

Hydraulic conductance characteristics of peach (*Prunus persica*) trees on different rootstocks are related to biomass production and distribution

LUIS I. SOLARI,¹ SCOTT JOHNSON¹ and THEODORE M. DEJONG^{1,2}

¹ Department of Plant Sciences, University of California, Davis, CA 95616, USA

² Corresponding author (tmdejong@ucdavis.edu)

Received July 28, 2005; accepted November 20, 2005; published online June 30, 2006

Summary We investigated hydraulic conductance characteristics and associated dry matter production and distribution of peach trees grafted on different rootstocks growing in the field. A single scion genotype was grown on a low ('K146-43'), an intermediate ('Hiawatha') and a high ('Nemaguard') vigor rootstock. 'K146-43' and 'Hiawatha' rootstocks had 27 and 52% lower mean leaf-specific hydraulic conductances, respectively, than the more vigorous 'Nemaguard' rootstock. Tree growth rates and patterns of biomass distribution varied significantly among rootstocks. Mean dry mass relative growth rates of trees on 'K146-43' and 'Nemaguard' were 66 and 75%, respectively, of the rates of trees on 'Nemaguard', and the scion to rootstock dry mass ratios of trees on 'K146-43' and 'Hiawatha' were 63 and 82%, respectively, of the ratio of trees on 'Nemaguard'. Thus, differences in dry matter distribution between the scion and rootstock, which may be a compensatory response to the differences in leaf specific hydraulic conductance among rootstocks, appeared to be related to differences in growth rates. Correspondingly, there was a positive linear relationship between the scion to rootstock dry mass ratio and the rootstock to scion hydraulic conductance ratio when conductance was normalized for dry mass. This study confirms that rootstock effects on tree water relations and vegetative growth potential result, at least in part, from differences in tree hydraulic conductance associated with specific peach rootstocks.

Keywords: dry matter partitioning, dwarfing rootstocks, hydraulic resistance, size-controlling rootstocks.

Introduction

Composite fruit trees combine different scion and rootstock genotypes, and certain rootstock genotypes can have a major influence on the vegetative growth and development of a tree. The growth interaction between scion and rootstock is a poorly understood phenomenon, and the physiological mechanism involved in rootstock regulation of vegetative tree growth has not been well characterized (see reviews by Rogers and Beakbane (1957), Lockard and Schneider (1981) and Webster (1995)). This physiological mechanism has been related to alterations

in the development of the vascular tissue at the graft union in apple trees (Soumelidou et al. 1994). The anatomical differences in the vascular tissue at the graft union (Beakbane 1956) have been reported to restrict the transport of plant growth regulators (Kamboj et al. 1997, 1999), mineral nutrients (Jones 1971, 1974) and water (Atkinson et al. 2003). However, there have been no conclusive studies directly linking these phenomena to rootstock effects on vegetative tree growth.

Studies with apple rootstocks (Olien and Lakso 1986, Cohen and Naor 2002) and peach rootstocks (Weibel et al. 2003) showed that specific rootstocks influence shoot growth rate and stem water potential. Tree water status is an important factor determining vegetative growth in peach trees. Berman and DeJong (1997) showed that changes in stem water potential occurring over a period of hours during the afternoon strongly influence shoot growth rate in the field. Basile et al. (2003a), who followed stem water potential and shoot growth rate during individual days and over a growing season on some of the same peach rootstocks characterized by Weibel et al. (2003), found a strong correlation between stem water potential and shoot growth over a day. Additionally, vegetative growth was correlated with cumulative water potential differences over a growing season (Basile et al. 2003a). More direct evidence that tree water status is involved in regulating vegetative growth among peach trees on different rootstocks has been obtained by Solari et al. (2006) who evaluated shoot growth rate responses of trees on different rootstocks to direct manipulations of stem water potential under field conditions and concluded that stem water potential is causally related to differences in relative shoot growth rate among peach trees on different rootstocks.

The capacity to transport water throughout a tree can be determined by measuring its hydraulic conductance. Tree hydraulic conductance determines the critical water potential for efficient water transport (Tyree and Sperry 1988) and trees tend to operate close to that critical water potential (Kolb and Sperry 1999) to maximize gas exchange (Jones and Sutherland 1991). Stomatal conductance should thus be related to the critical water potential to preserve the integrity of the hydraulic system. Measurements of the immediate responses of sto-

matal conductance and leaf gas exchange to manipulation of tree hydraulic conductance indicate that hydraulic conductance determines the water potential threshold at which stomatal limitation is induced (Sperry et al. 1993) on transpiration (Sperry and Pockman 1993) and carbon assimilation (Hubbard et al. 2001). These relationships indicate that hydraulic conductance influences tree growth potential. Tyree et al. (1998) studied the hydraulic conductances of pioneer and non-pioneer tropical trees and found that pioneer species with high hydraulic conductances tend to grow faster than non-pioneer species with low hydraulic conductances. It appears, therefore, that long-term tree growth potentials could be related to tree hydraulic architecture. This argument is similar to arguments in the literature on the hydraulic limitation of tree height (Ryan and Yoder 1997, Koch et al. 2004, Woodruff et al. 2004).

