The relationship of hydraulic conductance to root system characteristics of peach (*Prunus persica*) rootstocks

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Specific rootstocks can differentially influence the vegetative growth and development of fruit trees. However, the physiological mechanism involved in this phenomenon has been elusive. Recent research comparing different peach (Prunus persica L. Batsch) rootstocks suggests that the rootstock effect on vegetative growth in peach trees is associated to water relations and more specifically to differences in rootstock hydraulic conductance. This study was intended to confirm differences in hydraulic characteristics of similar size peach trees grafted on different rootstocks and to examine root system characteristics that could be associated with rootstock hydraulic limitations. Trees on rootstocks that were known to have a size-controlling effect when grown under field conditions had lower rootstock conductance than trees on the vigorous (control) rootstock when rootstock hydraulic conductance was measured with both the high-pressure and evaporative flow methods. Rootstocks with the lowest hydraulic conductance had less fine root surface area and length per unit root dry weight than the more vigorous (control) rootstock. However, contrary to previous field studies, in this study there were no significant differences in dry matter production and distribution among trees on the different rootstocks suggesting that whatever the normal growth control mechanism was, it did not differentially influence growth under the specific conditions of this study. This research confirmed that peach rootstocks exhibiting size-controlling behavior under field conditions differed in their hydraulic and morphological characteristics under controlled growth conditions even when those growth conditions negated the expression of the sizecontrolling behavior.

Introduction

A commercial fruit tree is generally a composite tree formed by grafting a scion onto a rootstock. Specific rootstocks clearly influence the vegetative growth and development of fruit trees. However, there is no widely accepted explanation of the underlying physiological mechanism behind this phenomenon (Webster 2004). Recent research has reported differences in hydraulic conductance among fruit trees grafted on different rootstocks (Basile et al. 2003b, Cohen and Naor 2002, Solari et al. 2006b). Tree hydraulic conductance appears to limit gas exchange at a critical water potential for

transpiration rate (Kolb and Sperry 1999) maximizing gas exchange without interrupting water transport (Jones and Sutherland 1991). Tree hydraulic conductance also appears to limit gas exchange below this critical water potential value (Yang and Tyree 1993). Experimental manipulations on tree hydraulics have shown immediate responses in stomatal conductance and consequently in tree transpiration (Saliendra et al. 1995) and carbon assimilation (Hubbard et al. 2001). These physiological responses may eventually affect the long-term growth

water transport (Tyree and Sperry 1988). Trees seem

to operate close to this critical water potential and

performance of the tree. Species with high hydraulic conductance tend to grow faster than species with low hydraulic conductance (Comas et al. 2002, Tyree et al. 1998). It appears therefore that the vegetative growth control mechanism of different rootstocks may be related to a hydraulic limitation mechanism. The variations in hydraulic conductance among peach rootstocks appear to influence the transpiration rate required to reach a water potential that induces stomatal limitations on carbon assimilation and results in different vegetative growth rates (Solari et al. 2006a). However, size scaling was necessary in previous rootstock hydraulic studies to normalize the comparisons among rootstocks because of their inherent differences in tree vegetative growth that occurred in the field. This normalization could have potentially confounded the results among rootstocks on dramatically different sized trees. There has been no study that has compared hydraulic conductance of sizecontrolling rootstocks on similar size trees to confirm their differences in hydraulic conductance without using scaling factors.

