Differences in Inflorescence Numbers and Endogenous Gibberellic Acid Levels in ‘Afterglow’ Bougainvillea

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ADDITIONAL INDEX WORDS. abscisic acid, ethephon, ethylene, photoperiod, plant growth regulator

SUMMARY. Bougainvillea (*Bougainvillea* sp.) plant inflorescence number will vary in response to multiple cues such as changes in temperature, water, light intensity, pruning, and photoperiod. Previous research reports that the application of plant growth regulators (PGRs) to bougainvillea grown under varying photoperiods improved inflorescence number, probably as a result of changes in gibberellic acid (GA) levels. There are many bioactive plant GAs, but we chose to investigate differences in gibberellic acid 3 (GA₃) levels and inflorescence number in response to the application of ethephon (2-cholorethylphosphonic acid) or abscisic acid (ABA) to ‘Afterglow’ bougainvillea (*Bougainvillea* × *buttiana*) grown under 14-hour photoperiod [long-day (LD)] conditions. Plants were 5 inches tall with seven visible lateral nodes and were grown in a greenhouse in 4-inch pots filled with 5-mm coarse aquarium zeolite. Ethephon was applied as a foliar spray at 0.05, 0.07, 0.10, 0.15, or 0.20 mg/plant. ABA was applied as a soil drench at 1, 1.5, 3, 6, 8, or 10 mg/plant. Endogenous levels of GA₃ were measured 1 and 48 days after treatment to calculate the change in GA₃ (ΔGA₃). A short day (SD) control of 8 hours was included to measure differences in inflorescence number and ΔGA₃ between photoperiods. ‘Afterglow’ plants grown under SD conditions had the greatest decrease in ΔGA₃ (−1.09 μg·g^{−1}) over 48 days and the most inflorescences (10.6) compared with LD control plants with a decrease in ΔGA₃ of −0.09 μg·g^{−1} and fewer inflorescences (1.0). Plants grown under LD conditions and treated with 0.05 mg/plant ethephon had inflorescence numbers (9.6) and levels of ΔGA₃ (−0.74 μg·g^{−1}) similar to the SD control. As ethephon rate increased to more than 0.05 mg/plant, inflorescence number on LD plants decreased and ΔGA₃ increased. Exogenous ABA rates of 1 mg/plant produced inflorescence numbers (1.4) and ΔGA₃ (−0.10 μg·g^{−1}) similar to the LD control. As the rate increased, ΔGA₃ increased and inflorescence number decreased. Plants treated with ABA rates of 3 mg/plant and more were defoliated and had no inflorescences.

Bougainvillea (*Bougainvillea* sp.) is a popular landscape ornamental plant in tropical and subtropical zones around the world, valued for its vigor and relative resistance to pests, disease, and drought;

variability in form; and bright floral display of colorful bracts. Inflorescences form in apical panicles on the current year’s wood, with number of inflorescences and timing of flowering varying based on differences in cultivars as well as in response to changes in temperature, irrigation, light intensity, pruning, and photoperiod (Hackett and Sachs,

1985; Norcini et al., 1994). ‘Afterglow’ bougainvillea (*Bougainvillea* × *buttiana*) plants grown under SDs (8 h) had visible inflorescences within 30 d, with 8 to 10 inflorescences per plant compared with no inflorescences on LD (14-h) plants after 30 d (Chng and Moore, 2016).

Inflorescence number on bougainvillea plants grown under LD conditions has been enhanced by the use of PGRs such as chlormequat, daminozide, paclobutrazol, and dikegualac, which act by inhibiting GA levels (Karagüzel, 1999; Liu and Chang, 2011b; Norcini et al., 1994). Gibberellic acids play an important role in flowering pathways (Campos-Rivero et al., 2017; Taiz et al., 2018). They promoted flowering in LD plants such as spinach [*Spinacia oleracea* (Metzger and Zeevaart, 1980)], and sweet william [*Silene armeria* (Talon and Zeevaart, 1990)], but exogenous applications of GA to ‘San Diego Red’ bougainvillea grown under SD conditions inhibited flowering (Even-Chen et al., 1979).