Recent studies on the hydraulic architecture of fruit trees have focused on the effects of different size-controlling rootstocks. In apple, the rootstock appears to affect tree hydraulic conductance (Cohen and Naor 2002, Atkinson et al. 2003). In contrast, in peach, Basile et al. (2003b) found that differences in rootstock-related specific hydraulic conductance were unrelated to differences in hydraulic conductance through the graft union. However, no studies have examined the possible link between differences in leaf function, shoot growth, whole-tree growth and biomass distribution associated with tree water relations and rootstock hydraulic conductance. In the accompanying paper (Solari et al. 2006), we demonstrate that differences in leaf function and shoot growth are associated with differences in water relations of trees on different size-controlling rootstocks. The goal of this study was to test the hypothesis that rootstock effects on tree water relations and vegetative growth potential result from differences in tree hydraulic conductance associated with particular peach rootstocks. Specifically, we investigated hydraulic conductance, dry matter production and distribution and vegetative growth characteristics of peach trees grafted on three different rootstocks growing in the field.

Materials and methods

The trees used in this experiment were the same as those used by Solari et al. (2006). 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 potentials (Weibel et al. 2003). The trees were propagated and grown for one season in a commercial nursery and then lifted, weighed, pruned to about 0.5 m above the graft union and planted in the field in February 2002. An additional five trees of each rootstock were set aside, dried at 60 °C and weighed to estimate the fresh to dry mass ratio at the time of planting. 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 fertilizer at the time of planting and then with 0.2 kg per tree of 15.5,0,0 fertilizer once per month. Trees were irrigated with micro-sprinklers once per week to replace estimated evapotranspiration. After about 7 months of field growth, hydraulic conductance and growth of the trees were measured in the field. The experiment was a complete randomized block design with 15 replications and measurement days as a blocking factor.

Hydraulic measurements were made on three trees, one per rootstock, on 15 days between 1000 and 1400 h in early October by the high-pressure flow method. This method measures hydraulic resistance (inverse of conductance) and involves quasi-steady and transient state measurements (Tyree et al. 1993, 1994). Hydraulic resistance (MPa s kg⁻¹) was calculated from the quasi-steady state ($R_{\text{quasi-steady state}}$) and transient state ($R_{\text{transient state}}$) measurements as:

$$R_{\text{quasi-steady state}} = \frac{P}{F} \quad (1)$$

$$R_{\text{transient state}} = \frac{dP}{dF} \quad (2)$$

where P is applied water pressure and F is water flow rate. The scion was cut above the graft union and the cut end was recut with a razor blade. Subsequently, the base of the scion was connected to a high-pressure flow meter (Dynamax, Houston, TX) and perfused for at least 30 min with deionized and degassed water to reach the quasi-steady state condition. The canopy was sprayed with water and covered with a plastic tarpaulin to minimize transpiration during measurements. Scion hydraulic resistance was measured by an alternating series of quasi-steady and transient state measurements. Immediately after measuring the scion hydraulic resistance, a wood segment that included the graft union was excised from the rootstock. The cut surface of the rootstock was recut with a razor blade and connected to the high-pressure flow meter. Rootstock hydraulic resistance was measured by a series of reverse water flow transient state measurements. Finally, the excised wood segment comprising mainly the scion, but including the graft union was connected to the instrument and wood segment hydraulic resistance was measured by quasi-steady state measurements first with the graft union and, subsequently, without the graft union. The tree or total hydraulic resistance (R_{tree}) was calculated as:

$$R_{\text{tree}} = R_{\text{scion}} + R_{\text{rootstock}} + R_{\text{wood segment}} \quad (3)$$

where R_{scion} , $R_{\text{rootstock}}$ and $R_{\text{wood segment}}$ are the scion, rootstock and wood segment (with the graft union) hydraulic resistance, respectively.

Hydraulic conductivity of the wood segment (K_h ; kg m MPa⁻¹ s⁻¹) with and without the graft union was calculated as:

$$K_h = \frac{L}{R_{\text{wood segment}}} \quad (4)$$

where L is wood segment length.

