Antitranspirational Efficacy and Longevity of Absciscic Acid and a Synthetic Absciscic Acid Analog in Pansies (*Viola × wittrockiana*)

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Abstract. Physiological antitranspirants can reduce financial risks to growers by temporarily preventing drought stress, improving product quality, and extending the shelf life of ornamental bedding plants. Exogenous absciscic acid (ABA) is an effective antitranspirant that induces stomatal closure in a rate-dependent manner, reducing transpirational water loss in many species. However, it may also cause chlorosis, which reduces product quality. Synthetic ABA analogs have similar effects on stomatal conductance (g_s) but are not known to induce chlorosis. We studied the effects of ABA and its analog 8' acetylene ABA methyl-ester (PBI 429) on g_s and net photosynthesis (P_n) in pansies (*Viola × wittrockiana*), compared the efficacy and longevity of each compound, and quantified the resulting chlorosis. Plants were treated with spray solutions of ABA (0 to 2000 mg·L⁻¹) and PBI 429 (0 to 200 mg·L⁻¹) and irrigated daily. Gas exchange and leaf chlorophyll measurements were made twice weekly for 2 weeks. Additional measurements were taken once or twice weekly through 47 days. Absciscic acid reduced leaf chlorophyll content and P_n in a rate-dependent manner for 14 days after application but reduced g_s for only 11 days, whereas PBI 429 reduced P_n and g_s similarly for 7 days and did not reduce leaf chlorophyll content. Reductions in g_s and P_n were greatest on the first day after treatment for both compounds. Our results demonstrate that ABA is more effective than PBI 429 at 100 and 200 mg·L⁻¹, but also causes chlorosis, whereas PBI 429 is an effective antitranspirant without this phytotoxic effect.

Ornamental bedding plants are the largest sector of the floriculture industry in the United States and have a wholesale value of over \$1.3 billion (U.S. Department of Agriculture, 2013). As a result of relatively recent shifts in sales strategies, ornamentals often spend an extended period of time in shipping and retailing (Waterland et al., 2010a; Yue and Behe, 2008), where they may be exposed to drought stress as a result of inadequate watering (Astacio and van Iersel, 2011a; Waterland et al., 2010a). This leads to rapid wilting and diminishes plant quality (Armitage, 1983; Starman et al., 2007). Some retailers now operate under the “pay-by-scan” system, a sales scheme in which growers are not paid for their products until they are scanned at a cash register. Thus, there is an increased risk of financial loss to growers if plants die or become unsalable as a result of lack of watering (van Iersel et al., 2009).

Absciscic acid is an integral part of plant drought response. Drought causes root cells to produce ABA, which is then translocated to leaves by way of the transpiration stream

(Davies et al., 2005; Malladi and Burns, 2007). Drought-induced ABA synthesis may also occur within the leaf tissue in some species (Christmann et al., 2007), and leaf ABA concentration is strongly correlated with g_s (Kim et al., 2012). When ABA reaches the guard cells, it initiates a signal cascade that results in the net movement of ions and water out of these cells, causing them to lose turgor pressure and reducing stomatal aperture (Grabov and Blatt, 1998; Kim et al., 2010). This hormone may also indirectly induce stomatal closure by decreasing the hydraulic conductivity of leaf vascular tissue (Pantin et al., 2012). Closing the stomates inhibits transpiration and allows plants to respond to drought by using less water (Buckley, 2005; Malladi and Burns, 2007).

Bedding plants treated with exogenous ABA are able to tolerate a temporary lack of watering with minimal wilting (Blanchard et al., 2007; Kim and van Iersel, 2011; Waterland et al., 2010a, 2010b; Weaver and van Iersel, 2014). However, ABA application also causes unwanted phytotoxic effects such as chlorosis and leaf abscission in some species (Astacio and van Iersel, 2011b; Blanchard et al., 2007; Kim and van Iersel, 2011; Waterland et al., 2010a; Weaver and van Iersel, 2014), and drench applications can

induce wilting (Astacio and van Iersel, 2011b; Sharma et al., 2006). These side effects limit the usefulness of ABA as a commercial holding agent (Blanchard et al., 2007; Petracek et al., 2005; van Iersel et al., 2009; Waterland et al., 2010a; Weaver and van Iersel, 2014).

