

# Daily shoot extension growth of peach trees growing on rootstocks that reduce scion growth is related to daily dynamics of stem water potential

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**Summary** We studied relationships between diurnal patterns of stem water potential ( $\Psi_{\text{STEM}}$ ) and stem extension growth of the same scion cultivar growing on three rootstocks with differing size-controlling potentials. The peach trees (*Prunus persica* (L.) Batsch) used in this field experiment consisted of an early-maturing freestone cultivar, 'Flavorcrest,' grafted onto three different rootstocks: Nemaguard (a vigorous seed-propagated control, *P. persica* × *P. davidiana* hybrid), Hiawatha (an intermediate vigor rootstock, derived from an open pollinated seedling of a *P. besseyi* × *P. salicina* hybrid) and K-146-43 (a semi-dwarfing rootstock, *P. salicina* × *P. persica* hybrid). Diurnal patterns of  $\Psi_{\text{STEM}}$  and stem extension growth were measured on six dates (March 29, April 12, April 26, May 10, May 24 and June 18) during the primary period of peach shoot extension growth. Rootstocks clearly affected diurnal patterns of  $\Psi_{\text{STEM}}$  and stem extension growth. Trees on K-146-43 had the lowest midday  $\Psi_{\text{STEM}}$  and stem extension growth. Differences among rootstocks in the amount of diurnal oscillation in  $\Psi_{\text{STEM}}$  explained stem extension rate differences induced by the three rootstocks. The sensitivity of shoot extension growth to tree water relations tended to decrease as the season progressed and was not apparent by mid-June. The results of the study indicate that water relations may play an important role in the dwarfing mechanism induced by size-controlling peach rootstocks.

**Keywords:** diurnal pattern of stem extension growth, diurnal pattern of stem water potential, dwarfing mechanism, dwarfing rootstocks, *Prunus persica*, water relations.

## Introduction

The physiological mechanism of the dwarfing effect induced by size-controlling rootstocks on the scion of compound trees is poorly understood. Several authors (Simons and Chu 1984, Ussahatanonta and Simons 1988, Soumelidou et al. 1994a, Salvatierra et al. 1998) have reported morphological and de-

velopmental anomalies (small vessels, swirling of vascular tissue, presence of necrotic areas, large amounts of non-conducting phloem) in the graft union of fruit trees grafted onto dwarfing rootstocks. Hence, it has been hypothesized that partial incompatibility between scion and dwarfing rootstock negatively affects the transport of water, solutes and hormones through the graft union. Jones (1984) correlated the dwarfing effect of apple rootstocks to a lower total solute content in the sap collected above the graft union compared to that extracted below the graft union. An influence of size-controlling rootstocks on leaf mineral content has also been reported for different fruit tree species (Simons and Swiader 1985, Tagliavini et al. 1992, Neilsen and Kappel 1996, Rosati et al. 1997, Ebel et al. 2000), but these effects may have been related to low nutrient uptake capability of the dwarfing rootstocks.

Lockard and Schneider (1981) hypothesized that dwarfing apple rootstocks were characterized by bark with a lower capability to transport auxins than invigorating rootstocks. They hypothesized that small amounts of auxins reaching the root system of dwarfing rootstocks would affect root growth, cytokinin production and, consequently, shoot growth. Successive studies in apple provided evidence that M9 dwarfing apple rootstock had lower basipetal auxin transport in apical shoots (Soumelidou et al. 1994b, Kamboj et al. 1997a, 1997b) and from scion leaves to roots (Kamboj et al. 1997a). Kamboj et al. (1999a) reported that cytokinin concentration in root pressure exudate and in shoot xylem sap was lower for dwarfing apple rootstocks than for invigorating rootstocks. Kamboj et al. (1999b) also reported that shoot bark of dwarfing rootstocks had higher concentrations of abscisic acid than vigorous rootstocks and speculated that abscisic acid may have an important role in polar auxin transport.

The central role of water in plant growth has been widely documented (Hsiao 1993, Kramer and Boyer 1995). Regulated water supply has been used as an agronomical tool to control vegetative growth in tree crops (Chalmers et al. 1981, Martin 1989). Berman and DeJong (1997a) modeled the diurnal

nal pattern of stem extension growth in peach as a function of temperature and stem water potential ( $\Psi_{\text{STEM}}$ ). There is also experimental evidence that the dwarfing mechanism of size-controlling rootstocks could be related to whole tree water relations. Giulivo and Bergamini (1982) reported that apple trees grafted onto dwarfing rootstocks (M9 and M26) had lower midday leaf water potentials ( $\Psi_{\text{LEAF}}$ ) than trees on invigorating rootstocks (M11 and seedling). Intermediate midday  $\Psi_{\text{LEAF}}$  were recorded in trees grafted onto semi-dwarf rootstocks (M111, MM104, MM106 and M7). Olien and Lakso (1984, 1986) also gave convincing evidence that midday  $\Psi_{\text{STEM}}$  measured on apple trees grafted onto M9 and M26 dwarfing rootstocks was lower than that of trees grafted on invigorating rootstocks (MM104, M7 and MM106). These authors suggested that the difference in midday  $\Psi_{\text{STEM}}$  could be related to low hydraulic conductivity of the root system of the dwarfing rootstock or at the graft union. This hypothesis could explain the results of Hussein and McFarland (1994), who reported that during the development of water stress, sap flow in apple trees on dwarfing rootstock (Mark) decreased faster than in trees on an invigorating rootstock (seedling). In addition, Olien and Lakso (1986) speculated that integration over the day and tree life of the  $\Psi_{\text{STEM}}$  differences induced by dwarfing apple rootstocks may have an effect on development and physiological functions of the tree, however the authors presented no experimental evidence to support this hypothesis.

