Mechanical Conditioning for Controlling Excessive Elongation in Tomato Transplants: Sensitivity to Dose, Frequency, and Timing of Brushing

Lauren C. Garner and Thomas Björkman

Department of Horticultural Sciences, New York State Agricultural Experiment Station, Cornell University, Geneva, NY 14456

Additional index words. Lycopersicon esculentum, mechanical conditioning, plug production

Abstract. During production of plug transplants, the high plant density results in rapid stem elongation as plants compete for light. The resulting tall, weak-stemmed plants are difficult to transplant and are easily damaged. One technique that can prevent excessive elongation is mechanical stimulation by brushing. Wide adoption of brushing is limited by a lack of information on how plants respond to variations in applying the technique. Our investigation examined how tomato (Lycopersicon esculentum cv. Oh8245) seedling growth responded to varying doses of mechanical stimulation, varying intervals between brush strokes during stimulation, time of day that stimulation was applied, and growth stage at which application started. Seedlings were grown in 288-cell flats at 2100 plants/m². Daily doses from 0 to 40 brush strokes were applied from canopy closure until the nontreated plants reached a canopy height of 15 cm. The final height was reduced by $\approx 20\%$ for all brushed treatments, with little further effect with >10 strokes/d. Intervals between strokes as long as 10 minutes resulted in the same reduction in the rate of stem elongation as the same daily dose applied in one continuous treatment. Treatments were similarly effective whether applied in the morning or late afternoon. Treatments begun at a canopy height of 6 (canopy closure), 8, or 10 cm gave similar reductions in the rate of stem elongation. Plants grew 6 mm·d⁻¹ when they were not treated and 3 mm·d⁻¹ when treated. Therefore, the final height was directly related to the number of treatment days. Stimulation appears to be sensed and integrated over at least half an hour and the reduction in the rate of stem elongation expressed over the subsequent daily cycle of growth. All results indicate that there is substantial flexibility in applying brushing for controlling elongation in tomato transplants.

Production of vegetable transplants in Canada and the northern United States is commonly done at high plant densities because the major production costs (greenhouse construction and heating) are related to the production area (Marr and Jirak, 1990). Commercial processing tomatoes are commonly grown in 288-cell plug trays at 2100 plants/m² (Garton 1990). Close spacing results in a number of morphological changes collectively referred to as the shade avoidance response. Plants that shade each other distribute a larger proportion of dry matter to stem elongation to compete for the limited amount of light in the plant canopy (Smith 1994). Shade avoidance is characterized by an increase in internode and petiole elongation and a reduction in leaf area, lamina thickness, and specific stem weight.

There are several drawbacks to excessive elongation: tall transplants with weak stems are difficult to handle and often lodge after transplanting, thereby increasing the risk of plant damage and disease. In addition, mechanical transplanters are designed to accommodate plants of a specified size. Taller plants catch in the mechanism, resulting in damaged or skipped plants in the field. For these machines to function properly, the plants must be "...uniform, short, and sturdy..." (Shaw 1993). However, unfavorable weather conditions can accelerate growth in the greenhouse or delay preparation of the field for transplanting. Height control, therefore, is an economic necessity for growers. Many methods are used to control transplant height, including plant growth regulators, withholding water or nutrients, temperature control, and clipping the shoots. These methods require high levels of management, often have long-term effects on plant growth, and may delay early yields (Adler and Wilcox, 1987; Hickman et al., 1989; Heins and Erwin, 1990; Jaworski et al., 1970; Latimer, 1992;) Vegetable transplant growers need a method for controlling transplant height that does not have these drawbacks (Price and Zandstra 1988). Such a method, which should be easy and inexpensive to apply on a large scale, currently is unavailable to most growers.

The simplest method of mechanical stimulation (brushing) can be applied by using a relatively non-abrasive material, such as bond typing paper (Biddington and Dearman, 1985), cardboard (Latimer, 1990), polyvinyl chloride pipe (Latimer and Thomas, 1991), or a wooden dowel (Baden and Latimer, 1991). Many plants are stimulated at once as the material is moved across the plant canopy contacting the leaves and bending the stems.