After the hydraulic measurements were completed, the scion was separated into leaves, stems and trunk and biomass determined after drying at 60 °C. The wood segment length and diameter with and without the graft union were measured with a digital caliper (Mitutoyo Corp., Tokyo, Japan). Total leaf area was measured with an LI-3100 area meter (Li-Cor, Lincoln, NE). At the end of the experiment, the rootstocks were mechanically excavated with a backhoe, washed, separated into root shank and extension roots and dried at 60 °C for at least two weeks to determine dry mass. Tree absolute growth rate (AGR; kg day⁻¹) was calculated as:

$$\text{AGR} = \frac{W_2 - W_1}{T_2 - T_1} \quad (5)$$

where W_2 and W_1 are tree dry mass at the end of growing season (T_2) and time of planting (T_1), respectively. Tree relative growth rate (RGR; day⁻¹) was calculated as:

$$\text{RGR} = \frac{\text{Log}_n(W_2) - \text{Log}_n(W_1)}{T_2 - T_1} \quad (6)$$

Net assimilation rate (NAR; kg m⁻² day⁻¹) was calculated as:

$$\text{NAR} = \frac{\text{RGR}}{\text{LAR}} \quad (7)$$

where leaf area ratio (LAR) is the leaf area per unit tree dry mass.

Statistical analyses of the data were performed with SAS statistical software (SAS Institute, Cary, NC). Analysis of variance was used to test the rootstock effect on dry matter production, distribution and growth of trees, and to test the rootstock effect on wood segment, rootstock and scion hydraulic conductance. Means separation among rootstocks was carried out with a 0.05 level of significance by the Tukey pairwise comparison test. Relationships among leaf area, scion, rootstock and tree hydraulic conductance and wood cross-sectional area and wood segment hydraulic conductivity were investigated by linear regression analysis, which was used also to investigate relationships among the ratio between the rootstock to scion hydraulic conductance per unit dry mass, scion to rootstock dry mass ratio and tree relative growth rate.

Results

At the time of field planting in February 2002, tree dry mass varied with rootstock ($P = 0.0001$). Trees with 'Nemaguard' and 'Hiawatha' had higher mean tree dry mass than trees on 'K146-43' (Table 1). Rootstock also affected scion, rootstock and tree dry mass at the end of the growing season ($P = 0.0001$). Trees on 'Nemaguard' had the highest mean scion, rootstock and, consequently, whole-tree dry mass followed by trees on 'Hiawatha' and 'K146-43' (Table 1). The final ratio between scion and rootstock dry mass was also affected by rootstock type ($P = 0.0002$). Trees grafted on 'Nemaguard' had the highest final mean scion to rootstock dry mass ratio followed by trees on 'Hiawatha' and 'K146-43' (Table 1).

Rootstock genotype affected tree absolute growth rates ($P = 0.0011$). Trees on 'Nemaguard' had the highest mean absolute growth rate followed by trees on 'Hiawatha' and 'K146-43' (Table 2). Correspondingly, tree dry mass relative growth rates differed among rootstocks ($P = 0.0157$). Trees on 'Nemaguard' had a higher mean dry mass relative growth rate than trees on 'K146-43' (Table 2). The tree growth analysis indicated that rootstock genotype significantly affected tree net assimilation rate ($P = 0.0077$). Trees on 'Nemaguard' had a higher mean net assimilation rate than trees on 'K146-43'.

Scion and rootstock hydraulic conductances differed among rootstocks at the end of the growing season ($P = 0.0005$ and 0.0006 , respectively). Trees on 'Nemaguard' had the highest mean scion and rootstock hydraulic conductances followed by trees on 'Hiawatha' and 'K146-43' (Figure 1). There were also differences in hydraulic conductance between the different components of the tree ($P = 0.027$). Rootstocks had lower mean hydraulic conductances than scions (Figure 1). Scion and rootstock contribution to whole-tree hydraulic resistance differed among trees according to rootstock ($P = 0.0287$ and 0.0075 , respectively). Rootstock hydraulic resistance contributed more to total hydraulic resistance in trees on 'K146-43' than in trees on 'Nemaguard'; the distribution of hydraulic resistance for trees on 'Hiawatha' was intermediate between the other two rootstocks (Figure 2).

Table 1. Dry matter production and distribution of 1-year-old peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks over a growing season. Each value is the mean of 15 trees $\pm$ standard error ($n = 45$). Values with different letters are significantly different at the 0.05 level of significance according to Tukey's mean comparison test.

