

Growth Reductions by Exogenous Abscisic Acid Limit the Benefit of Height Control in Diploid and Triploid Watermelon Transplants

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Abstract. Height control is important to produce compact vegetable transplants that are suitable for shipping and transplanting. Although abscisic acid (ABA) inhibits stem elongation, it can also induce other growth modifications. To optimize its application timing for effective height control, we examined age-dependent sensitivity of various growth variables to ABA in diploid ‘Summer Flavor 800’ and triploid ‘Summer Sweet 5244’ watermelon [*Citrullus lanatus* (Thunb.) Matsum & Nakai]. Seedlings were sprayed once with 1.9 mM ABA at 25, 18, or 11 days before transplanting (DBT) or twice with 0.95 mM ABA at 25 and 18 DBT. The application rate was 0.55 mg ABA per plant with a spray volume of 0.61 L·m⁻² (1.1 mL/plant). Only the single-spray treatment at 25 DBT (cotyledon stage) suppressed plant height by inhibiting petiole elongation. This effect was similar in both cultivars with 13% to 14% reductions at the transplanting stage compared with the untreated control. Undesirable growth modifications were also induced by ABA. In both cultivars, all ABA treatments caused 16% to 23% shoot biomass reductions mainly by inhibiting leaf expansion. Additionally, ABA treatments reduced stem diameter and root biomass in ‘Summer Flavor 800’. The double-spray treatment had similar growth-modulating effects as the single-spray treatments, except that it induced cotyledon abscission in ‘Summer Flavor 800’. These results suggest that although ABA applied at the cotyledon stage can reduce watermelon transplant height, the benefit is limited because of overall growth reductions, which can occur regardless of application timing. On the other hand, in triploid ‘Summer Sweet 5244’, moderate shoot growth delay by ABA may be of value as a growth-holding strategy when transplanting is delayed because of inclement weather at the time of field establishment. Importantly, field evaluations demonstrated that the growth modulation by ABA is only transient with no negative impact on marketable yield and fruit quality.

Vegetable transplant production in high-density plug trays can induce excessive stem elongation as a result of shade avoidance responses (Marr and Jirak, 1990; Smith, 1994). The resulting spindly transplants are generally considered unsuitable for shipping and transplanting, because they are susceptible to damage during these operations (Garner and Björkman, 1996; Shaw, 1993) and to wind damage in the field (Garner and Björkman, 1999; Latimer and Mitchell, 1988). Consequently, their field establishment can be

slow and non-uniform, potentially delaying early harvest and limiting marketable yield.

Height control is important for producing compact and high-quality vegetable transplants. Although several gibberellin inhibitors such as daminozide, paclobutrazol, and uniconazole are commercially used to produce compact plants in ornamentals and flowers (Gibson and Whipker, 2001; Whipker et al., 2000), they tend to have long-term growth inhibitory effects (Cantliffe, 1993; Latimer, 1991) and only uniconazole is currently registered for vegetable crops. Furthermore, the approved vegetables are limited mostly to solanaceous crops, including eggplant (*Solanum melongena* L.), pepper (*Cap-sicum annuum* L.), and tomato (*Solanum lycopersicum* L.). Alternatively, stem elongation can be reduced by mechanical stimulation such as brushing the upper canopy, shaking, and vibration by wind or forced aeration (Baden and Latimer, 1992; Björkman, 1999; Garner and Björkman, 1997). These mechanical conditioning methods inhibit stem elongation by stimulating ethylene production, which in turn inhibits cell elongation and promotes stem thickening (Hiraki and

Ota, 1975; Zarembinski and Theologis, 1994). However, their commercial application is limited by high costs of automation and labor (Latimer, 1998).

Abscisic acid can act as a physiological inhibitor of stem elongation in some vegetable transplants, including pepper, eggplant, tomato, and cucumber (*Cucumis sativus* L.) (Biai et al., 2011; Latimer and Mitchell, 1988; Yamazaki et al., 1995). In contrast to gibberellin inhibitors, ABA can be rapidly inactivated in plant tissues by oxidation or conjugation (Davies and Jones, 1991), suggesting that it may be more suitable for vegetable transplants because of its transient growth-inhibitory effects. The potential of ABA as a height control agent has been evaluated mainly in bell pepper seedlings. For example, Leskovar and Cantliffe (1992) reported that the concentration effect of ABA on stem elongation was quadratic with height suppression occurring above 10 μM. Biai et al. (2011) suggested that the effectiveness of height control by ABA is age-dependent and that ABA application should be initiated at the cotyledon stage. However, this recommendation is based solely on plant height, although other growth components are also known to be affected by ABA (Taiz and Zeiger, 2010). Moreover, high-dose applications of ABA have negative side effects such as leaf chlorosis and abscission (Agehara and Leskovar, 2012; Kim and van Iersel, 2011; Waterland et al., 2010). Therefore, the overall growth modification must be considered to further optimize ABA application methods for height control.

Seedless (triploid) watermelon is generally the most expensive vegetable to produce transplants, mainly because of the high cost of seeds, low seedling vigor (Grange et al., 2003), and extra care required for transplant production (Vavrina, 2002). Nonetheless, this highly valuable crop has been neither approved for the use of uniconazole, the only growth regulator currently available for height control of vegetable transplants, nor tested for ABA responses. The first objective of this study is, therefore, to examine the age-dependent sensitivity of various growth variables to ABA in diploid and triploid watermelon seedlings under greenhouse conditions. This information will be useful to determine the optimal application timing for the most effective height control. The second objective is to evaluate if the advantages of height control in ABA-treated transplants would be translated in improved field performance.