Synthetic ABA analogs are structurally similar to ABA, induce a comparable reduction in stomatal aperture, and do not cause chlorosis or abscission (Abrams et al., 1997; Flores and Dörffling, 1990; Jung and Grossman, 1985; Schubert et al., 1991; Sharma et al., 2006; Weaver and van Iersel, 2014). Because they can help alleviate drought stress without compromising product quality, ABA analogs could be effectively used as holding agents for ornamentals. In a comparison of two analogs, the compound PBI 429 was more efficacious than 8' methylene ABA methyl-ester (Sharma et al., 2005a). Furthermore, PBI 429 is more effective than ABA at delaying wilting and reducing water use in tomato (*Solanum lycopersicum*) (Sharma et al., 2005a, 2006). This analog is a promising commercial antitranspirant; however, it could be more persistent in the environment and plant tissue than ABA (Sharma et al., 2005b, 2006) and may cause a long-term reduction in tomato growth (Sharma et al., 2005a). Little is currently known about the duration of the effects of PBI 429. An ideal holding agent should limit plant water use for a short period of time but cease to affect the plant after purchase when it will likely encounter a more optimal growing environment.

In a previous study, we compared the efficacy of ABA and PBI 429 foliar sprays for extending shelf life in pansies (Weaver and van Iersel, 2014). These compounds reduced evapotranspiration similarly, but ABA consistently caused leaf chlorosis, whereas PBI 429 did not. We were unable to quantify the longevity of these effects or determine how they might affect photosynthesis and transpiration beyond the first few days after application because the plants were not rewetted. Without irrigation, drought causes stomatal closure, making it impossible to distinguish between spray treatment and drought-induced effects.

We investigated the efficacy and longevity of PBI 429 and ABA foliar sprays on well-watered pansies using g_s and leaf photosynthesis measurements. The objectives of this study were to determine which compound has a longer lasting effect on leaf gas exchange and to quantify chlorotic side effects over time.

Materials and Methods

Plant material. Pansy ‘Delta Premium Deep Blue’ plug seedlings were transplanted into square 10-cm pots filled with soilless substrate (Fafard 2P; Conrad Fafard Inc., Agawam, MA). Plants were grown in a greenhouse on ebb-and-flow benches and watered once daily with a fertilizer solution containing 100 mg·L⁻¹ nitrogen (15-5-15

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Cal-Mag, Everris, Marysville, OH; 15N–2.2P–12.45K). Subirrigation was used because overhead watering could wash off the spray solutions.

Spray solutions. Stock solutions of s-ABA, the biologically active isomer of ABA (10% s-ABA, VBC-30101; Valent BioSciences, Long Grove, IL), and PBI 429 (5% potassium salt of 8'-acetylene-ABA; Valent BioSciences) were diluted with a 10-mg·L⁻¹ surfactant solution composed of stock surfactant (10% Brij 98 Surfactant; Valent BioSciences) and deionized water. The range of concentrations (0, 100, 200, 500, 1000, or 2000 mg·L⁻¹ ABA and 0, 10, 20, 50, 100, or 200 mg·L⁻¹ PBI 429) was based on previous research (Astacio and van Iersel, 2011a, 2011b; Blanchard et al., 2007; Kim and van Iersel, 2011; van Iersel et al., 2009; Waterland et al., 2010a; Weaver and van Iersel, 2014) and allowed for direct comparison between the two compounds at equal concentrations (100 and 200 mg·L⁻¹).

Treatments were applied once the plants reached a marketable size, 24 d after transplanting. Four plants were sprayed with each of the 12 spray solutions using a 59-mL pump-style sprayer (Alberto-Culver USA, Inc., Melrose Park, IL) until all leaf surfaces were covered with a fine layer of mist. Three fully expanded leaves from the upper portion of the canopy were tagged on each plant, and all measurements were taken on these leaves.