Mechanical stimulation is, in principle, an excellent means of limiting undesirable stem elongation, and it also can increase stem strength and specific chlorophyll content (Latimer, 1991). Mechanical stimulation may avoid the detrimental effects of stressbased treatments and be more easily adapted to commercial use than temperature-based treatments. Furthermore, these changes in plant growth and morphology occur without long-term inhibition of plant growth. However, certain aspects of the physiological response to stimulation need to be better understood to develop a greenhouse treatment that can be adapted for growers' differing needs. The key questions that need to be answered for each growing condition are how much, how long, and when to treat. These questions were answered for tomato seedlings by investigating the growth response to varying doses of mechanical stimulation, the ability of the plant to sum the stimuli, the interaction with

Received for publication on 27 Dec. 1995. Accepted for publication 26 Apr. 1996. This research was supported by the New York State Tomato Research Association, Hatch Grant NYG632506 and a Cornell Graduate Research Assistantship to L.C.G. Use of trade names in this publication does not imply endorsement of the named products or criticism of similar ones not mentioned. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

the diurnal growth cycle, and the sensitivity to mechanical stimulation at different growth stages.

Materials and Methods

Plant culture. Experiments were conducted with the processing tomato, 'Ohio 8245' (Sunseeds, Hollister, Calif.). Seeds were planted in "No. 288 square deep" plastic plug trays (Landmark Plastics Corp., Akron, Ohio) with an individual cell volume of 6.5 ml and 2100 plants/m². This tray size is recommended for the commercial production of processing tomato transplants (Garton



Fig. 1. Applying brushing treatment to plug-grown tomato transplants. The transplants were stimulated mechanically by brushing with a piece of polystyrene foam with enough pressure to bend the stems slightly.

et al., 1987), and it is the most commonly used in New York. Seeds were sown at one seed per cell into a soilless growing medium (Pro-Mix BX, Premier Brands, Red Hill, Pa.).

The plants were maintained in a greenhouse and after emergence were fertilized two times per week at watering with 20N– 8.7P–16.6K soluble fertilizer at 100 ppm N (Peters Professional 20–20–20; Grace-Sierra Horticultural Products Co., Milpitas, Calif.). Transplants also were fertilized with Ca(NO₃)₂ with N at 50 ppm during the winter if incipient chlorosis was noted. The trays were placed on metal mesh benches to encourage air pruning of the root system. Supplemental light was provided by 1000-W, metal halide lamps providing 500 μ mol·cm⁻²·s⁻¹ for 12 h·d⁻¹ from November until May, unless otherwise noted.

A completely randomized design was used for all greenhouse experiments, with half flats (144 plants) used as the experimental units. All of the trays in a given experiment were placed together so that there were no gaps between neighboring trays. Cells at the edge of an experiment dried out quickly, consistently resulting in transplants that were stunted and overhardened. Guard rows three to four cells wide surrounded all experimental units so that edge plants were not sampled.

Brushing. The canopy was brushed with a $3 \times 20 \times 30$ -cm piece of polystyrene foam that allowed precise and uniform treatment of each experimental unit (Fig. 1). The brushing treatment was begun at canopy closure when most plants were at the first true leaf stage, except in the experiment where time of treatment initiation was the

Table 1. The effect of the number of brush strokes per day on the height, stem diameter, and shoot dry weight of processing tomato transplants. The repetitions of the experiment are identified by the month of seeding.

	Strokes/	Stem	Stem	Shoot dry
Statistic	day	length (cm)	diam (mm)	wt (mg)
	Jui	ne 1994 (n = 4)		
	0	13.8 ± 0.6	2.24 ± 0.04	86 ± 3
	10	13.5 ± 0.4	2.28 ± 0.02	82 ± 3
	20	13.0 ± 0.5	2.39 ± 0.03	78 ± 2
	40	12.1 ± 0.3	2.39 ± 0.02	75 ± 2
LSD ^Z		NA	0.09	8
F tests				
Overall		NS	**	*
Treated vs. nontreated		NS	**	*
	Ju	ly 1994 (n=4)		
	0	12.5 ± 0.5	2.44 ± 0.04	86 ± 7
	10	10.6 ± 0.4	2.39 ± 0.06	72 ± 3
	20	10.0 ± 0.5	2.35 ± 0.04	72 ± 4
	40	10.2 ± 0.3	2.36 ± 0.02	70 ± 3
LSD		1.4	NA	NA
F tests				
Overall		**	NS	NS
Treated vs. nontreated		**	NS	*
	Ap	ril 1995 (n = 6)		
	0	14.2 ± 0.4	2.34 ± 0.04	89 ± 4
	10	11.4 ± 0.4	2.34 ± 0.02	68 ± 2
	20	11.3 ± 0.6	2.51 ± 0.06	77 ± 5
	40	10.6 ± 0.4	2.52 ± 0.04	74 ± 5
LSD		1.3	0.12	13
F tests				
Overall		***	**	*
Treated vs. nontreated		***	*	*

^zFisher's protected LSD at P = 0.05. NA = not applicable.

