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Ethephon treatment promotes flower formation in bougainvillea

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ABSTRACT. Bougainvillea (*Bougainvillea* spp.) is an economically important ornamental flower in subtropical and tropical regions. This study examined bougainvillea shoots of different developmental stages, e.g., vegetative shoot, flowering shoot stage 1 with fully-developed thorn-inflorescence axis (FS1), flowering shoot stage 2 with visible flower bud (FS2), and flowering shoot stage 3 with blooming shoot (FS3) following their treatment with ethephon (2-chloroethylphosphonic acid). Experimental results indicated that ethephon treatment of bougainvillea's vegetative shoot accelerates its shoot maturity and enhances flower formation. The same treatment also increases endogenous ethylene production of the vegetative shoot, subsequently facilitating flower formation whereby the endogenous ACC content is lower than that of reproductive shoots (FS1, FS2, and FS3). Moreover, the ethephon treatment of reproductive bougainvillea shoots increases the ACC content beyond that of the vegetative shoot. Therefore, reproductive shoots produced more ethylene than vegetative shoots, subsequently inhibiting the development of flowers or even causing serious abscission of flower buds and leafs. This reveals that the role of ethylene in regulating the flowering control of bougainvillea is bidirectional. Results of this study demonstrate the significance of shoot maturity in the growth and flowering of the bougainvillea in which ethylene plays a major role.

Keywords: ACC content; *Bougainvillea* spp.; Ethephon; Ethylene; Flower formation; Shoot developmental stages.

Abbreviations: ACC, 1-aminocyclopropene-1-carboxylate; **Ethephon**, 2-chloroethylphosphonic acid; **FS1**, Flowering shoot stage 1 with the thorn-inflorescence axis developed fully; **FS2**, Flowering shoot stage 2 with visible flower bud; **FS3**, Flowering shoot stage 3 with blooming shoot.

INTRODUCTION

Bougainvillea (*Bougainvillea* spp.), a valued ornamental shrub-vine used in landscaping, is distributed from hot sunny areas to cool damp coastal regions worldwide. In Europe and North America, bougainvillea is also popular as a potted plant and in hanging baskets (Hackett and Sachs, 1967; Hackett et al., 1972). Various environmental conditions in which natural flowering of bougainvillea may occur include those of short photoperiods (Hackett and Sachs, 1968), low night temperatures (Hackett and Sachs, 1966; Norcini, 1993), high light intensity (Hackett and Sachs, 1968), water deficit (Henrard, 1976), shoot bending (Liu and Chang, 2011) and plant growth regulator use, e.g., chlormequat, daminozide (Hackett and Sachs, 1967), ancymidol (Criley, 1977), and dikegulac (Norcini et al., 1992; Norcini and Aldrich, 1994). However, some of these inductive conditions, e.g., water deficit and shoot bending, trigger ACC synthase gene expression, subsequently increasing ACC production and ultimately augmenting ethylene biosynthesis (Botella et al., 2000; Steed et al., 2004; Trusov and Botella, 2006).

As a gaseous hormone, ethylene is involved in the senescence of many plant vegetative organs and flowers, the ripening of fruits, and the enhancement of geophyte flowering (Halevy, 1995). Ethylene accelerates maturation of the Dutch iris, inducing small bulbs to bloom earlier, though it has no obvious effect on large bulbs or on the production of ACC (Imanishi et al., 1994; Botha et al., 1998). The treatment of spring barley with the ethylene-releasing agent ethephon enhances shoot maturity and increases their number of tillers (Dathe, 1992). The application of highly-concentrated ethylene promotes the vegetative growth of wheat, soy beans, lettuce, and potatoes, causing the flowers to bloom 10 days earlier than untreated ones (Wheeler et al., 1996). Ethylene is also responsible for the transfer from the vegetative to the flowering stage in pineapple (Min and Bartholomew, 1997; Van de Poel et al., 2009). That ethylene plays a role in promoting vegetative growth in some plants is mentioned above, but most plants' flower and flower bud abscission are also highly

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sensitive to the hormone. Such plants include: rose (Batista et al., 2009; Macnish et al., 2010), Christmas cactus (Serek and Reid, 1993), bougainvillea (Chang and Chen, 2001), geranium (Cameron and Reid, 2001), hibiscus (Reid et al., 2002), and kalanchoe (Zeddy et al., 2003). Ethylene transport can thus be bi-directional in regulating the flowering of some plants.

