Tactile Conditioning Increases Water Use by Tomato

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ABSTRACT. Mechanical conditioning can be used to control the height of vegetable and ornamental transplants. Previous research indicated that brushing plants increases cuticular water loss from detached leaves, which may be an indication of decreased drought resistance. This might decrease post-transplant survival of the plants. The objectives of this study were to determine the effect of brushing on growth and gas exchange by tomato (*Lycopersicon esculentum* Mill.) and quantify whole-plant water use during a slow dry-down period. Tomato plants were grown from seed in a greenhouse during Fall 1995. The brushing treatment started 11 days after seeding and consisted of 40 strokes, twice each day. After 39 days of treatment, brushing reduced height 32%, leaf area 34%, and shoot dry mass 29% compared to control plants. Brushing did not affect leaf gas exchange. Brushed plants had a higher stem water flux than control plants during the first 3 days of a 6-day dry-down period. Stem water flux was lower than that of control plants later in the cycle, presumably because brushed plants used more of the available water during the first 3 days. On the third day of the dry-down period, leaf conductance of brushed plants was 35% higher than that of control plants, resulting in a 10% higher transpiration rate per unit leaf area. Because brushed plants had less leaf area than controls, differences in whole-plant water use were small. Time to wilting was similar for the brushed and unbrushed plants (6 days after withholding water). It seems unlikely that brushing would have a major effect on drought tolerance of plants.

Height control of vegetable transplants and ornamental bedding plants is important for producing high-quality plant material. Traditionally, plant growth retardants have been used to control height of bedding plants (Latimer, 1991a). Some growth regulators are no longer available for use on food crops. One possible means for nonchemical height control of bedding plants is mechanical conditioning. Latimer (1991b) distinguishes two types of mechanical conditioning: tactile and nontactile stimulation. Tactile stimulation involves applying mechanical stress directly to the plant, for example, by rubbing the stem or brushing the shoots of the plants. Nontactile stimulation includes shaking potted plants or agitation by wind or forced aeration. Both methods can control plant height.

Brushing reduced the height of cucumber (*Cucumis sativus* L.), eggplant (*Solanum melongena* var. *esculentum* L. Nees), squash (*Cucurbita pepo* L.), tomato (*Lycopersicon esculentum* Mill.), and watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] (Latimer and Beverly, 1994; Latimer and Oetting, 1994) and reduced thrips and aphid populations on vegetable transplants (Latimer and Oetting, 1994). Latimer and Beverly (1994) also found that brushing cucurbit transplants increased water loss from detached leaves. This suggests that brushing decreases the drought tolerance of these plants. Drought tolerance is important for transplants, because they often are exposed to drought immediately after transplanting (Berkowitz and Rabin, 1988). Transplanting often reduces the effective root area, because of root damage and the destruction of root hairs (Kramer, 1983), resulting in transplant shock. Transplant shock can lead to water deficit stress, which may cause leaf abscission and reduced plant growth (Berkowitz and Rabin, 1988; Nitzsche et al., 1991). In extreme cases, transplant shock also can lead to plant death (Dufault, 1986).

Determining whether mechanical conditioning makes plants more vulnerable to drought stress is important, since brushed plants might be more susceptible to transplant shock. The objec-

tives of this research were to 1) describe the effects of brushing on growth and gas exchange by tomato and 2) determine whether brushed plants are more susceptible to drought during a slow dry-down period than unconditioned plants.

Materials and Methods

PLANT MATERIAL AND TREATMENTS. ‘Sunny’ tomato seeds were planted in 10 × 10-cm (510-mL) pots filled with a peat-lite potting mix (Redi-Earth; Grace Horticultural Products, Cambridge, Mass.) on 16 Oct. 1995. Plants were grown in a double-layered polyethylene greenhouse and thinned to one plant per pot shortly after germination. Plants were fertilized twice weekly with 20N–4.4P–16.6K water-soluble fertilizer (peat-lite special 20–10–20; The Scotts Co., Marysville, Ohio) containing 200 µg·g⁻¹ N, starting at the first true leaf stage. All plants were hand watered as necessary and kept well watered at all times. Greenhouse temperatures were maintained between 26 °C (days) and 18 °C (nights).

The brushing treatment began 11 d after planting (DAP) (first true leaf stage). Plants were brushed 40 times with a wooden pole twice daily (at 0830 and 1630 HR). The height of the bar was adjusted to strike only the upper third of the shoots (Baden and Latimer, 1992; Latimer and Oetting, 1994). Pots were placed in a plastic carrying tray during brushing to prevent them from falling over. Treatments were continued until 50 DAP. Pot volume and growing period in this experiment were not typical for commercial transplant production, but were chosen to produce plants that were large enough for stem water flux measurements.