Materials and Methods

Plant material. Seeds of two major watermelon cultivars in Texas, diploid ‘Summer Flavor 800’ and triploid ‘Summer Sweet 5244’ (Abbott & Cobb, Feasterville, PA), were sown on 16 Feb. 2010 in a polystyrene tray with 128 inverted pyramid cells each containing 35 mL of Peat-lite mix (Speedling Peat-lite; Speedling, Sun City, FL). Seedlings were grown in a commercial nursery greenhouse (Speedling, Alamo, TX) until they reached

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the optimal size for transplanting according to the nursery's commercial standard (typically 13 to 15 cm). Average daily air temperature during seedling growth ranged from 9 to 26 °C.

Treatments. There were five treatments for each cultivar: no spray control, three timings of a single spray with 1.9 mM (500 mg·L⁻¹) ABA, and one treatment of a double spray with 0.95 mM (250 mg·L⁻¹) ABA. The single spray was performed at 25, 18, or 11 DBT (17, 24, or 31 d after sowing), and the double spray was performed at 25 and 18 DBT. Seedlings had fully expanded cotyledons with one or two immature true leaves at the time of the first ABA application. Spray volume was set at 0.61 L·m⁻² (1.1 mL/plant), which wetted the leaves thoroughly to the dripping point. The application rate was 0.55 mg ABA per plant in all ABA treatments. We selected the spray concentration and volume based on our previous study that characterized growth-modulating effects and phytotoxicity of ABA in muskmelon seedlings over a range of concentrations from 0.24 to 7.57 mM (Agehara and Leskovar, 2012).

The formulation of ABA stock solution was VBC-30151 (Valent BioSciences, Libertyville, IL) containing 10% of S-ABA, a naturally occurring active form in plants. Test solutions were prepared immediately before each treatment by diluting the stock solution with irrigation water at the nursery. CapSil (Aquatrols, Paulsboro, NJ) was added at 0.05% (v/v) as an adjuvant according to the manufacturer's protocol (Valent BioSciences), which showed no significant effect on transplant growth in our preliminary experiment.

A CO₂-pressurized backpack sprayer (Model T; Bellspray, Opelousas, LA) was used to spray the ABA solutions evenly over the seedlings between 1000 and 1100 hr. The sprayer was equipped with three flat-fan nozzles (TP8002VS; TeeJet Technologies, Wheaton, IL) and a CO₂ cylinder with pressure maintained at 276 kPa.

Transplant growth measurements. All measurements were made at 25, 18, 11, and 1 DBT. Non-destructive measurement variables include stem and shoot height, petiole length, and leaf chlorophyll index, and destructive measurement variables include stem diameter, leaf number, leaf area, and shoot and root dry weight.

Six plants per replication (tray) were randomly selected before the first measurement. All non-destructive measurements were made repeatedly on the selected plants between 0800 and 1000 hr on each day. Stem height was measured from the medium surface to the shoot apex, and shoot height was measured up to the highest leaf tip by stretching the leaves. The length of the longest petiole was measured from the node to the leaf attachment point. Relative stem elongation rate (RSER, mm·cm⁻¹·d⁻¹) was calculated as follows:

$$RSER = (\ln H_2 - \ln H_1) / (t_2 - t_1) \times 10$$

where $\ln H_1$ and $\ln H_2$ are the natural logarithm of stem height (cm) at time one, t_1 , and time two, t_2 , respectively.

Leaf chlorophyll index was measured using a chlorophyll meter (SPAD-502; Konica Minolta Sensing, Tokyo, Japan) on two leaves differing in maturity, the youngest fully open leaf and the largest leaf. Two readings were taken per leaf on a leaf lamina between major leaf veins.

At each measurement time, three plants per replication were randomly sampled and roots were washed to remove the growth medium. Stem diameter was measured immediately below the cotyledonary node using a digital caliper (Absolute Digimatic Caliper Series 500; Mitutoyo, Kawasaki, Japan). The number of cotyledons and true leaves with unfolded laminae and visible petioles was counted. Leaf area was measured using an LI-3100 area meter (LI-COR, Lincoln, NE). Shoots and roots were separated and dried at 65 °C for 72 h to determine dry weight.

Field experiment. One day before transplanting, the seedling trays were transported in an enclosed trailer to the Texas A&M AgriLife Research and Extension Center in Uvalde, TX. Soil at the site was an Uvalde silty clay loam (fine-silty, mixed, hyperthermic Aridic Calcicustolls). At pre-plant, the surface (top 18 cm) soil had pH of 7.6, organic matter of 26 g·kg⁻¹, and high available macronutrient (phosphorus, potassium, and magnesium) levels (greater than 63 mg·kg⁻¹), according to soil tests by the Soil, Water and Forage Testing Laboratory at Texas A&M University in College Station, TX.

Seedlings were transplanted on raised beds (20 cm high and 1.6 m wide) in one row per bed on 30 Mar. 2010. A semiautomatic transplanter (RTME1100; Renaldo Sales

& Service, North Collins, NY) was used to control planting depth at the cotyledonary node with 91 cm-in-row spacing. Each plot was an 11-m long single row with 12 plants. There were 480 plants in total with a 1:1 diploid-to-triploid ratio, providing sufficient pollenizers (diploid watermelon) for optimum pollination of triploid watermelon plants. Pollinator bees were not used because native bees generally provide adequate pollination at the experiment site. All plots were irrigated through drip tapes (T-Tape 508-12-340; John Deere, Moline, IL) installed at 10-cm depth in the center of each bed. The drip tapes had emitters spaced 30 cm apart with a flow rate per emitter of 0.77 L·h⁻¹. Fertilizers at 80N-45P-17K kg·ha⁻¹ were applied in five split applications through the subsurface drip system. Standard pest management practices for watermelon were followed.

All field measurements were made repeatedly on the same plants (four plants per plot) from establishment to early harvest. Vine length was measured from the soil surface to the shoot apex. Leaf chlorophyll index was measured using the same method used in the greenhouse. Seedling survival was determined on a plot basis using all plants.

