>NS</td>
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*²Treatment significantly different from control by chi-square test, P < 0.05; chi-square = 3.841 for 1 df.
***NS: Nonsignificant or significant at 0.05 ≥ α > 0.01, 0.01 ≥ α > 0.001, or α ≤ 0.001, respectively, according to F test of contrast between treatments.
Expt. 3, the number of 2nd phylloclades was maximal when explants were cultured on media containing GA, 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 may have been due to greater hormone uptake in the former, possibly due to direct contact between the GA-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, at >0.01 mg-liter\(^{-1}\) (Table 5). GA 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 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 can stimulate leaf growth (Aloni and Pressman, 1980; Gray, 1957), it is feasible that GA 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-induced spine growth in ‘Crimson Giant’.

Intact plants and cultured phylloclades generally produced more new phylloclades as GA 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. Direct stimulation of stem growth via increased cell division and cell elongation has been demonstrated in several species after GA was applied (Sach, 1961), and GA would be expected to have similar effects on phylloclade growth. Also, GA 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 may have reversed the repression of vegetative growth by inhibiting flowering, thus allowing phylloclades to form. GA also promoted shoot growth in intact plants of *C. silvestri* (Sanderson et al., 1986), *M. elongata* (Sanderson et al., 1986), and *S. truncata* (Yonemura, 1959).

**Horticultural significance.** Applying GA, 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, at 5 mg-liter\(^{-1}\)3 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 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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