# Relationship of water status to vegetative growth and leaf gas exchange of peach (*Prunus persica*) trees on different rootstocks

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**Summary** We investigated relationships between tree water status, vegetative growth and leaf gas exchange of peach trees growing on different rootstocks under field conditions. Tree water status was manipulated by partially covering (0, ~30 and  $\sim$ 60%) the tree canopies on individual days and then evaluating the effects of tree water status on vegetative growth and leaf gas exchange. Early morning stem water potentials were approximately -0.4 MPa for trees in all treatments, but mean midday values ranged from -1.1 to -1.7 MPa depending on rootstock and canopy coverage treatment. Relative shoot extension growth rate, leaf conductance, transpiration rate and net CO<sub>2</sub> exchange rate differed significantly among trees in the different rootstocks and canopy coverage treatments. Shoot extension growth rate, leaf conductance, leaf transpiration rate and leaf net CO<sub>2</sub> exchange rate were linearly correlated with midday stem water potential. These relationships were independent of the rootstock and canopy coverage treatments, indicating that tree water relations are probably directly involved in the mechanism that imparts vegetative growth control by selected peach rootstocks.

Keywords: dwarfing rootstocks, leaf conductance, leaf photosynthesis, shoot growth, size-controlling rootstocks, stem water potential, water relations.

## Introduction

The well-documented interaction between shoot growth and root growth (Troughton 1977, Schulze 1983, Wilson 1988) is based on the complementary functions of shoots and roots. Several hypotheses have been advanced to explain this growth regulation between shoots and roots, and can be classified as having either a functional or a hormonal basis. Functional hypotheses propose that shoot growth is limited by the water or mineral nutrient supply from the roots, and that root growth is limited by the carbon supply from the shoots (Brouwer 1962). There is evidence that sucrose and nitrogen may be responsible for such shoot and root growth regulation (Minchin et al. 1994, Scheible et al. 1997). The hormonal hypotheses propose that shoot growth is influenced by plant growth regulators produced in roots and that root growth is influenced by plant growth regulators produced in shoots (Sachs 1972). Abscisic acid (Saab et al. 1990), cytokinins (Fetene and Beck 1993) and auxins (Reed et al. 1998) may be implicated in this shoot and root growth regulation. Although there have been some improvements in understanding shoot and root growth regulation over the years, there remains considerable disagreement on the underlying physiological mechanisms.

The present study pertains to the relationship between shoot and root that occurs in composite fruit trees. The composite fruit tree is a combination of two genotypes: scion (shoots) and rootstock (roots). It has been established that the rootstock can have a substantial influence on the vegetative growth and development of the tree; however, there is no convincing mechanistic explanation for this phenomenon. Various hypotheses, which have been reviewed by Rogers and Beakbane (1957), Lockard and Schneider (1981) and Webster (1995), propose that rootstocks have an effect on vegetative growth by influencing the tree hormonal status (Kamboj et al. 1999), mineral nutrition status (Jones 1971) or water status (Olien and Lakso 1986). It has been argued that the differences in rootstock effects on one or more of these processes account for the observed differences in the vegetative growth of the trees. The rootstock effect on these processes has been related to the different rootstock capacities to transport plant growth regulators (Kamboj et al. 1997), water (Cohen and Naor 2002) and mineral nutrients (Jones 1974) throughout the tree. However, there have been no conclusive studies directly linking any of these processes to rootstock effects on tree vegetative growth. The hypotheses that have been advanced remain to be conclusively demonstrated and refined before a satisfactory mechanistic explanation of rootstock action is clearly understood.

Recent research has identified a series of rootstocks that cause differing amounts of vegetative growth in peach trees. A comparative study of these peach rootstocks showed that specific rootstocks had significant effects on shoot growth rate and stem water potential during the day (Weibel et al. 2003). The differences in shoot growth rates appeared to correspond with differences in stem water potential among rootstocks. Similar results were previously reported for apple rootstocks by Olien and Lakso (1986) who suggested that such differences in stem water potential may be related to differences in the hydraulic conductance of the rootstocks. Higgs and Jones (1990) reached similar conclusions that were later confirmed by Cohen and Naor (2002). Additional evidence for a comparable phenomenon occurring in peach rootstocks came from a study by Basile et al. (2003a) on the same peach rootstocks that had been studied by Weibel et al. (2003). Basile et al. (2003a) followed stem water potential and shoot growth rate during the day over the early part of the growing season and found a strong positive correlation between changes in stem water potential and shoot growth rate over a day. More importantly, vegetative growth was correlated with cumulative stem water potential differences over a growing season. Therefore, it appears that the effect of the peach rootstocks on tree vegetative growth may be caused by differences in tree water status. However, no study has directly evaluated the response of shoot growth rate to water potential manipulations among peach trees on different rootstocks.