 $NS^{*,**}$ Main effects within column nonsignificant at P = 0.05 or significant at P < 0.05, 0.01, or 0.001, respectively.

variable. Treatments were continued until the brushed plants reached an average canopy height of ≈ 15 cm, which is the appropriate height for the mechanical transplanter. Plants within a given experiment were treated between 8:00 AM and 9:00 PM, except in experiments where time of day was the variable.

Measurements. During the treatment period of each experiment, the stem growth was estimated intwoways (as appropriate to the experiment). The canopy height of each experimental unit was estimated every 1 to 3 d by gently placing a note card on top of the canopy and measuring the distance from the soil surface to the note card. The stem length was used to estimate the rate of stem elongation. The height of 10 randomly selected plants from each experimental unit was measured from the soil level to the growing point three times per week. The leaves extended beyond the growing point so that the canopy height was several centimeters greater than the stem length. Height measurements were taken before the daily treatment application, taking care to avoid disrupting the plant canopy. At the end of each experiment, the stem length, stem

diameter, and shoot dry weight of sample plants from each experimental unit were measured on 20 sample plants. Stem diameter was measured with a caliper 1 cm above the point of attachment of the cotyledons. Dry weights of shoots were measured after drying in a forced-air oven at 80 °C for \geq 48 h.

Statistical analysis. Data were analyzed by one-way analysis of variance and regression analysis (Schaefer and Farber, 1992). Differences were detected by orthogonal contrasts and Fisher's protected least significant difference procedure (LSD) with 95% confidence level. Fisher's protected LSD was applied so that the error rate of each pairwise comparison was about equal to the overall error rate of the F test (Ott, 1993).

Dose response. The range of treatment levels was chosen based on a preliminary trial in which a dose of 10 daily strokes was ineffective, whereas a dose of 40 daily strokes, while effective for height control, damaged the leaves slightly. Blocks of 144 plants were stroked daily 10, 20, or 40 times back and forth with a piece of styrofoam. These treatments correspond to brushing for \approx 12, 25, or 50 s, respectively. An unbrushed control treatment also was included. The experiment was conducted three times with four or six replications. The seeding dates were 10 June 1994, 19 July 1994, and 17 Apr. 1995. The third repetition coincided with the commercial production season. Treatments began when the average canopy height was \approx 6 cm (18 to 27 d after seeding) and lasted 11, 16, and 14 d, respectively.

Interval between strokes. Each experimental unit was brushed with 10 back-and-forth strokes each day, but the time interval between pairs of strokes was varied. The four brushed treatments were 0.01 (continuous stimulation), 0.1, 1, and 10 min between strokes. The control treatment was not brushed; therefore, the total treatment time varied from 12 s to 40 min. The experiment was conducted twice, seeded 1 July 1994 and 23 Aug. 1994, with four replications each time. Treatments were begun when the average canopy height was \approx 8.5 and 6.5 cm, respectively, and continued for 9 d. Canopy heights were measured every day during the treatment period and were used to calculate the average stem elongation rate for each experimental unit for the 9 d of treatment.

Measurement of growth periodicity. To determine the time of day at which stem elongation was most rapid, the stem elongation of nontreated tomato transplants growing in a greenhouse without supplemental lighting was measured using linear displacement transducers (World Precision Instruments, Miami). The transducers were connected by a piece of dacron thread to the base of the petiole of the newest fully expanded leaf of 3- to 4-week-old tomato transplants. The base of the stem was held by a clamp to maintain its position constant relative to the rest of the apparatus. This apparatus did not appear to affect transplant growth. Electric signals from the transducers were amplified, digitized (MP-100; BioPac, Goleta, Calif.), and stored on a computer using AcqKnowledge software (Wester and Nakazawa 1992). Stem elongation was recorded every 10 s, and the rate of stem elongation was calculated based on a running average of every 10 data points. The elongation of two plants was measured simultaneously for periods of several days. To minimize physical disturbance and uneven growth, the transplants were maintained in a plug tray that was set in a plastic flat containing a thin layer of the fertilizer solution to supply a constant source of water and nutrients to the plants. The experiments were conducted during Apr. and May 1995. The data are displayed by representative stem elongation plots produced with Igor software (Wavemetrics, Lake Oswego, Ore.).

Time of day. In this experiment, plants were brushed either in the morning (between 8:00 AM and 9:00 AM) or in the afternoon

(between 4:00 PM and 5:00 PM) with 30 back-and-forth strokes. The treatment lasted for 12 d. The experiment was conducted twice with six replications each time; the seeding dates were 22 Feb. and 13 Mar. 1995. Plants received natural daylight (max 500 μ mol·cm⁻²·d⁻¹ for \approx 12 h·d⁻¹, with sunrise between 6:00 and 6:30 AM and sunset between 6:00 and 6:30 PM. Plants also received supplemental lighting from 8:00 AM to 5:00 PM.