To determine the effect of brushing on plant water use under drought conditions, stem water flux of some of the control and brushed plants was monitored during a 6-d dry-down period. The growing medium was watered to saturation at the start of the measurements (42 DAP) and the plants did not receive additional water. The pots were enclosed in plastic bags to minimize soil evaporation. This may have caused buildup of CO₂ and depletion of O₂ in the pots. However, the bags did not make a perfect seal around the stem of the plants and there was some gas exchange between the pots and the atmosphere by diffusion. In addition, as the plants used the water in the pots, it was replaced by air, providing a continuous source of oxygen to the roots of the plants.

MEASUREMENTS. Plant height was measured 37, 41, 45, and 50

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Fig. 1. Average height of control (●) and brushed (■) tomato plants. The brushing treatment was started 11 d after planting. Plants were brushed twice a day with 40 strokes using a wooden pole. Error bars represent the standard error. Error bars not shown are within the limit of the symbol.

DAP to assess the effect of brushing on stem elongation. The apices of two plants were damaged by the brushing treatment, after which these plants were no longer included in the height measurements. Transpiration, leaf conductance (g_s), and net photosynthesis per unit leaf area (P_{net}) were measured on well-watered tomato plants three times (31, 36, and 46 DAP) with a gas exchange system (CIRAS-1; PP systems, Haverhill, Mass.). Photosynthetic photon flux density during these measurements was 210, 480, and 370 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. Leaf gas-exchange data also were collected on the third and fifth day of the dry-down experiment (45 and 47 DAP). Ambient CO_2 concentrations were kept at 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ for the measurements. All measurements were taken on the uppermost fully expanded leaf between 1130 and 1300 HR.

Leaf number, leaf area, and leaf and stem dry mass were determined at 50 DAP. Specific leaf area was calculated from these data as leaf area/leaf dry mass. The experimental design was a randomized complete block with 10 replications, using single plants as experimental units. Since plants from four of the replications were used to determine the water used by the plants during dry-down, only six replications were left from 42 to 50 DAP. Data were analyzed using general linear models (SAS Institute, Cary, N.C.).

Water flux through stems of control and brushed plants was monitored during the 6-d dry-down period with stem-flow gauges (Flow32; Dynamax, Inc., Houston, Texas) using the heat-balance method (Baker and van Bavel, 1987; Sakuratani, 1981). Calculated stem flow is very sensitive to the thermal conductance of the stem flow gauge, especially under conditions of low transpiration in the greenhouse in late fall and winter. In this experiment,

thermal conductance of the gauges was determined from the comparison between stem water flux and gravimetric transpiration measurements.

Cumulative stem water flux and whole-plant transpiration are very similar over a period of several days. The difference between these two measurements represents the change in the amount of water that is stored in the plant. Although this can be significant during short periods, over several days this difference is negligible. Total transpiration of the individual plants was determined gravimetrically five times per day during the dry-down period. Cumulative transpiration at the end of the 5-d measurement period was used to calculate the thermal conductance of the individual stem flow gauges. Calculated stem water flux was then compared to the gravimetric transpiration measurements during the experiment. The correlation between calculated stem flow and measured transpiration was high for all gauges ($r^2 = 0.988$ or higher, slope = 0.972 ± 0.023), indicating that calculated thermal conductances were accurate. Stem water flux was very low after the first 5 d and no longer

could be measured accurately with the stem-flow gauges. All plants were severely wilted at the sixth day of the drying period.

This dry-down experiment was conducted in a randomized complete-block design with four replications. The flow data were transformed using $\sqrt{(\text{flow rate} + 1)}$ to stabilize the variance before statistical analysis. The transformed data were analyzed by analysis of variance, but reported means are based on the raw data.

Results and Discussion

PLANT GROWTH AND GAS EXCHANGE. Brushing significantly reduced the height of the tomato plants (Fig. 1). Differences in plant height between treatments were small (7.3 mm) but significant at 37 DAP, and increased rapidly when the height of control plants increased exponentially from 37 to 50 DAP. Height increase of brushed plants during this period was much slower, and, at the end of the experiment, brushed plants were 73 mm (32%) shorter than control plants. Latimer and Oetting (1994) observed a similar reduction (40%) in the stem length of tomato plants due to brushing. The effects of brushing on plant height increased rapidly during the period of rapid stem elongation (Fig. 1).