Another consideration when studying rootstock effects on tree water relations is leaf function. Tree water status is an important internal factor that affects leaf gas exchange (Schulze and Hall 1982). Stomatal conductance exhibits a negative feedback response to leaf water potential. This proposed stomatal regulatory mechanism has recently received considerable experimental support (Saliendra et al. 1995, Fuchs and Livingston 1996, Comstock and Mencuccini 1998). These studies used the root pressurization method to independently manipulate water status in order to evaluate stomatal responses. They showed that leaf water potential could account for the stomatal responses under various environmental conditions.

There have been several attempts to compare tree water status and leaf gas exchange among trees on different rootstocks. Olien and Lakso (1986) found no relationship between stem water potential and stomatal conductance among apple rootstocks that were associated with different amounts of vegetative growth control. A similar result was also reported by Higgs and Jones (1990) although in their study stomatal conductance differed significantly among apple rootstocks. In contrast, Cohen and Naor (2002) found a positive relationship between tree water status and canopy conductance among trees on the same rootstocks used by Olien and Lakso (1986) and Higgs and Jones (1990). Therefore, it appears that a direct connection among rootstocks and the relationship between tree water relations and leaf conductance remains elusive.

We tested the hypothesis that rootstock effects on vegetative growth result from differences in tree water status. Specifically, we investigated water status, vegetative growth and leaf gas exchange of peach trees on different rootstocks growing in the field. We focused on how vegetative growth and leaf gas exchange respond to direct manipulation of water status of trees growing on different rootstocks. The experiment was designed to determine the relationships among tree water status, vegetative growth and leaf gas exchange. This objective was achieved by temporarily covering the canopies of trees growing on three different rootstocks to differing extents and then evaluating how the resulting differences in tree water status affected vegetative growth and leaf gas exchange.

#### Materials and methods

One-year-old peach trees (Prunus persica var. nectarina, cv. 'Mayfire'), grafted on three different rootstocks were grown at the Kearney Agricultural Center, Parlier, CA. The selected rootstocks have previously been shown to impart low (Prunus salicina Lindl. × Prunus persica L. Batsch hybrid, cv. 'K146-43'), intermediate (Prunus besseyi Bailey × Prunus salicina Lindl. hybrid, cv. "Hiawatha") and high (Prunus persica L. Batsch × Prunus davidiana hybrid, cv. "Nemaguard") vegetative growth potential (Weibel et al. 2003). The trees were propagated and grown for one season in a commercial nursery and then lifted, pruned to about 0.5 m above the graft union and planted in the field in February 2002. After planting, cultural management practices were conducted as in a commercial orchard. The soil was amended with 0.5 kg per tree of 15,15,15 (N,P,K; Hydro Agri, Oslo, Norway) at the time of planting and then with 0.2 kg per tree of 15.5,0,0 fertilizer (N,P,K) once per month. Trees were irrigated with microsprinklers once per week to replace the estimated evapotranspiration.

The tree water status manipulation experiment and physiological measurements were conducted during July. Tree canopies were partially covered (0, -30 and -60%) on specific days to manipulate tree water status. Tree canopies were covered the afternoon before the day of physiological measurements. Prior to covering each tree canopy, the basal diameter of each major shoot on the tree was recorded with a digital caliper (Mitutoyo, Tokyo, Japan) and used to estimate the number of shoots that needed to be covered in order to obtain the desired canopy coverage percentage. Later, a significant correlation between shoot diameter and leaf area confirmed these estimations ( $r^2 = 0.79$ , P = 0.002). Individual shoots were wrapped with polyethylene film and then completely covered with an aluminum-impregnated reflective foil (Advanced Foil Systems, Ontario, USA). Air temperature was measured in canopy-covered and exposed trees with a Fluke 2190A/Y2001 thermocouple digital thermometer (Fluke, Everett, WA). Canopy temperatures did not differ significantly between covered canopies and exposed canopies (data not shown). The experiment was a 3 × 3 factorial in a complete randomized block design with five replications, two trees per replication and measurement days as a blocking factor.