Hackett and Sachs (1985) suggested that GAs stimulate sinks for available plant resources that compete with developing inflorescence primordia, and the removal of young leaves reduces GA levels, potentially shifting resources to inflorescences (Hackett and Sachs, 1985). Gibberellins are senescence-repressing hormones with active forms that decline in leaves as they age, whereas ethylene and ABA levels increase in senescing leaves and are considered senescence-promoting hormones that accelerate leaf and inflorescence senescence (Taiz et al., 2018). There are many bioactive GAs in plants, but we chose to focus on gibberellic acid 3 (GA₃) because this is a commercially available plant hormone that can

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Units			
To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
29,574	fl oz	μL	3.3814 × 10 ^{−5}
29.5735	fl oz	mL	0.0338
0.3048	ft	m	3.2808
2.54	inch(es)	cm	0.3937
25.4	inch(es)	mm	0.0394
1	μmho/cm	μS·cm ^{−1}	1
28.3495	oz	g	0.0353
28,350	oz	mg	3.5274 × 10 ^{−5}
1	ppm	mg·L ^{−1}	1
1	ppm	μg·g ^{−1}	1
1	ppm	μL·L ^{−1}	1
(°F − 32) ÷ 1.8	°F	°C	(°C × 1.8) + 32

be applied to moderate plant growth and flowering, and it has been heavily investigated (Campos-Rivero et al., 2017; Hackett and Sachs, 1967; Taiz et al., 2018).

Leaf senescence is enhanced by the plant hormones ethylene and ABA (Taiz et al., 2018). Bending shoots of 'Taipei Red' bougainvillea resulted in greater ethylene production, leading to enhanced inflorescence number (Liu and Chang, 2011a). In a follow-up study, application of ethephon, a synthetic ethylene-releasing compound, to vegetative 'Taipei Red' bougainvillea shoots produced more inflorescences than vegetative control plants. However, foliar applications of ethephon to flowering shoots caused inflorescence and bud drop (Liu and Chang, 2011b). Unfortunately, Liu and Chang (2011a, 2011b) only investigated one rate of ethephon (0.15 mg/plant) and did not measure changes in endogenous GA levels. They suggested that adequately controlling the response to ethylene during shoot development would facilitate inflorescence control.

In a preliminary study, we observed that the application of ethephon at rates of 0.07 to 0.15 mg/plant to 'Afterglow' bougainvillea grown under SD conditions increased the number of inflorescences after 30 d, but had limited success in improving inflorescence number under LD conditions (Chng and Moore, 2018). Ethephon rates of 0.3 mg/plant applied to plants grown under both SD and LD conditions resulted in complete defoliation 3 d after treatment (Chng and Moore, 2018). The objective of this study was to monitor differences in inflorescence number and endogenous GA₃ levels in response to the application of five rates of ethephon and ABA to LD plants.

Materials and methods

On 1 Oct. 2016, 65 rooted cuttings of 'Afterglow' bougainvillea were grown in a greenhouse in 4-inch pots filled with 100% 5-mm coarse aquarium zeolite (Pentair Aquatic Eco-systems, Apopka, FL). Zeolite was used to minimize potential flowering in response to drought or environmental stress because it holds moisture better than perlite, and was sterile and chemically inert (Liu and Chang, 2011a, 2011b; Ma and Gu, 2012).

At planting, 'Afterglow' bougainvillea were fertilized with 10 mg·L⁻¹ of nitrogen (Peters Professional Bloom Booster 10N-13.5P-16.6K; JR Peters, Allentown, PA). We continued to apply the fertilizer at the same rate once per week throughout the remainder of the experiment. Plants were watered with 50 mL tap water [electrical conductivity = 516 μS·cm⁻¹, pH = 8.3] every 2 d.

On 14 Oct. 2016, plants were actively growing, with some plants showing signs of inflorescence initiation. To ensure that all plants were at the same physiological state before treatment, all plants were sprayed with 1.2 mg/plant of ethephon (Florel; Monterey Lawn and Garden Products, Fresno, CA) to induce leaf and inflorescence senescence. All plants were single stems that were pruned to remove the apical bud and to reduce plants to a mean height of 5 inches with seven visible lateral nodes.