For several species of azalea, shoots older than 15 weeks respond to temperature, photoperiod, and Cycocel treatments (Shanks and Link, 1968) with a higher flower density than those of younger shoots. Mango shoots 8 weeks and older are more responsive to lower temperatures in forming flower buds than 2 or 4 week-old shoots are (Núñez-Elisea and Davenport, 1995). According to Ramina et al. (1979), the dry/fresh weight ratio and the content of soluble substances of bougainvillea increase with an increasing leaf area and with a larger number of developing inflorescences. This observation reveals that an increased assimilate accumulation in the reproductive shoots enhances flowering in bougainvillea, and indicates that the branch growth of woody plants must reach a certain maturity before the flower bud forms.

The bougainvillea inflorescence originates from a determinate shoot adjacent to an indeterminate vegetative axillary bud at each node (Figure 1). A thorn-inflorescence refers to a typical thorn containing a developing axis. The fully developed axis is defined as inflorescence hereafter (Hackett and Sachs, 1967). Although bougainvillea has axillary buds accompanying the growth of shoots, the shoot with accelerated growth is non-flowering. Abortion of the inflorescences at various stages of shoot development is a conspicuous phenomenon in bougainvillea. It was previously mentioned that the bending of bougainvillea shoots increases the flowering of buds, the blossom size of flowers and the endogenous ACC content. Shoot bending also resulted in greater ethylene production, causing earlier maturation and flowering. Ethylene may be an important factor in the flowering of bougainvillea (Liu and Chang, 2011). However, which shoot developmental stages of ethylene-sensitive are the least studied. The aim of this research, then, is to elucidate how shoot developmental stages and ethephon affect the flower formation of bougainvillea. The results will provide a basis for future research on the control of flowering in bougainvillea.

MATERIALS AND METHODS

Plant material

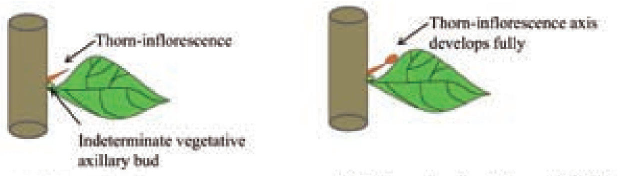
One-year-old seedlings of potted 'Taipei Red' bougainvillea were obtained from a commercial bougainvillea nursery and planted in 7-inch pots filled with 2,900 mL medium, composed of field soil and peat in a ratio of 7:3. The seedlings were on average 54.2 cm tall with a mean of 16.2 nodes. During the experimental period, the plants were thoroughly watered every 1 to 3 days, when the surface of the medium appeared slightly dry. Each pot was fertilized monthly with 3 g of 14-14-14 Osmocote.

Effect of ethephon on shoot developmental stages

The shoots were first categorized into several classes (Figure 1). Vegetative shoots that exhibited strong growth with prolific and dense leaves. Their florets did not develop fully on the thorn-inflorescence axis; peduncles became thorns. Flowering shoot stages (FS1 to FS3) were characterized as follows: FS1) fully developed thorn-inflorescence axes and florets with elongated peduncles that remained soft and with a tendency towards reproductive growth; FS2) visible flower buds and well-developed, FS3) flower buds in full bloom on the blooming shoot. Plants at each of these four described shoot developmental stages were sprayed with 75 mg L^{-1} ethephon (2-chloroethylphosphonic acid). Ethephon was sprayed once, 50 mL per each pot. After treatment, the plants were grown in a greenhouse where the shoot developmental stage-specific effect of ethephon on flower formation, flower drop and leaf drop could be observed. Each developmental stage was represented by five potted plants. The control plants were at the vegetative shoot stage and received no ethephon treatment.