The scarcity of suitable dwarfing rootstocks for peach has limited knowledge about size-control mechanisms in this species. Several promising size-controlling peach rootstocks are being evaluated at the University of California (Weibel 1999, DeJong et al. 2001). Weibel (1999) analyzed the diurnal patterns of stem extension growth and  $\Psi_{\text{STEM}}$  of peach trees grafted on size-controlling rootstocks using Nemaguard as a vigorous control. His work indicated that peach trees on Nemaguard rootstock tended to have slightly higher  $\Psi_{\text{STEM}}$  and stem extension growth rate during the day than trees on size-controlling rootstocks. However, Weibel (1999) conducted his study relatively late in the growing season, when shoot growth may already have slowed (DeJong et al. 1987) and differences in tree size may have masked rootstock effects on tree water relations.

The present work was initiated to test the hypothesis that if size-controlling rootstocks affect scion growth via water relations, this should be clearly detectable during the first part of the growing season (DeJong et al. 1987). The current study focused on three of the peach rootstocks studied by Weibel (1999). These were K-146-43, the most dwarfing rootstock in the trial; Hiawatha, a rootstock that produces trees of intermediate vigor, and Nemaguard, a vigorous rootstock used in commercial production. The purpose of the research was to study the relationships between diurnal patterns of  $\Psi_{\text{STEM}}$  and stem extension growth of the same scion cultivar growing on these three rootstocks. Specifically, the experiment was designed to (1) evaluate the influence of size-controlling peach rootstocks on the diurnal patterns of shoot growth and  $\Psi_{\text{STEM}}$

throughout the first half of the growing season, (2) correlate potential differences in daily shoot growth with differences in  $\Psi_{\text{STEM}}$  and (3) evaluate seasonal patterns of correlations between differences in stem growth and water relations.

## Materials and methods

### Experimental orchard

The study was carried out at the Kearney Agricultural Center of the University of California (Parlier, California, USA) during 2001. Peach trees (*Prunus persica* (L.) Batsch) used in the field experiment were an early-maturing freestone cultivar, 'Flavorcrest,' grafted on three different rootstocks: Nemaguard (a vigorous, seed-propagated *P. persica* × *P. davidiana* hybrid), Hiawatha (an intermediate vigor, open pollinated seedling of a *P. besseyi* × *P. salicina* hybrid) and K-146-43 (a semi-dwarfing *P. salicina* × *P. persica* hybrid). Trees were planted in 1996 and grown with a Kearney Agricultural Center perpendicular 'V' (DeJong et al. 1995) training system in a North-South orientation (the trees were spaced 4.88 × 1.98 m for Nemaguard, and 4.88 × 1.83 m for Hiawatha and K-146-43).

The experiment was conducted on five trees per rootstock within a larger trial designed to evaluate horticultural performance. Routine pest control treatments were provided according to a commercial protocol for fruit production. Trees were flood irrigated as necessary for 100% replacement of the computed evapotranspiration ( $ET_C = ET_O \times K_C$ ). The variable  $ET_O$  was calculated with the Penman-Monteith model and  $K_C$  was computed according to Goldhamer and Snyder (1989). Trees were irrigated at 2-week intervals until the end of May. In June, irrigation was reduced to once per week. All fruits were removed (April 11) to avoid the influence of crop load on shoot growth (Berman and DeJong 1997b) and tree water relations (Bianco et al. 1995). The trees were not summer-pruned during the experiment.

### Stem extension growth measurements

Diurnal patterns of stem extension growth rate were determined on six dates (March 29, April 12, April 26, May 10, May 24 and June 18). On the first measurement date (March 29) trees still bore fruit, but because the fruits were very small (full bloom occurred on March 7), we assumed that the effect of crop load on transpiration and shoot growth was negligible.

Stem extension was evaluated according to Berman and DeJong (1997a) with some modifications. Three homogeneous watersprouts (vigorous upright shoots arising from epicormic buds) per tree were selected (15 shoots per rootstock) on each date. On the first three dates, watersprouts from the lower part of the tree were used, whereas on the last three dates, when the canopies were starting to close, watersprouts from the external and mid-height part of the tree were used to avoid shading effects of the top of the tree. The evening before the measurement day, three fine permanent ink marks (10 mm apart) were made on each stem starting at the first visible

internode. The distance between two consecutive marks (two measurements per watersprout) was measured with a digital caliper (Mitutoyo, Tokyo, Japan) six times per day at 3- to 6-h intervals. The shortest intervals corresponded to late morning, afternoon and evening measurements, when the largest fluctuations in stem extension growth rate were expected to occur (Berman and DeJong 1997a). Stem growth was evaluated as relative extension growth rate (RER) computed as follows:

$$\text{RER} = \frac{L_H - L_K}{tL_K}$$

where  $L_H$  is the distance (mm) between two consecutive ink marks measured at time of day  $H$ ,  $L_K$  is the distance (mm) between the same ink marks at the previous measurement time of day ( $K$ ) and  $t$  is the time (h) between the two measurements. Daily RER was also computed for each segment of shoot delimited by ink marks. Means of the RER values relative to the two segments from the same shoot were computed for each measurement time of day. Time of day was expressed as Pacific standard time.

#### Water status measurements

Stem water potential measurements were made according to McCutchan and Shackel (1992) on the same six dates and at the same time of day as stem extension measurements. Starting on the second measurement date (April 12), an additional  $\Psi_{\text{STEM}}$  measurement was taken at 1400 h. On each date, one of the measurements was taken just before dawn (predawn  $\Psi_{\text{STEM}}$ ). Plastic bags covered with aluminum foil were placed over two shaded mature leaves per tree at least one hour before measurement in order to allow  $\Psi_{\text{LEAF}}$  to equilibrate with the water potential of the stem where leaves were attached. Leaves were sampled near the base of the trunk. Stem water potential was measured with a pressure chamber (Model 3005, Soil Moisture Equipment, Santa Barbara, CA).

