Inadequate watering during retail diminishes the salability and shelf life of plants (Armitage, 1983), resulting in economic losses for growers and/or retailers. One way to reduce water use and extend the shelf life of plants in retail settings is by the application of exogenous ABA (Barrett and Campbell, 2006), although the duration of the effects is dependent on species, application rate, and application method (Blanchard et al., 2007; Kim and van Iersel, 2011; Sharma et al., 2006; van Iersel et al., 2009; Waterland et al., 2010a, 2010b). The effects of ABA can be profound and have commercial implications. Until recently, use of ABA was cost-prohibitive for horticultural applications and relegated to research. However, breakthroughs in microbiology have made it possible to produce ABA at much lower costs (Petracek et al., 2005) and Valent BioSciences registered ABA as a plant growth regulator for use on ornamental plants with the U.S. Environmental Protection Agency in 2010 (Runkle, 2009). As such, there is potential for the use of ABA as a plant growth regulator in commercial horticulture, although there are still questions of possible phytotoxic responses and deleterious long-term effects (Abrams et al., 1997; Kim and van Iersel, 2011; Waterland et al., 2010b), including flower abscission (Barrett and Bartuska, 2011). ABA is known to affect a myriad of plant processes, including stomatal conductance. In addition, the plants in the second study were to examine the short-term effects of ABA applications of ABA increase the shelf life of bedding plants has recently been examined with encouraging results. When ABA (250 mg L\(^{-1}\)) is applied as a sprench (spraying the leaves and allowing the excess solution to moisten the substrate), the shelf life of ‘New Guinea’ impatiens (Impatiens balsamina L.) is prolonged by almost 6 d, although the same rate extends the shelf life of verbena (Verbena hybrida) by only 1 d (Blanchard et al., 2007). Other studies have found that drench applications of ABA increase the shelf life of hydrangea (Hydrangea macrophylla) by up to 11 d (van Iersel et al., 2009) and of salvia (Salvia splendens) by up to 5 d (Kim and van Iersel, 2011), depending on the rate. Work on six different annual bedding plants found that a 500-mg L\(^{-1}\) ABA drench increases shelf life of marigold (Tagetes patula) by 3 d and is more effective than a foliar spray of the same rate. On the other hand, pansy (Viola ×wittrockiana) responds better to a spray than a drench application, demonstrating that application method is as important of a consideration as rate (Waterland et al., 2010a). However, there are still questions about exogenous ABA on plant water use such as its effects on ET and how quickly it affects leaf gas exchange. In addition, the plants in the studies mentioned previously were all subjected to drought stress. Little work has been done comparing the effects of ABA on well-watered plants. We conducted two studies to quantify the effects of ABA drenches on tomato. Tomatoes were used as the model crop because they are responsive to ABA applications (Sharma et al., 2006). The objectives of the first study were to evaluate the effects of exogenous ABA on the ET of drought-stressed and well-watered tomatoes and to quantify how ABA affects the time to wilting. The objectives of the second study were to examine the short-term effects of ABA drenches on \(g_s\), \(E\), and \(P_n\) of tomato.
Materials and Methods

Evapotranspiration and shelf life. Tomatoes ‘Sweeter 100’ were seeded in 72-cell trays and grown on an ebb and flow bench providing a nutrient solution containing 100 mg L\(^{-1}\) nitrogen (15-5-15 Cal-Mag; Scotts, Marysville, OH; 15N–2.2P–12.45K) for 20 d. Seedlings were transplanted on 10 Sept. 2009 into 10-cm round pots filled with soilless substrate (Fafard 2P; Conrad Fafard Inc., Agawam, MA) and grown on the load cell system (see subsequently) in a glass greenhouse at the University of Georgia in Athens, GA. The tomatoes were fertilized with 2.6 g/plant of controlled-release fertilizer (Osmocote14-14-14, Scotts; 14N–6.16P–11.62K) as a top dressing and watered by hand daily. A data logger (CR10; Campbell Scientific Inc., Logan, UT) recorded environmental conditions using a quantum sensor (QSO-sun; Apogee Instruments, Logan, UT) and a temperature and humidity sensor (HMP50; Vaisala, San Jose, CA). Daily minimum and maximum temperatures were 18.9 ± 2.7 and 26.0 ± 5.2 °C, minimum and maximum vapor pressure deficit were 0.168 ± 0.09 and 0.953 ± 0.858 kPa, and daily light integral was 11.8 ± 4.3 mol m\(^{-2}\) d\(^{-1}\) (mean ± sn in the period before the ABA treatments.

