Ethephon Foliar Sprays Are Influenced by Carrier Water Alkalinity and Ambient Air Temperature at Application

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Abstract. The plant growth regulator (PGR) ethephon [(2-chloroethyl) phosphonic acid; ETH] can be sprayed on floriculture crops to inhibit internode elongation, hinder apical dominance, increase lateral branching, and abort flower buds and flowers. However, the efficacy of ETH can be reduced as the pH of the carrier water used to mix the spray solution or temperature increase. Therefore, our objective was to quantify how the efficacy of ethephon sprays is influenced by carrier water alkalinity (CaCO_3 ; ALK) and the air temperature at application (TEMP). Young plants of verbena (*Verbena peruviana*) ‘Aztec Blue Velvet’, ivy geranium (*Pelargonium × peltatum*) ‘Precision Pink’, and petunia (*Petunia × hybrida*) ‘Easy Wave Neon Rose’ were transplanted into 11-cm-diameter containers and grown in a greenhouse with an average daily air temperature (ADT) set point of 21 °C. Before the ETH spray application(s), the ADT in each greenhouse compartment was changed from a set point of 21 °C to 14, 17, 20, 23, or 26 °C for ≈24 hours. Plants were sprayed with 0, 250, 500, or 750 $\text{mg}\cdot\text{L}^{-1}$ ETH mixed with carrier water containing ≈50, 150, or 300 $\text{mg}\cdot\text{L}^{-1}$ CaCO_3 2 and 3 weeks (Expt. 1) or 1 or 2 weeks (Expt. 2) after transplant. Generally, high ALK had a negative effect on spray efficacy. For example, an increase in ALK from 50 to 300 $\text{mg}\cdot\text{L}^{-1}$ CaCO_3 resulted in one and five fewer ivy geranium and verbena branches, respectively. In addition, as application TEMP increased above 23 °C, chemical efficacy generally decreased in all species. For instance, as ETH increased from 0 to 750 $\text{mg}\cdot\text{L}^{-1}$ across ALKs, inflorescence number of ivy geraniums increased from 7 to 18 at a TEMP of 23 °C, but was unaffected at 26 °C. Based on our results, we can conclude that both ALK and TEMP influence ETH efficacy and are additional factors for greenhouse growers to consider when making applications.

A common production challenge for greenhouse producers of floriculture crops is excessive stem elongation and/or poor branching that leads to unmarketable plants and reduced profits. To increase plant densities, meet market or buyer height specifications for shipping, and produce compact, well-branched, and aesthetically appealing plants, greenhouse growers use a wide vari-

ety of chemical plant growth regulators or retardants (PGRs) (Blanchard and Runkle, 2007; Currey et al., 2016a). The most commonly used PGRs are gibberellin inhibitors that control extension growth by inhibiting various steps in the gibberellin biosynthetic pathway (Rademacher, 2000). Although the PGR ethephon [(2-chloroethyl) phosphonic acid; ETH] is not a gibberellin inhibitor, it has been reported to influence the production of gibberellins (Furukawa et al., 1997).

Ethephon breaks down to release the plant hormone ethylene (C_2H_4) as well as chlorine (Cl^-), and hydrogen phosphate (H_2PO_4^-) (Biddle et al., 1976). It is labeled for foliar spray applications on floriculture crops to increase lateral branching, abort flowers and flower buds, and inhibit internode elongation (Currey et al., 2016b; Hayashi et al., 2001); although not labeled, recent research has shown that it can be effective as a substrate drench (Currey et al., 2016b; Miller et al., 2012). The increase in lateral branching is due to an inhibition of apical dominance (Andersen, 1976), and the control of flowering is due to ethylene-induced flower and flower bud abscission (Roberts et al., 1984). Ethylene also causes a rearrangement of the microfibrils in cell walls, resulting in a reduction of

extension growth and increased stem diameter (Ridge, 1973). In addition, high ethephon concentrations can inhibit root growth and development (Feldman, 1984).

Before spray applications, the liquid ethephon is mixed with water, known as carrier water, to form the spray solution. The evolution of the liquid ethephon to the gaseous and active compound, ethylene, is hypothesized to influence the efficacy of foliar sprays due to the changing duration of exposure and concentration of ethylene surrounding and absorbed by the plant. However, this evolution and, therefore, the efficacy of ethephon applications can be influenced by a variety of factors, including temperature and spray solution pH (Klein et al., 1979; McReynolds and Kossuth, 1985).