Stomatal conductance was measured around solar noon on April 26 with a steady state porometer (LI-1600, Li-Cor, Lincoln, NE). Three well-lit mature leaves per tree (15 leaves per rootstock) were selected for the measurements.

#### Vegetative measurements

On June 19, the trunk circumference of the 15 trees was measured at 20 cm from the ground and trunk cross-sectional area (TCSA) was computed. On June 20, all the watersprouts on the 15 trees in the experiment were harvested. The total number of watersprouts per tree and total watersprout fresh mass per tree were determined. Watersprout dry mass and length (main shoot length plus sylleptic shoot length) were calculated from a subsample of five average sized watersprouts from each rootstock. The fresh subsamples were weighed, oven-dried at 65 °C to constant mass and weighed again to determine dry mass and the fresh to dry mass ratio.

#### Calculation of integrated daily $\Psi_{\text{STEM}}$ fluctuation and cumulative integrated $\Psi_{\text{STEM}}$ fluctuation

To quantify the daily oscillation in  $\Psi_{\text{STEM}}$ , an integrated daily  $\Psi_{\text{STEM}}$  fluctuation was calculated by subtracting  $\Psi_{\text{STEM}}$  at any moment from the daily maximum measured  $\Psi_{\text{STEM}}$  (usually the predawn value), and integrating this difference over a 24-h period (the integrated daily  $\Psi_{\text{STEM}}$  fluctuation was expressed in MPa h). We used this integrated value because the Berman and DeJong (1997a) model was based on the premise that stem extension growth is more closely related to fluctuations in  $\Psi_{\text{STEM}}$  than to absolute values of  $\Psi_{\text{STEM}}$ .

To quantify the seasonal effect of the integrated daily  $\Psi_{\text{STEM}}$  fluctuations on watersprout growth, a "cumulative integrated  $\Psi_{\text{STEM}}$  fluctuation" was calculated for each tree on the three rootstocks. This value was calculated as the integral of the daily  $\Psi_{\text{STEM}}$  fluctuation over the season (between the first and the last measurement date; a total of 81 days).

#### Temperature measurements

Temperatures were measured at a CIMIS (California Irrigation Management Information System) weather station located within 1 km of the experimental site.

#### Statistical analysis

All analyses were performed with SPSS software (SPSS, Chicago, IL). One-way analysis of variance (ANOVA) was used to evaluate the effects of the three rootstocks on the different parameters and a Tukey test with a 95% confidence interval was used as a *post hoc* test for mean separation.

Repeated measures analyses were performed to test the overall significance of the effects of rootstock, time and rootstock  $\times$  time interactions on the daily patterns (performed separately on each of the six dates) of stem RER and  $\Psi_{\text{STEM}}$ , and the seasonal patterns of daily stem RER, midday  $\Psi_{\text{STEM}}$  and integrated daily  $\Psi_{\text{STEM}}$  fluctuations. In the repeated measures analyses performed on the daily patterns of stem RER, single watersprouts were used as the experimental units, whereas in all other repeated measures analyses, a single tree was considered the experimental unit.

#### Results

At the end of the experiment (June 20), trees grafted on K-146-43 had the lowest TCSA, number of watersprouts per tree, and watersprout fresh and dry mass per tree (Tukey test;  $P \leq 0.05$ ) (Table 1). Hiawatha had an intermediate watersprout production and TCSA, but its TCSA was not significantly different from that of Nemaguard (Table 1). The scion cultivar TCSA and watersprout production of trees on K-146-43 was only one third that of trees on Nemaguard (Table 1).

Diurnal patterns of stem RER had a similar shape for all three rootstocks (Figures 1 and 2). On the six dates, peaks of stem growth rate occurred in the afternoon between 1400 and 1900 h, whereas the lowest growth rates occurred early in the morning and late at night. No significant differences in stem RER among rootstocks were found at any time of the day on

Table 1. Total numbers, and fresh and dry masses of watersprouts per tree and trunk cross-sectional area (TCSA) for trees on Nemaguard, Hiawatha and K-146-43. Each value is the mean of five trees.

Rootstock	Watersprouts			TCSA (cm <sup>2</sup> )
	Total number	Fresh mass (kg tree <sup>-1</sup> )	Dry mass (kg tree <sup>-1</sup> )	
Nemaguard	87.0 c <sup>1</sup>	14.2 c	5.2 c	182.4 b
Hiawatha	60.4 b	9.6 b	3.5 b	143.3 b
K-146-43	31.4 a	4.1 a	1.5 a	57.4 a

<sup>1</sup> Means followed by a different letter within a column are significantly different at the 5% level according to Tukey's test.

March 29 and April 12 (an unusually cool day) (Figure 1). Around 0300 and 0900 h on April 26, stem RERs in trees on K-146-43 were significantly lower than those in trees on Nemaguard or Hiawatha (Tukey test;  $P \leq 0.05$ ) (Figure 1), and around 2200 h, trees on Hiawatha had lower stem RERs than trees on Nemaguard (Tukey test,  $P \leq 0.05$ ). Around 0300 h on May 10 (Figure 2), stem RERs were lower in trees on K-146-43 than in trees on Nemaguard (Tukey test;  $P \leq 0.05$ ). In addition, differences in stem RER among rootstocks were also visible around 2000 h (ANOVA;  $P \leq 0.063$ ). Around 0900 and 2000 h on May 24, trees on K-146-43 and Hiawatha had lower stem RERs than trees on Nemaguard (Tukey test;

$P \leq 0.05$ ). On the last measurement date (June 18), no significant differences in stem RER among rootstocks were detected (Figure 2). On each date, the repeated measures analysis detected significant effects ( $P \leq 0.05$ ) of the rootstock and the time on the diurnal pattern of stem RER (Table 2), whereas the rootstock  $\times$  time interaction was significant only on May 24.