ABA stock solution (10% w/w s-ABA, the biologically active form of ABA, VBC-30101; Valent BioSciences, Libertyville, IL) was diluted with deionized water to yield concentrations of 0, 62.5, 125, 250, 500, and 1000 mg L\(^{-1}\). This range of concentrations was chosen based on prior research that showed high efficacy at concentrations of 250 to 2000 mg L\(^{-1}\), although concentrations higher than 1000 mg L\(^{-1}\) resulted in significant leaf abscission in annual salvia (Salvia splendens; (Kim and van Iersel, 2011)). ABA applications were made on 13 Oct. 2009, ≈1 month after transplanting. The tomatoes were watered to the runoff point the next afternoon as well as the previous day. ABA solution applied to the substrate surface. ABA was applied in 1-mL aliquots. Substrate moisture was maintained at 50% for the well-watered plants and 25% for the unwatered plants

To collect gas exchange data, the cuvette of a portable leaf photosynthesis system (Ciras-2; PP Systems, Amesbury, MA) was clamped onto the uppermost, fully expanded leaf of a plant before treatment and leaf gas exchange was recorded every 5 min. Once stable readings were achieved and pretreatment data were gathered for 3 h. Plants were drenched with 100 mL of deionized water or 250 mg L\(^{-1}\) ABA solution made from ABA stock solution (VBC-30101; Valent BioSciences). This concentration was chosen based on the results from the ET and shelf life study to minimize the risk of negative side effects of the ABA while being effective in reducing ET.

Two plants (one ABA treatment and one control) were measured per day over the course of 11 d (8 Feb. through 18 Feb. 2011). A total of five replications (two treatments × five replications) were used, although stable readings were not achieved for one ABA-treated plant, resulting in only four usable replications for this treatment. To determine instantaneous water use efficiency (WUE), \(P_e\) was divided by \(E\). Leaf gas exchange data were normalized by expressing them as a percentage of the pretreatment rate and analyzed by analysis of variance (SAS 9.2; SAS Institute, Cary, NC).

Results and Discussion

Evapotranspiration and shelf life. Cumulative ET increased over time in a stepwise manner, because the plants used more water during the day than at night, when the stomata are closed and the vapor pressure deficit is smaller (Fig. 2). ABA-treated plants had lower ET than control plants, indicating that ABA caused stomatal closure, limiting transpiration water loss. A reduction in the cumulative ET of the unwatered, ABA-treated plants was apparent within 1.5 h (\(P = 0.007\)) and similar differences were seen in the well-watered plants starting 4.5 h after ABA application (\(P < 0.03\); Fig. 2). ABA effects on cumulative ET remained significant throughout the remainder of the study, both in the unwatered and well-watered treatments (\(P < 0.001\)). By the end of the second day after ABA application, unwatered control plants had used 82 mL of water, plants treated with 62.5 mg L\(^{-1}\) ABA had used 74 mL, and plants treated with 125 to 1000 mg L\(^{-1}\) ABA had used only 49 to
Fig. 2. Cumulative evapotranspiration of tomato during a 13 d period as affected by 100-mL drenches with different concentrations of ABA. Plants were either well-watered (top) or unwatered (bottom) after ABA application and changes in weight were recorded using load cells connected to a data logger. Significant effects of ABA drenches on cumulative ET were first noted 4.5 h after ABA application in the well-watered plants ($P < 0.03$) and 1.5 h after ABA application in the unwatered plants ($P < 0.007$) and persisted throughout the remainder of the study. Data represent the mean ± SE ($n = 2$). ABA = abscisic acid; ET = evapotranspiration.