Fruits were harvested on 1 and 14 July and graded based on the U.S. Dept. of Agriculture (USDA) grade standards (USDA, 2006). Marketable fruits were at least U.S. No. 1 grade with a minimum size of 4.54 kg. Other fruits were graded as unmarketable fruit. Number and fresh weight of marketable and unmarketable fruits were determined. Among the marketable fruits harvested on 1 July (peak harvest), three fruits per plot were sampled

Table 1. Stem and shoot height of diploid 'Sumer Flavor 800' and triploid 'Summer Sweet 5244' watermelon seedlings as affected by abscisic acid (ABA) applied as a single high dose at different growth stages or repeated low doses.^z

Cultivar	Treatment ^y	Stem ht (cm)				Shoot ht (cm)
		DBT				
		25	18	11	1	1
SF 800	Control	1.97	3.14 a ^w	3.43 a	3.96	15.7 a
	11 DBT (1.9 mM)	—	—	—	3.85	15.9 a
	18 DBT (1.9 mM)	—	—	3.32 ab	3.96	15.7 a
	25 DBT (1.9 mM)	—	2.44 b	3.13 b	3.58	13.5 b
	25 + 18 DBT (0.95 mM)	—	2.90 a	3.33 ab	3.77	15.0 ab
Orthogonal contrasts ^x		P value				
	Control vs. ABA	—	—	—	0.226	0.168
	ABA × 1 vs. × 2	—	—	—	0.860	0.934
SS 5244	Control	2.41	3.67a	3.93 a	4.22	14.0 a
	11 DBT (1.9 mM)	—	—	—	4.16	14.3 a
	18 DBT (1.9 mM)	—	—	3.91 ab	4.20	13.1 ab
	25 DBT (1.9 mM)	—	2.90 c	3.56 b	3.67	12.2 b
	25 + 18 DBT (0.95 mM)	—	3.36 b	3.85 ab	4.17	12.8 ab
Orthogonal contrasts		P value				
	Control vs. ABA	—	—	—	0.286	0.096
	ABA × 1 vs. × 2	—	—	—	0.341	0.488

^zStem height was measured from the medium surface to the shoot apex, and shoot height was measured up to the highest leaf tip by stretching the leaves.

^yTreatments were as follows: no spray control, three timings of a single spray with 1.9 mM ABA, and one treatment of a double spray with 0.95 mM ABA. In all treatments, the application rate was 0.55 mg ABA per plant with the spray volume of 0.61 L·m⁻² (1.1 mL/plant).

^xOrthogonal contrasts tested two hypotheses: control vs. all ABA treatments (control vs. ABA) and all single-spray treatments vs. double-spray treatment (ABA × 1 vs. × 2).

^wFor each cultivar, least squares means (n = 4) in a column with the same letter are not significantly different (Tukey-Kramer test, P < 0.05).

SF 800 = Sumer Flavor 800; SS 5244 = Summer Sweet 5244; DBT = day before transplanting.

and cut transversely along the equator for quality assessment. Mesocarp firmness was measured using a digital force meter (DFM10; AMETEK, Largo, FL) with an 11-mm diameter round-head probe. Soluble solids content was measured using a digital refractometer (PR-101; Atago, Tokyo, Japan) on unfiltered juice squeezed from the mesocarp tissue. Three and two readings were taken per fruit for firmness and soluble solids content, respectively.

Statistical design and analysis. In the greenhouse, five treatments for each cultivar were replicated four times with one tray per replication in a completely randomized block design. The same experimental design was used in the field. The two cultivars could not be compared at the same development stage because of relatively slow germination and early seedling growth of ‘Summer Sweet 5244’, which are typical to triploid watermelon (Grange et al., 2003; Hodges, 2007).

Consequently, the two cultivars were analyzed separately.

All data analyses were run in SAS (Version 9.2; SAS Institute, Cary, NC), and *P* values less than 0.05 were considered statistically significant. Treatment effects were tested using the restricted maximum likelihood method with the DDFM=KR option in the MIXED procedure. Pre-treatment data were included as covariates. Two additional tests were run in the MIXED procedure: the Tukey-Kramer test for multiple comparisons of least squares means and orthogonal contrasts for testing two specific hypotheses. First, we hypothesized that all ABA treatments have equivalent growth-modulating effects, thereby comparing the control with the pooled ABA treatments. Second, we hypothesized that ABA has different effects based on whether it is applied once at 1.9 mM or twice at 0.95 mM, thereby comparing the pooled single-spray treatments with the double-spray treatment. When heteroscedasticity was indicated by a likelihood ratio test, the MIXED procedure was run with the GROUP option in the REPEATED statement.

To assess the linear association between two dependent variables, the data were fit to a simple linear regression model using the REG procedure. The association was considered nonsignificant when the slope was not significantly different from zero.

Table 2. Relative stem elongation rate (RSER) of diploid ‘Sumer Flavor 800’ and triploid ‘Summer Sweet 5244’ watermelon seedlings as affected by abscisic acid (ABA) applied as a single high dose at different growth stages or repeated low doses.

Cultivar	Treatment ^z	RSER (mm·cm ⁻¹ ·d ⁻¹)		
		25–18	18–11	11–1
SF 800	Control	0.66 a ^y	0.14 bc	0.14
	11 DBT (1.9 mM)	—	—	0.11
	18 DBT (1.9 mM)	—	0.06 c	0.17
	25 DBT (1.9 mM)	0.35 b	0.35 a	0.13
	25 + 18 DBT (0.95 mM)	0.54 a	0.20 b	0.12
SS 5244	Control	0.59 a	0.11 bc	0.07
	11 DBT (1.9 mM)	—	—	0.05
	18 DBT (1.9 mM)	—	0.07 c	0.10
	25 DBT (1.9 mM)	0.27 c	0.29 a	0.05
	25 + 18 DBT (0.95 mM)	0.45 b	0.19 ab	0.06

^zTreatments are as described in Table 1.

^yFor each cultivar, least squares means (n = 4) in a column with the same letter are not significantly different (Tukey-Kramer test, *P* < 0.05).