Shoot growth was measured by photographing three shoot tips of each tree every 3 h from 0600 to 2100 h. The uppermost shoot tips were initially marked with ink between the first visible node and seventh node where most of the extension growth occurs over a day (Berman and DeJong 1997*a*). The shoot tips were photographed with a Nikon Coolpix 995 digital camera (Nikon, Tokyo, Japan). Millimetric paper was used as a reference scale and background for each photograph. A stand was constructed to keep the shoot tip and millimetric paper at a constant distance, inline and squared with the lens of the camera. Later, the images were analyzed with SigmaScan image analyzer software (SPSS, Chicago, IL). Instant relative shoot extension growth rate (RSEGR $_i$ ) was calculated as:

$$RSEGR_{i} = \frac{Log_{n}(L_{2}) - Log_{n}(L_{1})}{T_{2} - T_{1}}$$
(1)

where  $L_2$  and  $L_1$  are the shoot lengths at times  $T_2$  and  $T_1$  and relative shoot extension growth rate has units of  $h^{-1}$ .

Stem water potential was measured on three leaves per tree by the pressure chamber method (Scholander et al. 1965) at predawn and then every 3 h from 0600 to 2100 h. Stem water potential was estimated by enclosing fully mature leaves in an aluminum-foil-coated polyethylene bag, allowing the leaf to equilibrate with the water potential of the stem for at least 1 h (Begg and Turner 1970). The excised covered leaves from the base of the selected shoots were pressurized with a pressure chamber (Model 3005, Soil Moisture Equipment, Santa Barbara, CA).

Leaf conductance, net CO<sub>2</sub> exchange rate and transpiration rate were measured on five fully mature and well-exposed leaves of each tree with an LI-6400 infrared gas analyzer (Li-Cor, Lincoln, NE) every 3 h from 0600 to 1800 h. Reference CO<sub>2</sub> concentration in the leaf chamber was controlled at 400  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. Photosynthetic photon flux (PPF), reference air temperature and relative humidity in the leaf chamber were similar to the environment during the day and all measurements were made on clear, sunny days. In addition, intercellular CO2 concentration versus leaf net CO2 assimilation curves were determined on fully mature well-exposed leaves with an LI-6400 infrared gas analyzer by changing the reference CO<sub>2</sub> concentration in the leaf chamber, in a stepwise manner, from 0 to 800  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. For these measurements, PPF, reference air temperature and relative humidity in the leaf chamber were set to 1000  $\mu mol~m^{-2}~s^{-1},~25~^\circ C$  and 70%, respectively.

Statistical analyses of the data were made with SAS statistical software (SAS Institute, Cary, NC). Multiple linear regression analysis was used to test the rootstock and canopy coverage effects on diurnal variations of relative shoot extension growth rate, stem water potential, leaf conductance, net CO<sub>2</sub> exchange rate and transpiration rate. Mean separation among rootstock and canopy coverage treatments were carried out with a 0.05 level of significance by the Tukey pairwise comparison test. Midday stem water potential was estimated by finding the minimum of the fit polynomial function for each rootstock and canopy coverage combination treatments on each measurement day. Mean relative shoot extension growth rate was estimated by fitting an exponential function to the shoot extension growth over time for each combination of rootstock and canopy coverage treatments. Mean leaf conductance, net CO2 exchange rate and transpiration rate were also estimated by integrating the respectively fit polynomial functions for each combination of rootstock and canopy coverage treatments for each measurement day. Multiple linear regression analyses were used to examine the relationship between midday stem water potential and mean relative shoot extension growth rate, leaf conductance, net CO<sub>2</sub> exchange rate and transpiration rate among trees on different rootstocks. Nonlinear regression analysis was used to estimate the parameters of the relationship between intercellular  $CO_2$  concentration and leaf net  $CO_2$  assimilation rate among trees in the rootstock and canopy coverage treatments. Analysis of variance was used to evaluate the rootstock and canopy coverage effects on these parameters.