There are several methods available for estimating hydraulic conductance in plants. The conventional methods used to estimate hydraulic conductance are the evaporative flow methods, which involve the measurement of a steady-state evaporative flux density associated with a specific soil to leaf water potential gradient. Alternative methods are the pressure flow methods, which involve applying a known positive water pressure to the inflow end of a root or shoot system and measuring the water flow rate. In theory, these methods should not produce the same hydraulic conductance values because the direction, pattern and/or condition of the hydraulic pathway are not the same under pressure and evaporation-induced water flow (Tyree et al. 1994, Yang and Tyree 1994). For example, the high-pressure flow method measures root hydraulic conductance while water flows opposite to the normal direction of water flow in roots. The pressure flow methods are also more sensitive to high-conductance pathways than the evaporative flow methods. Additionally, the pressure flow methods may not take into consideration natural embolisms in the conductive tissues. However, the evidence indicates that values obtained by these methods may be quite similar in the end. Tsuda and Tyree (1997) compared an evaporative flow method with the high-pressure flow meter. They demonstrated that the high-pressure and evaporative flow methods yielded consistent values of hydraulic conductance. Basile et al. (2003b) and Solari et al. (2006b) used the high-pressure flow meter to measure the hydraulic conductance of field-grown peach trees on different rootstocks and reported substantial differences in hydraulic conductance among rootstocks.

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However, there has been no comparative rootstock study that validates these results using an alternative method to measure hydraulic conductance.

The root hydraulic system can be separated into a radial and axial conductance. The radial conductance is generated by the radial water movement from the root surface to the conductive tissue, whereas the axial conductance is generated by the axial water movement through the conductive tissue. The axial is much larger than the radial hydraulic conductance. This has been theoretically analyzed by Landsberg and Fowkes (1978) and later experimentally demonstrated by Frensch and Steudle (1989). These components depend on the topology, morphology and anatomy of the root system (Doussan et al. 1998). Vercambre et al. (2002) theoretically explained how root topology can influence the axial hydraulic conductance. Aspects of root morphology such as root diameter have been related to the radial hydraulic conductance in several species (Rieger and Litvin 1999). The root anatomy may also add to the hydraulic conductance of the root system. Studies indicate that root hydraulic conductance is affected by anatomical changes in the radial water pathway (North and Nobel 1998, Zimmermann and Steudle 1998).

There has been some research on root morphology and anatomy in relation to root hydraulic conductance in fruit trees. Syvertsen and Graham (1985) reported significant differences in root hydraulic conductance per unit root length among citrus rootstocks. More importantly, the root hydraulic conductance per unit root length generally reflected the relative growth potential that these citrus rootstocks impart to the tree in the field. These differences in root hydraulic conductance per unit root length among the citrus rootstocks were later related to anatomical differences across the root cylinder (Huang and Eissenstat 2000).

The present study was designed to confirm rootstockrelated differences in the hydraulic conductance by using the high-pressure and evaporative flow methods in similar size peach trees growing on rootstocks that were known to induce differing amounts of scion vigor when grown under orchard conditions. Three of the four rootstocks used in this study were previously reported to differ in hydraulic conductance when grown under field conditions (Solari et al. 2006b). This study was also intended to evaluate the root system topological and/or morphological characteristics that could potentially explain differences in rootstock hydraulic conductance among specific peach rootstocks. These technically challenging objectives were achieved by transplanting and growing peach trees grafted on selected rootstocks in containers and maintaining high levels of soil water availability. However, there was the possibility that the growth performance and dry matter production and distribution of these peach trees could be affected by root confinement (Ran et al. 1992, Richards and Rowe 1977, Rieger and Marra 1994). Therefore, growth parameters should be analyzed with caution and no definite conclusion should be drawn regarding tree growth data in this experiment.