Rootstock	Initial tree dry mass (kg)	Final tree dry mass (kg)	Final scion dry mass (kg)	Final rootstock dry mass (kg)	Final scion/rootstock dry mass ratio
'Nemaguard'	0.11 $\pm$ 0.01 a	2.80 $\pm$ 0.16 a	2.07 $\pm$ 0.11 a	0.74 $\pm$ 0.04 a	2.80 $\pm$ 0.22 a
'Hiawatha'	0.10 $\pm$ 0.01 a	1.26 $\pm$ 0.16 b	0.87 $\pm$ 0.12 b	0.39 $\pm$ 0.04 b	2.31 $\pm$ 0.25 b
'K146-43'	0.04 $\pm$ 0.01 b	0.36 $\pm$ 0.14 c	0.23 $\pm$ 0.11 c	0.13 $\pm$ 0.03 c	1.77 $\pm$ 0.27 c

Table 2. Vegetative growth characteristics of 1-year-old peach trees on 'Nemaguard', 'Hiawatha' and K146-43 rootstocks over a growing season. Each value is the mean of 15 trees $\pm$ standard error ($n = 45$). Values with different letters are significantly different at the 0.05 level of significance according to Tukey's mean comparison test. Abbreviation: DM = dry mass.

Rootstock	Absolute growth rate (g day ⁻¹)	Relative growth rate (DM) (day ⁻¹)	Leaf area ratio (m ² kg ⁻¹)	Net assimilation rate (g m ⁻² day ⁻¹)
'Nemaguard'	10.74 $\pm$ 0.60 a	0.0141 $\pm$ 0.08 a	2.34 $\pm$ 0.10a	6.08 $\pm$ 0.42a
'Hiawatha'	4.87 $\pm$ 0.66 b	0.0106 $\pm$ 0.09 ab	2.30 $\pm$ 0.13a	4.65 $\pm$ 0.45ab
K146-43	1.37 $\pm$ 0.59 c	0.0093 $\pm$ 0.08 b	2.13 $\pm$ 0.14a	4.37 $\pm$ 0.41b

Hydraulic conductance of the wood segment with the graft union differed according to rootstock ($P = 0.0034$). 'Nemaguard' had the highest mean graft union wood segment hydraulic conductance followed by 'Hiawatha' and 'K146-43' (Figure 1). However, the contribution to whole tree hydraulic resistance of the wood segment that included the graft union did not differ significantly among trees on different rootstocks (Figure 2). There was a significant positive linear correlation between wood cross-sectional area and the hydraulic conductivity of the wood segment with the graft union (Table 3), and neither the rootstock nor the graft union significantly affected this relationship. Furthermore, the interaction effects among rootstock, graft union and wood cross-sectional area did not significantly affect the hydraulic conductivity of the wood segment with the graft union. Although there was a tendency for hydraulic conductivity to be lower in wood segments without the graft union than in wood segments that included the graft union, the slopes of the relationships were not significantly different. Wood segment hydraulic conductivity data for all

the rootstocks and wood segments with and without the graft union fit the same relationship (Figure 3).

Scion, rootstock and tree hydraulic conductances were correlated with leaf area ($P = 0.0001$, 0.022 and 0.0039, respectively) and rootstock had no effect on these relationships (data not shown). There was a significant interaction effect between rootstock and leaf area on rootstock hydraulic conductance and consequently on tree hydraulic conductance ($P = 0.025$ and 0.046, respectively). Mean rootstock hydraulic conductance per unit leaf area differed significantly with rootstock; 'Nemaguard' having the highest and 'K146-43' the lowest value, and 'Hiawatha' having an intermediate value (Figure 4a). However, mean tree hydraulic conductance per unit leaf area differed significantly only between 'Nemaguard' and 'K146-43'.

Scion, rootstock and tree hydraulic conductances were correlated with scion ($P = 0.0016$), rootstock ($P = 0.0087$) and tree ($P = 0.0045$) dry mass, respectively (data not shown). Rootstock influenced the rootstock and tree hydraulic conduc-

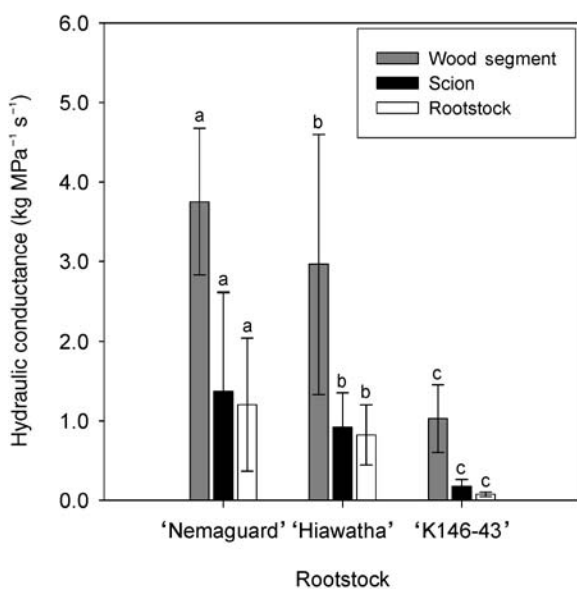


Figure 1. Wood segment with graft union, scion and rootstock hydraulic conductance of 1-year-old peach trees on 'Nemaguard', 'Hiawatha' and K146-43 rootstocks. Each bar value is the mean of 15 trees $\pm$ standard error ($n = 45$). Within a tree component, values with different letters are significantly different among rootstocks at the 0.05 level of significance according to Tukey's mean comparison test.