Carrier water quality, specifically pH and alkalinity or the presence of calcium (Ca) and magnesium (Mg), is known to affect the efficacy of many agricultural chemicals, including weak acid herbicides (Chahal et al., 2012), insecticides, and miticides (Cloyd, 2007). For example, Mueller et al. (2006) found that glyphosate activity was less in solutions with $>250 \text{ mg}\cdot\text{L}^{-1}$ Ca and Mg. Calcium and Mg cations have also been reported to lessen the activity of 2,4-dichlorophenoxyacetic acid (2,4-D) and dicamba (Nalewaja and Matysiak, 1993). In addition, water pH >7.0 can cause weak acid herbicides, such as glyphosate, 2,4-D, and dicamba, to become negatively charged, thus inhibiting absorption by the leaf cuticle and cell membrane (Chahal et al., 2012). Carrier water, particularly its alkalinity and pH, also can play a role in the chemical composition and evolution of PGRs, thus influencing efficacy (Camberato et al., 2014; Hammer, 2001).

The evolution of ethephon to ethylene increases as the spray solution pH increases above 4.5 (Klein et al., 1979; Warner and Leopold, 1969). The rapid release of ethylene from solution results in a phase change from liquid to gas, reducing the ethylene influx through stomata, and thus reducing chemical efficacy. Camberato et al. (2014) classified ethephon as a strong acid and reported that the addition of 500 $\text{mg}\cdot\text{L}^{-1}$ ethephon [Collate® (21.7% a.i.); Fine Americas, Inc., Walnut Creek, CA] to reverse osmosis carrier water with a pH of 5.3 or 8.2, resulted in a final spray solution pH of 2.4 and 2.5, respectively. However, the reduction in final solution pH was minimal when the solution was dilute and the carrier water had a high alkalinity. For example, when carrier water with 293 $\text{mg}\cdot\text{L}^{-1}$ CaCO_3 and pH of 7.3 was mixed with 250 and 750 $\text{mg}\cdot\text{L}^{-1}$ ethephon, the final solution pH was 6.4 and 3.8, respectively.

Groundwater wells are a common greenhouse water source for irrigation and chemical mixing in the United States (Biernbaum, 1994). In the United States, ≈60% of groundwater sampled by DeSimone et al. (2015) used for drinking water had a high alkalinity, containing 120 $\text{mg}\cdot\text{L}^{-1}$ or higher CaCO_3 , whereas only 20% contained $<60 \text{ mg}\cdot\text{L}^{-1}$ CaCO_3 . Groundwater containing high carbonate concentrations is largely due to carbonate-rock aquifers,

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particularly limestone aquifers, releasing compounds such as CaCO_3 as rocks dissolve (DeSimone et al., 2015). Of the top 15 floriculture-producing states, Florida, Illinois, Michigan, Ohio, Texas, and Southern California (USDA, 2016) are in regions with high-alkalinity water (Briggs and Ficke, 1977; DeSimone et al., 2015).

Air temperature also influences the efficacy of many agricultural chemicals, including herbicides (Ganie et al., 2017), insecticides (Longstaff, 1988), and PGRs (Biddle et al., 1976). For example, herbicide efficacy generally increases as temperature increases for chemicals that are quickly metabolized (Ganie et al., 2017). Glyphosate efficacy is greater when applied at 35 °C compared with applications at 24 °C (McWhorter et al., 1980), whereas more slowly metabolized herbicides, such as mesotrione, have a greater efficacy when applied at lower temperatures (e.g., 25/15 °C compared with 40/30 °C day/night) (Godar et al., 2015). At high temperatures, the half-life of ethephon is less due to the rapid evolution from ethephon to ethylene (Biddle et al., 1976; Klein et al., 1979; Loughheed and Franklin, 1972). However, we have found no research conducted in a greenhouse environment to determine how average daily air temperature (ADT) during and following application (TEMP) affects the efficacy of ethephon on bedding plants.