SF 800 = Sumer Flavor 800; SS 5244 = Summer Sweet 5244; DBT = day before transplanting.

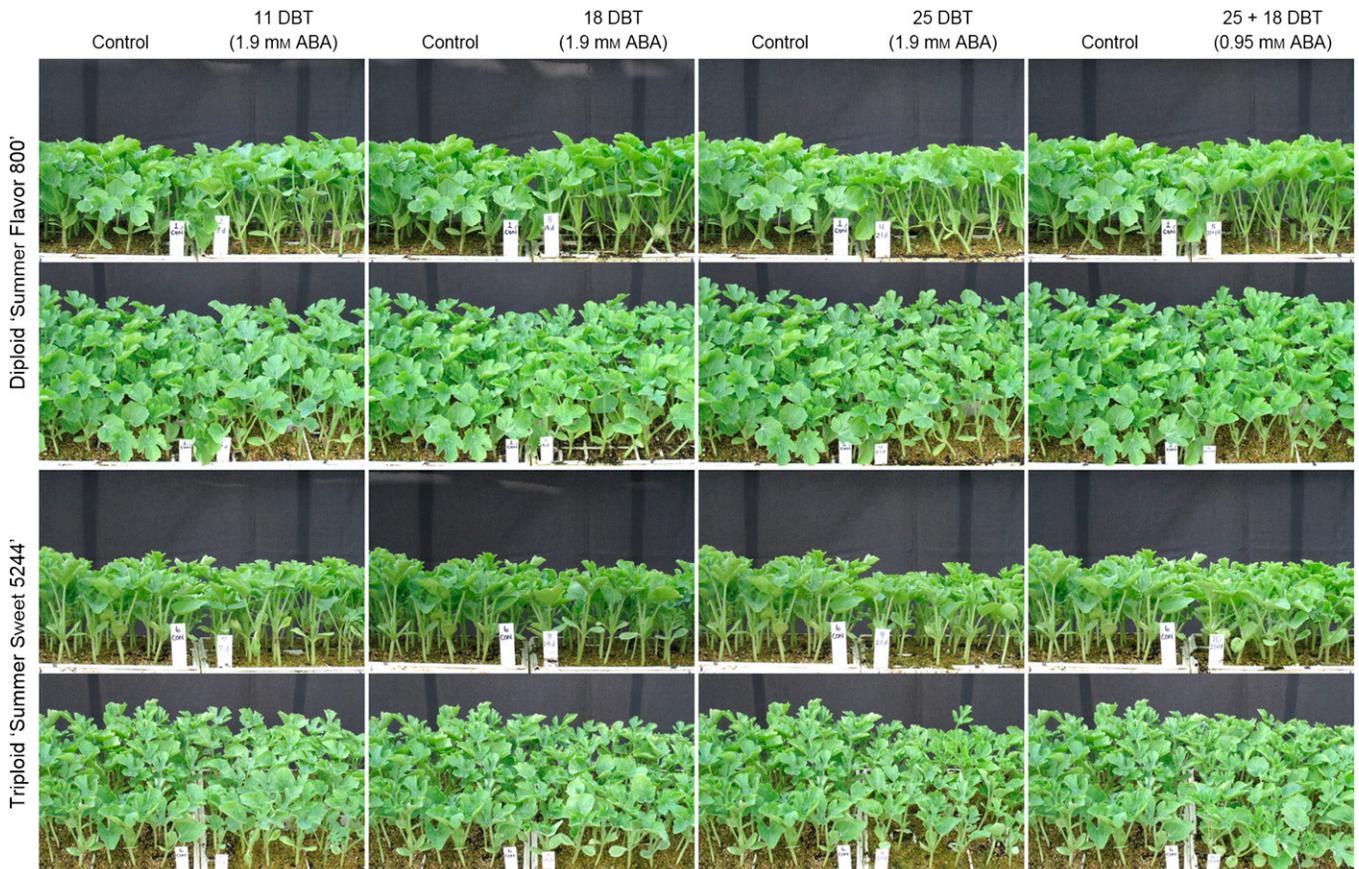


Fig. 1. Diploid ‘Summer Flavor 800’ and triploid ‘Summer Sweet 5244’ watermelon seedlings 1 d before transplanting (DBT). Treatments were as follows: no spray control, three timings of a single spray with 1.9 mM ABA, and one treatment of a double spray with 0.95 mM ABA. In all treatments, the application rate was 0.55 mg ABA per plant with the spray volume of 0.61 L·m⁻² (1.1 mL/plant). Height and leaf area reductions by the 25 DBT treatment were readily visible in both cultivars. Cotyledon abscission was induced by the 25 + 18 DBT treatment in ‘Summer Flavor 800’. ABA = abscisic acid.

Results

Stem and shoot height. Pre-treatment stem height was 1.97 cm in ‘Summer Flavor 800’ and 2.41 cm in ‘Summer Sweet 5244’ (Table 1). In the control, RSER decreased during the experiment (Table 2), whereas stem height increased steadily to 3.96 cm in ‘Summer Flavor 800’ and 4.22 cm in ‘Summer Sweet 5244’ (Table 1). Exogenous ABA inhibited stem elongation similarly in the two cultivars. In ‘Summer Flavor 800’, RSER calculated over 7 to 10 d after ABA applications at 25, 18, and 11 DBT was reduced by 47% (0.66 vs. 0.35 mm·cm⁻¹·d⁻¹), 54% (0.14 vs. 0.06 mm·cm⁻¹·d⁻¹), and 17% (0.14 vs. 0.11 mm·cm⁻¹·d⁻¹), respectively (Table 2). In ‘Summer Sweet 5244’, the corresponding reductions for the 25, 18, and 11 DBT treatments were 54% (0.59 vs. 0.27 mm·cm⁻¹·d⁻¹), 40% (0.11 vs. 0.07 mm·cm⁻¹·d⁻¹), and 29% (0.07 vs. 0.05 mm·cm⁻¹·d⁻¹), respectively. These reductions were significant only for the 25 DBT treatment in both cultivars. During the subsequent measurement periods, however, the 25 DBT treatment showed higher RSER than the control by 154% in ‘Summer Flavor 800’ (0.14 vs. 0.35 mm·cm⁻¹·d⁻¹) and by 158% in ‘Summer Sweet 5244’ (0.11 vs. 0.29 mm·cm⁻¹·d⁻¹). As a result, final stem height

showed no significant difference among the treatments, ranging from 3.58 to 3.96 cm in ‘Summer Flavor 800’ and from 3.67 to 4.22 cm in ‘Summer Sweet 5244’ (Table 1).