## Results

VEGETATIVE GROWTH AND WATER RELATIONS OF PEACH ROOTSTOCKS

The rootstock and canopy coverage treatments had significant effects on stem water potential over a day (Figure 1). Mean



Figure 1. Diurnal patterns of stem water potential of peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Individual values represent the mean for two trees on a given measurement day (n = 540). Upper panel: lines represent fitted simple quadratic regressions for each rootstock. 'Nemaguard':  $y = 0.01x^2 - 0.37x + 1.18$ ,  $r^2 = 0.68$ ; 'Hiawatha':  $y = 0.02x^2 - 0.44x + 1.47$ ,  $r^2 = 0.71$ ; and K14-43:  $y = 0.02x^2 - 0.45x + 1.51$ ,  $r^2 = 0.67$ . Lower panel: lines represent the fitted simple quadratic regression for each canopy coverage treatment. 0%:  $y = 0.02x^2 - 0.50x + 1.76$ ,  $r^2 = 0.83$ ; 30%:  $y = 0.02x^2 - 0.41x + 1.39$ ,  $r^2 = 0.71$ ; and 60%:  $y = 0.01x^2 - 0.34x + 1.09$ ,  $r^2 = 0.69$ .

midday stem water potential differed significantly among trees in the different rootstock (P = 0.0039) and canopy coverage (P = 0.0001) treatments (Figure 2). Trees grafted on 'Nemaguard' had a higher mean midday stem water potential than trees on 'Hiawatha' and 'K146-43'. Trees with 60% of their canopies covered had the highest mean midday stem water potential followed by trees with 30 and 0% of their canopies covered. There was no significant interaction effect between rootstock and canopy coverage treatment on midday stem water potential. Predawn stem water potential did not differ significantly among trees in the different rootstock or canopy coverage treatments (data not shown). Mean predawn stem water potential was -0.425 MPa.

The rootstock and canopy coverage treatments had significant effects on relative shoot extension growth rate over a day (Figure 3). Mean relative shoot extension growth rate differed significantly among trees in the different rootstock (P =0.0213) and canopy coverage (P = 0.0036) treatments (Figure 4). Trees grafted on 'Nemaguard' had a higher mean relative shoot extension growth rate than trees on 'K146-43'. In addition, trees with 60% of their canopies covered had the highest mean relative shoot extension growth rate followed by trees with 30 and 0% of their canopies covered. The interaction term between rootstock and canopy coverage treatments was not significant for relative shoot extension growth rate.

Daily mean leaf conductance, net  $CO_2$  exchange rate and transpiration rate differed significantly among trees in the different rootstock (P = 0.0004, 0.0341 and 0.0063, respectively) and canopy coverage (P = 0.0058, 0.0201 and 0.0029, respectively) treatments (Figure 5). Trees grafted on 'Nemaguard'



Figure 2. Midday stem water potentials in the 0, 30 and 60% canopy coverage treatments in peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Values represent the mean for 10 trees  $\pm$  standard error (n = 90). Values not connected by the same letter are significantly different among rootstocks and canopy coverage treatments with a 0.05 level of significance according to Tukey's mean comparison test.



Figure 3. Diurnal patterns of relative shoot extension growth rate of peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Individual values represent the mean for two trees on a given measurement day (n = 540). Upper panel: lines represent fitted simple quadratic regressions for each rootstock. 'Nemaguard':  $y = 0.002x^2 - 0.047x + 0.270$ ,  $r^2 = 0.76$ ; 'Hiawatha':  $y = 0.002x^2 - 0.044x + 0.255$ ,  $r^2 = 0.77$ ; and K14-43:  $y = 0.002x^2 - 0.038x + 0.224$ ,  $r^2 = 0.66$ . Lower panel: lines represent the fitted simple quadratic regression for each canopy coverage treatment. 0%:  $y = 0.002x^2 - 0.042x + 0.253$ ,  $r^2 = 0.65$ ; 30%:  $y = 0.002x^2 - 0.042x + 0.253$ ,  $r^2 = 0.69$ ; and 60%:  $y = 0.002x^2 - 0.047x + 0.270$ ,  $r^2 = 0.64$ .

had higher mean leaf conductance, net  $CO_2$  exchange rates and transpiration rates than trees on 'Hiawatha' and 'K146-43'. In addition, trees with 60% of their canopies covered had higher mean leaf conductances, net  $CO_2$  exchange rates and transpiration rates than trees with 30 or 0% of their canopies covered. The relationship between intercellular  $CO_2$  concentration and leaf net  $CO_2$  assimilation rate did not differ significantly among rootstock and canopy coverage treatments (Figure 6). There were no significant interaction effects between rootstock and canopy coverage treatments on the measured leaf gas exchange parameters.