Materials and methods

One-year-old peach trees (Prunus persica var. nectarina, cv. Mayfire) grafted on four different rootstocks were grown at the experimental fields of the Department of Pomology, Davis, CA. The rootstocks used for this experiment were previously documented to impart low (Prunus salicina Lindl. \times P. persica L. Batsch hybrid, cv. K146-43), intermediate (Prunus besseyi Bailey × P. salicina Lindl. hybrid, cv. Hiawatha and P. salicina Lindl. \times *P. persica* L. Batsch hybrid, cv. P30-135) and high (P. persica L. Batsch \times Prunus davidiana hybrid, cv. Nemaguard) tree vigor (Weibel et al. 2003). The trees were propagated and grown for one season in a commercial nursery and then dug up, weighed, pruned to approximately 0.2 m above the graft union and planted in 40-l plastic containers in May, 2003. An additional five trees on each rootstock were dried at 60°C and weighed to estimate the fresh to dry weight ratio. The soil medium consisted of Turface fritted clay (Profile Products LLC, Buffalo Grove, IL) amended with 0.5 kg per tree of 18-6-12 Multicote fertilizer (N-P-K, Schultz Co., Bridgeton, MO). The containers were covered with an insulating aluminum foil (Advanced Foil Systems Inc., Ontario, CA) to prevent over heating of roots. The trees were irrigated once a day to maintain the soil medium at near maximum water holding capacity. After about 4 months of growth in ambient field conditions, trees were moved to a controlled environment room at the Controlled Environment Facility at University of California, Davis, 2 days before each series of intensive measurements. The environmental conditions in the controlled environment room were set at 14 h of light at 1000 μ mol photons m⁻² s⁻¹ photosynthetic photon flux density, 25/20°C air temperature and 60/80% relative humidity during the light and dark periods, respectively. The experiment was a complete randomized block design with 10 replications and measurement days as a blocking factor.

Hydraulic measurements were made during August. The evaporative and pressure flow methods were used to measure the hydraulic resistance (inverse of conductance) of trees. The evaporative flow method, as previously mentioned, involved the measurement of tree transpiration rates and water potential gradients. These measurements were carried out on sets of four trees, one for each rootstock, in the controlled environment room. The containers were enclosed in plastic bags to prevent evaporation from the soil medium during measurements. The tree hydraulic resistance (R_{tree}) was calculated as:

$$R_{\rm tree} = -\frac{\Psi_{\rm leaf} - \Psi_{\rm soil}}{E}$$

where Ψ_{leaf} is the leaf water potential, Ψ_{soil} the soil water potential, *E* the tree transpiration rate and tree hydraulic resistance is measured in MPa s kg⁻¹. In addition, the rootstock to stem hydraulic resistance ($R_{\text{rootstock+stem}}$) was calculated as

$$R_{\rm rootstock+stem} = -\frac{\Psi_{\rm stem} - \Psi_{\rm soil}}{E}$$

where $\Psi_{\rm stem}$ is the stem water potential. Tree transpiration rate was gravimetrically measured with an ES100L digital scale (Ohaus Corp., Pine Brook, NJ) every 2 h, five times during the light period. The trees were irrigated soon after each weighing to replace the water transpired and maintain the soil medium at water holding capacity. Leaf and stem water potential were measured at the same time as tree transpiration measurements by using the pressure chamber method (Scholander et al. 1965). The excised leaves from the selected shoots were pressurized with a 3005-model pressure chamber (Soil Moisture Equipment, Santa Barbara, CA). Leaf water potential was measured by sampling fully mature and well-exposed leaves, whereas stem water potential was measured by enclosing a fully mature leaf in an aluminum foil covered polyethylene bag, allowing the leaf to equilibrate with the water potential of the stem (Begg and Turner 1970). Stem water potential was also measured during the dark period and assumed to be in equilibrium with the soil medium water potential. Hydraulic measurements using the high-pressure flow method were made on the same trees (sets of four trees, one for each rootstock) between 1000 and 1400 h a week after the evaporative flow method measurements. The highpressure flow method involved guasi-steady and/or transient state measurements of hydraulic resistance (Tyree et al. 1993b, 1994). The hydraulic resistance in quasi-steady $(R_{\text{quasi-steady state}})$ and transient $(R_{\text{transient state}})$ state measurements were calculated as

$$R_{\text{quasi-steady state}} = \frac{P}{F}$$
$$R_{\text{transient state}} = \frac{dP}{dF}$$

where *P* is applied water pressure, *F* the water flow rate and hydraulic resistance is measured in MPa s kg^{-1} . The