Stem water potential followed similar, nearly symmetric diurnal patterns throughout the season (Figures 1 and 2). Within each rootstock, the diurnal pattern became more pronounced as the season progressed. Maximum  $\Psi_{STEM}$  values occurred in the night and early morning, whereas the lowest values occurred between 1000 and 1400 h depending on measurement date (Figures 1 and 2). Differences in  $\Psi_{STEM}$  among rootstocks were observed at predawn (Figures 1 and 2). Predawn  $\Psi_{STEM}$  was significantly higher (Tukey test;  $P \leq 0.05$ ) in trees on K-146-43 and Hiawatha than in trees on Nemaguard throughout the season. Predawn  $\Psi_{STEM}$  did not differ significantly between trees on Hiawatha and trees on K-146-43 on most of the measurement dates (Tukey test;  $P \leq 0.05$ ). Predawn  $\Psi_{STEM}$  differences between trees on K-146-43 and Nemaguard (and also between trees on Hiawatha and Nemaguard) increased as the season progressed (0.018 MPa on March 29 and 0.128 MPa on June 18) (Figures 1 and 2). On each date, the repeated measures analysis detected significant effects ( $P \leq 0.05$ ) of rootstock (not significant on March 29), time and rootstock  $\times$  time interactions on the diurnal pattern of  $\Psi_{STEM}$  (Table 3).

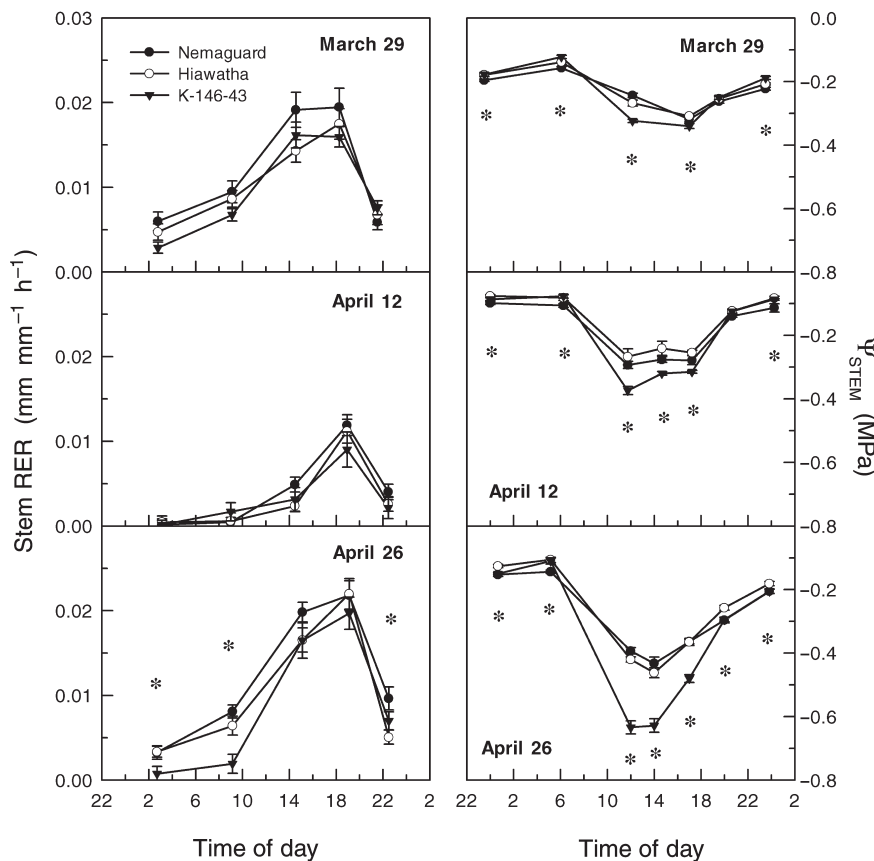


Figure 1. Diurnal patterns of stem relative extension growth rate (RER) and stem water potential ( $\Psi_{STEM}$ ) for trees on Nemaguard, Hiawatha and K-146-43 on March 29, April 12 and April 26, 2001. Bars indicate the standard error of the mean. Asterisks indicate significant differences between rootstocks at the 5% level based on one-way ANOVA.