Gas exchange. Net photosynthesis and g_s were measured using a portable photosynthesis meter and attached leaf cuvette with a light-emitting diode light source that provided a photosynthetic photon flux density (PPFD) of 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Ciras-2; PP Systems, Amesbury, MA). The reference CO₂ concentration in the leaf cuvette was maintained near 380 $\mu\text{mol}\cdot\text{mol}^{-1}$ during gas exchange measurement. Vapor pressure deficit (VPD) in the leaf cuvette was between 0.4 and 2.1 kPa. Plants were treated with the spray solutions on Day 1 of the study. Measurements were taken 1 d before (Day 0) and after (Day 2) treatment and then twice weekly for the first 4 weeks after application. Sampling frequency was reduced to once a week for the remainder of the 47-d study. Leaf abscission began after Day 15 and introduced bias into the data because the least healthy, most chlorotic leaves abscised. Therefore, only data from the first 15 d of the study are presented. Gas exchange measurements were taken around solar noon to eliminate variation within treatments as a result of circadian rhythms or diurnal fluctuations in photosynthetic activity.

Environmental conditions. Greenhouse environmental conditions were measured using a quantum sensor (Apogee SQ-110; Apogee Instruments, Logan, UT) and temperature and relative humidity sensor (HMP50; Vaisala) connected to a data logger (CR-10; Campbell Scientific, Logan, UT). The daily light integral (DLI) was calculated from the PPFD data, whereas temperature and relative humidity were used to calculate the VPD (summarized in Fig. 1).

Fig. 1. Daily light integral (DLI) and daily minimum and maximum temperature and vapor pressure deficit (VPD) during the first 16 d of the study.

Fig. 2. Leaf chlorophyll over time in pansies as affected by foliar sprays of abscisic acid (ABA, top) or 8'-acetylene methyl-ester abscisic acid (PBI 429, bottom) at a range of concentrations. Significant effects of ABA concentration were first observed 4 d after ABA application (L = linear effect of log(concentration+10); * $P < 0.05$; ** $P < 0.01$; NS = nonsignificant).

Leaf chlorophyll. Leaf chlorophyll content was measured using a leaf chlorophyll meter (SPAD-502; Minolta, Ramsey, NJ) immediately after gas exchange measurement on the same leaves.

Statistics. Plants were arranged in a randomized complete block design. Statistical analysis was performed using SAS (SAS 9.2; SAS Institute, Cary, NC). The data were analyzed separately for each measurement day because of treatment by time interactions and unequal variance over time. Regression analysis was performed after log transformation of the ABA and analog compound concentrations [$\log(\text{concentration}+10)$] to determine rate-dependent effects. Pairwise comparisons were used to compare the effects of ABA and PBI 429 applied at equal concentrations (100 and 200 $\text{mg}\cdot\text{L}^{-1}$).

Because ABA can affect leaf P_n by inducing both stomatal closure and chlorosis, P_n data from Day 0 to 12 were analyzed using correlations with g_s , SPAD readings, VPD, and DLI to determine which factors may have affected P_n . This analysis was followed by stepwise regression to quantify the effects of g_s , SPAD readings, VPD, DLI, and their interactions on P_n . Significant factors were added to the model one at a time using forward selection ($P < 0.05$). The relative importance of the significant factors was determined based on partial R^2 values, which indicate how much of the variation in the P_n data can be explained by the different factors remaining in the model.

Results and Discussion

Leaf chlorophyll. Rate-dependent chlorosis was observed in the ABA-treated plants beginning at 4 d after spray application (Day 5) (Fig. 2). This effect persisted through 47 d after treatment (data not shown). Plants treated with 1000 and 2000 $\text{mg}\cdot\text{L}^{-1}$ ABA had chlorotic stems and leaves and exhibited flower bleaching (not quantified). Exposure to exogenous ABA causes chlorosis in many species (Astacio and van Iersel, 2011b; Blanchard et al., 2007; Kim and van Iersel, 2011; van Iersel et al., 2009; Waterland et al., 2010a; Weaver and van Iersel, 2014). This effect may be the result of ABA-induced ethylene production (Sharp et al., 2000; Zhang et al., 2009), although Waterland et al. (2010b) found that 1-methylcyclopropene (an ethylene action inhibitor) did not prevent ABA-induced chlorosis and suggested that interactions with cytokinins and gibberellins may be responsible. However, the exact mechanism is still unclear. No chlorosis was observed in the plants treated with PBI 429 at any concentration (Fig. 2). A general, but nonsignificant downward trend in leaf chlorophyll was observed in all PBI 429 and control treatments (Fig. 2). This was likely the result of leaf aging (Constable and Rawson, 1980) or root restriction (Dubik et al., 1990).