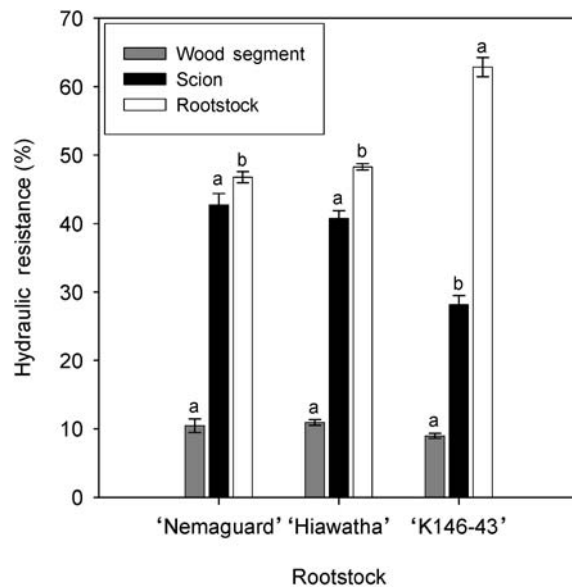


Figure 2. Percent contributions of wood segment with graft union, scion and rootstock to whole-tree hydraulic resistance of 1-year-old peach trees on 'Nemaguard', 'Hiawatha' and K146-43 rootstocks. Each bar value is the mean of 15 trees $\pm$ standard error ($n = 45$). Within a tree component, values with different letters are significantly different among rootstocks at the 0.05 level of significance according to Tukey's mean comparison test.

Table 3. Summary of statistical analysis for the effects of rootstock, graft union and wood cross-sectional area (WCSA) on the hydraulic conductivity of the wood segment.

Source	DF	Sum of squares	Mean square	F Ratio	P > F
Rootstock	2	601.6578	300.829	1.6933	0.1979
Graft	1	3.6787	3.679	0.0207	0.8864
WCSA	1	1574.9175	1574.917	8.8646	0.0051
Rootstock × Graft	2	41.6677	20.834	0.1173	0.8897
Rootstock × WCSA	2	34.1238	17.062	0.0960	0.9087
Graft × WCSA	1	4.0726	4.073	0.0229	0.8805
Rootstock × Graft × WCSA	2	60.6567	30.328	0.1707	0.8437

tance relationship ($P = 0.0057$ and 0.024 , respectively; data not shown). There was a significant interaction effect between rootstock and dry mass on rootstock and tree hydraulic conductance ($P = 0.0106$ and 0.0065 , respectively). Trees on 'Nemaguard' and K146-43 had the highest and lowest rootstock and tree hydraulic conductance per unit dry mass, respectively (Figure 4b).

There were positive linear correlations between rootstock to scion hydraulic conductance per unit dry mass ratio and scion to rootstock dry mass ratio ($P = 0.048$, Figure 5), and rootstock to scion hydraulic conductance per unit dry mass ratio and tree dry mass relative growth rate ($P = 0.057$, Figure 6). Because neither the rootstock nor the interaction term had a significant effect on these relationships, the scion to rootstock dry mass ratio and relative tree growth rate data for all the rootstocks fit the same relationships (Figures 5 and 6).

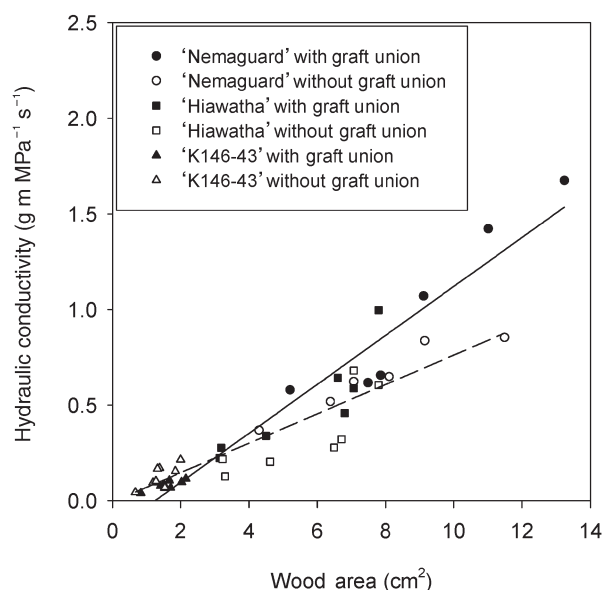


Figure 3. Relationships between the wood cross-sectional area and wood segment hydraulic conductivity with and without the graft union of 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Each value is for an individual wood segment ($n = 60$). Solid and dashed lines represent the fitted linear regression for wood segments with and without the graft union, respectively. Equations of fitted linear regressions are $y = 0.13x - 0.16$, $r^2 = 0.94$ and $y = 0.08x - 0.01$, $r^2 = 0.86$.