1-Aminocyclopropene-1-carboxylate (ACC) content

ACC measurements were determined from 1 cm internodes segments of the tested plants (cut from 10 cm below the apical bud). The method developed by Lizada and Yang (1979) was modified to perform the analyses. All samples were washed in test tubes with 5 mL of 80% EtOH for subsequent extraction in a hot water bath at 70°C for 20 minutes, followed by centrifuging. This procedure was repeated twice, and the mixture of the two extracts was further concentrated in a vacuum until it became anhydrous. Distilled water was then added to the concentrated sample to a final volume of 1 mL. The prepared



(A) Vegetative shoot **(B) Flowering shoot stage 1（FS1)**

(C) Flowering shoot stage 2 (FS2) **(D) Flowering shoot stage 3 (FS3)**

Figure 1. Sketch map of different stages of shoot development in bougainvillea (A) Florets on thorn-inflorescence axis do not fully develop, and peduncle becomes a thorn (B) Thorn-inflorescence axis fully develops, peduncle elongates and remains soft (C) Flowering shoot with visible flower bud (D) Flowering shoot with fully blooming shoot.

samples were stored in test tubes at 0°C to be analyzed within two weeks.

To perform the analyses, 0.5 mL supernatant was mixed with 0.1 mL $HgCl_2$ (50 mM) twice: 0.1 mL ACC (100 mM) was added to one system; nothing was added to the other. Their final volumes were each brought to 1.8 mL with distilled water; the mixture was placed in test tubes sealed with sleeve stoppers. While the tubes were submerged in crushed ice, 100 μL of a mixture (2:1, v/v) of iced 5% NaOCl and saturated NaOH was added to each test tube. The contents were vortexed for 5 seconds and then each tube was returned to the crushed ice for 2.5 minutes. They were then vibrated for 1 second and 1 mL of the gas was extracted for analysis using a GC-14A gas chromatograph (Shimazdu, Japan).

Ethylene production rate

Three leaves previously treated with ethephon were detached from three samples (replicates) for each stage of shoot development on days 1, 3 and 7, and were then incubated in a 25 mL sealed plastic jar at temperatures ranging from 20-28°C for 2 h. Following incubation, air samples were taken from the headspace for ethylene analysis by a Shimadzu GC-14A gas chromatograph. Ethylene production rates were calculated and expressed as nL g^{-1} h^{-1}.

Table 1. Effect of ethephon (75 mg L^{-1}) on flower formation at different stages of shoot development in bougainvillea.

Treatment	Mean days to first flower buds	Mean node of first flower buds	Number of flower buds
Control	40.7[1]a[2]	22.4 a	11.8 b
Vegetative shoot	21.4 b	21.6 a	17.2 a
$LSD_{0.05}$	3.2	4.1	10.9

[1]Each value represents the mean of five replicates.

[2]Significant differences between treatments are designated by letters a and b (LSD test, *P*<0.05).

Experimental design and statistical analyses

During the experiment, weekly records were made of the number of nodes and time of the first flower bud, number of flower buds, flower drops, flower bud drops and leaf drops. The experimental design was based on complete randomized design (CRD). The results were statistically analyzed based on analysis of variance (ANOVA) to test the least significant difference (LSD) for evaluating whether the results of various treatments differ from each other (P<0.05). CoStat 6.2 (CoHorrt Software, Monterey, CA, USA) was used for conducting the analyses and SigmaPlot 8.0 (Systat software, Inc., Richmond, CA, USA) was used for graphic plotting of the results.

RESULTS

Effect of ethephon on flower formation

Shoots at various degrees of maturity (Figure 1) were treated using the ethylene-releasing agent ethephon in order to observe how ethylene affected shoot developmental stages of bougainvillea. Bougainvillea treated with ethephon during the vegetative shoot stage resulted in a shortened flower formation time and an increase in the number of flower buds (19.3 days and 5.4 flower buds, respectively (Table 1) compared to the untreated control group.