Stomatal conductance. Both compounds reduced g_s in a concentration-dependent manner (Fig. 3). These effects lasted through Day 8 (though not significant on Day 5) in

the PBI 429-treated plants and through Day 12 in those treated with ABA. The greatest reductions in g_s were observed on the first day (Day 2) after treatment (Fig. 3). Absciscic acid is rapidly absorbed by plant tissue and its effects take place within 1.5 h (Astacio and van Iersel, 2011a). Leaf and root tissue PBI 429 concentrations are highest soon after foliar application and decrease over time (Sharma et al., 2005b).

The g_s for the 0- $\text{mg}\cdot\text{L}^{-1}$ ABA treatments on the day after spray application was 592 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, whereas those treated with 2000 $\text{mg}\cdot\text{L}^{-1}$ had a g_s of 96 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, a reduction of 84%. Plants treated with 100 $\text{mg}\cdot\text{L}^{-1}$ PBI 429 had 34% lower g_s than control plants. In the 200- $\text{mg}\cdot\text{L}^{-1}$ PBI 429 treatments, g_s was 40% lower than control plants. The reduction in g_s observed in the 100- $\text{mg}\cdot\text{L}^{-1}$ ABA treatment was 455 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ or 77%. Thus, the lowest ABA concentration was more effective than any of the PBI 429 treatments (Fig. 3).

Pairwise comparisons of both compounds applied at equal concentrations also indicate that ABA is more effective than PBI 429 at reducing g_s . At the 100- $\text{mg}\cdot\text{L}^{-1}$ concentration, ABA reduced g_s by 216 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (61%) more than the equivalent PBI 429

treatment on Day 2 of the study ($P = 0.01$) and by 212 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (52%) more on Day 5 ($P < 0.05$). In the 200- $\text{mg}\cdot\text{L}^{-1}$ treatments, ABA was more effective than PBI 429 on Day 2 $\times$ 195 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (61%, $P < 0.05$) and by 114 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (55%, $P < 0.01$) on Day 12.

Net photosynthesis. Net photosynthesis was affected in a manner similar to g_s during the first 12 d of the study. Both compounds reduced P_n in a rate-dependent manner (Fig. 4). This is consistent with the idea that a reduction in stomatal aperture will lead to a decrease in P_n by restricting the diffusion of CO_2 into the leaf tissue, thereby limiting the amount of carbon available for photoassimilation (Buckley, 2005; Pantin et al., 2012). No effect on P_n was found in the plants treated with PBI 429 beyond 7 d after treatment (Fig. 4). This corresponds to the duration of the decrease in g_s observed in these plants (Fig. 3). In the ABA-treated plants, P_n was inhibited in a dosage-dependent manner for 14 d (Fig. 4).

Like with g_s (Fig. 3), the greatest decreases in P_n occurred on the day immediately after spray application and in plants treated with the highest concentrations of each compound (Fig. 4). At this time, the plants treated with 2000 $\text{mg}\cdot\text{L}^{-1}$ ABA had P_n 92% lower than the

Fig. 3. Stomatal conductance (g_s) over time in pansies as affected by foliar sprays of abscisic acid (ABA, top) or 8' acetylene methyl-ester abscisic acid (PBI 429, bottom) at a range of concentrations. Significant effects of ABA and PBI 429 concentrations were first observed 1 d after treatment (L = linear and Q = quadratic effect of $\log(\text{concentration}+10)$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = nonsignificant).

control plants and P_n was 41% lower than control plants in the 200-mg·L⁻¹ PBI 429 treatments. The 100-mg·L⁻¹ ABA treatments had P_n 89% lower than control plants, a reduction greater than the 41% decrease induced by the highest PBI 429 concentration (200 mg·L⁻¹; Fig. 4).