At 1 DBT, shoot height was three to four times higher than stem height (Table 1) because of petiole elongation (Fig. 1). The 25 DBT treatment had 14% and 13% lower shoot height than the control in ‘Summer Flavor 800’ (15.7 vs. 13.5 cm) and ‘Summer Sweet 5244’ (14.0 vs. 12.2 cm), respectively, whereas other ABA treatments were not significantly different from the control. The reductions in shoot height were highly correlated with the inhibition in petiole elongation (Fig. 2). Among the ABA treatments, neither multiple comparisons nor orthogonal contrasts detected a significant difference in shoot height of both cultivars. Height suppression with shortened petioles was readily visible in the 25 DBT treatment (Fig. 1).

Stem diameter. Stem diameter at 1 DBT was smaller in the ABA treatments than in the control by 4% to 7% in ‘Summer Flavor 800’ (5.54 vs. 5.17 to 5.32 mm) and by 1% to 6% in ‘Summer Sweet 5244’ (5.16 vs. 4.87 to 5.09 mm) (Fig. 3). These reductions were not significant, except when all ABA treatments in ‘Summer Flavor 800’ were pooled (5.26 mm) by orthogonal contrasts.

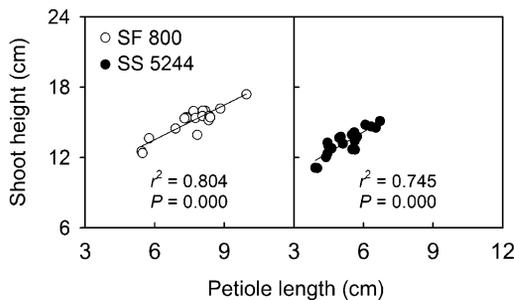


Fig. 2. Linear correlation between shoot height and petiole length of diploid ‘Summer Flavor 800’ (open symbol) and triploid ‘Summer Sweet 5244’ (black symbol) seedlings 1 d before transplanting. Treatments are as described in Figure 1.

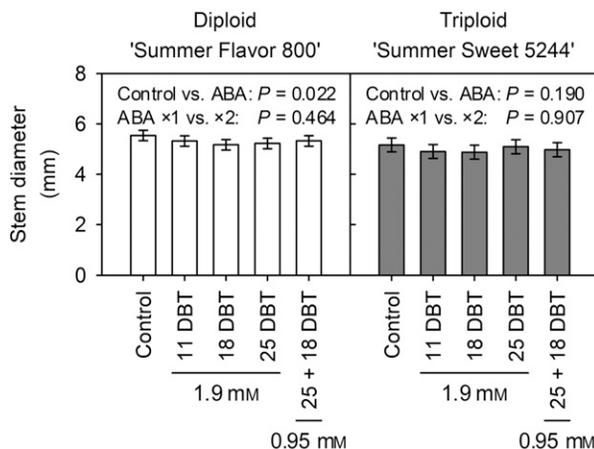


Fig. 3. Stem diameter of diploid ‘Summer Flavor 800’ (open bar) and triploid ‘Summer Sweet 5244’ (gray bar) seedlings 1 d before transplanting (DBT) as affected by abscisic acid (ABA) applied as a single high dose at different growth stages or repeated low doses. Treatments are as described in Figure 1. Data are least squares means \pm 95% confidence intervals ($n = 4$). Orthogonal contrasts tested two hypotheses: control vs. all ABA treatments (control vs. ABA) and all single-spray treatments vs. double-spray treatment (ABA $\times 1$ vs. $\times 2$).

Leaf growth. Cotyledon abscission was severe in the 25 + 18 DBT treatment of ‘Summer Flavor 800’ (Fig. 1), reducing cotyledon number by 46% (2.00 vs. 1.08) and area by 41% (7.55 vs. 4.42 cm²) compared with the control (Fig. 4A–B). In this cultivar, orthogonal contrasts also found significant differences in two additional hypothesis tests. First, the pooled ABA treatments had smaller number (2.00 vs. 1.67) and area (7.55 vs. 6.26 cm²) of cotyledons than the control. Second, the pooled single-spray treatments had a larger number (1.86 vs. 1.08) and area (6.87 vs. 4.42 cm²) of cotyledons than the 25 + 18 DBT treatment. In ‘Summer Sweet 5244’, cotyledon abscission by ABA was minimal and nonsignificant.

True leaves measured at 1 DBT showed similar responses to ABA in the two cultivars; none of the ABA treatments affected leaf number (Fig. 4A), whereas the 25 DBT treatment reduced leaf area by 17% compared with the control (40.4 vs. 33.7 cm² in ‘Summer Flavor 800’ and 42.1 vs. 34.9 cm² in ‘Summer Sweet 5244’) (Fig. 4B). These leaf area reductions were readily visible (Fig. 1). Contrasting results in the two cultivars were also found by orthogonal contrasts. The pooled ABA treatments had a smaller leaf area than the control in ‘Summer Sweet 5244’ (42.1 vs. 37.6 cm²), whereas the pooled single-spray treatments had a smaller leaf area than the 25 + 18 DBT treatment in ‘Summer Flavor 800’ (36.7 vs. 40.7 cm²).