Treatment initiation. Brushing was begun at three mean canopy heights: 6, 8, and 10 cm. The corresponding stem lengths were 4.0, 5.2, and 6.4 cm. The experiment was seeded 22 Feb. 1995 with six replications. Treated plants were brushed daily with 30 back-and-forth strokes.



Fig. 2. Dose response. Plants were treated beginning at canopy closure, when the stem length was ≈5 cm. The treatments differed in the number of back-and-forth strokes applied daily with a piece of polystyrene foam. The treatments were applied for ≈2 weeks. The final stem length (soil to meristem) was measured when plants were at marketable stage (canopy height 15 cm). The bars are the sE of the four replicates. The circles, triangles, and squares are the first, second, and third repetition of the experiment.



Fig. 3. The relationship between plant height and shoot biomass. The squares are brushed treatments of the second dosage experiment, and the circles are non-treated controls. The regression line for the pooled data is $DW = 7.1 \text{ mg}\cdot\text{cm}^{-1} \times \text{height} - 1.8 \text{ mg}$. $R^2 = 0.77$

Results

Dose response. Mechanical stimulation by brushing resulted in a significant reduction in the final height of plug-grown tomato plants. The response to increasing doses was not linear: treated plants were shorter than those that had not been brushed, but there was not a consistent difference in height among the brushed treatments (Table 1). The shape of the response curve differed between repetitions of this experiment (Fig. 2). The average shoot dry weight of treated plants was significantly lower than that of nontreated plants, and the dry weight was closely related to the stem length (Fig. 3). The treated plants had a more uniform appearance that the nontreated plants. Torn or yellow leaves were rare, and when they did occur, they were on plants that received 40



Fig. 4. Interval between strokes. With a constant dose of 10 brush strokes, the interval between strokes was varied to determine whether small doses could be accumulated over time. The stem elongation rate was calculated for the 9 d of treatment. The nontreated control had an infinite interval. The bars are the se.



Fig. 5. Diurnal variation in stem elongation rate of nontreated tomato transplants. The change in stem length was measured continuously under the growing conditions used throughout these experiments. The lighter lines are traces of two plants on 27 Apr. 1995, and the heavier lines are two plants on 19 to 20 May 1995.

strokes/d. The large effect of the first 10 strokes compared to additional treatment suggests that there is an increment of elongation that is easily suppressed by mechanical stimulation and that further reduction of the elongation rate is not possible without the risk of plant damage.

Time interval between strokes. The daily treatment was applied using different intervals between strokes to test the ability of the plants to integrate a discontinuous stimulus. There were no significant differences in final canopy height or stem elongation rate among four brushing intervals that varied exponentially from 0.01 to 10 min (Fig. 4).

Time of day. Slowing elongation by brushing should have the greatest effect if it is done so that the inhibition occurs when the rate of stem elongation is greatest. Transducer measurements of the diurnal growth cycle showed that stem elongation was greatest from late afternoon until morning (Fig. 5). The specific time at which rapid stem elongation occurred varied from day to day, but on any given day, both of the plants being measured responded at the same time.

Brushing was similarly effective in the morning (preceding the minimum growth rate) or in the late afternoon (preceding rapid growth). Both reduced height significantly (Table 2). In only one repetition did the time of day have a significant effect on plant height, with a 26% reduction by the morning treatment and an 18% reduction by the afternoon treatment. In the second repetition, the trend was similar but nonsignificant. There was no significant effect of the treatment time on stem diameter or shoot dry weight.

Stage of growth at treatment initiation. The growth stage at which brushing was started had a significant effect on the final plant height (Table 3). Brushing treatments were begun at canopy closure (canopy height 6 cm) and at two later dates when the canopy was 8 and 10 cm tall. A reduction in the stem elongation rate was noticeable within 2 to 4 d of the beginning of treatment (Fig. 6). The rate of stem elongation of the stimulated plants was the same once brushing begun, regardless of treatment. Brushed plants elongated at 0.27 cm·d⁻¹, which was about half the rate of nontreated plants (0.59 cm·d⁻¹). Differences in height at the end of the experiment depended directly on the duration of the treatment (Fig. 7). The final stem length of the plants was reduced by ≈ 3 mm·d⁻¹ of treatment, regardless of when the treatments began. Some tender large leaves tore if treatments were begun when the canopy height was 10 cm.