Pairwise comparisons showed that ABA was, at times, more effective than PBI 429 when applied at equal rates. In the 100-mg·L⁻¹

treatments, ABA reduced P_n by 87% more than PBI 429 ($P < 0.001$) on Day 2, by 83% more on Day 5 ($P < 0.0001$), and by 71% more on Day 8 ($P < 0.05$). ABA was more effective at the 200-mg·L⁻¹ concentration as well with P_n 49% ($P < 0.05$) lower than PBI 429-treated plants on Day 2, 54% ($P < 0.01$) lower on Day 5, and 49% ($P < 0.05$) lower on Day 12 (Fig. 4). The lack of consistent, significant differences between the effects of ABA and

PBI 429 agrees with recent work by de la Rosa et al., (2014). They found that leaf gas exchange in *Prunus persica* trees is very responsive to drought but that these data also have a large cv, reducing the likelihood of statistical significance.

Environmental conditions, chlorosis, and gas exchange. Variations occurred within all treatments between measurement days for both g_s (Fig. 3) and P_n (Fig. 4) and were correlated with fluctuations in greenhouse DLI (Fig. 1). This suggests that although the internal light source on the leaf cuvette provided a consistent *PPFD*, the resulting measurements were affected by ambient light levels, possibly because leaves did not have sufficient time to adjust to the 1000- $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD* light source. The average measurement time in this study was 5 min. Dark-adjusted leaves take as long as 20 min to achieve maximum stomatal aperture when exposed to a red light source, although stomatal opening occurs much more rapidly when even a very weak (5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) blue light source is also applied (Shimazaki et al., 2007). The Ciras-2 provides *PPFD* using white light-emitting diode (LED)s that emit light over a broad spectrum of wavelengths. Nonetheless, we cannot rule out the possibility that the leaves did not fully adjust to the measurement light. Further research is necessary to determine the influence of ambient light on leaf gas exchange measurements.

Correlation and stepwise regression analysis were used to determine which factors were associated with P_n . Significant correlations existed between P_n and g_s ($r = 0.68$, $P < 0.0001$), VPD ($r = -0.67$, $P < 0.0001$), leaf chlorophyll content ($r = 0.46$, $P < 0.0001$), and DLI ($r = 0.36$, $P < 0.0001$). The correlation between DLI and P_n supports our hypothesis that the leaves did not fully acclimated to the 1000- $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD* light source during gas exchange measurement and may explain why neither P_n nor g_s was affected by PBI 429 on Day 5, when DLI was low. Because VPD does not have a direct effect on P_n , this correlation was likely the result of the effect of VPD on g_s ($r = -0.74$, $P < 0.0001$); high VPD resulted in stomatal closure, which in

Fig. 4. Net photosynthesis over time in pansies as affected by foliar sprays of abscisic acid (ABA) or 8' acetylene methyl-ester abscisic acid (PBI 429) at a range of concentrations. Significant effects of ABA and PBI 429 concentrations were first observed 1 d after treatment (L = linear and Q = quadratic effect of $\log(\text{concentration}+10)$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = nonsignificant).

Fig. 5. The relationship between net photosynthesis (P_n) and stomatal conductance (g_s , left) and leaf chlorophyll content (right) of pansy. Data from all ABA and PBI429 treatments and measurements days are combined in this figure. Note that plants with a high g_s typically have high P_n , whereas low chlorophyll is associated with low P_n .

turn reduced P_n . The correlations among P_n , g_s , and leaf chlorophyll content (Fig. 5) were expected because stomatal closure reduces CO_2 diffusion into the leaf, whereas chlorosis reduces light absorption and is associated with low leaf nitrogen content and photosynthetic capacity (Chapman and Barreto, 1997; Evans, 1989). However, plotting P_n vs. g_s and leaf chlorophyll suggests that the effects of g_s and leaf chlorophyll were not truly linear (Fig. 5). Instead, high g_s was associated with high P_n , but P_n was highly variable at low g_s (less than 400 $mmol\cdot m^{-2}\cdot s^{-1}$). This is likely related to an interactive effect of g_s and DLI on P_n (see below). Conversely, low leaf chlorophyll levels were consistently associated with low P_n , but there was a large range of P_n at high leaf chlorophyll levels. Treatment-induced stomatal closure likely contributed to low P_n on the days immediately after treatment when leaf chlorophyll content had not yet declined.