Figure 4. Relative shoot extension growth rates in the 0, 30 and 60% canopy coverage treatments in peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Values represent the mean of 10 trees  $\pm$  standard error (n = 90). Values not connected by the same letter are significantly different among rootstocks and canopy coverage treatments with a 0.05 level of significance according to Tukey's mean comparison test.

There was a significant negative correlation (P = 0.0012) between exposed leaf area and midday stem water potential (Figure 7). The interaction term between rootstock and exposed leaf area was also significant for midday stem water potential (P = 0.0112).

Daily mean relative shoot extension growth rate, leaf conductance, net  $CO_2$  exchange rate and transpiration rate were significantly correlated with midday stem water potential (P =0.0101, 0.0076, 0.0193 and 0.00917, respectively). These relationships were not significantly affected by either the rootstock or the canopy coverage treatments (Figures 8 and 9).

### Discussion

The different rootstock and canopy coverage treatments had significant effects on tree water status, vegetative growth and leaf gas exchange over a day (Figures 1 and 2). Despite regular weekly irrigations, midday stem water potentials of the trees were somewhat lower than commonly measured in field-grown peach trees in central California (Weibel et al. 2003, Basile et al. 2003*a*). However, it is unlikely that limited soil water availability was responsible for the differences among treatments observed in these experiments because all trees recovered to similar predawn stem water potentials (–0.425 MPa). In addition, if lack of soil water was a factor, trees with the smallest canopies (i.e., trees on 'K146-43' root-stock) should have had the highest midday stem water potentials as observed in the canopy coverage treatments. The rather



Figure 5. Daily mean leaf conductance, net  $CO_2$  exchange rate and transpiration rate in the 0, 30 and 60% canopy coverage treatments in peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Values represent the mean of 10 trees ± standard error (n = 90). Values not connected by the same letter are significantly different among rootstocks and canopy coverage treatments with a 0.05 level of significance according to Tukey's mean comparison test.



Figure 6. Relationship between intercellular CO<sub>2</sub> concentration and leaf net CO<sub>2</sub> assimilation rate of peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Individual values are from individual trees on a given measurement day (n = 225). The solid line represents the fitted Farquhar and Von Caemmerer CO<sub>2</sub> assimilation model for all the combinations of rootstock and canopy coverage treatments.  $A = (78.9 (\pi - 76.1)/(\pi + 213.4)) - 20.7$ ,  $r^2 = 0.84$ .

low midday stem water potential values that we observed probably reflect the hot (36.4 °C mean maximum air temperature) and dry (29.6% mean minimum realive humidity)



Figure 7. Relationship between exposed leaf area and midday stem water potential of peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Individual values represent the mean for two trees on a given measurement day (n = 90). The solid line represents the fitted simple linear regression for each rootstock. 'Nemaguard': y = -0.08x - 0.83,  $r^2 = 0.51$ ; 'Hiawatha': y = -0.20x - 1.10,  $r^2 = 0.62$ ; and K14-43: y = -1.30x - 0.98,  $r^2 = 0.71$ .



Figure 8. Relationship between midday stem water potential and relative shoot extension growth rate of 0, 30 and 60 percent of canopy covered peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' root-stocks. Individual values represent the mean for two trees on a given measurement day (n = 90). The solid line represents the fitted simple linear regression for all the combinations of rootstock and canopy coverage treatments. y = 0.004x - 0.129,  $r^2 = 0.47$ .

weather that prevailed during the measurement period and the fact that the experiment was conducted in an open field with no ground cover and a highly reflective soil surface.

Differences in midday stem water potential corresponded with differences in relative shoot extension growth rate among rootstock and canopy coverage treatments (Figures 2 and 4). Additionally, the daily relative shoot extension growth rate pattern was similar to the daily stem water potential pattern among rootstock and canopy coverage treatments (Figures 1 and 3). Stem water potential and relative shoot extension growth rate decreased during the morning and increased during the afternoon. Differences in relative shoot extension growth occurred simultaneously with differences in stem water potential during the afternoon and evening. However, differences in shoot extension growth rates among treatments were not apparent during the morning despite the differences in stem water potential. These responses are similar to the shoot growth responses to mild water stress reported by Berman and DeJong (1997b) where differences in shoot extension growth rates were primarily apparent during the afternoon even though differences in stem water potential were apparent in the morning. According to the growth model proposed by Berman and DeJong (1997a), this temporal pattern can be explained by the relatively lower temperatures in the morning compared with later in the afternoon, and the decline in stem water potentials during this period.