We hypothesize that a high rate of evolution from ethephon to ethylene influences the efficacy of ethephon sprays. Rapid evolution due to high carrier water CaCO_3 (ALK) when carrier water pH is high, as well as a high TEMP, will theoretically reduce ethephon spray efficacy. Therefore, our objectives were to determine how the efficacy of foliar ethephon sprays applied to aggressive bedding plant species is influenced by ALK and TEMP.

Materials and Methods

Plant material. Cuttings of verbena (*Verbena peruviana*) ‘Aztec Blue Velvet’ were stuck in 102-cell liner trays, and ivy geranium (*Pelargonium x peltatum*) ‘Precision

Pink’ were stuck in 104-cell liner trays, whereas petunias (*Petunia x hybrida*) ‘Easy Wave Neon Rose’ were sown in 288-cell plug trays by commercial propagators (Tagawa Greenhouses, Inc., Brighton, CO, or Dickman Farms, Auburn, NY). On receipt, on 12 Oct. 2016 (Expt. 1, all species), 14 Dec. 2016 (Expt. 2, petunia and verbena), or 21 Dec. 2016 (Expt. 2, ivy geranium), rooted liners and plugs were transplanted into round, 11-cm-diameter (600-mL) containers filled with a 70% peatmoss, 21% perlite, and 9% vermiculite substrate mixture (Suremix; Michigan Grower Products, Inc., Galesburg, MI). Plants were irrigated as needed with reverse osmosis water supplemented with 13N–3P–15K water-soluble fertilizer providing (in $\text{mg}\cdot\text{L}^{-1}$) 125 nitrogen, 12 phosphorus, 100 potassium, 65 Ca, 12 Mg, 1.0 iron and copper, 0.5 manganese and zinc, 0.3 boron, and 0.1 molybdenum (MSU Orchid RO Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Greenhouse environment. Plants were grown in connecting glass-glazed greenhouse compartments with an ADT and vapor pressure deficit set point of 21 °C and 0.70 kPa, respectively. The photoperiod was 16 h (0600 to 2200 hr) consisting of natural photoperiods (lat. 43° N) and day-extension lighting from high-pressure sodium lamps that provided a supplemental photosynthetic photon flux density of $77 \pm 13 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ when the outdoor light intensity was below $\approx 440 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Exhaust fans, evaporative-pad cooling, radiant steam heating, and supplemental lighting were controlled by an environmental control system (Integro 725; Priva North America, Vineland Station, ON, Canada). In each greenhouse compartment, a shielded and aspirated 0.13-mm type E thermocouple (Omega Engineering, Stamford, CT) recorded the air temperature, and a quantum sensor (SQ-500-SS Full-Spectrum Quantum Sensor; Apogee Instruments, Logan, UT) placed at canopy height recorded the light intensity. A CR-1000 datalogger (Campbell Scientific, Logan, UT) collected the environmental data every 15 s and hourly means were recorded. The mean daily light integrals $\pm$ SD during Expts. 1 and 2

were $10.3 \pm 4.1 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and $12.0 \pm 3.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, and the mean ADTs $\pm$ SD during Expts. 1 and 2 were 21.8 ± 1.6 °C and 20.7 ± 0.7 °C, respectively.

Ethephon treatments. Sulfuric acid (95% to 98%, H_2SO_4 ; J.T. Baker, Center Valley, PA) was added to well water to achieve target carrier water concentrations of ≈ 50 , 150, or 300 $\text{mg}\cdot\text{L}^{-1}$ CaCO_3 with actual concentrations reported in Table 1, and a handheld colorimeter (HI775 Checker HC; Hanna Instruments, Woonsocket, RI) was used to determine the CaCO_3 following a colorimetric reaction with an alkalinity reagent (HI775–26; Hanna Instruments). The adjusted well water was mixed with ethephon [Collate® (21.7% a.i.), Fine Americas, Inc.] to create 0, 250, 500, or 750 $\text{mg}\cdot\text{L}^{-1}$ solutions (Table 1). PGR solution pH was measured with a portable pH meter [portable waterproof pH/ED/TDS meter (high range) HI991301; Hanna Instruments]. Solution pH and ALK were measured for each treatment and the means $\pm$ SD are reported in Table 1.