Brushing reduced plant height and decreased leaf area by 34%, leaf dry mass by 31%, stem dry mass by 23%, and total shoot dry mass by 29% compared to the controls (Table 1). The leaves of brushed plants were epinastic, giving the plants a slightly wilted appearance. Specific leaf area and number of leaves were not affected by the brushing treatment. The lower dry mass as the result of brushing was similar to that observed by Latimer and Oetting (1994). A decrease in leaf area expansion as a result of brushing was found by Latimer and Beverly (1994) in some cucumber, squash, and watermelon cultivars, while other cultivars did not show a significant decrease in leaf area. Brushing effects on leaf number also were cultivar dependent. Heuchert and Mitchell

Table 1. Average number of leaves, leaf area, leaf stem and shoot dry mass (DM), specific leaf area (SLA), and leaf to stem ratio of greenhouse-grown tomato plants as affected by tactile conditioning.

Treatment	Leaves (no.)	Leaf area (m^2/plant)	Leaf DM (g/plant)	Stem DM (g/plant)	Shoot DM (g/plant)	SLA ($\text{m}^2\cdot\text{g}^{-1}$)	Leaf to stem mass ratio
Control	7.0	0.0675	4.57	1.93	6.50	0.0148	2.37
Brushed	7.0	0.0448***	3.14***	1.48***	4.62***	0.0143	2.11***

***Significantly different from the control at $P = 0.001$ according to F tests.

Table 2. Transpiration, leaf conductance (g_s), and net photosynthesis (P_{net}) of well-watered greenhouse-grown tomato plants as affected by mechanical conditioning (brushing). The brushing treatment was started at 11 d after planting (DAP).

DAP	Treatment	Transpiration ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	g_s ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	P_{net} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
31	Control	2.24	220	3.15
	Brushed	2.21	206	3.60
36	Control	2.86	222	6.82
	Brushed	2.78	215	6.34
46	Control	3.87	318	6.92
	Brushed	4.09*	369*	6.43

*Significantly different from the control treatment at $P = 0.10$ according to F tests.

(1983) found that nontactile stimulation of tomato with a gyratory shaker had similar effects on leaf area, leaf and shoot dry mass, and plant height as seen in this study. Stroking the upper part of the shoot or shaking the containers by hand also causes a significant reduction in plant height and dry mass (Mitchell et al., 1977). Epinasty of tomato leaves as a result of mechanical agitation of plants has been reported previously by Mitchell et al. (1975). The brushing treatment altered carbon distribution within the tomato plants; brushed plants had a significantly lower leaf to stem mass ratio (Table 1), indicating that these plants allocated a larger fraction of carbohydrates to the stems. The results of this study may have been influenced by the relative large container volume (510 mL) and long growing period (50 d), which are atypical for tomato transplant production. However, the observed treatment effects were similar to those in other studies, suggesting that growth was affected similarly.

Brushing did not affect leaf conductance or transpiration rates of well-watered plants during most of the experiment, except 46 DAP, when brushed plants had a slightly higher leaf conductance and transpiration rate (Table 2). The lack of a brushing effect on P_{net} is in apparent contradiction with decreased shoot dry mass of the brushed plants, since photosynthesis is the driving force for almost all dry matter production. However, carbon fixation depends on the photosynthetic rate per unit leaf area and on the total amount of

light absorbed by the plant (Lawlor, 1995). The amount of light a plant intercepts depends on its leaf area and leaf angle (Acocck, 1991). Because brushed plants allocated a larger fraction of their carbohydrates to stem dry matter than control plants, they produced less leaf area, thus decreasing the total amount of light intercepted by the plants. The epinastic growth habit of the brushed leaves may have decreased the amount of intercepted light and, thus, whole-plant photosynthesis even more. It is also possible that brushing had a transient effect on leaf gas exchange, since measurements in this study were taken about 4 h after the brushing treatment. Shaking, a nontactile form of mechanical conditioning, caused a temporary reduction (<4 h) in leaf transpiration and photosynthesis of soybean [*Glycine max* (L.) Merrill] (Pappas and Mitchell, 1985).

Whole-plant photosynthesis was not determined in this study, but the combination of similar P_{net} and smaller leaf area of brushed plants suggests that whole-plant photosynthesis was higher for control than brushed plants. This explains the difference in shoot dry mass between the two treatments. Mitchell et al. (1977) also reported that P_{net} of tomato plants was unaffected by mechanical conditioning. They found a close correlation between leaf area development and dry matter production and concluded that differences in dry matter production were the result of differences in leaf area, and not of conditioning effects on P_{net} . Their conclusion is supported by the results of this study.