41 mL (Fig. 2, bottom). By Day 8, the control plants had used most of the available water (301 mL) and were wilting, whereas the ABA-treated plants were still transpiring as a result of remaining water availability in the substrate (Fig. 2). Compared with the unwatered plants, cumulative ET after 13 d was much higher in the well-watered control plants (567 mL) than in the unwatered controls (335 mL, 41% less) (Fig. 2). Differences in cumulative ET between unwatered and well-watered plants were smaller for ABA-treated plants, e.g., 365 mL versus 293 mL (20% less) for the well-watered and unwatered plants treated with 1000 mg L$^{-1}$ (Fig. 2).

The reduced water use of the ABA-treated plants shows that ABA effectively closed stomata, limiting E. This is consistent with previous reports (Jiang and Hartung, 2008; Kim and van Iersel, 2011; Walton, 1980; Waterland et al., 2010c), which indicated that ABA limits $g_s$. Walton (1980) reported that ABA levels in leaves were inversely related to stomatal aperture but concluded that ABA levels alone are not a great indicator of $g_s$, because only a portion of ABA in the leaves is involved with regulating stomata (Walton, 1980). We found that ABA drenches reduced water use quickly (within 1.5 h) and there was a clear relationship between the ABA concentration of the drench solution and cumulative ET for both the unwatered and well-watered treatments, suggesting that ABA levels are correlated with stomatal closure. This inverse relationship between cumulative ET and ABA concentration was to be expected, because ABA is largely responsible for limiting $g_s$ by controlling ion flux in and out of guard cells (Walton, 1980) and Kim (2011) showed that there was a strong relationship between leaf ABA concentrations and $g_s$ of petunia (Petunia ×hybrida). Because we applied ABA as a drench, these results also indirectly corroborate the conclusions of Jiang and Hartung (2008) that ABA is transported from the roots through the xylem to the leaf tissue and we have since found that ABA drenches increase leaf ABA concentrations of tomato in a dose-dependent manner (Astacio and van Iersel, 2012).

The ABA concentration also affected daily ET with the unwatered control plants using 35 mL on the first full day after ABA application, plants in the 62.5 mg L$^{-1}$ ABA treatment using only 25 mL, and higher ABA concentrations reducing daily ET even more, to 15 to 18 mL (Fig. 3, bottom). On Day 3, the daily ET of the unwatered control plants was 45 mL, whereas the ABA-treated plants used 27 to 28 mL. Unwatered control plants had higher daily ET than unwatered, ABA-treated plants during the first 5 d, but on Day 6, daily ET of the unwatered control plants dropped sharply and the plants started to wilt. Daily ET started to decrease on Day 7 in the unwatered 62.5 mg L$^{-1}$ ABA treatment and on Day 8 for the unwatered 125 and 250 mg L$^{-1}$ ABA treatments (Fig. 3, bottom), indicating the onset of drought stress. From Day 9 to 12, daily ET was highest with the highest ABA concentrations (500 to 1000 mg L$^{-1}$ ABA), presumably because these treatments had the most water left. These findings are similar to those reported by Kim and van Iersel (2011), who found that ABA drenches slowed water loss from the substrate with the substrate volumetric water content of the control treatments dropping to 0.1 m$^3$ m$^{-3}$ after 2 d, whereas the 1000- and 2000-mg L$^{-1}$ plants reached 0.1 m$^3$ m$^{-3}$ after 8 and 9 d, respectively. In addition, van Iersel et al. (2009) reported that hydrangeas not treated with ABA used 50% of the available water within 7 d, whereas the substrate of plants treated with 500 and 1000 mg L$^{-1}$ ABA still had 80% and greater than 90% of the plant available water left, respectively, at this time. Waterland et al. (2010c) showed that ABA drenches reduced $g_s$ of drought-stressed chrysanthemum (Chrysanthemum ×morifolium) at 1 d after the ABA drench, but $g_s$ was very low (less than 50 mmol m$^{-2}$ s$^{-1}$) in both control and ABA-treated plants after 3 d. The effect of ABA on $g_s$ presumably disappeared after 3 d because control plants had used most of the available water in the substrate, thus inducing drought stress and stomatal closure, whereas ABA-treated plants had low $g_s$ as a result of the ABA application. The exact duration of ABA-induced reductions in ET is likely to depend on species, ABA concentration and application method, plant water use (e.g., plant size, environmental conditions), and the amount of water available in the substrate at the time of ABA application (e.g., container size, substrate properties).