Ethephon solutions were applied at a volume of $0.2 \text{ L}\cdot\text{m}^{-2}$, 14 and 21 d after transplant for Expt. 1, and 7 (verbena and ivy geranium) or 14 d (petunia) after transplant for Expt. 2. Before the foliar ethephon spray applications were initiated, the ADT in each of the separate glass-glazed greenhouse compartments was changed from a constant set point of 21 °C to 14, 17, 20, 23, or 26 °C for ≈ 24 h with actual temperatures reported in Table 2. After ≈ 24 h, the ADT was changed back to 21 °C for the remainder of the study.

Data collection and analysis. For both experiments, the date of first open flower was recorded, and length of the longest stem and branch number (>2.5 cm) was measured at first spray application and at first open flower. The stem length and branch number at the first spray application were subtracted from the stem length and branch number, respectively, at first open flower to determine the increase in stem length and branch number with these values being used for analysis and are henceforth referred to as “stem length” and “branch number.” In Expt. 2, inflorescence number at first open flower was recorded for ivy geranium.

Table 1. The pH and alkalinity (ALK) of well water acidified to create 0, 250, 500, and 750 $\text{mg}\cdot\text{L}^{-1}$ ethephon spray solution concentrations (ETH) from carrier water with a target ALK of 50, 150, or 300 $\text{mg}\cdot\text{L}^{-1}$ CaCO_3 , the pH and ALK of the carrier water, the ETH added, and the ALK and pH of the final spray solutions.

Well water		Adjusted carrier water				Spray water solution	
ALK ($\text{mg}\cdot\text{L}^{-1}$ CaCO_3)	pH	ALK ($\text{mg}\cdot\text{L}^{-1}$ CaCO_3)		pH	ETH ($\text{mg}\cdot\text{L}^{-1}$)	ALK ($\text{mg}\cdot\text{L}^{-1}$ CaCO_3)	pH
		Target	Actual				
338 $\pm$ 10	7.3 $\pm$ 0.2	300	301 $\pm$ 2	7.3 $\pm$ 0.2	0	301 $\pm$ 2	7.3 $\pm$ 0.2
338 $\pm$ 10	7.3 $\pm$ 0.2	300	301 $\pm$ 2	7.3 $\pm$ 0.2	250	200 $\pm$ 3	6.5 $\pm$ 0.1
338 $\pm$ 10	7.3 $\pm$ 0.2	300	301 $\pm$ 2	7.3 $\pm$ 0.2	500	85 $\pm$ 11	6.1 $\pm$ 0.1
338 $\pm$ 10	7.3 $\pm$ 0.2	300	301 $\pm$ 2	7.3 $\pm$ 0.2	750	2 $\pm$ 2	3.6 $\pm$ 0.2
338 $\pm$ 10	7.3 $\pm$ 0.2	150	151 $\pm$ 1	6.4 $\pm$ 0.2	0	151 $\pm$ 1	6.4 $\pm$ 0.2
338 $\pm$ 10	7.3 $\pm$ 0.2	150	151 $\pm$ 1	6.4 $\pm$ 0.2	250	47 $\pm$ 3	5.8 $\pm$ 0.1
338 $\pm$ 10	7.3 $\pm$ 0.2	150	151 $\pm$ 1	6.4 $\pm$ 0.2	500	0 $\pm$ 0	3.3 $\pm$ 0.2
338 $\pm$ 10	7.3 $\pm$ 0.2	150	151 $\pm$ 1	6.4 $\pm$ 0.2	750	0 $\pm$ 0	2.8 $\pm$ 0.2
338 $\pm$ 10	7.3 $\pm$ 0.2	50	52 $\pm$ 1	5.8 $\pm$ 0.2	0	51 $\pm$ 1	5.8 $\pm$ 0.2
338 $\pm$ 10	7.3 $\pm$ 0.2	50	52 $\pm$ 1	5.8 $\pm$ 0.2	250	0 $\pm$ 0	3.3 $\pm$ 0.1
338 $\pm$ 10	7.3 $\pm$ 0.2	50	52 $\pm$ 1	5.8 $\pm$ 0.2	500	0 $\pm$ 0	2.8 $\pm$ 0.1
338 $\pm$ 10	7.3 $\pm$ 0.2	50	52 $\pm$ 1	5.8 $\pm$ 0.2	750	0 $\pm$ 0	0.6 $\pm$ 0.2

Mean values reported are the average of four spray treatments across two experiments.