Some of the effects of brushing on plant morphology and physiology may be hormonal. Ethylene, auxin, gibberellins, cytokinins, and abscisic acid may be involved in the response of plants to mechanical stress (reviewed by Mitchell, 1996). Mechanical conditioning can increase ethylene evolution of plants (Biro and Jaffe, 1984), which can cause leaf epinasty. Mechanical stress also decreases the gibberellin-like activity of the treated tissues (Beyll and Mitchell, 1983), which may be important in internode elongation. It seems likely that the effects of brushing depend on different hormones and their interactions.

CONDITIONING EFFECTS ON PLANT WATER USE DURING A DRY-DOWN PERIOD. Plant water use was studied during a 6-d drying period. During the first 3 d of the dry-down period, stem water flux (Fig. 2)

Fig. 2. Stem water flux through brushed (---) and control (—) tomato plants during a slowly developing drought stress. All pots were watered to saturation before the start of the measurements and did not receive additional water. *Significant differences between the two treatments ($P < 0.05$). Stem water flux on day 6 was too low to be measured accurately and plants were severely wilted on this day.

Fig. 3. Cumulative water flow through the stems of brushed (---) and control (—) tomato plants during a slowly developing drought. Data are shown as cumulative water flow (A) and as cumulative stem flow in the brushed plants as a percentage of the control treatment (B), which emphasizes differences during the earlier part of the dry-down period. Error bars represent the standard error.

conductance, and it is not clear if cuticular conductance was affected by the mechanical conditioning.

Stem water flux was much lower during days 4 and 5 than during the first 3 d of the dry-down period for control and brushed plants. Since the cumulative water flow of the brushed plants after 3 d was higher than that of the controls (Fig. 3), brushed plants had less available water left in the growing medium at the start of day 4. This resulted in a bigger decrease in water flux through the brushed plants during the fourth and fifth day compared to the control plants.

Leaf conductance of control plants was higher than that of brushed plants during the fifth day of the drying period (81 vs. 52 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), but the difference was not statistically significant. The slightly higher leaf conductance, combined with a larger leaf area, explains the higher stem water flux in control plants during the fourth and fifth day of the period. Total cumulative water flow over the 5-d period was identical for plants in both treatments (Fig. 3). Presumably, almost all the available water had been taken up by the plants at that time and severe wilting was seen on the sixth day of the drying period.

Although the pattern of water use during a dry-down period was clearly affected by the brushing treatment, the differences were small. No differences in time to wilting were seen between the two treatments. Brushed plants had higher water use per unit leaf area than control plants during the dry-down period, but this was partially compensated for by their smaller leaf area. Since the differences in whole-plant water use were relatively small, it does not seem likely that brushing would make plants more susceptible to water-deficit stress after transplanting.

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was closely related to solar radiation (data not shown). The cloudy weather on the first day apparently limited plant water uptake. This was expected, since transpiration strongly depends on the amount of radiation a plant absorbs (Salisbury and Chandler, 1993). Despite sunny conditions on the fourth and fifth day of the drying period, water flux was lower than during the second and third day (Fig. 2), presumably because the water supply had become a limiting factor for transpiration. No reliable data were collected on the sixth day because of extremely low stem water fluxes.

Stem water fluxes for the two treatments were similar during the mornings of the first 3 d of the dry-down period, but brushed plants had a higher stem water flux (whole-plant water uptake) during the afternoons of the first 3 d (Fig. 2). Since brushed plants had a lower leaf area than control plants, water flux per unit leaf area was higher in brushed plants throughout the first 3 d of the dry-down period. This is in apparent contradiction with the findings of Mitchell et al. (1977), who reported that transpiration rates (per unit leaf area) were unaffected by mechanical conditioning, but whole-plant transpiration was decreased by the conditioning because of the smaller leaf area. However, the mechanical conditioning in Mitchell et al (1977) consisted of shaking whole containers or rubbing the upper part of the stem gently with the thumb and forefinger. The leaves were not physically disturbed in either of their conditioning treatments, while brushing can possibly result in subtle leaf damage, causing an increase in the leaf conductance to water vapor. Shoot abrasion may also make plants more susceptible to disease (Shawish and Baker, 1982).

Latimer and Beverly (1994) found that brushing increased water loss from detached leaves of cucurbit transplants, presumably because of an increase in cuticular conductance to water. An increase in cuticular water loss also could explain the stem flow data, since it would result in higher transpiration rates per unit leaf area. Gas-exchange data collected during the afternoon of the third day of the dry-down period indicated that conductance of leaves of brushed plants was significantly higher than that of control plants (421 vs. 311 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $P = 0.03$), resulting in a 10% higher transpiration rate (3.43 vs. 3.10 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $P = 0.06$). These measurements cannot differentiate between stomatal and cuticular

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