Stepwise regression indicated that P_n could be described as a function of the interaction between g_s and DLI (partial $r^2 = 0.54$, $P < 0.0001$) and leaf chlorophyll content (partial $r^2 = 0.03$, $P < 0.0001$). The interactive effects of g_s and DLI on P_n further supports our hypothesis that leaves were not fully acclimated to the constant PPFD of the LED light source; P_n was higher on days with high DLI even when g_s was similar.

Over time, g_s and P_n decreased in all treatments including the controls (Figs. 3 and 4). This was likely caused by leaf aging (Constable and Rawson, 1980) as well as shading (Frantz and Bugbee, 2005) because the measured leaves became shaded by new growth as the study progressed. Chlorosis further contributed to the decline in P_n (Fig. 2).

Relation to previous research. Plant responses to both ABA (Waterland et al., 2010a) and PBI 429 (Sharma et al., 2006) are species-specific. Identical PBI 429 treatments are more effective at reducing water use in tomatoes than in marigolds (Sharma et al., 2005b), and inconsistent responses to similar ABA treatments occur in different bedding plant species (Blanchard et al., 2007; Waterland et al., 2010a). Effects also vary depending on the mode and rate of application (Sharma et al., 2005a; Waterland et al., 2010a). Root drenches of PBI 429 are more effective than foliar sprays in tomatoes (Sharma et al., 2005a), and pansies are highly responsive to ABA spray applications, whereas marigolds are affected more by root drenches (Waterland et al., 2010a). Many species exhibit rate-dependent responses to ABA (Astacio and van Iersel, 2011a; Blanchard et al., 2007; Kim and van Iersel, 2011; van Iersel et al., 2009; Waterland et al., 2010a, 2010b; Weaver and van Iersel, 2014) and PBI 429 (Sharma et al., 2005a, 2006; Weaver and van Iersel, 2014); the magnitude of effects is expected to be proportional to the concentration applied for either compound.

Two studies compared ABA and PBI 429 root drench applications in tomatoes (Sharma et al., 2005a, 2006) and showed that PBI 429

was more effective using visual observations and leaf relative water contents in transplanted seedlings (Sharma et al., 2005a) and container weights of seedlings in growth chambers (Sharma et al., 2006). Although these effects were likely caused by a reduction in stomatal aperture, gas exchange was not directly measured (Sharma et al., 2005a, 2006). Additionally, the plants were treated with more highly concentrated PBI 429 solutions (288 to 2881 $mg\cdot L^{-1}$) than those used in our study (Sharma et al., 2005a, 2006). In tomatoes, large and rapid decreases in root hydraulic conductance can occur after ABA drench application and lead to reduced leaf water content and wilting. This ABA-induced wilting is independent of the stomatal response (Astacio and van Iersel, 2011b). The effects of PBI 429 on tomato root system hydraulics have not yet been studied.

We demonstrated that ABA is more effective than PBI 429 at inducing stomatal closure in pansies when applied at the same concentration and volume. Previously, we found that the two compounds have similar effects on evapotranspiration in pansies (Weaver and van Iersel, 2014). These findings seemingly contradict the results of prior research, which demonstrated that PBI 429 is more effective than ABA (Sharma et al., 2005a, 2006). However, it is difficult to make comparisons between our studies and others (Schubert et al., 1991; Sharma et al., 2005a, 2005b, 2006) because of differences in the mode and rates of application, types of measurements, plant species, and the possibility of unobserved effects on root hydraulics.

Conclusions

Spray applications of ABA and PBI 429 reduce g_s and P_n of pansies in a dosage-dependent manner for several days after treatment with the greatest reductions occurring on the day immediately after spray application. When applied at the same rate, ABA more effectively and persistently inhibits gas exchange than PBI 429. Foliar ABA application also causes rate-dependent leaf chlorosis, which likely contributes to a prolonged reduction in P_n , even after ABA effects on g_s have dissipated and may negatively affect plant marketability and performance. Although it was found to be less potent, PBI 429 is a more practical holding agent than ABA for pansies because it is effective at causing a short-term reduction in g_s with no observed phytotoxic side effects.

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