Effect of ethephon on flowering

During the vegetative shoot stage, bougainvillea treated with ethephon had more flower buds and flowers than the untreated control group. Plants treated with ethephon during the vegetative shoot stage and the FS1 stage with fully developed thorn-inflorescence axes exhibited 0% flower and flower bud drop. The application of ethephon during the FS2 stage when flower buds were visable, or the FS3 stage with blooming shoots, resulted in a flower drop of 85% (FS2) and 100% (FS3), ultimately reaching 100% after 7 days; whereas the flower bud drop had already reached 100% by 3 days. Treating the plant with ethephon during FS2 and FS3 stages caused an obvious flower and

Table 2. Effect of ethephon (75 mg L^{-1}) on the flower drop, flower bud drop and leaf drop percentage of different shoot developmental stages of bougainvillea.

Treatment	Thorn-inflorescence at treatment			Flower drops (%) Days after treatment		Flower buds drops (%) Days after treatment		Leaf drops (%) Days after treatment	
	Bloom No.	Bud No.	Total No.	3	7	3	7	3	7
Control	11.8[1]b[2]	16.6 b	28.4	0.0 c	0.0	0.0	0.0	3.7 d	23.5 c
Vegetative shoot	17.2 a	22.6 a	39.8	0.0 c	0.0	0.0	0.0	7.4 d	20.9 c
FS1	--	--	--	0.0 c	0.0	0.0	0.0	23.7 c	44.9 b
FS2	--	--	--	85.0 b	100.0	100.0	100.0	62.0 b	90.0 a
FS3	--	--	--	100.0 a	100.0	100.0	100.0	100.0 a	100.0 a
$LSD_{0.05}$	10.9	1.1	--	2.5	--	--	--	11.2	19.1

[1]Each value represents the mean of five replicates.

[2]Significant differences between treatments are designated by letters a, b, c and d (LSD test, *P*<0.05). FS1: Flowering shoot stage 1 with the thorn-inflorescence axis developed fully; FS2: Flowering shoot stage 2 with visible flower bud; FS3: Flowering shoot stage 3 with blooming shoot. Control plant was at the vegetative shoot stage without ethephon treatment.

flower bud drop (Table 2). The leaf drop was insignificant for both the control and for the ethephon treated plants at the vegetative shoot stage. After 3 days, the leaf drop was 3.7% for the control and 7.4% for the treated plants at the vegetative shoot stage; after 7 days, the leaf and flower drop were 23.5%, and 20.9%, respectively. Treating bougainvillea at developmental stages FS1, FS2, and FS3 with 75 mg L^{-1} ethephon, resulted in a leaf drop of 23.7%, 62.0%, 100%, respectively, after 3 days and 44.9%, 90.0%, 100%, respectively, after 7 days.

ACC content of shoot developmental stages

Vegetative shoots of bougainvillea contained less ACC (0.045 nmole g^{-1}) than the FS1 stage (0.243 nmole g^{-1}), the FS2 (0.295 nmole g^{-1}) and the FS3 stage (0.735 nmole g^{-1}) (Figure 2).

Effect of ethephon on ethylene production

The FS3 stage of bougainvillea contained more ethylene (2.17 nL g^{-1} h^{-1}) than the FS2 stage (2.01 nL g^{-1} h^{-1}), the FS1 stage (1.82 nL g^{-1} h^{-1}), the vegetative stage (1.72 nL g^{-1} h^{-1}) and the control (1.21 nL g^{-1} h^{-1}) at 7 days. Ethylene increased with an increasing duration of the ethephon treatment (Figure 3).

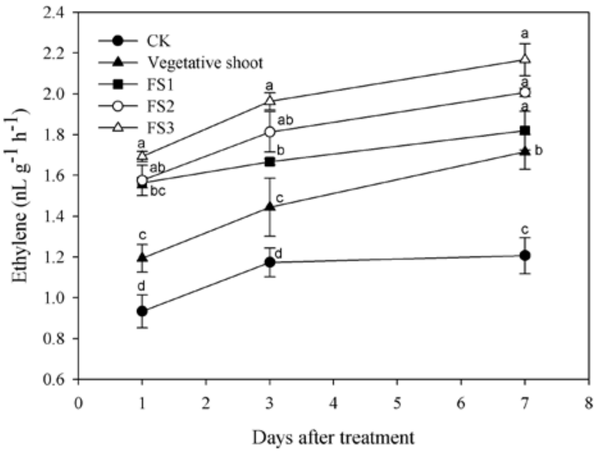


Figure 3. Effect of different stages of shoot development on ethylene production (nL g^{-1} h^{-1}) treated with ethephon (75 mg L^{-1}). FS1: Flowering shoot stage 1 with the thorn-inflorescence axis fully developed; FS2: Flowering shoot stage 2 with visible flower bud; FS3: Flowering shoot stage 3 with blooming shoot. Control plant was at the vegetative shoot stage without ethephon treatment. The vertical bars represent the mean ± standard error ($n = 3$). Significant differences between treatments are designated by letters a, b, c and d (LSD test, $P<0.05$).