Discussion

The results of these experiments confirm the usefulness of mechanical stimulation as a means to control excessive elongation in tomato transplants. They also provide measures of the responsiveness of the transplants to the main parameters of the treatment. The commercial use of mechanical stimulation to control transplant height currently is quite limited. Of sugar beet (*Beta vulgaris*) growers in Japan, \approx 35% use brushing to control transplant size (Fletcher, 1984). Brushing has been tested on a small scale with tomato transplants in commercial greenhouses (Latimer and Thomas, 1991; Schnelle et al. 1994). Our results should make implementation on a broader scale possible.

Dose response. The optimum dose for treatment appears to be a broad range between 10 and 40 brush strokes/d. The mechanical stimulation resulting from movement of transplants during everyday handling, greenhouse ventilation, and watering is not sufficient to control height. The appropriate dose is one that provides enough control for the grower to accommodate changes in weather or delivery time. The seasonal differences were consistent with a higher dose being necessary when the plants were more prone to excessive elongation.

There appears to be an increment of growth that is eliminated by the mild mechanical stimulation reported here and that this response is easily saturated. Of course, more intense treatment will stress the plant to ultimately reduce growth to zero. These reductions in growth appear to be different responses to mechanical stimulation. Our interpretation is that the mild stimulation in our study provides a developmental cue and is not a reduction in growth due to stress.

A graded response to varying stimulation intensities has been described in many species. The response has occurred in growth and in the expression of touch-induced genes that regulate growth. In studies using several levels of stimulation, there was a graded increase in growth inhibition with increased mechanical stimulation in aster (Callistephus chinensis), dusty miller (Senecio bicolor), and petunia (Petunia) (Autio et al., 1994); lettuce (Wurr et al., 1986); tomato (Heuchert and Mitchell, 1983); and chrysanthemum (Beyl and Mitchell, 1977). These studies have not distinguished a biphasic response with a saturable response at small doses. In Arabidopsis, expression of the TCH genes that code for regulatory proteins is greater and lasts longer with increasing doses of mechanical stimulation (Braam and Davis 1990). The TCH4 gene, which codes for a wall-stiffening enzyme, xyloglucan endotransglycosylase, has the same response to varying doses of mechanical stimulation (Xu et al. 1995).

Brushing had a small effect on stem diameter, in some cases increasing it by $\approx 5\%$ at higher doses. To our knowledge, an increase in the stem diameter of tomatoes as a result of brushing has not been reported previously. Brushing often has no effect on the stem diameter, although some tomato cultivars respond to brushing with a reduction in diameter (Johjima and Latimer, 1992). Even when the stem diameter is not affected, there can be an increase in stem strength and rigidity (Heuchert et al., 1983). Our results indicate that it is possible to apply brushing in a dose that reduces height without decreasing the stem diameter.

Mechanical stimulation also has reduced the shoot dry weight of tomatoes with either brushing (Johjima and Latimer ,1992; Latimer and Thomas, 1991) or shaking (Mitchell et al., 1977). The should be limited to only as much stimulation as is necessary for the needed height control.

Brushing does not damage tomato transplants if treatments are applied carefully. In fact, brushing often improves tomato transplant appearance (Latimer and Thomas, 1991; Schnelle et al., 1994); we found a more uniform canopy and a better ability to maintain that appearance when the flats were transported.

Time interval. The time interval between strokes experienced by a given plant is small when flats are treated individually. For treatment of commercial quantities, such as whole benches, the interval may be longer. The effect of individual brush strokes would not be additive if some occur during a refractory period. Conversely, the individual strokes could be perceived as a series of individual subthreshold stimuli. Therefore, our objective in these experiments was to determine whether increasing the time interval between brush strokes can provide the same amount of height control as continuous brushing.

We found that the interval between strokes could be at least 10 min and still result in the same amount of height control as continuous brushing. The individual strokes are large enough stimuli to be perceived individually, and they are not followed by a refractory period. If either of these were the case, the long intervals would have had little or no effect. Furthermore, individual strokes with long time intervals were not perceived as separate treatments. If that had occurred, long intervals would have had a greater effect than continuous brushing. The response can be brief enough for either of these phenomena to occur. In beans, stem elongation ceases ≈ 6 min after mechanical stimulation and begins to recover after only 30 min (Jaffe, 1976). Longer intervals (2 to 6 h) are perceived as separate treatments. Tomato plants that received two or more daily shaking treatments responded more than those receiving the same dose in a single daily application (Mitchell et al., 1975; Piszczek and Jerzy, 1987).