Leaf chlorophyll index of the youngest fully open leaf and the largest leaf was unaffected by ABA in both cultivars (data not shown). Accordingly, leaf chlorosis was not noticeable in all ABA treatments (Fig. 1).

Dry matter accumulation and partitioning. Shoot dry matter accumulation at 1 DBT was inhibited by all ABA treatments in the two cultivars (Fig. 5A). The reductions were 17% to 21% in ‘Summer Flavor 800’ (391 vs. 309 to 325 mg) and 16% to 23% in ‘Summer Sweet 5244’ (465 vs. 357 to 388 mg) compared with the corresponding controls.

Root dry matter accumulation at 1 DBT was inhibited by ABA only in ‘Summer Flavor 800’ (Fig. 5B). The 11 DBT treatment (59 mg) had the smallest and nonsignificant inhibition, whereas other ABA treatments (55 to 57 mg) significantly reduced root dry weight by 22% to 25% compared with the control (73 mg). In this cultivar, the pooled ABA treatments (57 mg) also had significantly lower root dry weight than the control. A similar but nonsignificant trend for ABA treatments ($P = 0.061$) was found in ‘Summer Sweet 5244’. Root-to-shoot ratio was unaffected by ABA, ranging from 0.17 to 0.19 in ‘Summer Flavor 800’ and from 0.13 to 0.15 in ‘Summer Sweet 5244’ (Fig. 5C).

In both cultivars, shoot dry weight was positively correlated with leaf area, whereas it had no significant correlation with shoot height and stem diameter (Fig. 6).

Field growth, yield, and fruit quality. Seedling survival rate and leaf chlorophyll index showed no significant difference among the treatments (data not shown). Seedling loss

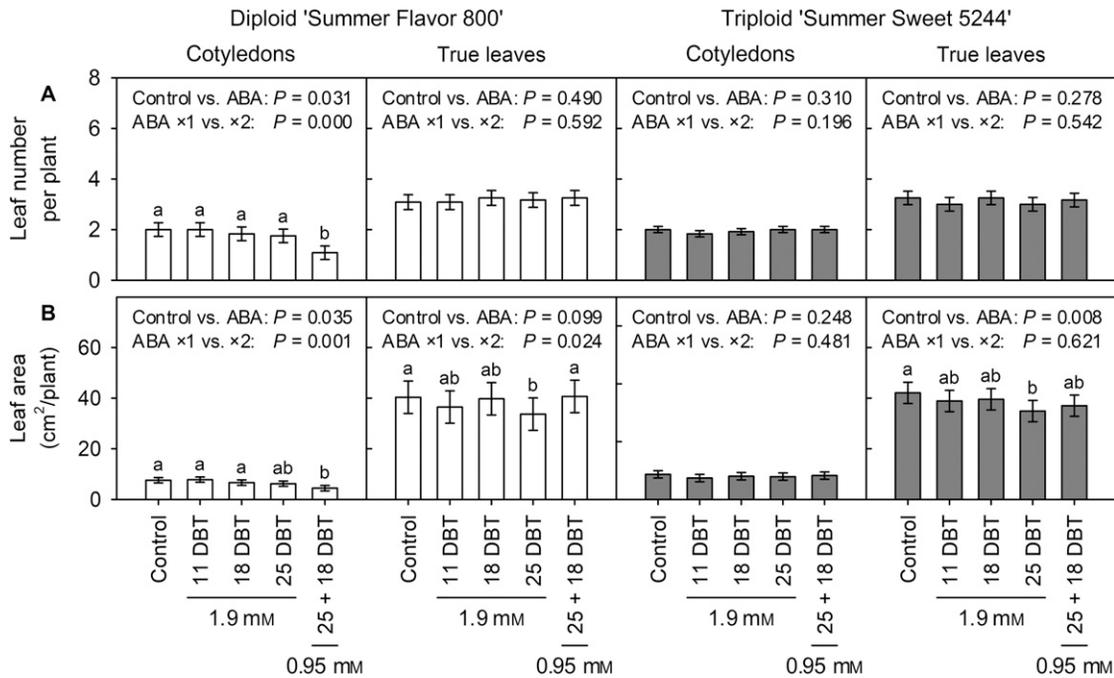


Fig. 4. Leaf growth of diploid 'Summer Flavor 800' (open bar) and triploid 'Summer Sweet 5244' (gray bar) seedlings 1 d before transplanting (DBT) as affected by abscisic acid (ABA) applied as a single high dose at different growth stages or repeated low doses: (A) leaf number and (B) leaf area. Treatments and statistical comparisons are as described in Figures 1 and 3, respectively. Means with the same letter are not significantly different (Tukey-Kramer test, $P < 0.05$).