DISCUSSION

Ethephon was applied at four developmental stages of shoots to observe the stage-specific effect of ethylene on bougainvillea flower formation. According to the results, when bougainvillea is in the vegetative growth stage, its ACC content is relatively low. Additionally, spraying ethephon increases endogenous ethylene production, subsequently accelerating maturation of the shoots. When the shoots are in the reproductive growth stage (FS1 to FS3), the increasing ACC content causes the sprayed ethephon to adversely impact shoot development because excessive ethylene leads to serious leaf and flower drop. The above observation indicates ethylene's bi-directional movement in adjusting bougainvillea's flowering.

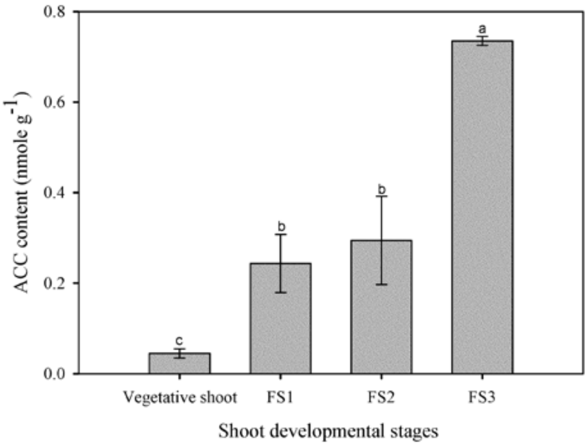


Figure 2. ACC content (nmole g^{-1}) at different stages of shoot development in bougainvillea. FS1: Flowering shoot stage 1 with the thorn-inflorescence axis fully developed; FS2: Flowering shoot stage 2 with visible flower bud; FS3: Flowering shoot stage 3 with blooming shoot. The vertical bars represent the mean ± standard error ($n = 3$). Significant differences between treatments are designated by letters a, b and c (LSD test, $P<0.05$).

This phenomenon is related to the observation by Day et al. (2002) that the age and size of woody plants affects their development; in addition, various maturing shoots may have different hormone distributions. Moreover, this observation is also related to nutrient diversion as proposed by Sachs (1977). As is hypothesized, there is competition for nutrients between bougainvillea's young leaves and flowering buds. Notably, a situation in which a nutrient originally destined for the growth of young leaves is directed to a location where flowering buds are developing, suppresses the shoot growth. Tse et al. (1974) mentioned that treating the bougainvillea, in which all young leaves with PBA (N-benzyl-α-(tetrahydro-2H-pyran-2yl)-adenine) have been removed, causes the plant to increasing accumulation of assimilates at the tip. Ramina et al. (1979) also confirmed that PBA treatment increases the soluble solid and cumulative dry weight of bougainvillea. Thus, the floral axis tips receive information on the accumulation of assimilates, and in addition, the increasing accumulation of assimilates facilitates the formation of flowering buds. Li et al. (2000) also noted that the mature shoot of bamboo affects the nutrient distribution within the plant; a larger number of mature shoots increases production. Zhou and Xi (1993) observed that treating the mature shoot with mixtalol causes different photosynthesis activities and production. This observation indicates that responses to chemical reagents for the plant fluctuate at various growth stages.