The experiment was organized in a randomized complete-block design with a three-way factorial arrangement. Plants were blocked by TEMP (five levels), ALK (three levels), and ETH (four levels) with six plants per treatment combination and were randomized in a common greenhouse environment after PGR applications. The experiment was performed twice over time for the three species evaluated. Analysis of variance and Student's *t* test were performed using JMP (version 12.0.1; SAS Institute, Inc., Cary, NC).

Results

Expt. 1. In Expt. 1, ETH×ALK, ETH×TEMP, and ALK×TEMP interacted to influence time to flower of ivy geranium, whereas only ETH×ALK and ETH×TEMP influenced time to flower of petunia (Table 3). For example, an increase in carrier water ALK (from 50 to 300 mg·L⁻¹ CaCO₃) hastened time to flower of ivy geranium and petunia by 5 and 11 d, respectively, across TEMP when ETH was sprayed at 250 mg·L⁻¹ (Fig. 1). Conversely, an increase in ALK (from 50 to 300 mg·L⁻¹ CaCO₃) for petunia and ivy geranium sprayed with 750 mg·L⁻¹ ETH delayed flowering at 5 and 0 d, respectively. TEMP and ETH influenced time to flower for verbena, as plants sprayed at 14 °C flowered 5 d later than those sprayed at 26 °C, and increasing ETH from 500 to 750 mg·L⁻¹ caused a 3-d delay in flowering (Table 3; Fig. 1).

Branch number of ivy geranium at flowering was influenced by the interaction of TEMP×ALK×ETH, whereas only TEMP and ETH influenced branch number of verbena (Table 3). For instance, as TEMP increased from 14 to 26 °C, verbena branch number increased from 12 to 18 branches across ETH and ALK (Fig. 2).

Increase in stem length for ivy geranium and petunia was influenced by the interaction of TEMP×ALK×ETH (Table 3). Verbena was influenced by ALK×ETH and ETH×TEMP interactions. For example, increasing ALK (from 150 to 300 mg·L⁻¹ CaCO₃) resulted in similar stem length when ETH was 250 mg·L⁻¹. However, when 750 mg·L⁻¹ ETH was sprayed, the stem length was 1.2 cm shorter when the ALK was 150 than 300 mg·L⁻¹ CaCO₃ (Fig. 2). At a TEMP of 23 °C, stem length of verbena at flowering was 4.0 cm longer when sprayed with 250 mg·L⁻¹ ETH compared with 750 mg·L⁻¹ ETH (Fig. 2). However, at a TEMP of 26 °C, stem length increased by only 1.8 cm.

Expt. 2. Ivy geranium and verbena flowered 23 and 21 d later, respectively, as ETH increased from 0 to 750 mg·L⁻¹ at 23 °C; however, there was no difference at 26 °C (Table 4; Fig. 3). Time to flower of verbena was influenced by the interaction of ETH×ALK (Table 4). For example, flowering of verbena was not delayed by increasing ETH from 500 to 750 mg·L⁻¹ at an ALK of 50 mg·L⁻¹ CaCO₃, whereas flowering was delayed by 7 d as ETH increased from 500 to 750 mg·L⁻¹ at an ALK of 300 mg·L⁻¹ CaCO₃.

Table 2. Average daily air temperature during and 24 h after spray application (TEMP) for two experiments and three spray applications.

TEMP set point (°C)	Expt.	Spray (no.)	Actual TEMP (°C)
14	1	1	16.1 ± 1.6
	1	2	17.3 ± 1.6
	2	1	14.3 ± 1.0
17	1	1	20.0 ± 1.0
	1	2	20.3 ± 1.1
	2	1	17.3 ± 1.0
20	1	1	21.0 ± 0.6
	1	2	24.2 ± 3.4
	2	1	20.2 ± 0.9
23	1	1	24.6 ± 0.7
	1	2	25.0 ± 1.5
	2	1	23.1 ± 1.2
26	1	1	27.0 ± 0.8
	1	2	26.9 ± 0.7
	2	1	25.9 ± 1.0

Data were collected every 15 s with means logged every hour.