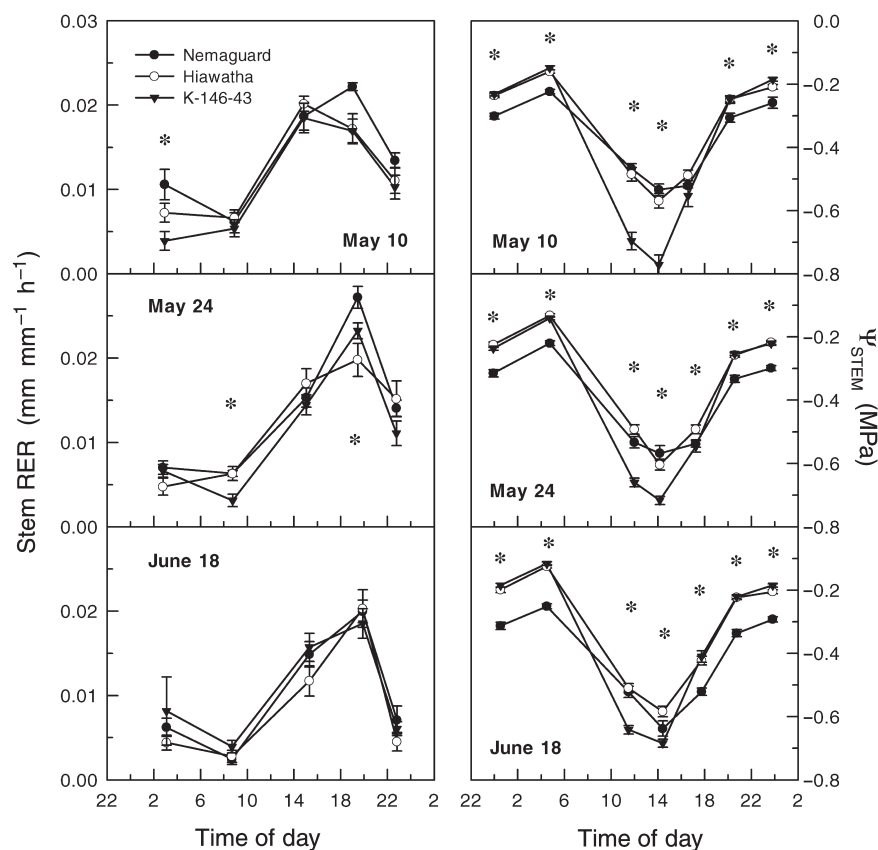


Figure 2. Diurnal patterns of stem relative extension growth rate (RER) and stem water potential ( $\Psi_{STEM}$ ) for trees on Nemaguard, Hiawatha and K-146-43 on May 10, May 24 and June 18, 2001. Bars indicate the standard error of the mean. Asterisks indicate significant differences between rootstocks at the 5% level based on one-way ANOVA.

Table 2. Significance of the effects of rootstock, time and rootstock  $\times$  time on the diurnal pattern of stem relative extension growth rate on six dates evaluated by repeated measures analysis. An individual watersprout was considered as the experimental unit.

Source	Probability					
	March 29	April 12	April 26	May 10	May 24	June 18
Rootstock	0.0191	0.0370	0.0034	0.0006	0.0357	0.1600
Time	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Rootstock $\times$ time	0.3815	0.6251	0.2302	0.3244	0.0050	0.7321

Table 3. Significance of the effects of rootstock, time and rootstock  $\times$  time on the diurnal pattern of stem water potential ( $\Psi_{STEM}$ ) on six dates evaluated by repeated measures analysis. An individual tree was considered as the experimental unit.

Source	Probability					
	March 29	April 12	April 26	May 10	May 24	June 18
Rootstock	0.5550	0.0006	0.0001	0.1094	0.0015	0.0001
Time	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Rootstock $\times$ time	0.0001	0.0002	0.0001	0.0001	0.0001	0.0001

Early in the season (March 29), trees on K-146-43 had mid-day  $\Psi_{STEM}$  values that were significantly lower (Tukey test;  $P \leq 0.05$ ) than trees on Nemaguard and Hiawatha (Figures 1–3). The daily maximum  $\Psi_{STEM}$  difference (always occurring around solar noon) between trees on K-146-43 and trees on Nemaguard tended to increase as the season progressed until

May 10 (0.08 MPa on March 29 and April 12; 0.24 MPa on April 26 and May 10). No significant differences (Tukey test;  $P \leq 0.05$ ) in midday  $\Psi_{STEM}$  were found between trees on Hiawatha and Nemaguard throughout the season (Figures 1–3). The repeated measures analysis detected significant effects ( $P \leq 0.05$ ) of rootstock, time and the rootstock  $\times$  time

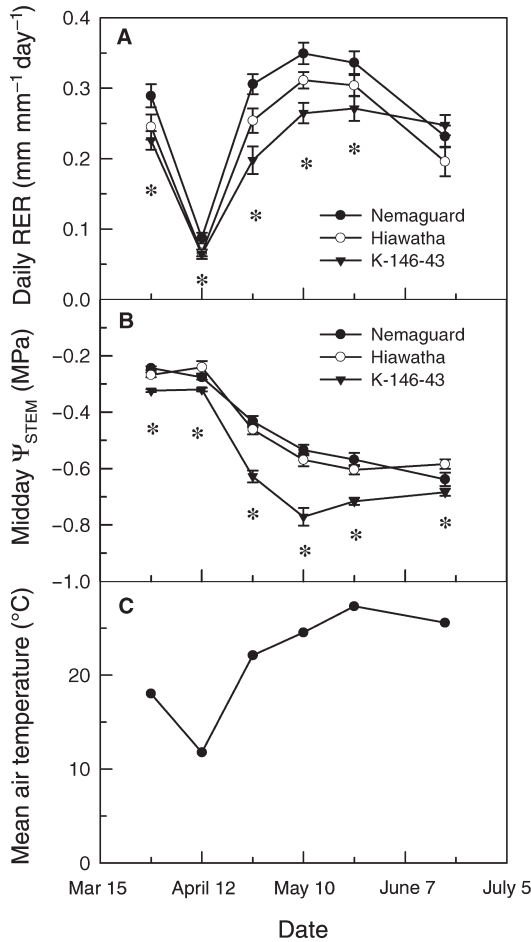


Figure 3. Seasonal patterns of (A) daily stem relative extension growth rate (RER), (B) midday stem water potential ( $\Psi_{STEM}$ ) of trees on Nemaguard, Hiawatha and K-146-43 and (C) mean air temperature. Bars indicate the standard error of the mean. Asterisks indicate significant differences between rootstocks at the 5% level based on one-way ANOVA.

interaction on the seasonal pattern of midday  $\Psi_{STEM}$  (Table 4).

Rootstocks significantly affected daily stem RER throughout the growing season (ANOVA;  $P \leq 0.05$ ), except on June 18 (Figure 3). Trees on K-146-43 had a daily stem RER that was significantly lower than trees on Nemaguard (Tukey test;

Table 4. Significance of the effects of rootstock, time and rootstock  $\times$  time on the seasonal patterns of daily stem relative extension growth rate (RER), midday stem water potential ( $\Psi_{STEM}$ ) and integrated daily  $\Psi_{STEM}$  fluctuation evaluated by repeated measures analysis. An individual tree was considered as the experimental unit.