For implementing this technique on a commercial scale, the treatment easily could be automated by modifying an irrigation boom. The interval may be several minutes, but the plant's response permits substantial flexibility.

Time of day. Stem elongation in herbaceous dicots is usually highest at the end of the light period and at the beginning of the dark

reduction in dry weight is gradual with greater stimulation (Autio et al., 1994; Heuchert and Mitchell, 1983) and is likely due to a change in the rate of photosynthesis, respiration, or both (Keller and Steffen 1995). Photosynthesis can be reduced as a result of transient stomatal closure following stimulation (Pappas and Mitchell, 1985).

Also, the shorter plants produced by brushing were correspondingly lower in dry weight. Unlike the elongation response, there was not a low dose that caused only redistribution of assimilates to produce shorter but stockier plants. Therefore, brushing is of value as a method of slowing growth temporarily if necessary, rather than as a method of increasing stockiness in all transplants. The amount of brushing

Table 2. The effect of time of day of brushing on tomato transplant growth.

Seeding	Time of day	Stem	Stem	Shoot dry
date	of treatment	length (cm)	diam (mm)	wt (mg)
February 1995	Nontreated	12.56 ± 0.39	2.30 ± 0.01	88 ± 2
	Morning	9.03 ± 0.19	2.28 ± 0.03	69 ± 5
	Evening	10.10 ± 0.40	2.34 ± 0.02	82 ± 2
LSD ^Z		1.02	NA	NA
F tests				
Overall		***	NS	NS
Treated vs. nontreated		***	NS	NS
Morning vs. evening		*	NS	NS
March 1995	Nontreated	12.3 ± 0.22	2.34 ± 0.02	86 ± 2
	Morning	8.87 ± 0.30	2.20 ± 0.04	72 ± 3
	Evening	8.95 ± 0.28	2.21 ± 0.03	72 ± 2
LSD		0.82	0.09	7
F tests				
Overall		***	**	***
Treated vs. untreated		***	**	***
Morning vs. evening		NS	NS	NS

^zFisher's protected LSD at P = 0.05. NA = not applicable.

^{NS,*,**,***}Main effects within column nonsignificant at P = or 0.05 significant at P < 0.05, 0.01, or 0.001, respectively.

Table 3. The effect of the stage of plant growth at the initial brushing treatment on height, stem diameter, and shoot dry weight of tomato transplants.

Canopy ht at treatment start (cm)	Stem length (cm)	Stem diam (mm)	Shoot dry wt (mg)
6	7.12 ± 0.45	1.88 ± 0.06	56 ± 5
8	7.99 ± 0.49	1.96 ± 0.08	61 ± 5
10	8.36 ± 0.52	1.96 ± 0.05	63 ± 4
nontreated	10.55 ± 0.31	2.06 ± 0.05	76 ± 6
LSD ^z	1.33	NA	NA
F test	***	NS	NS

²Fisher's protected LSD at P = 0.05.

^{NS, ***}Main effects within column nonsignificant at P = 0.05 or significant at P < 0.001, respectively.



Fig. 6. Treatment initiation. The treatment was begun at initial canopy heights of 6, 8, and 10 cm at the times indicated by vertical lines. The bars are the sE. The mean elongation rate was 5.9 mm d⁻¹ in the controls and before treatment began and 2.7 mm d⁻¹ after the treatment began.



Fig. 7. The effect of the number of days that treatment was applied on the stem length of tomato transplants. The duration of the treatment was varied by changing the date on which the treatment was begun. The regression line is height $= 10.6 \text{ cm} - 0.28 \text{ cm} \cdot d^{-1}$ of treatment $R^2 = 0.61$

period (Behringer and Davies, 1993; Beyl and Mitchell, 1977), which was true in the tomato seedlings grown under our commercial transplant–production conditions. However, the plants were more responsive to brushing in the morning than in the afternoon when it would have suppressed peak growth. In a similar experiment with seismic stress, tomatoes were unaffected by the time of day that they were shaken (Heuchert and Mitchell 1983), but chrysanthemums were more sensitive in the morning (Beyl and Mitchell 1977). The reduction may have been due to mechanical stimulation causing stomatal closure because photosynthesis would be reduced only in the morning treatment because the evening treatment was followed by darkness.

Since the time of day made little difference, the timing of the treatment, therefore, is quite flexible. It is more important to treat the plants when injury and the spread of disease are minimized; usually, that period occurs in the morning when the plants are neither wilting nor wet.