Plants were kept vegetative for 3 weeks under LD conditions by supplementing the natural daylight (around 11 h) with white light-emitting diode lights supplying 70 μmol·m⁻²·s⁻¹ photosynthetic photon flux, measured using a handheld quantum meter (Apogee Instruments, Logan, UT). After 3 weeks (4 Nov. 2016), new growth had formed from existing buds, creating denser plants without increasing overall height. Plants were ready for treatments on 5 Nov. 2016. All plants except a control group of five replicate plants continued to receive supplemental lighting for the duration of the experiment. Plants that served as controls were covered with a black plastic 5-gal container from 4:00 PM to 8:00 AM to create a SD photoperiod.

Plants grown under LD conditions were treated once either with ethephon (Florel) or ABA (ProTone; Valent Biosciences, Libertyville, IL). Ethephon was applied as a foliar spray of 0, 0.05, 0.07, 0.10, 0.15, or 0.20 mg/plant. ABA was applied as a soil drench of 0, 1, 1.5, 3, 5, 8, or 10 mg/plant. Each treatment rate contained five replicates (i.e., five individual potted plants).

The plants were arranged in a completely randomized design in an open-sided greenhouse exposed to ambient average air temperatures (80/64 °F day/night) and 76.0% relative humidity (RH) at the University of Florida, Fort Lauderdale

Research and Education Center, Davie, FL. Weather data were collected by the Florida Automated Weather Network system located 3 m from the greenhouse. This experiment was repeated to confirm results with 65 'Afterglow' rooted cuttings placed in the greenhouse on 3 Dec. 2016; defoliation on 17 Dec. 2016; and treatments on 7 Jan. 2017. Average temperatures and RH were similar in the repeat of the experiment.

Inflorescences on each plant were counted 48 d after treatment (23 Dec. 2016 and 24 Feb. 2017). Based on previous experiments, inflorescence appearance on 'Afterglow' bougainvillea occurred from 30 to 48 d after initiating conditions conducive to flowering (Chng and Moore, 2016, 2018). One inflorescence was defined as an individual thorn-inflorescence axil, regardless of how many florets were attached to the peduncle.

GA DETERMINATION. The levels of GA₃ in the leaf tissue were determined using an adapted version of the spectrophotometric method developed by Holbrook et al. (1961) and further modified by Berrios et al. (2004). Chemicals and reagents used were zinc acetate solution [21.9 g zinc acetate (Acros Organics, Fair Lawn, NJ) dissolved in deionized (DI) water and 1 mL glacial acetic acid (Thermo Fisher Scientific, Waltham, MA) made up to 100 mL]; potassium ferrocyanide solution [10.6 g analytical-grade potassium ferrocyanide (Acros Organics) dissolved in 100 mL DI water]; dilute hydrochloric acid (HCl) 35% (Thermo Fisher Scientific); and GA₃ standard [analytical-grade GA₃ (Acros Organic)] dissolved in ethanol (Thermo Fisher Scientific) at various concentrations for calibration].

Fresh tissue was harvested from plants, and 200 mg from each replicate was weighed and homogenized in 0.5 mL methanol, then centrifuged at 6000 g_n for 3 min. The extract was transferred to a glass vial to which 1 mL ethanol and 1 mL DI water was added, followed by 1 mL zinc acetate solution, and the mixture was shaken vigorously and left to stand for 2 min at room temperature. One milliliter of the potassium ferrocyanide solution was then added to the mixture and vortexed for 10 s, then left to stand for 10 min and vortexed for

another 10 s. The resulting precipitate was filtered using filter paper (P8, Thermo Fisher Scientific); the clear extract was retained for analysis. A 500- μ L sample of the extract was transferred into a test tube. When the sample was ready to be analyzed, 800 μ L dilute HCl was added to the test tube, which was then shaken vigorously and pipetted into a quartz cuvette to be analyzed in the ultraviolet spectrophotometer (Cary 100; Varian, Palo Alto, CA), with absorbance measured at 254 nm over 2 min. The differentials of the resulting curves were measured against a calibration curve constructed before the experiment using known concentrations of GA₃ standard solutions of 0.125, 0.25, 0.5, and 1.0 μ L·L⁻¹. The resulting quotient is the concentration of GA₃ in the sample.