Table 3. Analysis of variance for ethephon spray solution concentration (ETH), carrier water alkalinity (ALK), and average daily air temperature at application (TEMP) effects on time to flower and increase in stem length and branch number at first open flower of ivy geranium, verbena, and petunia in Expt. 1.

	Time to flower	Branch number at flowering	Stem length at flowering
<i>Ivy Geranium</i>			
ETH	***	***	*
ALK	*	**	NS
TEMP	***	***	*
ETH*ALK	**	*	*
ETH*TEMP	*	***	NS
ALK*TEMP	***	NS	NS
TEMP*ALK*ETH	NS	*	*
<i>Verbena</i>			
ETH	***	**	***
ALK	NS	NS	***
TEMP	***	***	***
ETH*ALK	NS	NS	**
ETH*TEMP	NS	NS	**
ALK*TEMP	NS	NS	NS
TEMP*ALK*ETH	NS	NS	NS
<i>Petunia</i>			
ETH	***	— ^z	***
ALK	***	—	***
TEMP	***	—	***
ETH*ALK	***	—	***
ETH*TEMP	**	—	**
ALK*TEMP	NS	—	NS
TEMP*ALK*ETH	NS	—	*

^zData not collected.

NS, *, **, ***Nonsignificant or significant at *P* ≤ 0.05, 0.01, or 0.001, respectively.

At 23 °C, the number of ivy geranium, petunia, and verbena branches at first open flower increased from 5 to 11, 38 to 94, and 18 to 48 branches, respectively, as ETH increased from 0 to 750 mg·L⁻¹; however, no differences were observed at 26 °C (Table 4; Fig. 4). As ALK increased from 50 to 300 mg·L⁻¹ CaCO₃, ivy geranium and verbena had 1 and 5 fewer branches, respectively, regardless of ETH. At 17 °C, petunia had 14 fewer branches as ALK increased from 50 to 300 mg·L⁻¹ CaCO₃; however, plants grown at 26 °C had the same number of branches, regardless of ALK (Fig. 4).

Ivy geranium and verbena stem length was similar at a TEMP of 26 °C as ETH increased from 0 to 750 mg·L⁻¹; however, at 20 °C, ivy geranium stem length was 2.9 cm shorter, and for verbena, was 4.6 cm longer as ETH increased from 0 to 750 mg·L⁻¹ (Table 4; Fig. 4). In addition, stem length of

ivy geranium and verbena were 1.7 and 0.9 cm less, respectively, as ALK increased from 50 to 300 mg·L⁻¹ CaCO₃. Similar to other growth and developmental parameters, petunia stem length was unaffected by ALK at a TEMP of 26 °C (Fig. 4).

At a TEMP of 26 °C, ivy geranium inflorescence number was similar as ETH increased from 0 to 750 mg·L⁻¹, but was different at TEMP ≤ 23 °C (Table 4; Fig. 3). For example, at 23 °C ivy geranium inflorescence number increased from 7 to 18 as ETH increased from 0 to 750 mg·L⁻¹.

Discussion

Increasing the ETH in spray solutions can help enhance plant responses to ethephon in two ways. First, there is an increase in the active ingredient, ethephon, and greater ethylene release resulting in more robust plant responses (Currey et al., 2016b). Second,

Fig. 1. Time to flower for petunia, verbena, and ivy geranium sprayed with 0, 250, 500, or 750 mg·L⁻¹ ethephon concentrations (ETH), with carrier water alkalinities of 50, 150, or 300 mg·L⁻¹ CaCO₃, and target average daily air temperatures at application of 14, 17, 20, 23, or 26 °C in Expt. 1. Each bar represents a mean of six plants, and error bars represent SE.

Fig. 2. Increase in branch number and stem length from application to first open flower for verbena and ivy geranium and increase in stem length from application to first open flower for petunia sprayed with 0, 250, 500, or 750 mg·L⁻¹ ethephon concentrations (ETH), with carrier water alkalinities (ALKs) of 50, 150, or 300 mg·L⁻¹, and target average daily temperatures at application (TEMPs) of 14, 17, 20, 23, or 26 °C in Expt. 1. Letters indicate mean separation across TEMPs, ALKs, and ETHs by Student's *t* test at *P* ≤ 0.05 within a species. Each bar represents a mean of six plants, and error bars represent SE.

ethephon is a strong acid; therefore, increasing ETH also results in a lower spray solution pH (Camberato et al., 2014). Moreover, because the rate of ethephon conversion into ethylene increases as pH increases (Klein et al., 1979; Warner and Leopold, 1969) and

the prolonged ethephon release of ethylene is hypothesized to increase efficacy, ETH influences plant responses, as our results confirm (Table 1).