scion was cut above the graft union, connected to the high-pressure flow meter (Dynamax Inc., Houston, TX) and immersed in a large tub of deionized water. Water temperature in the tub was determined with a Fluke 2190A/Y2001 thermocouple digital thermometer (Fluke Corp., Everett, WA). The scion was perfused for at least 20 min with deionized and degassed water to reach the quasi-steady state condition. Scion hydraulic resistance was measured by an alternating series of quasi-steady state and transient state measurements. Immediately after measuring the scion hydraulic resistance, leaves were removed from the scion and stem hydraulic resistance was measured after reaching a quasi-steady state condition. Subsequently, a wood segment that included the graft union was cut off from the rootstock. The container with the rootstock was immersed in another large tub of deionized water and connected to high-pressure flow meter. The rootstock hydraulic resistance was measured by a series of reverse water flow transient state measurements. Finally, the wood segment that had been previously removed was connected to the instrument and the hydraulic resistance was measured by guasi-steady state measurements. The tree hydraulic resistance (R_{tree}) was calculated as

$$R_{\text{tree}} = R_{\text{scion}} + R_{\text{rootstock}} + R_{\text{wood segment}}$$

where R_{scion} , $R_{rootstock}$ and $R_{wood segment}$ are the scion, rootstock and wood segment (with the graft union) hydraulic resistance, respectively. Furthermore, the rootstock to stem hydraulic resistance ($R_{rootstock+stem}$) was calculated as

$$R_{\text{rootstock}+\text{stem}} = R_{\text{rootstock}} + R_{\text{wood segment}} + R_{\text{stem}}$$

where R_{stem} is the stem hydraulic resistance.

In addition, the leaf hydraulic resistance (R_{leaf}) was calculated with both methods as

$$R_{\text{leaf}} = R_{\text{tree}} - R_{\text{rootstock+stem}}$$

The scion biomass was separated into leaves, stems and trunk at the end of the hydraulic measurements. The total leaf area was measured with a LI-3100 area meter (Li-Cor Inc., Lincoln, NE). The rootstock biomass was washed and separated into root shank and extension roots. Approximately 20% by weight of extension roots of each tree was sampled to evaluate the root system topological and morphological characteristics. The extension roots were positioned in a waterproof plexiglass tray filled with deionized water and scanned on an Epson Expression 1680 digital scanner (Epson America Inc., Long Beach, CA). The images were analyzed with WinRhizo software (Regent Instruments Inc., Quebec, Canada), which is an image analysis system specifically designed for washed root measurements. The software can be used to carry out topological and morphological root analyses as a function of the whole root systems and root diameter classes. In this study, the number of root tips was used as topological or branching pattern indices, whereas root diameter, length and surface area were used as morphological indices. The fresh biomass was dried at 60°C for at least 2 weeks to determine dry matter.

Statistical analyses of the data were done with SAS statistical software (SAS Institute Inc., Cary, NC). Analysis of variance was used to test the rootstock effect of the production and distribution of dry matter. Analysis of variance was also used to test the rootstock and hydraulic method effects on different hydraulic components of the tree. Mean separation among rootstocks was carried out at a 0.05 level of significance by the Tukey pairwise comparison test. Multiple linear regression analysis was used to examine different root extension allometric relationships among rootstocks. Multiple analyses of variance were used to test the rootstock effect on root surface area per unit dry weight for different root diameter classes.

Results

Tree dry weight was slightly different among trees on different rootstocks at the beginning of the experiment (P = 0.0025). Trees grafted on Hiawatha and Nemaguard had higher initial dry weight than trees on K146-43, whereas the initial dry weight of trees grafted on P30-135 was in between them (Table 1). However, there were no significant differences in scion and rootstock dry weights at the end of the experiment and consequently the scion to rootstock dry weight ratio was also not significantly different among trees on different rootstocks (Table 1).