Tissue samples for GA analysis were collected 1 and 48 d after treatment. Difference in GA₃ was calculated as Δ GA₃ = GA_{3 d48} - GA_{3 d1}. We pooled the analyses for the two runs of this experiment to get 10 replications to determine Δ GA₃. A correlation analysis between number of inflorescences per plant and Δ GA₃ was performed to look for a relationship between Δ GA₃ and inflorescence number in LD plants. The correlation analysis was performed separately for the ethephon and ABA treatments.

All statistical analyses were performed using the R statistical software

package (R Foundation for Statistical Computing, Vienna, Austria). Differences in inflorescence number and Δ GA₃ among the 13 treatments were analyzed using analysis of variance (ANOVA) with mean separation using Tukey's honestly significant difference test. The experiment was repeated to confirm results. We ran an ANOVA to compare the two sets of data and decided to pool the data after finding no differences between the two runs of the experiment ($P < 0.220$).

Results and discussion

'Afterglow' bougainvillea plants grown under SD conditions had more inflorescences than plants grown under LD conditions [9.6 vs. 1.8, respectively; $P < 0.01$ (Table 1)]. 'Raspberry Ice' (*Bougainvillea glabra*), 'Taipei Red', 'Rainbow Gold', and 'San Diego Red' also had more inflorescences under SD conditions than LD conditions (Even-Chen et al., 1979; Liu and Chang, 2011b; Ma and Gu, 2012; Norcini et al., 1992). However, photoperiod is only one trigger for inflorescence number in bougainvillea.

Bougainvillea will eventually produce inflorescences under LD conditions in response to other environmental cues such as temperature, light intensity, and irrigation, as well as in response to PGRs (Hackett and Sachs, 1985; Karagüzel, 1999; Liu and Chang, 2011b; Norcini et al.,

1992, 1994). 'Afterglow' plants grown under LD conditions and treated with ethephon at 0.05 mg/plant had inflorescence numbers (10.6) similar to SD control plants (9.6) (Table 1). Both were greater than the LD control (1.8). As ethephon rate applied to LD plants increased from 0.05 to 0.10 mg/plant, the number of inflorescences decreased, with fewer inflorescences than the LD control at rates of 0.10, 0.15, and 0.20 mg/plant (Table 1). We did not observe any leaf drop at these ethephon rates.

However, we observed 100% leaf loss on LD plants 4 d after treatment with ABA at rates of 6, 8, and 10 mg/plant. At ABA rates of 1 mg/plant, we observed inflorescence numbers similar to the LD control, with less inflorescences as rates increased (Table 1). 'Afterglow' plants that lost all leaves were slow to recover. Inflorescence development in bougainvillea might be a function of leaf number (Ramina et al., 1979; Tse et al., 1974). Young leaves were reported to be a source of GAs that stimulated sinks competing with developing inflorescences for resources (Hackett and Sachs, 1985; Tse et al., 1974). Research supports that GA is an inhibitor of inflorescence development in bougainvillea (Even-Chen et al., 1979; Hackett and Sachs, 1985; Norcini et al., 1992, 1994), and the application of PGRs that inhibit GAs promote inflorescence number in bougainvillea (Karagüzel, 1999; Liu

Table 1. Mean number of inflorescences and mean difference in gibberellic acid (Δ GA₃) of 5-inch (12.7-cm) 'Afterglow' bougainvillea plants grown in a greenhouse in 4-inch (10.2-cm) pots filled with coarse aquarium zeolite and subjected to short-day (8 h) or long-day (14 h) photoperiods in Fort Lauderdale FL. Long day plants were treated once with ethephon or abscisic acid (ABA). Ethephon was applied as a foliar spray of 0, 0.05, 0.07, 0.10, 0.15, or 0.20 mg/plant. ABA was applied as a soil drench of at 0, 1, 1.5, 3, 5, 8, or 10 mg/plant.^z