Source	Probability		
	Daily stem RER	Midday $\Psi_{STEM}$	Integrated daily $\Psi_{STEM}$ fluctuation
Rootstock	0.0040	0.0001	0.0001
Time	0.0001	0.0001	0.0001
Rootstock $\times$ time	0.0574	0.0007	0.0048

$P \leq 0.05$ ) on each measurement date, except on the last day (Figure 3). Trees on Hiawatha appeared to have intermediate daily stem RER on most measurement dates (Figure 3), but no significant differences were detected between trees on Hiawatha and other rootstocks (Tukey test;  $P \leq 0.05$ ). The seasonal patterns of daily stem RER were similar in the three rootstocks, but some differences were found on the last two measurement dates, when trees on Nemaguard and Hiawatha had a decrease in daily stem RER, whereas daily stem RER of trees on K-146-43 was nearly constant (Figure 3). The sharp drop in daily stem RER in trees on all rootstocks on April 12 was related to temperature (Figure 3). The repeated measures analysis detected significant effects ( $P \leq 0.05$ ) of rootstock and time on the seasonal pattern of daily stem RER (Table 4).

Significant differences in integrated daily  $\Psi_{STEM}$  fluctuation among rootstocks were detected on each date (Figure 4). The integrated daily  $\Psi_{STEM}$  fluctuation of trees on K-146-43 was significantly (Tukey test;  $P \leq 0.05$ ) greater than that of trees on Nemaguard (Figure 4). Trees on Hiawatha had intermediate integrated daily  $\Psi_{STEM}$  fluctuation values throughout the season, and were statistically different from trees on Nemaguard on March 29 and June 18 (Tukey test;  $P \leq 0.05$ ). On the other hand, differences in integrated daily  $\Psi_{STEM}$  fluctuation between trees on Hiawatha and K-146-43 were significant (Tukey test;  $P \leq 0.05$ ) throughout the season. In addition, the repeated measures analysis detected significant effects ( $P \leq 0.05$ ) of rootstock, time and rootstock  $\times$  time interactions on the seasonal pattern of integrated daily  $\Psi_{STEM}$  fluctuation (Table 4).

For each measurement date, mean values of daily stem RER per tree were regressed against mean values of integrated daily  $\Psi_{STEM}$  fluctuation per tree (Figure 5). Significant negative linear relationships between the two parameters were found on March 29 ( $r^2 = 0.48$ ;  $P = 0.004$ ), April 26 ( $r^2 = 0.46$ ;  $P = 0.005$ ) and May 10 ( $r^2 = 0.53$ ;  $P = 0.002$ ). However, daily

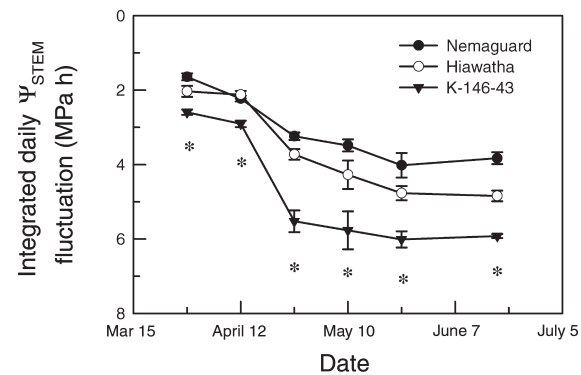


Figure 4. Seasonal patterns of integrated daily stem water potential ( $\Psi_{STEM}$ ) fluctuation for trees on Nemaguard, Hiawatha and K-146-43. The integrated daily  $\Psi_{STEM}$  fluctuation represents the difference in  $\Psi_{STEM}$  from the maximum measured  $\Psi_{STEM}$  (usually the predawn value) integrated over a 24-h period and expressed as MPa h. Bars indicate the standard error of the mean. Asterisks indicate significant differences between rootstocks at the 5% level based on one-way ANOVA.

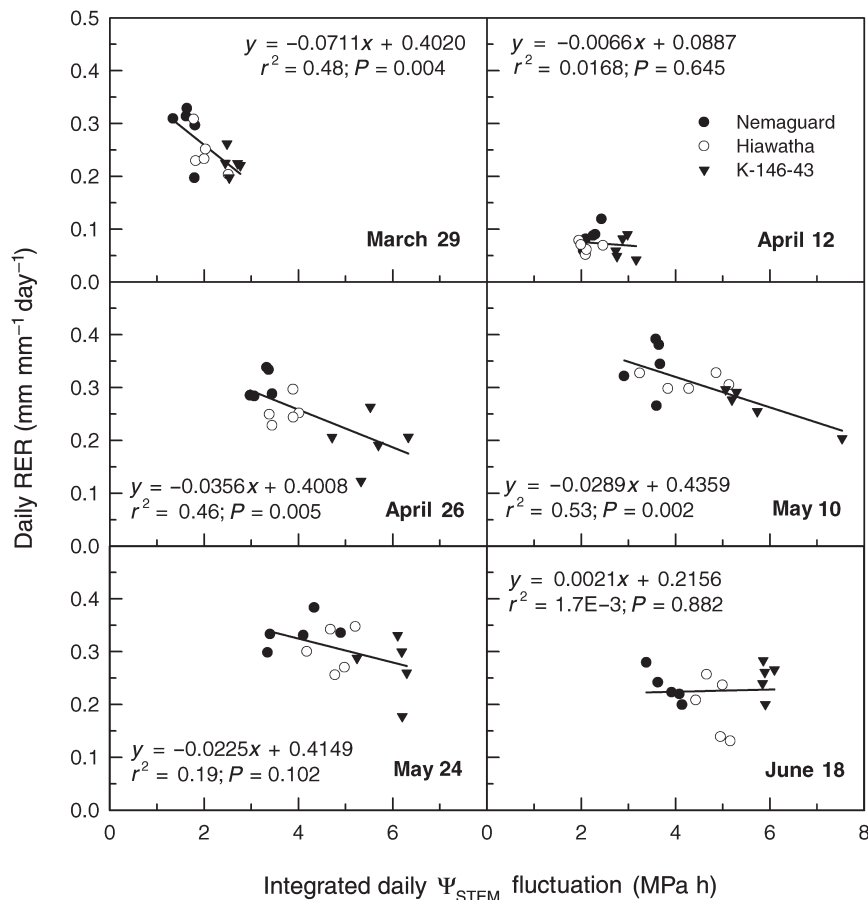


Figure 5. Relationships between daily stem relative extension growth rate (RER) and integrated daily stem water potential ( $\Psi_{STEM}$ ) fluctuation on March 29, April 12, April 26, May 10, May 24 and June 18, 2001 (see Figure 4 for details). Each point represents data from a single tree. Trees on different rootstocks are represented with different symbols.

stem RER was uncorrelated with integrated daily  $\Psi_{STEM}$  fluctuations on the other three measurement dates.