There were no significant interaction effects between the method and rootstock in hydraulic conductance that justified analyzing both effects independently. Tree hydraulic conductance was significantly different among trees grafted on the four rootstocks (P = 0.0343). Trees grafted on Nemaguard had higher mean tree hydraulic conductance than trees on K146-43 (Fig. 1). Trees on P30-135 and Hiawatha had intermediate tree hydraulic conductance values. There were no significant differences in scion and wood segment hydraulic conductance among trees on different rootstocks as determined by the high-pressure flow method (Fig. 2). According to this method, the significant differences among rootstocks in tree hydraulic conductance were only related to

Table 1. Dry matter production and distribution of 1-year-old peach trees on Nemaguard, P30-135, Hiawatha and K146-43 rootstocks. Individual values represent the mean of 10 trees \pm standard error (n = 40). Values not connected by the same letter are significantly different at a 0.05 level of significance according to Tukey's mean comparison test.

Rootstock	lnitial tree dry weight (kg)	Final tree dry weight (kg)	Final scion dry weight (kg)	Final rootstock dry weight (kg)	Final scion/rootstock dry weight ratio
Nemaguard	$0.13\pm0.02a$	$0.40\pm0.05a$	$0.28\pm0.04a$	$0.12\pm0.02a$	$2.33\pm0.30\text{a}$
P30-135	$0.11\pm0.02ab$	$0.39\pm0.06a$	$0.26\pm0.04a$	$0.13\pm0.02a$	$2.00\pm0.23a$
Hiawatha	$0.14\pm0.02a$	$0.40\pm0.06a$	$\textbf{0.28} \pm \textbf{0.05a}$	$0.12\pm0.02a$	$2.33\pm0.35a$
K146-43	$0.10\pm0.01b$	$0.38\pm0.07\text{a}$	$0.26\pm0.06\text{a}$	$0.12\pm0.02a$	$2.17\pm0.24a$

significant differences in rootstock hydraulic conductance (P = 0.0177). Trees grafted on Nemaguard, P30-135 and Hiawatha and K146-43 had high, intermediate and low mean rootstock hydraulic conductance, respectively (Fig. 2). Rootstock hydraulic conductance was also significantly different among rootstocks when scaled by the root surface area (P = 0.0405). Trees on Nemaguard had higher rootstock hydraulic conductance per unit surface area than those on Hiawatha and K146-43, whereas trees on K146-43 had lower rootstock hydraulic conductance per unit surface area than those on P30-135 and Nemaguard (Fig. 3).

Leaf and tree hydraulic conductance estimates significantly differed between high-pressure and evaporative flow methods (P < 0.0001). The high-pressure flow method yielded higher estimates of mean leaf and tree hydraulic conductance than the evaporative flow method (Fig. 4). Rootstock to stem hydraulic conductance estimates were also significantly different between methods (P = 0.0146). However, this time the high-pressure flow method yielded lower estimates of mean rootstock to stem hydraulic conductance than the evaporative flow method (Fig. 4).

The number of root tips and root surface area was significantly correlated with the root dry weight (P < 0.0001 and 0.0001, respectively). The rootstock had a significant effect on number of root tips and root area (P < 0.0001 and 0.0001, respectively). However, the interaction effect between the rootstock and root dry



40 Wood Segment Hydraulic conductance (10⁻⁴ kgMPa⁻¹s⁻¹) □ Scion Rootstock 30 а 20 10 ah ab 0 Nemaguard P30-135 Hiawatha K146-43 Rootstock

Fig. 1. Tree hydraulic conductance of 1-year-old peach trees on Nemaguard, P30-135, Hiawatha and K146-43 rootstocks. Individual bar values represent the mean of 10 trees \pm standard error bars (n = 40). Values not connected by the same letter are significantly different among rootstocks within a tree component at a 0.05 level of significance according to Tukey's mean comparison test.

Fig. 2. Wood segment, scion and rootstock hydraulic conductance of 1year-old peach trees on Nemaguard, P30-135, Hiawatha and K146-43 rootstocks measured using the high-pressure flow method. Individual bar values represent the mean of 10 trees \pm standard error bars (n = 40). Values not connected by the same letter are significantly different among rootstocks within a tree component at a 0.05 level of significance according to Tukey's mean comparison test.