Photoperiod	Chemical	Rate (mg/plant) ^z	Inflorescences [mean $\pm$ SE (no.)] ^y	Δ GA ₃ [mean $\pm$ SE (μ g·g ⁻¹)] ^{y,x}
Short day	None	0	10.6 $\pm$ 0.11 a ^w	-1.09 $\pm$ 0.19 a
Long day	None	0	1.0 $\pm$ 0.12 c	-0.09 $\pm$ 0.15 c
Long day	Ethephon	0.05	9.6 $\pm$ 0.17 a	-0.74 $\pm$ 0.17 a
Long day	Ethephon	0.07	5.2 $\pm$ 0.15 b	-0.28 $\pm$ 0.11 b
Long day	Ethephon	0.10	0.5 $\pm$ 0.15 d	0.30 $\pm$ 0.18 d
Long day	Ethephon	0.15	0.4 $\pm$ 0.10 d	0.28 $\pm$ 0.13 d
Long day	Ethephon	0.20	0.4 $\pm$ 0.11 d	0.29 $\pm$ 0.13 d
Long day	ABA	1	1.4 $\pm$ 0.16 c	-0.10 $\pm$ 0.14 c
Long day	ABA	1.5	0.3 $\pm$ 0.12 d	0.29 $\pm$ 0.18 d
Long day	ABA	3	0.4 $\pm$ 0.10 d	0.27 $\pm$ 0.15 d
Long day	ABA	5	0.0 $\pm$ 0.0 d	0.69 $\pm$ 0.11 e
Long day	ABA	8	0.0 $\pm$ 0.0 d	0.70 $\pm$ 0.13 e
Long day	ABA	10	0.0 $\pm$ 0.0 d	0.77 $\pm$ 0.19 e

^z1 mg = 3.5274 $\times$ 10⁻⁵ oz.

^yValues are means of 10 replicates. Results were pooled for both runs of this experiment.

^x Δ GA₃ = GA_{3 d48} - GA_{3 d1}; 1 μ g·g⁻¹ = 1 ppm.

^wMeans followed by the same lowercase letter within a column are not significantly different by Tukey's honestly significant difference test at $\alpha = 0.05$.

and Chang, 2011b; Norcini et al., 1994).

Short day control ‘Afterglow’ plants had a greater decrease in ΔGA_3 over 48 d than LD control plants (Table 1). ‘Afterglow’ plants treated with ethephon at 0.05 mg/plant had a decrease of ΔGA_3 similar to the SD control. Only ‘Afterglow’ plants treated with ABA at 1 mg/plant had a decrease in ΔGA_3 , which was similar to the LD control (Table 1). The number of ‘Afterglow’ inflorescences and ΔGA_3 correlated negatively for both ethephon (correlation coefficient = -0.915 , $P = 0.011$) and ABA (correlation coefficient = -0.885 , $P = 0.046$) treatments. In spinach (LD plant), GA levels were low in plants when they were grown under SD conditions, and plants maintained a rosette form (Metzger and Zeevaart, 1980; Taiz et al., 2018). However, when spinach plants were moved to LDs, GA levels increased and resulted in flowering, suggesting that GA metabolism was affected by daylength (Metzger and Zeevaart, 1980; Taiz et al., 2018).

The application of ethephon to vegetative shoots of ‘Taipai Red’ increased 1-aminocyclopropane-1-carboxylic acid (ACC) contents, a precursor to ethylene, which increased ethylene production and accelerated maturation of shoots, improving flowering (Liu and Chang, 2011b). Reproductive shoots also had greater ACC contents than vegetative shoots, suggesting that factors that increase ACC synthesis such as drought or application of ethephon improve flowering. However, excess ethylene in reproductive shoots led to inflorescence and leaf drop (Liu and Chang, 2011b). Greater ethylene production was associated with earlier maturing and flowering when shoots of bougainvillea were bent (Liu and Chang, 2011a, 2011b). Ethylene and ABA are regarded as senescence-promoting and stress-produced hormones, and their levels tend to increase as plants age (Taiz et al., 2018). However, GAs are senescence-repressing hormones and their levels decline as leaves age (Taiz et al., 2018). In our

study, the application of low rates of ethephon and ABA to LD ‘Afterglow’ plants resulted in a decrease in GA_3 and at least one inflorescence.

Our results suggest that the use of ethephon and ABA at low rates might be another tool for improving inflorescence number in ‘Afterglow’ bougainvillea when other PGRs are unavailable or when light levels, temperature, irrigation, and daylength are harder to manage. It is apparent that inflorescence control in bougainvillea involves multiple cues that vary with cultivar and the environment in which they are grown, and will require more study to link the many variables into an accurate inflorescence model.

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