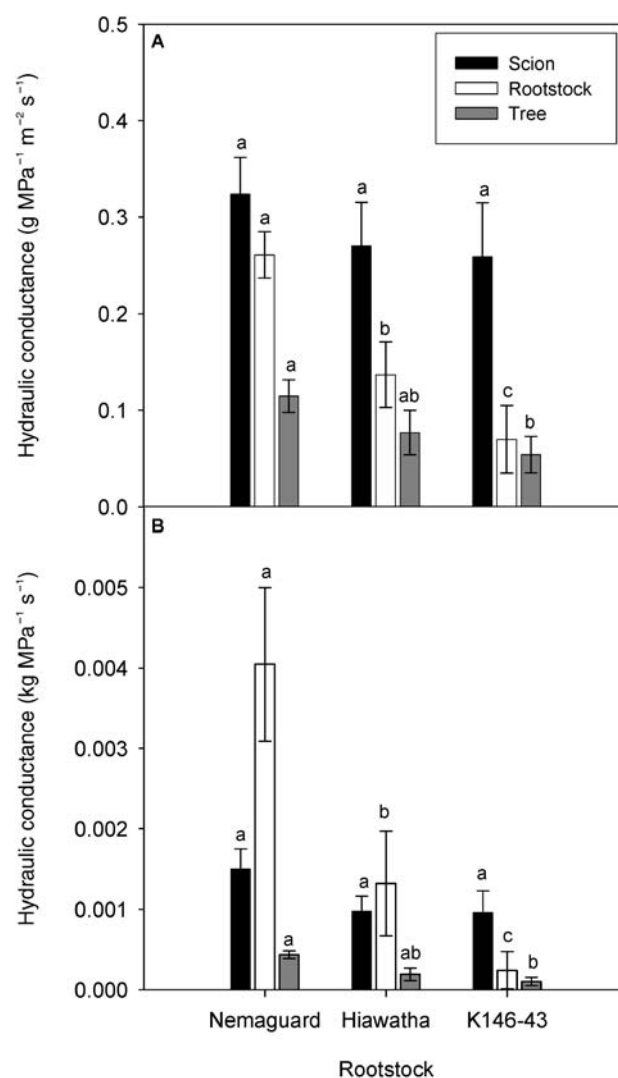


Figure 4. Scion, rootstock and tree hydraulic conductance per unit leaf area and dry mass of 1-year-old peach trees on 'Nemaguard', 'Hiawatha' and 'K146-43' rootstocks. Within a tree component, values with different letters are significantly different among rootstocks at the 0.05 level of significance. (A) each bar value is the mean of 15 trees $\pm$ standard error ($n = 45$) calculated from slopes of the fitted linear regressions between leaf area and hydraulic conductance. (B) each bar value is the mean of 15 trees $\pm$ standard error ($n = 45$) calculated from slopes of the fitted linear regressions between dry mass and hydraulic conductance.

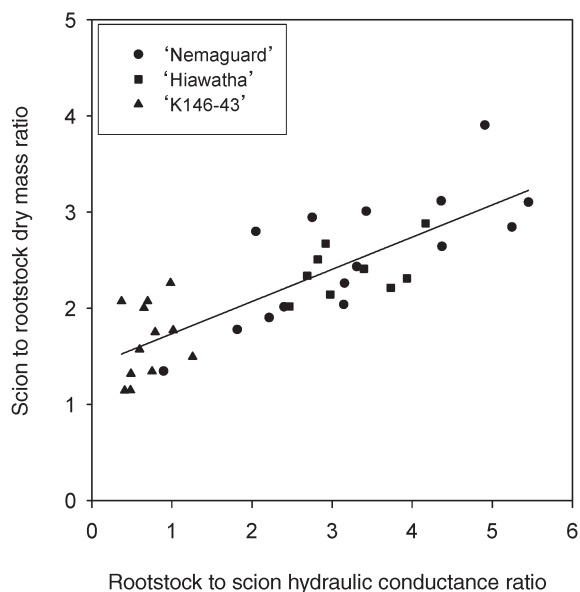


Figure 5. Relationships between the ratio of rootstock to scion hydraulic conductance (per unit dry mass) and the ratio of scion to rootstock dry mass of 1-year-old peach trees on Nemaguard, 'Hiawatha' and "K146-43" rootstocks. Each value is for an individual tree ($n = 45$). The solid line represents the fitted linear regression for all the rootstocks.