In the well-watered treatments, ABA reduced daily ET in a dose-dependent manner through Day 5, consistent with the report by Petracek et al. (2005). Water use was similar in all treatments after Day 5, suggesting that the ABA might have lost its effectiveness. Likewise, Waterland et al. (2010c) found that $g_s$ of well-watered chrysanthemum was reduced at 1 and 3 d after ABA drenches but that $g_s$ of ABA-treated plants was similar to that of control plants at 9 d after ABA application. This is likely the result of exogenous ABA in the plants being catabolized. The half-life of ABA in tomato was reported to be only 7 h (Zeevaart and Creelman, 1988). This rapid catabolism of ABA helps explain the importance of ABA dose on the longevity of the response. Treating plants with greater doses of ABA results in higher leaf tissue concentrations of
ABA (Astacio and van Iersel, 2012) and it would therefore take longer for enough ABA to be catabolized for concentrations to drop to levels where they no longer reduce \( g_s \). Generally, ABA drenches delayed wilting in unwatered plants longer as ABA concentration increased \((P < 0.0001)\). Control plants wilted after 6 to 7 d, whereas the plants treated with 62.5 mg L\(^{-1}\) ABA wilted after 9 d and plants treated with 500 and 1000 mg L\(^{-1}\) ABA after 13 to 15 d (Fig. 4). The time to wilting was prolonged by overcast weather on Days 2, 3, and 5, shortly after the ABA applications (Fig. 1). Wilting was only noted in the unwatered plants; well-watered plants did not wilt. Similar results of shelf life extension were also described for salvia and hydrangea after ABA applications (Kim and van Iersel, 2011; van Iersel et al., 2009) as well as a variety of bedding plants (Blanchard et al., 2007; Sharma et al., 2006; Waterland et al., 2010a, 2010c). These and other studies have found that exogenous ABA can extend the shelf life of common bedding plants from 1 d in the case of verbena (Blanchard et al., 2007), 4 d for chrysanthemum (Waterland et al., 2010c), 4.3 d for petunia (Waterland et al., 2010a), and up to 11 d for hydrangea (van Iersel et al., 2009). In addition, van Iersel et al. (2009) reported that ABA drenches reduced \( g_s \) of unwatered hydrangea for 9 d. We found similar results with tomato, in particular with the well-watered plants in which ABA reduced daily ET for 5 d, after which ABA lost its efficacy (Fig. 3, top). Foliar chlorosis and leaf abscission were negative side effects of the ABA treatments (results not shown). Chlorosis of lower leaves of plants treated with 250 to 1000 mg L\(^{-1}\) was first noted 2 d after ABA applications, and leaf abscission occurred after 4 or 5 d, after which abscission tapered off. Chlorosis has been frequently mentioned as a side effect of high doses of ABA (Blanchard et al., 2007; Kim and van Iersel, 2011; van Iersel et al., 2009; Waterland et al., 2010b). Symptoms were more severe with higher ABA concentrations, which was also reported when salvia (Kim and van Iersel, 2011), hydrangea (van Iersel et al., 2009), or pansy (Waterland et al., 2010b) was treated with high levels of exogenous ABA. Because leaf abscission reduces leaf area, this may further reduce plant water use and delay wilting in addition to the direct effects of ABA on \( g_s \).