In Expt. 1, nearly all crops and growth parameters were influenced by the interaction

of ETH×ALK, where differences in ALK effects are more pronounced when lower ETH was used (Table 3). To illustrate, ivy geranium and petunia flowering was delayed to a greater extent as the ALK of a 250 mg·L⁻¹ ETH solution increased from 50 to 300 mg·L⁻¹

Table 4. Analysis of variance for ethephon spray solution concentration (ETH), carrier water alkalinity (ALK), and average daily air temperature at application (TEMP) effects on time to flower and increase in stem length and branch number at first open flower of ivy geranium, verbena, and petunia in Expt. 2.

	Time to flower	Branch number at flowering	Stem length at flowering	Inflorescence number
<i>Ivy Geranium</i>				
ETH	*** ^z	***	***	***
ALK	**	**	**	NS
TEMP	***	***	NS	***
ETH*ALK	NS	NS	NS	NS
ETH*TEMP	***	***	*	***
ALK*TEMP	NS	NS	NS	NS
TEMP*ALK*ETH	NS	NS	NS	NS
<i>Verbena</i>				
ETH	***	***	***	— ^z
ALK	**	***	**	—
TEMP	***	***	***	—
ETH*ALK	**	NS	NS	—
ETH*TEMP	***	***	***	—
ALK*TEMP	NS	NS	NS	—
TEMP*ALK*ETH	NS	NS	NS	—
<i>Petunia</i>				
ETH	***	***	NS	—
ALK	**	NS	*	—
TEMP	***	***	NS	—
ETH*ALK	NS	NS	NS	—
ETH*TEMP	***	***	NS	—
ALK*TEMP	***	*	*	—
TEMP*ALK*ETH	*	NS	NS	—

^zData not collected.

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Fig. 3. Time to flower for petunia, verbena, and ivy geranium and inflorescence number at first open flower of ivy geranium sprayed with 0, 250, 500, or 750 mg·L⁻¹ ethephon concentrations (ETH), with carrier water alkalinities (ALKs) of 50, 150, or 300 mg·L⁻¹ CaCO₃, and target average daily air temperatures at application (TEMPs) of 14, 17, 20, 23, or 26 °C in Expt. 2. Letters indicate mean separation across TEMPs, ALKs, and ETHs by Student's *t* test at $P \leq 0.05$ within a species. Each bar represents a mean of six plants, and error bars represent SE.

CaCO₃, than at an ETH of 750 mg·L⁻¹ where there were slight to no differences in days to flower between ALKs. This may be due to the differences in solution pH. When ALK is high, low ETH does not neutralize carrier water pH as much as high ETH (Table 1). However, when the ALK is low, lower ETH results in a greater reduction in solution pH. This may be why there was less difference among ALKs

when high ETH was sprayed, but there were greater differences when lower ETH was sprayed.

In Expt. 2, ivy geranium and verbena were influenced by ALK, but generally not the interaction of ALK and either TEMP or ETH (Table 4). In contrast, petunia was influenced by the interaction of ALK×TEMP. In most cases, as ALK increased from 50 to 300

mg·L⁻¹ CaCO₃, branch number and days to flower were less, whereas stem length at flowering increased (Figs. 3 and 4). Differences between species may be due to a variety of factors, including epicuticular wax (Beaudry and Kays, 1987), pubescence affecting airflow around the leaf, stomatal characteristics including whether the plant has amphi- or hemistomatous leaves (Beaudry and

Fig. 4. Increase in branch number and stem length from application to first open flower for petunia, verbena, and ivy geranium sprayed with 0, 250, 500, or 750 mg·L⁻¹ ethephon concentrations, with carrier water alkalinities of 50, 150, or 300 mg·L⁻¹ CaCO₃, and target average daily temperatures at application of 14, 17, 20, 23, or 26 °C in Expt. 2. Each bar represents a mean of six plants, and error bars represent SE.