Fig. 3. Rootstock hydraulic conductance per unit root surface area of Nemaguard, P30-135, Hiawatha and K146-43 rootstocks. Individual bar values represent the mean of 10 trees \pm standard error bars (n = 40). Values not connected by the same letter are significantly different among rootstock and method combinations at a 0.05 level of significance according to Tukey's mean comparison test.

weight was only significantly different for root surface area (P < 0.0001). Trees grafted on Nemaguard and P30-135 had a higher mean root surface area per unit dry weight than those grafted on Hiawatha and K146-43 (Table 2). The root length was also significantly correlated with the root dry weight (P < 0.0001), and rootstocks again had a significant effect on this relationship (P < 0.0001). The interaction effect between the rootstock and root dry weight was also significantly different for root length (P < 0.0001). Trees grafted on Nemaguard and P30-135 had the highest mean root length per unit dry weight followed by those grafted on Hiawatha and K146-43 (Table 2). Furthermore, root diameter differed among rootstocks (P < 0.0001). Trees grafted on K146-43 had the



Fig. 4. Leaf, rootstock to stem and tree hydraulic conductance measured using the evaporative and high-pressure flow methods. Individual bar values represent the mean of 40 trees \pm standard error bars (n = 80). Values not connected by the same letter are significantly different among rootstock and method combinations at a 0.05 level of significance according to Tukey's mean comparison test.

highest root diameter and Nemaguard the lowest, whereas those grafted on Hiawatha and P30-135 had intermediate root diameter (Table 2). The root surface area per unit dry weight was also significantly different among rootstocks for different root diameter classes (P < 0.0001). In most cases, trees grafted on Nemaguard had the highest mean root surface area per unit dry weight of fine roots (root diameter <2 mm) followed by those grafted on P30-135, Hiawatha and K146-43 (Fig. 5).

Discussion

In the present study, peach rootstocks had an effect on the whole tree hydraulic conductance (Fig. 1). However,

Table 2. Extension root topological and morphological characteristics of Nemaguard, P30-135, Hiawatha and K146-43 rootstocks. Individual values represent the mean of 10 trees \pm standard error (n = 200). Values not connected by the same letter are significantly different at a 0.05 level of significance according to Tukey's mean comparison test.

Rootstock	Specific number of tips (10 ⁵ kg)	Specific surface area (m ² kg ⁻¹)	Specific length (10 ³ m kg ⁻¹)	Diameter (10 ⁻³ m)	
Nemaguard	$\textbf{27.92} \pm \textbf{2.47a}$	66.17 ± 4.56a	$26.35\pm2.15a$	$0.74\pm0.01c$	
P30-135	$21.85\pm2.23a$	63.66 ± 3.54a	$24.48\pm1.71a$	$0.78\pm0.01b$	
Hiawatha	$22.69\pm2.07a$	55.07 ± 3.35b	$19.06\pm1.40b$	$0.78\pm0.01b$	
K146-43	$20.11\pm1.09a$	$44.19\pm2.69b$	$14.46 \pm 1.05 c$	$0.88\pm0.01a$	



Fig. 5. Root surface area per unit dry weight of Nemaguard, P30-135, Hiawatha and K146-43 rootstocks. Individual bar values represent the mean of 10 trees \pm standard error bars (n = 40). Values not connected by the same letter are significantly different among rootstocks within a root diameter class at a 0.05 level of significance according to Tukey's mean comparison test.