Treating mustard plants with ethephon at their vegetative growth stage transfers assimilates to their reproductive organs, increases their photosynthesis rate and dry weight and enhances flower formation (Khan, 2005). Ethylene biosynthesis was also promoted in vegetative bud formation in wild-type tobacco (Ma and Li, 2006). According to Lin et al. (2005), a significant amount of ACC of culture medium promotes flowering in bamboo. Some studies have attributed the flowering of Bromeliaceae to the increasing endogenous ethylene production and endogenous ACC content that raises the plant sensitivity to ethylene (Min and Bartholomew, 1993; Min and Bartholomew, 1996). We found similar results with bougainvillea: it had low ACC content during vegetative growth and the application of ethephon enhanced ethylene, thus promoting plant maturity and the formation of flowering buds. Bougainvillea contains a higher endogenous ACC content during the reproductive growth stages FS1, FS2, and FS3, than during the vegetative growth stage. Additionally, the application of ethephon causes a serious flower bud, flower and leaf drop, in which ethylene increases with an extended treatment. Moreover, treating bougainvillea with STS when its flowers are fully blooming alleviates the problem of flower and leaf drop and increases flower longevity (Chang and Chen, 2001). The present study also confirmed that the use of the inhibitor 1-MCP to treat bougainvillea after flowering increases flower longevity (data not shown).

Natural flowering occurs when plants are exposed to inductive stress conditions, e.g., water deficit and shoot bending (Henrard, 1976). According to our results, however, young bougainvillea plants (e.g., vegetative growth stage) are already sensitive to external flowering formation agents (e.g., ethephon or ethylene). Young plants may still need to develop certain sensitivity towards natural flowering formation. The above observations are consistent with those of Van de Poel et al. (2009). The sensitivity of an active ingredient and the magnitude of the evoked response is related to the ethylene receptor and signal transduction physiology (Trewavas, 1991). However, although bougainvillea plants at the vegetative shoot stage can sense externally-applied ethylene and transfer the signal resulting in flowering, they do not yet respond toward natural flowering. From this developmental stage, the ability to synthesize ethylene *de novo* (at the level of the axillary buds) appears to be a primary controlling factor to respond to natural flowering formation. Importantly, no flowering occurs if young plants can not yet increase their ethylene production (at the level of the axillary buds) in response to natural flowering formation.

The results presented here demonstrate that the developmental stage of bougainvillea shoots significantly affects its flower development. With respect to maturity of the shoots, above observations confirm that bougainvillea has a low ACC content during the vegetative growth period. Applying ethephon at this developmental stage would thus increase ethylene production, as well as promote shoot maturity and flower bud maturity. During the reproductive stages FS1to FS3, these plants have a higher ACC content, explaining why ethylene inhibits the development of flowering buds. Moreover, applying ethephon adversely impacts the subsequent development of flowering buds; excessive ethylene leads to a serious leaf drop and flower drop. Therefore, adequately controlling the response of bougainvillea to ethylene during its different shoot development stages would greatly facilitate the flower control.

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益收生長素促進九重葛花芽之形成

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九重葛為熱帶及亞熱帶重要的觀賞盆花。以不同枝條成熟度的九重葛枝條 (營養生長枝條、刺花序軸肥大的枝條、花苞可見的枝條、已開花枝條) 處理益收生長素 (ethephon)，觀察不同枝條成熟度對九重葛生長及開花之影響。結果顯示：九重葛在營養生長時期，施用 ethephon 可以加速枝條成熟，促進九重葛的花芽形成，顯示出乙烯會促進九重葛的花芽形成，且因營養生長時期其內生 ACC 含量低於生殖生長階段，故此時處理 ethephon 可提高九重葛內生乙烯含量而達到促進花芽形成之效果；而在生殖生長時期 (刺花序軸肥大、花苞可見和盛花)，因此時內生 ACC 含量高於營養生長階段，故此時處理 ethephon 會因過多的乙烯而抑制花芽發育，反而不利之後花苞的發育，甚至會造成嚴重的落苞及落葉現象。故推論在不同枝條成熟度處理乙烯對九重葛花芽形成有不同的影響，在營養生長時期乙烯可促進九重葛花芽形成，但在生殖生長時期則否，在九重葛花期調節上具有雙向之作用。由以上結果可得知枝條成熟度的時期對九重葛的花芽形成甚為重要，而乙烯扮演一關鍵之角色。

關鍵詞：ACC 含量；九重葛；益收生長素；乙烯；花芽形成；枝條成熟度。