Kays, 1988), and the presence of gibberellin (Furukawa et al., 1997). Higher concentrations of epicuticular wax result in a lower rate of ethephon evolution to ethylene (Beaudry and Kays, 1987). As airflow increases, ethephon or ethylene is more likely to be carried away from the leaf before the compound can enter the stomata into the leaf tissue (Beaudry and Kays, 1988). Because ethephon sprays are applied to the adaxial leaf surface, whether plants have stomata on only the abaxial (hemistomatous) or both abaxial and adaxial surface (amphistomatous) can affect ethylene flux (Beaudry and Kays, 1988).

Generally, stem elongation was less as ETH increased and ALK decreased. This is because of ethylene affecting cell expansion in two ways: by decreasing the overall rate of expansion (Ridge and Osborne, 1969), and by changing the directionality of growth (Ridge, 1973). Turgor pressure exerts outward-directed force in equal directions on the cell wall. Directionality of cell expansion is determined by cellulose microfibril orientation within the cell wall. Newly formed cells in the center of the meristem contain isodiametric-oriented microfibrils resulting in a round cell.

However, as the cells mature, microfibrils are most commonly aligned transversely to promote anisotropic growth and an increase in length more than width (Baskin, 2005). Ethylene causes a rearrangement of the microfibrils in cell walls of the plant from transverse to longitudinal causing lateral cell expansion, less in stem elongation, and an increased stem diameter (Ridge, 1973). However, verbena in Expt. 2 had the opposite response. Researchers have found that in some plants, including rice (*Oryza sativa*; Furukawa et al., 1997), celery-leaved buttercup (*Ranunculus sceleratus*; Musgrave and Walters, 1973), water starwort (*Callitriche platycarpa*; Musgrave et al., 1972), and marsh and curly dock (*Rumex palustris* and *Rumex crispus*; Voesenek and Blom, 1989), ethylene can cause elongation especially when under water stress (Bleecker and Kende, 2000). This phenomenon may be influenced by gibberellins and may be species dependent (Furukawa et al., 1997).

Air temperature at application did not have the same effect between Expt. 1 and Expt. 2 (Tables 3 and 4). This may be due to the differences in experimental design. In Expt. 1, plants were sprayed twice and

exposed to TEMP treatments for a total of ≈96 h compared with only ≈24 h for plants in Expt. 2. The differences in days to flower, for instance, between experiments may be due to differences in ADT influencing growth and development in addition to the TEMP affecting spray efficacy. For example, time to flower of verbena in Expt. 1 was hastened by 5 d when the TEMP was 26 °C compared with 14 °C (Fig. 1). Similarly, Kaczperski et al. (1991) reported that flowering of petunia 'Snow Cloud' was hastened as temperature increased from 10 to 30 °C and Moccaldi and Runkle (2007) reported that as temperatures increased from 14 to 27 °C, the rate of development of salvia (*Salvia splendens*) 'Vista Red' and marigold (*Tagetes patula*) 'Bonanza Yellow' increased.

In Expt. 2, plants sprayed at TEMPs between 14 and 23 °C generally had responses similar to the ETH and ALK treatments; however, the responses of plants sprayed at TEMPs of 26 °C more closely resembled those sprayed with 0 mg·L⁻¹ ETH (Figs. 3 and 4). This may be because of the short half-life of ethephon owing to the rapid evolution from ethephon to ethylene at 26 °C

(Biddle et al., 1976; Klein et al., 1979; Loughheed and Franklin, 1972). Klein et al. (1979) demonstrated that the half-life of ethephon decomposition decreases dramatically regardless of pH or vapor pressure as temperature increases from 20 to 30 °C. This also supports the idea that the interactions of ETH×TEMP and ALK×TEMP are largely attributed to the difference at high TEMP, meaning that at higher TEMP, the evolution is rapid and results in reduced spray efficacy regardless of solution pH.

Conclusions

To have the greatest ethephon efficacy, sprays should be applied when greenhouse TEMPs are ≤23 °C. High ETH is not influenced by ALK as much as low ETH. Therefore, reducing ALK will have the greatest increase in spray efficacy when low ETH (250 mg·L⁻¹) is being sprayed; however, there is still a benefit to decreasing ALK of the carrier water of high-ETH sprays.

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