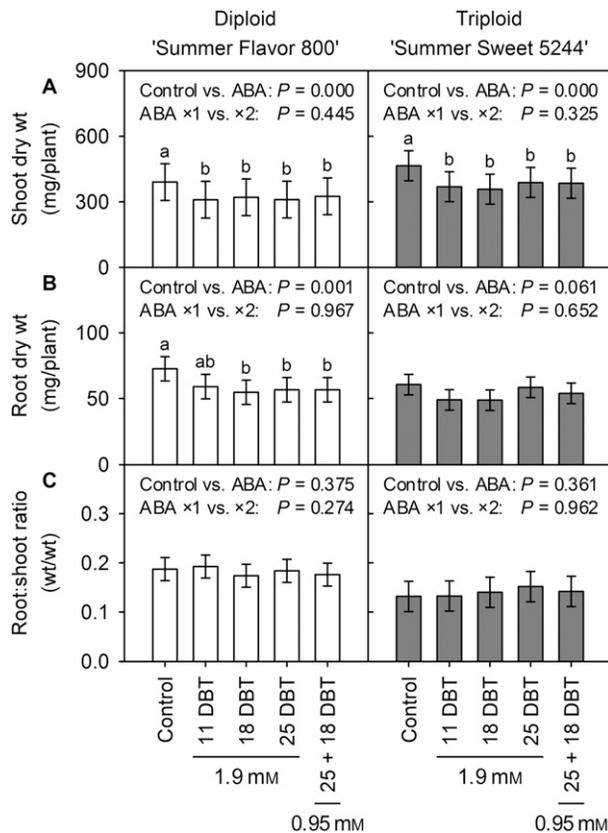


Fig. 5. Dry matter accumulation and partitioning of diploid 'Summer Flavor 800' (open bar) and triploid 'Summer Sweet 5244' (gray bar) seedlings 1 d before transplanting (DBT) as affected by abscisic acid (ABA) applied as a single high dose at different growth stages or repeated low doses: (A) shoot dry weight, (B) root dry weight, and (C) root-to-shoot ratio. Treatments and statistical comparisons are as described in Figures 1 and 3, respectively. Means with the same letter are not significantly different (Tukey-Kramer test, $P < 0.05$).

was attributable mainly to wind damage before vine development, averaging 15% in 'Summer Flavor 800' and 11% in 'Summer Sweet 5244'. Vine length showed no significant difference among the treatments in 'Summer Flavor 800' (Table 3). By contrast, vine development of 'Summer Sweet 5244' was delayed in the ABA-treated plants with vine length at 44 d after treatment (DAT) ranging from 52% to 77% of the control. These reductions were significant when all ABA treatments were pooled and compared with the control (87 vs. 57 cm). At the initial stage of fruit set (65 DAT), however, the ABA-treated plants had equivalent vine development compared with the control. Yield and fruit quality variables showed no significant difference among the treatments in both cultivars (Table 4).

Discussion

ABA effects on watermelon transplant height. A single spray of 1.9 mm ABA at the cotyledon stage (25 DBT) suppressed watermelon transplant height by inhibiting petiole elongation. This effect was similar in the two cultivars, diploid 'Summer Flavor 800' and triploid 'Summer Sweet 5244', with 13% to 14% reductions at the transplanting stage compared with the control. Exogenous ABA has been reported to inhibit stem elongation in many species (Bai et al., 2011; Latimer and Mitchell, 1988; Leskovar and Cantliffe, 1992; Yamazaki et al., 1995). Although the advantage of this height control effect may be limited for watermelon transplants

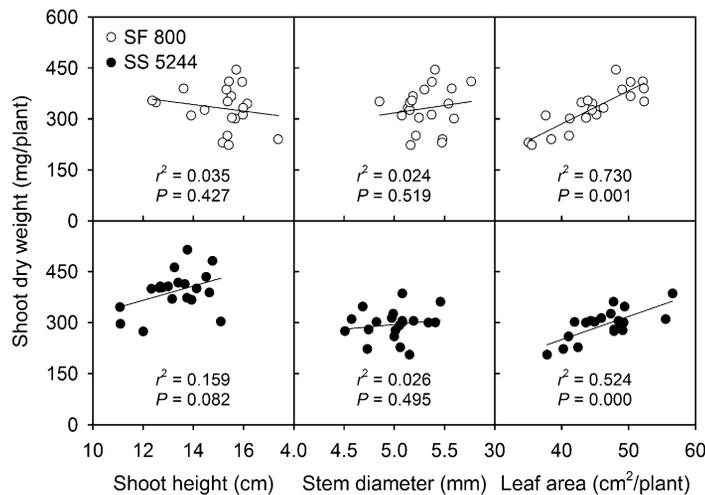


Fig. 6. Linear correlation between shoot dry weight and other growth variables of diploid 'Summer Flavor 800' (open symbol) and triploid 'Summer Sweet 5244' (black symbol) seedlings 1 d before transplanting. Treatments are as described in Figure 1.

Table 3. Vine development of diploid 'Sumer Flavor 800' and triploid 'Summer Sweet 5244' watermelon as affected by abscisic acid (ABA) applied during transplant growth as a single high dose at different growth stages or repeated low doses.

Cultivar	Treatment ^a	Vine length (cm)		
		Days after transplanting		
		23	44	65
SF 800	Control	7.8	78	284
	11 DBT (1.9 mm)	7.5	74	304
	18 DBT (1.9 mm)	9.7	70	296
	25 DBT (1.9 mm)	6.9	74	293
	25 + 18 DBT (0.95 mm)	9.7	91	323
	Orthogonal contrasts ^b			P value
	Control vs. ABA	0.548	0.970	0.465
	ABA × 1 vs. × 2	0.133	0.136	0.371
SS 5244	Control	6.7	87	282
	11 DBT (1.9 mm)	6.0	67	260
	18 DBT (1.9 mm)	6.6	45	262
	25 DBT (1.9 mm)	5.6	65	279
	25 + 18 DBT (0.95 mm)	4.8	51	270
	Orthogonal contrasts			P value
	Control vs. ABA	0.527	0.019	0.424
	ABA × 1 vs. × 2	0.399	0.482	0.876

^aTreatments are as described in Table 1.

^bOrthogonal contrasts are as described in Table 1.

SF 800 = Sumer Flavor 800; SS 5244 = Summer Sweet 5244; DBT = day before transplanting.

because of their relatively short stems, our results suggest that ABA is still effective in improving transplant compactness by shortening petiole length.

Undesirable growth modifications by ABA. In addition to height suppression, other growth modifications were induced by ABA. In both watermelon cultivars, all ABA treatments reduced shoot biomass compared with the control to a similar extent. The reductions ranged from 16% to 23%, which were highly associated with leaf area reductions. These results suggest that ABA inhibits leaf expansion more strongly than shoot elongation, thereby causing shoot growth reductions. Delaying transplant growth is not desirable for commercial nurseries because it prolongs the transplant production cycle and increases the cost of production.