The differences in stem water potential corresponded with differences in leaf conductance among rootstock and canopy coverage treatments (Figures 2 and 5). However, the differences in leaf conductance did not explain the differences in



Figure 9. Relationship between midday stem water potential and leaf conductance, net CO<sub>2</sub> exchange and transpiration rates in the 0, 30 and 60% canopy coverage treatment in peach trees on Nemaguard, Hiawatha and K146-43 rootstocks. Individual values represent the mean for two trees on a given measurement day (n = 90). Lines represent the fitted simple linear regression for all combinations of rootstock and canopy coverage treatments. y = 0.067x + 21.050,  $r^2 = 0.62$ ; y = 0.028x + 8.450,  $r^2 = 0.62$ ; and y = 126x + 332,  $r^2 = 0.71$ .

stem water potential because leaf conductance was highest in the trees with the lowest stem water potentials. Leaf conductance was presumably a major determinant of the observed differences in leaf net  $CO_2$  exchange rate among rootstocks and canopy coverage treatments because there were no significant differences in intrinsic photosynthetic capacity (Figure 6) as indicated by the relationship between intercellular  $CO_2$  concentration and leaf net  $CO_2$  assimilation rate (Schulze and Hall 1982). Steinberg et al. (1989) also reported a stomatal limitation on photosynthesis in water-stressed peach trees. Thus, the results show that rootstock and canopy coverage treatments had similar effects on tree water status, vegetative growth and leaf gas exchange, implying a similar physiological response.

It is well documented that when a tree canopy is partially covered there is a significant decrease in tree transpiration and an increase in water potential (Figure 7) that in turn affects shoot growth rate (Berman and DeJong 1997a) and leaf gas exchange (Whitehead et al. 1996). The evidence suggests that the compensatory responses in shoot growth rate and leaf gas exchange following partial canopy coverage are generated by changes in water potential. Long-term partial canopy coverage or leaf removal treatments would be expected to have a pronounced effect on the accumulation and distribution of dry matter (Meinzer and Grantz 1990), but such effects would not be expected in response to our short-term coverage treatments. Therefore, the rootstock effects on vegetative growth and leaf gas exchange in our current experiments appear to be causally related to the measured differences in tree water status. This is further demonstrated by integrating the effects of rootstock and canopy coverage on the relationships between tree water status and vegetative growth and leaf gas exchange (Figures 8 and 9). Relative shoot extension growth rate was linearly related to stem water potential across both rootstock and coverage treatments (cf. Basile et al. 2003a). Furthermore, leaf conductance, and consequently leaf net CO2 exchange and transpiration rates, were also linearly related to stem water potential across both treatments. Given the short term nature of the coverage treatments, these differences in leaf performance were not translated directly into the measured differences in relative shoot extension growth rates in response to the canopy coverage treatments through differences in carbohydrate supply to the growing shoot tips (Berman and DeJong 1997a). However, the depressed CO<sub>2</sub> exchange rates measured in the trees on the size-controlling rootstocks would be expected to have long-term consequences on the overall carbon budget of the trees and these effects would probably be compounded over time.

Our results support the initial hypothesis that tree water status is involved in the regulation of vegetative growth of scions on different peach rootstocks. It appears that tree water status had a direct effect on shoot growth potential among trees on different rootstocks. Tree water status also had a significant effect on leaf conductance regulation of gas exchange potentially affecting shoot carbon gain and, consequently, long-term growth potential. These differences in shoot growth potential compounded over a growing season may give rise to large differences in seasonal dry matter accumulation among trees on different rootstocks. However, these results do not exclude the possibility that other factors, including plant growth regulators, also influence scion vegetative growth among trees on various peach rootstocks. More research is needed to determine whether the differences in tree water status are related to intrinsic characteristics of peach rootstocks, such as differences in hydraulic conductance. Studies indicate that apple rootstocks may have different capacities to transport water (Olien and Lakso 1986; Cohen and Naor 2002). This may be the case for the peach rootstocks under study because the slopes of the relationship between exposed leaf area and midday stem water potential relative to total leaf area differed among rootstocks (Figure 7). Furthermore, Basile et al. (2003b) showed that there appear to be significant differences in the hydraulic conductance of a vigorous and a size-controlling peach rootstock. The significance of tree water status as a mechanism controlling vegetative growth among the peach rootstocks used in this study depends on clear documentation that the same rootstocks differ in hydraulic properties.

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