**Short-term gas exchange responses.** ABA drenches quickly and effectively closed stomata and limited transpirational water loss. Significant reductions in \( E, g_s, \) and \( P_n \) were seen 55 to 60 min after ABA application \((P < 0.05; \text{Fig. 5})\). After 2 h, ABA reduced \( E, g_s, \) and \( P_n \) by 66%, 72%, and 55% respectively, compared with the control plants (Fig. 5). These reductions continued until the end of the 3-h study, when ABA reduced \( E, g_s, \) and \( P_n \) by 71%, 77%, and 61%, respectively, compared with control plants (Fig. 5). A rapid physiological response to ABA is consistent with the findings that ABA drenches (250 to 2000 mg L\(^{-1}\)) reduced \( g_s \) and \( E \) of salvia within 3 h (Kim and van Iersel, 2011) and that \( g_s \) of hydrangea was negatively correlated with ABA concentration within 1 d after treatment (van Iersel et al., 2009). Boldt (2008) used split-root systems to determine how the duration of root exposure to ABA affected \( g_s \) of well-watered chrysanthemum and found that an exposure as short as 7.5 min was enough to induce stomatal closure within 4 h. Walton (1980) reported that there was a 50% increase in ABA within 30 min after water stress was initiated, indicating that endogenous ABA levels can fluctuate quickly in response to stress.

ABA tended to increase WUE with the ABA-treated plants having a 28% higher WUE than control plants, although the difference...
was never significant ($P \geq 0.086$; Fig. 5). However, the data suggest that ABA-induced stomatal closure increases WUE. This concept has found practical applications in horticulture. For example, plants can be stimulated to produce ABA by implementing partial root zone drying, which involves exposing part of the root system to dry soil. The resulting increase in endogenous ABA induces stomatal closure and increases WUE (Davies et al., 2002). This raises the question of whether WUE can be increased using exogenous ABA applications as well.

The effect of the ABA applications on $E$ and $g_s$ is consistent with previous reports that ABA is largely responsible for controlling $g_s$, which in turn greatly affects $E$ (Kim and van Iersel, 2011; Walton, 1980) and photosynthesis (Franks and Farquhar, 2001; Liang et al., 1997). Reductions in $g_s$, resulting from drought stress can in turn lead to reduced $P_n$ (Farquhar and Sharkey, 1982). Liang et al. (1997) reported that drought-stress-induced ABA increases led to the reduction of both $g_s$ and $P_n$ of two tropical tree species over a period of 4 d and that recovery to pre-stress rates after rewetting is species-dependent, because only one of the tree species was able to fully recover. Furthermore, other research examined the effect of injecting ABA into the petioles of attached soybean (Glycine max) leaves and found that quantum yield and photosynthetic capacity were significantly reduced (Ward and Bunce, 1987). Conversely, Franks and Farquhar (2001) treated half of the Tradescantia virginiana plants in the study with 793 mg L$^{-1}$ ABA solution for 13 d and reported that photosynthetic capacity was not significantly affected, although the ABA-treated plants had lower $g_s$ and higher WUE. They concluded that studies in which photosynthesis appears to be diminished could be the result of patchy distribution of stomatal regulation by ABA and that many studies that have reported lower $P_n$ rates after ABA treatment were done in the short-term, whereas their experiment was conducted over the long-term (Franks and Farquhar, 2001). These conclusions are supported by Bradford et al. (1983), who found that long-term treatment with 2.6 and 7.9 mg L$^{-1}$ ABA solution as a spray had marginal effects on photosynthesis of tomato. Our findings indicate that ABA has a clear limiting effect on $g_s$ and $P_n$, although future studies will be necessary to fully elucidate the role of ABA in limiting $P_n$ and specifically the role of stomatal versus non-stomatal factors, because findings are still controversial.

**Conclusions**

The use of ABA as a commercial means to extend the shelf life of retail plants shows promise. Leaf gas exchange measurements indicated that ABA drenches closed stomata and reduced transpiration within 1 h of the application. Daily ET of well-watered plants was reduced by ABA drenches for 5 d, whereas ABA delayed wilting and extended the shelf life of unwatered plants by 2 to 8 d, depending on the ABA concentration. This effect would be beneficial in extending the salability of retail plants. Negative side effects of the ABA drenches, chlorosis and leaf abscission, were noted and generally became more pronounced as ABA concentration increased. The lowest effective rate of ABA should be applied to extend shelf life without imposing side effects.

**Literature Cited**


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