Additional undesirable growth modifications were observed only in diploid 'Summer

Flavor 800'. First, stem diameter was reduced by ABA, suggesting that ABA may weaken stem strength and thus limit the benefit of height control. This effect is a drawback to ABA treatments compared with mechanical transplant conditioning methods, which can both shorten and thicken stems by stimulating ethylene production (Garner and Björkman, 1996, 1997; Hiraki and Ota, 1975; Latimer, 1998). Another drawback was the strong inhibition of root biomass accumulation. Large root systems are important to facilitate pulling of transplants from trays (Vavrina, 2002), whereas insufficient roots can result in severe transplant shock (Agehara and Leskovar, 2012). Furthermore, cotyledon abscission, a sign of poor transplant quality, was induced by the double-spray treatment. The ABA-induced abscission can be attributed to the stimulation of ethylene production (Gepstein and Thimann, 1981), which mediates

degradation of the cell wall and middle lamella by inducing the synthesis of hydrolytic enzymes (Mishra et al., 2008; Taylor et al., 1991; Tucker et al., 1991).

In contrast to shoot height, other growth variables showed cultivar-dependent responses to ABA with more undesirable growth inhibitions occurring in 'Summer Flavor 800' than in 'Summer Sweet 5244'. Such information is important in developing ABA application methods optimized for diploid and triploid watermelon cultivars.

Age-dependent sensitivity to ABA. For pepper transplants, Biai et al. (2011) suggest that ABA application should be initiated at the cotyledon stage for maximal height suppression. However, this recommendation is based solely on plant height, although other growth variables are also known to be affected by ABA (Taiz and Zeiger, 2010). In the two watermelon cultivars used in this study, age-dependent sensitivity to ABA was evident in shoot height and leaf area. In all cases, growth inhibition was maximal when 1.9 mM ABA was applied at the cotyledon stage, during which relative growth rate was most rapid. This similar age-dependent sensitivity of the two growth variables to ABA raises a dilemma in deciding the optimal application timing, because ABA can limit plant photosynthetic capacity as a tradeoff for height control. However, moderately restricted leaf expansion of transplants in greenhouses may be beneficial in reducing transplant shock under stressful field conditions, because it reduces plant water use by limiting transpirational area (Agehara and Leskovar, 2012).

Single versus double application of ABA. To avoid undesirable side effects of ABA such as leaf chlorosis and abscission (Agehara and Leskovar, 2012; Kim and van Iersel, 2011; Waterland et al., 2010), repeated application of low doses may be a more effective strategy than applying a single high dose. As opposed to our assumption, cotyledon abscission was induced only by the double-spray treatment in diploid 'Summer Flavor 800', whereas other growth variables showed minimal differences between the two application strategies in both cultivars. These results suggest that to prevent cotyledon abscission, repeated application of ABA is not recommended for watermelon transplants even at low doses.

ABA effects are minimal after transplanting. Field performance must be evaluated to justify the advantages of transplant growth modification in nurseries. Except for the relatively slow vine development, the ABA-treated plants had similar growth, yield, and fruit quality compared with the control plants. Their initial slow growth could be attributable simply to an insufficient leaf area and root system to support new growth.

It is important to note that all transplants used in the field experiment were shipped from the nursery in trays and thus were minimally damaged. In common commercial operations, mechanical injury often occurs when transplants are pulled from trays and

Table 4. Marketable yield and fruit quality of diploid ‘Sumer Flavor 800’ and triploid ‘Summer Sweet 5244’ watermelon as affected by abscisic acid (ABA) applied during transplant growth as a single high dose at different growth stages or repeated low doses.

Cultivar	Treatment ^z	Marketable yield			Firmness (N)	SSC (°Brix)
		(fruit no./plant)	(kg/fruit)	(t·ha ⁻¹)		
SF 800	Control	1.25	8.55	55.8	13.0	9.71
	11 DBT (1.9 mm)	1.24	8.30	54.8	13.1	9.54
	18 DBT (1.9 mm)	1.08	8.23	50.1	13.9	10.36
	25 DBT (1.9 mm)	1.21	8.03	51.6	13.4	10.10
	25 + 18 DBT (0.95 mm)	1.14	8.50	51.3	13.0	9.69
Orthogonal contrasts ^y			P value			
Control vs. ABA		0.766	0.579	0.740	0.680	0.583
ABA × 1 vs. × 2		0.882	0.551	0.944	0.607	0.447
SS 5244	Control	1.02	7.57	42.2	11.0	9.78
	11 DBT (1.9 mm)	0.96	7.19	36.7	10.7	9.56
	18 DBT (1.9 mm)	1.05	6.69	37.9	10.5	9.28
	25 DBT (1.9 mm)	1.10	6.81	40.6	11.8	9.23
	25 + 18 DBT (0.95 mm)	1.00	6.94	36.1	12.5	9.86
Orthogonal contrasts			P value			
Control vs. ABA		0.978	0.127	0.616	0.702	0.415
ABA × 1 vs. × 2		0.870	0.912	0.779	0.174	0.183

^zTreatments are as described in Table 1.

^yOrthogonal contrasts are as described in Table 1.

SSC = soluble solids content; SF 800 = Sumer Flavor 800; SS 5244 = Summer Sweet 5244; DBT = day before transplanting.

packed in boxes at high density for shipment (Cantliffe, 1993). Therefore, our field data may not reflect the advantage of height suppression to minimize damage during commercial shipping operations.

Practical implications of growth inhibition by ABA. Although foliar spray of ABA at the cotyledon stage can reduce watermelon transplant height, the benefit is limited by overall growth reductions, which can occur regardless of application timing. On the other hand, moderate shoot growth delay by ABA in triploid ‘Summer Sweet 5244’ may be of value as a growth-holding strategy when transplanting is delayed because of inclement weather at the time of field establishment. Importantly, field evaluations suggest that the growth modulation by ABA is only transient with no negative impact on marketable yield and fruit quality.

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