The cumulative integrated  $\Psi_{STEM}$  fluctuation was highly correlated ( $r^2 = 0.83$ ;  $P \leq 0.0001$ ) to the watersprout length at

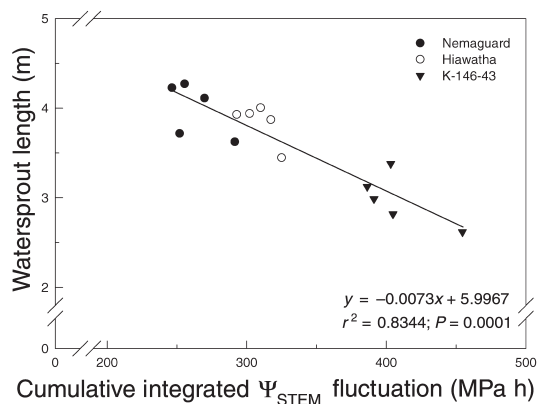


Figure 6. The relationship between mean watersprout length and cumulative integrated stem water potential ( $\Psi_{STEM}$ ) fluctuation for trees on Nemaguard, Hiawatha and K-146-43. Cumulative integrated  $\Psi_{STEM}$  fluctuations were calculated as integrals over the season (between the first and last measurement date; a total of 81 days) of the integrated daily  $\Psi_{STEM}$  fluctuations for each tree on the three rootstocks.

the end of the experiment (Figure 6).

On April 26, leaf stomatal conductance measured for trees on Nemaguard was  $507.8 \pm 34.3$  mmol m<sup>-2</sup> s<sup>-1</sup>, whereas trees on K-146-43 and Hiawatha had a leaf stomatal conductance of  $376.3 \pm 18.2$  and  $394.1 \pm 17.5$  mmol m<sup>-2</sup> s<sup>-1</sup>, respectively. Leaf stomatal conductances of trees on K-146-43 and Hiawatha were significantly lower (Tukey test;  $P \leq 0.05$ ) than those of trees on Nemaguard, whereas no significant differences were detected between trees on K-146-43 and Hiawatha.

## Discussion

The parameters measured to characterize tree growth highlighted dramatic rootstock effects on tree vigor. Results of our study confirm the size-controlling potential of the K-146-43 rootstock and the intermediate vigor of Hiawatha as reported previously (Weibel 1999, DeJong et al. 2001).

Throughout the experiment, diurnal patterns of stem RER, independent of the rootstock, were similar to those reported previously for peaches (Berman and DeJong 1997b). Trees on the three rootstocks had low stem RER during nighttime, even when trees were close to full hydration (just prior to dawn) and during the morning when plant dehydration occurred, whereas stem RER was high in the afternoon during  $\Psi_{STEM}$  re-

covery. Therefore, the relationship between stem RER and  $\Psi_{\text{STEM}}$  showed hysteresis, which was expected according to previous descriptions of both stem extension (Naor and Wample 1996) and diameter growth (Klepper et al. 1971). The presence of hysteresis indicates that another factor interacts with  $\Psi_{\text{STEM}}$  in determining the diurnal changes in stem RER. A previous study (Berman and DeJong 1997a) indicated that the primary factor driving the diurnal fluctuations of stem RER was air temperature. These authors demonstrated that the diurnal rate of change of  $\Psi_{\text{STEM}}$ , rather than  $\Psi_{\text{STEM}}$  by itself, could be used as a secondary factor with temperature to predict diurnal patterns of stem RER. The results of this study support these findings. Early in the morning, when temperature was increasing, stem RER did not keep pace with increases in temperature because  $\Psi_{\text{STEM}}$  was decreasing, whereas during the late afternoon, when temperature was decreasing, rapid growth was maintained as long as  $\Psi_{\text{STEM}}$  was recovering. Stem RER decreased again at night because of the low nighttime temperature, even though trees continued hydrating until dawn.

The main effect of the size-controlling rootstocks on stem RER occurred in the morning, but on May 10 and 24, some differences were also detected during the afternoon growth peak. There appeared to be a slight seasonality in the time of day at which the differences occurred, with differences occurring mainly in the morning early in the growing season and also in the afternoon later in the season.

The repeated measures analysis detected significant effects of rootstock on stem RER on the first five measurement dates (Table 2), even though on April 12, the difference among rootstocks in stem RER was less clear (Figure 1). These results suggest that size-controlling rootstocks affected shoot RER most when all conditions were favorable for maximum shoot growth. But on the low temperature day (April 12) and late in the season (June 18), the effect of the size-controlling rootstocks appeared to be weaker (Figure 3). The latter reduced rootstock effect on stem RER appeared to be related to the progressive slowing of stem growth later in the vegetative season as previously reported for peaches (DeJong et al. 1987). In the current experiment, stem RER of the trees on Nemaguard and Hiawatha decreased between the last two measurement dates. Weibel (1999) also indicated that K-146-43 and Hiawatha peach rootstocks had a slight effect on stem RER during late June.