Discussion

Scion and rootstock hydraulic conductances varied significantly among rootstocks according to tree vigor, and scion hydraulic conductance was greater than rootstock hydraulic conductance for trees on each rootstock (Figure 1). These results

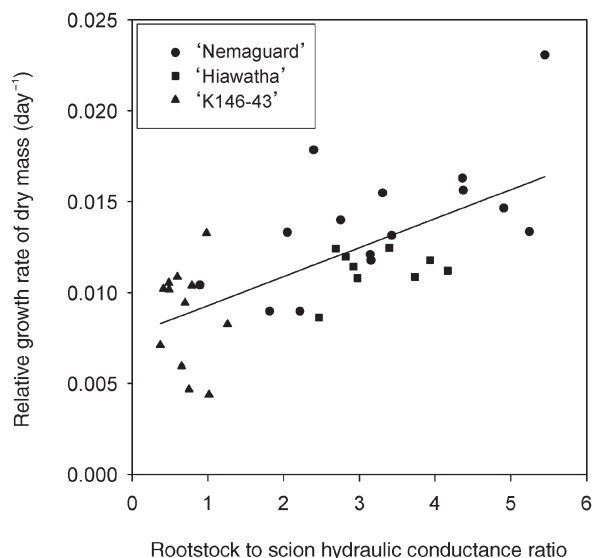


Figure 6. Relationships between the ratio of rootstock to scion hydraulic conductance (per unit dry mass) and dry mass relative growth rate of 1-year-old peach trees on Nemaguard, Hiawatha and 'K146-43' rootstocks. Each value is for an individual tree ($n = 45$). The solid line represents the fitted simple linear regression for all rootstocks.

corroborate previous studies showing that the root system is the main hydraulic resistance in peach trees (Rieger 1989, Basile et al. 2003b) and other tree species (Running 1980, Tsuda and Tyree 1997). However, the contributions of scion and rootstock hydraulic resistances to whole-tree hydraulic resistance varied among the rootstocks, with scion and rootstock accounting for about 30–45 and 45–60% of whole-tree resistance, respectively. As tree vigor decreased, the contribution of the rootstock to whole-tree hydraulic resistance increased (Figure 2). Olien and Lakso (1986) reported a similar trend in the contributions of scion and rootstock to whole-tree hydraulic resistance in apple trees. The differences in hydraulic resistance distribution among trees on different rootstocks were not explained by differences in dry matter distribution (Table 1; Figure 1), suggesting that there are specific differences in hydraulic properties among trees on different rootstocks.

Wood segment hydraulic conductivity ranged from 0.5 to $18 \times 10^{-4} \text{ kg MPa}^{-1} \text{ s}^{-1}$, similar to values reported for apple rootstocks (Atkinson et al. 2003). However, the contribution of the wood segment with the graft union to whole-tree hydraulic resistance was only about 10% for all the rootstocks studied (Figure 2). The linear relationship between wood cross-sectional area and wood segment hydraulic conductance was similar among rootstocks and also similar in the presence and absence of the graft union (Table 3; Figure 3). When the hydraulic conductances of wood segments with and without graft unions were analyzed separately there was a non-significant tendency for the segments without the graft union to have lower hydraulic conductances than the segments with the graft union. Therefore, it is unlikely that the graft union itself is responsible for any xylem-based differences in transport processes associated with the growth performance of trees on the peach rootstocks tested. This finding contrasts with previous studies on apple rootstocks showing that the graft union limits transport of plant growth regulators (Kamboj et al. 1997 and 1999), mineral nutrients (Jones 1971 and 1974) and water (Atkinson et al. 2003) from rootstocks as a result of disorganization of the vascular tissue where the scion and rootstock join (Soumelidou et al. 1994). In peach, however, it is the rootstock itself that apparently limits water transport through the tree.

The rootstocks did not affect scion hydraulic conductance per unit leaf area, but affected rootstock hydraulic conductance per unit leaf area (Figure 4a). Consequently, whole-tree hydraulic conductance per unit leaf area also differed among rootstocks (Figure 4a). Rootstock hydraulic conductance per unit leaf area ranged from about 0.5 to $4 \times 10^{-4} \text{ kg MPa}^{-1} \text{ m}^{-2} \text{ s}^{-1}$, which is in the range of published values (Olien and Lakso 1986, Cohen and Naor 2002, Basile et al. 2003b). Because rootstock hydraulic conductance per unit leaf area appeared to be related to differences in dry matter distribution among rootstocks (Table 1), we also expressed hydraulic conductance per unit dry mass of the tree components. Hydraulic conductance per unit dry mass varied from 0.4 to $40 \times 10^{-4} \text{ MPa}^{-1} \text{ s}^{-1}$ (Figure 4b) and was within the range reported for tropical trees (Tyree et al. 1998). Figure 4b also shows that differences in rootstock hydraulic conductance were more clearly separated among rootstock genotypes when hydraulic conductance was

expressed per unit dry mass, and that the differences in hydraulic conductance between the trees grafted on the three rootstocks were almost entirely located in the root of the tree. Nemaguard rootstock appeared to have a more efficient hydraulic system that could maintain a more favorable tree water status than 'K146-43' for a given transpiration rate, and 'Hiawatha's hydraulic performance was intermediate.