there were no differences among rootstocks in wood segment hydraulic conductance that included the graft union (Fig. 2). This result contradicts those of previous studies carried out on apple rootstocks, which suggest that the graft union limits the transport of plant growth regulators (Kamboj et al. 1999), mineral nutrients (Jones 1971) and water (Atkinson et al. 2003) from different rootstocks. The differences in tree hydraulic conductance among trees on different rootstocks appeared to be localized in the rootstock as determined by the highpressure flow method (Fig. 2). These results were comparable to those of previous studies carried out on some of the same or similar peach rootstocks grown in orchard conditions (Basile et al. 2003b, Solari et al. 2006b). Although there were no significant differences in root dry matter production, the rootstocks still differed significantly in root surface area (Table 2). Additional information was obtained when the rootstock hydraulic conductance was scaled by root surface area. There were significant differences in rootstock hydraulic conductance per unit surface area as determined by the highpressure flow method (Fig. 3). These results suggest that the differences in rootstock hydraulic conductance may be associated to differences in the efficiency of the root to uptake water across the root surface.

The hydraulic conductance values clearly differed between the high-pressure and evaporative flow methods

(Fig. 4). The differences in rootstock to stem hydraulic conductance between methods may be related to the rootstock hydraulic conductance measurements. The high-pressure flow method measures rootstock hydraulic conductance opposite to the normal direction of water flow during transpiration (Tyree et al. 1994). This flow direction may have decreased the solute potential inside fine roots by reverse osmosis, which in turn may have changed the driving force and consequently the water flow during measurements. This might explain the lower values in rootstock to stem hydraulic conductance by using the high-pressure compared to the evaporative flow method.

In contrast, the high-pressure flow method yielded higher tree hydraulic conductance values than the evaporative method (Fig. 4). This meant that leaf hydraulic conductance values were different between methods. Leaves are generally more sensitive to natural embolisms than other tree parts. This adaptive feature is known as vulnerability segmentation (Tyree et al. 1993a). The highpressure flow method does not consider native state embolism because air bubbles are dissolved during measurements. Furthermore, the high-pressure flow method may have altered the leaf pathway compared to the evaporative flow method (Yang and Tyree 1994). This might explain the differences in tree hydraulic conductance between methods. However, these methods gave similar comparative results among rootstocks despite the differences in absolute values of hydraulic conductance.

The efficiency of water acquisition may be affected by the topology, morphology and anatomy of the root system. In this study, the peach rootstocks did not have a significant effect on root branching pattern as indicated by the number of root tips per unit dry weight for each rootstock (Table 2). However, the rootstocks, as previously mentioned, differed in root surface area per dry weight. The differences in root surface area were clearly related to differences in root diameter and length (Table 2). Similar morphological studies have reported significant differences in root hydraulic conductance that were correlated with root length per unit weight in citrus rootstocks (Syvertsen and Graham 1985). Rieger and Litvin (1999) also reported a significant inverse correlation between root diameter and root hydraulic conductivity across various Prunus species. The differences in root diameter among rootstocks in the present study were related to fine roots, which represented approximately 90% of the total root area (Fig. 5). Although no anatomical studies were carried out on the rootstocks used in the present study, differences in root anatomy may potentially affect rootstock hydraulic resistance in these peach trees. Several studies have related hydraulic conductivity with anatomical features of the root system (North and Noble 1998, Zimmermann and Steudle 1998). In particular, Huang and Eissenstat (2000) and Eissenstat and Achor (1999) correlated the differences in root hydraulic conductivity among citrus rootstocks to anatomical characteristics of the exodermis. Furthermore, water channels or aquaporins may be also involved in the differences in specific hydraulic conductance among these peach rootstocks. Recent genetic manipulation studies have shown the important function that aquaporins play in controlling water transport across the root (Lian et al. 2004, Martre et al. 2002, Siefritz et al. 2002). The anatomical and molecular aspects of water transport on these specific rootstocks will be addressed in a future study.