Stage of growth at treatment initiation. It may be advantageous to delay the beginning of treatment, either to limit the amount of handling of the plants or because the plants are growing on schedule. In earlier experiments using mechanical stimulation to control tomato transplant height, brushing was begun at the cotyledon stage (Baden and Latimer, 1991; Latimer and Thomas, 1991; Schnelle et al., 1994). Our experiments show that it is not necessary to begin treatments at such an early stage. Waiting until at least the first true-leaf stage to begin treatments reduces the risk of damage to the growing point and reduces the spread of disease by shortening the treatment period. Significant height control can be achieved without plant damage if treatments are begun before the canopy is 10 cm high. However, the amount of height control depends on the number of days the plants are treated. This effectively reduces the number of times that growers need to treat the plants. There is a large window of opportunity in which to begin treating transplants, providing growers with the flexibility to treat only if the plants are growing taller than appropriate for the scheduled finishing date.

Beginning the treatment period when the plant canopy was 10 cm tall often resulted in visible leaf damage. Uniform brushing was difficult because the plants laid down and became entangled. Also, the leaves were much more delicate and succulent at this stage of growth. The leaves were easily ripped and many developed pale or necrotic leaf margins 1 to 2 d after the treatments had begun. No such difficulties or damage were observed when the treatment applications that were begun at 6- and 8-cm canopy heights. When brushing was begun at these shorter heights, the plants were still easy to treat when they reached canopy heights of ≥ 10 cm. This result suggests that young leaves acclimate to the stress of brushing.

The results of all these experiments are consistent with the model that there is an increment of growth that is easily eliminated by mechanical stimulation, and the effect of the stimulation is expressed over ≈ 1 d. The data fit all the following predictions from that model. A relatively small amount of mechanical treatment, but one that significantly exceeds that caused by normal greenhouse operations, will eliminate the responsive increment of the stem elongation. When that increment of the stem elongation rate is eliminated, additional treatment will not be very effective. Brief stimuli are amassed over time and are expressed over the next day, so that the intervals between individual stimuli will not affect the response. If the response lasts ≈ 1 d, then the same response will be observed regardless of the time of day. Furthermore, the effect of the treatment will depend on the number of days that it was applied.

In the dose experiment that was performed during the local commercial growing season for tomato transplants, there was a significant amount of height control (20% to 25% reduction in height), a significant increase in stem caliper, a modest reduction in dry weight, and no visible plant damage. There was damage only if the first treatment was delayed until the canopy consisted of large succulent leaves. Taken together, these results suggest that brushing is a flexible treatment that can be modified easily to provide effective height control with minimal dry-weight reduction and plant damage.

Literature Cited

- Adler, P.R. and G.E. Wilcox 1987. Salt stress, mechanical stress, or chlormequat chloride effects on morphology and growth recovery of hydroponic tomato transplants. J. Amer. Soc. Hort. Sci. 112:22–25.
- Autio, J., I. Voipio, and T. Koivunen. 1994. Responses of aster, dusty miller, and petunia seedlings to daily exposure to mechanical stress. HortScience 29:1449–1452.
- Baden, S.A. and J.G. Latimer. 1991. An effective system for brushing vegetable transplants for height control. HortTechnology 2:412–414.
- Behringer, F.J. and P.J. Davies. 1993. The early time course of the inhibition of stem growth of etiolated pea seedlings by fluorescent light. Plant Growth Regula. 12:341–345.
- Beyl, C.A. and C.A. Mitchell. 1977. Characterization of mechanical stress dwarfing in chrysanthemum. J. Amer. Soc. Hort. Sci. 102:591–594.
- Biddington, N.L. and A.S. Dearman. 1985. The effect of mechanicallyinduced stress on the growth of cauliflower, lettuce and celery seedlings. Ann. Bot 55:109-119.
- Braam, J. and R.W. Davis. 1990. The mechanosensory pathway in *Arabidopsis*: Touch induced regulation of expression of calmodulin and calmodulin-related genes and alterations of development. Current Topics Plant Biochem. and Physiol. 9:85–100.
- Fletcher, B. 1984. Sugar beet growing in Japan. British Sugar Beet Rev. 52:8–10.
- Garton, R. 1990. Greenhouse production of vegetable transplants. Ag Canada, Ottawa.

Garton, R.W., J.K. Muehmer, and E.J. Tomecek. 1987. Growing vegetable transplants in plug trays. Ont. Ministry Agr. and Food Factsheet 87-007.