Rootstocks did not affect the time of day when minimum  $\Psi_{\text{STEM}}$  occurred, but there were clear effects of the rootstocks on diurnal fluctuations of  $\Psi_{\text{STEM}}$  (Figures 1 and 2, Table 3). Trees on the most size-controlling rootstock, K-146-43, consistently had the highest predawn  $\Psi_{\text{STEM}}$  and the lowest midday  $\Psi_{\text{STEM}}$  on each measurement date. This apparent disagreement between the rootstock effects on predawn  $\Psi_{\text{STEM}}$  and midday  $\Psi_{\text{STEM}}$  was unexpected. Predawn water potential has been commonly used to estimate the water potential of soil around the root system (Kramer 1983). A strong correlation between predawn water potential and soil water content has been shown previously for similar irrigation management

strategies and soil conditions (Girona et al. 1993). Hence, the differences in predawn  $\Psi_{\text{STEM}}$  between rootstocks probably indicate that the trees on Nemaguard had higher water consumption than trees on Hiawatha and K-146-43. This may be related to the larger canopy size and presumably greater water use induced by the more vigorous Nemaguard rootstock. However, this putative greater water use did not appear to negatively influence leaf stomatal behavior because trees on Nemaguard had higher stomatal conductances than reported previously for nonstressed peach trees (e.g., Marsal and Girona 1997). However, the advantage of a relatively high predawn  $\Psi_{\text{STEM}}$  for the K-146-43 root system did not translate into a higher midday  $\Psi_{\text{STEM}}$  compared to trees on Nemaguard. A higher leaf stomatal conductance of trees on K-146-43 might explain this incongruence, but considering that leaves of trees on K-146-43 appeared to have the lowest stomatal conductance, this phenomenon is more likely related to other factors such as low water absorption capability of the root system compared to the transpiration demand of the canopy or a high hydraulic resistance of the root system or graft union. The latter hypothesis was suggested by Olien and Lakso (1986) to explain the lower  $\Psi_{\text{STEM}}$  values of apple trees on M9 and M29 dwarfing rootstocks compared to trees on invigorating rootstocks.

On the other hand, trees on Hiawatha had midday  $\Psi_{\text{STEM}}$  very similar to trees on Nemaguard, but the daily fluctuation of  $\Psi_{\text{STEM}}$  was larger for trees on Hiawatha than on Nemaguard because trees on Hiawatha had higher predawn  $\Psi_{\text{STEM}}$  (Figures 1 and 2). Thus, differences in midday  $\Psi_{\text{STEM}}$  did not appear to explain differences in vigor between trees on Nemaguard and Hiawatha (Figures 1–3, Table 1). Berman and DeJong (1997a) demonstrated that the rate of change of  $\Psi_{\text{STEM}}$  during a given interval of time during the day was more closely related to the stem elongation rate during the same period than was actual  $\Psi_{\text{STEM}}$ . Similarly, in the present study, diurnal changes in  $\Psi_{\text{STEM}}$  appeared to characterize rootstock effects on tree water relations better than  $\Psi_{\text{STEM}}$  values, as indicated by the rootstock  $\times$  time interaction. These interactions were highly significant even on the days when there was no significant rootstock effect (March 29, May 10; Table 3). Moreover, comparison of the daily patterns of  $\Psi_{\text{STEM}}$  and stem RER early in the season (Figure 1; March 29) with patterns later in the season (Figure 2; May 25, June 18) indicated that the magnitude of the changes and the timing of patterns of both parameters were linked. Thus, we hypothesized that there was a seasonal developmental effect related to rootstock differences in the hydration/dehydration events occurring during a 24-h period.

Daily stem RER of trees on the different rootstocks appeared to be affected mainly by temperature (Figure 3), but on each date, the stem RER differences among rootstocks appeared to be driven primarily by the integrated daily  $\Psi_{\text{STEM}}$  fluctuation (Figures 3 and 4). Thus, the rootstock effect on daily stem RER appeared to be correlated with the rootstock effect on integrated daily  $\Psi_{\text{STEM}}$  fluctuation.

The significant negative linear relationships between daily stem RER and integrated daily  $\Psi_{\text{STEM}}$  fluctuation (Figure 5)



suggested that the effects of the rootstock on watersprout growth and the amount of daily oscillation of  $\Psi_{STEM}$  were linked. However, if the measurement from April 12 is excluded (when low temperatures presumably masked rootstock effects on shoot growth), the slope of the regression line decreased as the season progressed. Thus, early in the season, shoot growth appeared to be most sensitive to the differences in water relations caused by rootstocks. Daily stem RER sensitivity to integrated daily  $\Psi_{STEM}$  fluctuation appeared to decrease progressively throughout the season and disappeared between May 24 and June 18. Because differences in water relations among trees on the three rootstocks were still present in these later measurements, it is possible that the insensitivity of shoot growth later in the season was related to ontogenetic changes in growth rate (DeJong et al. 1987). Alternatively, it may have been related to increasing competition among shoots at the canopy level in more vigorous trees. The highly significant relationship between watersprout length and cumulative integrated  $\Psi_{STEM}$  fluctuation (Figure 6) suggests that the large differences in vegetative vigor of trees on the three peach rootstocks are associated with differences in the daily dynamics of cumulative  $\Psi_{STEM}$  associated with the rootstocks. In addition, the integrated  $\Psi_{STEM}$  parameters appeared to explain vigor differences both among rootstocks and among trees on the same rootstock (Figure 6). Additional research is needed to determine the cause of the differences in daily dynamics of cumulative  $\Psi_{STEM}$  between these rootstocks and to investigate the relationships between individual shoot extension rates and the total number and size of watersprouts per tree.

Limited understanding of the physiology of the dwarfing mechanism in fruit tree rootstocks has been a major limitation to the development of suitable dwarfing rootstocks for commercial orchards of species like peaches and cherries. Our results indicate that water relations are involved in the dwarfing mechanism expressed by the peach rootstocks analyzed in the present study. However, our results do not exclude the possibility that, for these rootstocks, other mechanisms such as root–shoot hormonal signals may play a role in the final expression of the dwarf phenotype in the scion.

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