Although there were differences in rootstock hydraulic conductance, the rootstocks did not have a major effect on dry matter production and distribution (Table 1). These results contradict those of previous field studies carried out on the same peach rootstocks (Solari et al. 2006b, Weibel et al. 2003). The conflicting results in tree growth of the current study compared to previous studies are difficult to reconcile but it should be noted that in the previous experiments the trees were planted in natural soils in the field. In the current experiment, tree growth may have been initially controlled by the rootstocks but subsequently pot size may have been the dominant factor controlling tree growth. It is well documented that treatments causing root restriction affect vegetative growth of various tree species (Richards and Rowe 1977, Tschaplinski and Blake 1985, Webster et al. 2000). Ran et al. (1992) and Rieger and Marra (1994) showed that restricting the soil volume available for the growth of the root system severely reduced dry matter production of peach trees. Mandre et al. (1995) also found differences in dry matter distribution with root confinement in peach trees. Similar responses to root confinement were also reported in the field by Webster et al. (2000) and Williamson and Coston (1990) in peach and apple trees, respectively. More importantly, Webster et al. (2000) observed that apple rootstocks did not have an effect on tree growth when trees were grown in containers despite their differences in vegetative growth potentials under normal field conditions. Therefore, it is very possible that root confinement was an overriding factor limiting the growth of the trees in this experiment that prevented the trees from exhibiting the differences in growth normally associated with these rootstocks.

In addition, the daily watering and type of soil used in these experiments may have acted to minimize the growth effects of rootstock-related differences in rootstock hydraulic conductance because the water potential gradient between the roots and the soil was kept to a minimum and the plants certainly did not experience the same type of fluctuations in soil water availability as would be common under field conditions. Mean midday stem water potentials of the plants in this experiment growing outside under ambient filed conditions ranged between -1.09 and -1.13 MPa and from -0.77 to -0.80 MPa when they were in the growth chamber. These values and ranges of differences were much less than those that have been reported for trees on the same rootstocks growing in orchard field conditions (Basile et al. 2003a, Solari et al. 2006a). Thus, differences in hydraulic conductance between rootstocks would not be expected to have as great of an effect on leaf function and growth of trees growing in the more moderate conditions of this experiment compared to trees growing in orchard field conditions.

The specific peach rootstocks used in this study did show differences in rootstock hydraulic conductance even though the trees were of similar size. The differences in root hydraulic conductance were correlated with differences in root morphology among the different rootstocks. The differences in root surface area per unit dry weight among rootstocks may have conferred more efficient soil exploration of the root system for water acquisition. In addition, the rootstocks may have also had different efficiencies in water transport because of differences in root diameter. The rootstocks differed in the diameter of fine roots, where most of the water uptake is presumed to occur in the root system. This may have had a direct effect on the radial hydraulic conductance, which is the most important hydraulic component in the root system (Frensch and Steudle 1989). Under field conditions, the hydraulic limitations imposed by the different rootstocks can be minimized by changing the tree dry matter distribution and/or decreasing the tree transpiration, with the consequence of affecting the vegetative growth potential of the tree (Solari et al. 2006a, b). These compensatory responses can reduce the water uptake rate per unit root area preventing a critical loss of hydraulic conductance. Hacke et al. (2000) demonstrated this concept by planting loblolly pine in soils with contrasting hydraulic properties. The soils had different hydraulic sensitivity to soil water potential. Differences in soil hydraulic conductivity were compensated for by adjustments in the root to leaf area ratio of the loblolly pine.

As discussed above, this study demonstrated that peach rootstocks differed in their hydraulic properties in accordance with previously reported differences in rootstock associated tree vigor. Furthermore, there were differences in root morphology among these rootstocks that appeared to be consistent with the differences in root hydraulic properties. This study did not rule out the possibility that other mechanisms may also be involved in the size-controlling phenomenon associated with these rootstocks. However, it is interesting to note that if other mechanisms are usually involved they also were not expressed in the particular experimental setup used in the present experiments. If the size-controlling behavior exhibited in the orchard by these rootstocks (Basile et al. 2003a, Solari et al. 2006b, Weibel et al. 2003) was because of hormonal interactions between root and shoot it would be even more difficult to explain the lack of size-controlling behavior observed in this potted plant study.

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