- Heins, R., and J. Erwin. 1990. Understanding and applying DIF. Greenhouse Grower February:73–78.
- Heuchert, J.C., J.S. Marks, and C.A. Mitchell. 1983. Strengthening of tomato shoots by gyratory shaking. J. Amer. Soc. Hort. Sci. 108:801–805.
- Heuchert, J.C. and C.A. Mitchell. 1983. Inhibition of shoot growth in greenhouse-grown tomato by periodic gyratory shaking. J. Amer. Soc. Hort. Sci. 108:795–800.
- Hickman, G.W., E.J. Perry, R.J. Mullen, and R. Smith. 1989. Growth regulator controls tomato transplant height. Calif. Agr. 43:19–20.
- Jaffe, M.J. 1976. Thigmomorphogenesis: Electrical resistance and mechanical correlates of the early events of growth retardation due to mechanical stimulation in beans. Zeitschrift fur Pflanzenphysiologie 78:24–32.
- Jaworski, C.A., R.E. Webb, S.A. Garrison, E.L. Bergman, and S. Shannon. 1970. Growth-retardant-treated tomato transplants. HortScience 5:255–256.

- Johjima, T. and J.G. Latimer. 1992. Brushing influences transplant growth and subsequent yield of four cultivars of tomato and their hybrid lines. J. Amer. Soc. Hort. Sci. 117:384–388.
- Keller, E. and Steffen K. L. 1995. Increased chilling tolerance and altered carbon metabolism in tomato leaves following application of mechanical stress. Physiol. Plant. 93:519–525.
- Latimer, J.G. 1990. Drought or mechanical stress affects broccoli transplant growth and establishment but not yield. HortScience 25:1233– 1235.
- Latimer, J.G. 1991. Mechanical conditioning for control of growth and quality of vegetable transplants. HortScience 26:1456–1461.
- Latimer, J.G. 1992. Drought, paclobutrazol, abscisic acid, and gibberellic acid as alternatives to daminozide in tomato transplant production. J. Amer. Soc. Hort. Sci. 117:243–247.
- Latimer, J.G. and P.A. Thomas. 1991. Application of brushing for growth control of tomato transplants in a commercial setting. HortTechnology 1:109–110.
- Marr, C.W. and M. Jirak. 1990. Holding tomato transplants in plug trays. HortScience 25:173–176.
- Mitchell, C.A., H.C. Dostal, and T.M. Seipel. 1977. Dry weight reduction in mechanically dwarfed tomato plants. J. Amer. Soc. Hort. Sci. 102:605– 608.
- Mitchell, C.A., C.J. Severson, J.A. Wott, and P.A. Hammer. 1975. Seismomorphogenic regulation of plant growth. J. Amer. Soc. Hort. Sci. 100:161–165.
- Ott, R.L. 1993. An introduction to statistical methods and data analysis. Duxbury Press, Belmont, Calif.
- Pappas, T. and C.A. Mitchell. 1985. Influence of seismic stress on photosynthetic productivity, gas exchange, and leaf diffusive resistance of *Glycine max* (L.) Merrill cv. Wells II. Plant Physiol. 79:285–289.
- Piszczek, P.M. and M. Jerzy. 1987. The response of tomato (*Lycopersicon esculentum* Mill.) transplants to mechanical stress. Acta Agrobotanica 40:5–14.
- Price, H.C. and B.H. Zandstra. 1988. Maximize transplant performance. Amer. Veg. Grower April:10–16.
- Schaefer, R.L. and E. Farber. 1992. The student addition of MINITAB, Release 8. Addison-Wesley Publishing Co., New York.
- Schnelle, M.A., B.D. McCraw, and T.J. Schmoll. 1994. A brushing apparatus for height control of bedding plants. HortTechnology 4:275–276.
- Shaw, L.N. 1993. Changes needed to facilitate automatic transplanting. HortTechnology 3:418–420.
- Smith, H. 1994. Sensing the light environment: The functions of the phytochrome family, p. 377–416. In: R.E. Kendrick and Kronenberg (eds.). Photomorphogenesis in plants. Kluwer Academic, Boston.
- Wester, M. and R. Nakazawa. 1992. AcqKnowledge: Waveform data analysis for the Macintosh version 2.0.1. BioPac Systems, Goleta, Calif.
- Wurr, D.C.E., J.R. Fellows, and P. Hadley. 1986. The influence of supplementary lighting and mechanically-induced stress during plant raising on transplant and maturity characteristics of crisp lettuce. J. Hort. Sci. 61:325–330.
- Xu, W., M.M. Purugganan, D.H. Polisensky, D.M. Antosiewicz, S.C. Fry, and J. Braam. 1995. Arabidopsis *TCH4*, regulated by hormones and the environment, encodes a xyloglucan endotransglucosylase. Plant Cell 7:1555–1567.