The significant effect of rootstocks on tree dry matter production at the end of the growing season (Table 1) is in agreement with earlier studies (Weibel et al. 2003). Differences in dry matter production among trees on different rootstocks were associated with differences in absolute growth rates and relative growth rates of the trees (Table 2). Because relative growth rate is a function of net assimilation rate and leaf area ratio of plants, differences in dry mass relative growth rate among trees on different rootstocks were associated with differences in calculated canopy net assimilation rates (Table 2). These differences in canopy net assimilation rate correspond to differences in individual leaf net assimilation rates measured over individual days in a companion study (Solari et al. 2006). We have no information on the fraction of assimilated carbon respired by trees on these rootstocks. However, differences in dry matter distribution among trees on the three rootstocks may have influenced the proportion of carbon used in respiration by trees on the different rootstocks and, hence, also contributed to the differences in estimated canopy net assimilation rate. Despite the variations in dry matter distribution, trees on the different rootstocks did not have statistically different leaf area ratios, implying that the differences in dry mass relative growth rates of trees on the different rootstocks were determined mainly by differences in carbon assimilation rates and biomass distribution.

The relationship between rootstock to scion hydraulic conductance ratio and the scion to rootstock dry mass ratio (Figure 5) indicates that the whole-tree response to the decrease in rootstock hydraulic efficiency relative to scion hydraulic efficiency was to allocate proportionately more biomass to roots. Young peach trees show a similar response to water stress (Steinberg et al. 1990). Thus, not only was net assimilation rate of trees on the size-controlling rootstocks affected by the reduction in hydraulic conductance (Table 3), but also partitioning of assimilates between the scion and rootstock with greater investment in the roots than the shoots. The combination of these responses resulted in a clear relationship between the rootstock to scion hydraulic conductance ratio and tree dry mass relative growth rate (Figure 6). This relationship provides direct evidence that the size-controlling behavior of the studied rootstocks was linked to the relative rootstock to scion hydraulic efficiency of each rootstock/scion combination. Because a common scion genotype was used for all trees, the explanation for the differences among trees must lie in the differences in hydraulic conductance among rootstocks.

These results, together with the findings presented in the accompanying paper (Solari et al. 2006), demonstrate how specific rootstocks influence the vegetative growth of peach trees, and confirm traditional concepts of the relationships between shoot and root growth (Brouwer 1962). The more size-control-

ling rootstocks had lower leaf specific hydraulic conductance than the more vigorous rootstocks, indicating that vigorous rootstocks maintained a higher tree water status than size-controlling rootstocks. In turn, this difference caused differences in daily shoot growth and leaf net assimilation rates (Solari et al. 2006), subsequently affecting whole-tree net carbon assimilation rates in the field (Table 2). Furthermore, these rootstocks had a pronounced effect on shoot growth because shoot growth is highly responsive to differences in stem water potential (Berman and DeJong 1997). In addition, root growth was favored compared with scion growth in the more dwarfing rootstock to compensate for the lower rootstock hydraulic conductance (Figure 5). The different physiological responses among rootstocks with different hydraulic properties eventually resulted in different vegetative growth rates of the trees (Figure 6).

Although water relations and rootstock hydraulic conductance play a mechanistic role in the physiology of size-control in the peach rootstocks we studied, these results do not exclude the possibility that other factors, including plant growth regulators, are involved in controlling vegetative growth of trees on these and other size-controlling rootstocks. It also remains to be determined whether the differences in rootstock hydraulic conductance among the different rootstocks are associated with differences in root system architecture.

Acknowledgments

We thank Dr. Larry Williams for the use of his equipment and laboratory. We are grateful to the field personnel at Kearney Agricultural Center for assistance in horticulture operations and experimental measurements.

References

- Atkinson, C.J., M.A. Else, L. Taylor and C.J. Dover. 2003. Root and stem hydraulic conductivity as determinants of growth potential in grafted trees of apple (*Malus pumila* Mill.) J. Exp. Bot. 54: 1221–1229.
- Basile, B., J. Marsal and T.M. DeJong. 2003a. Daily shoot extension growth of peach trees growing on rootstocks that reduce scion growth to daily dynamics of stem water potential. Tree Physiol. 23: 695–704.
- Basile, B., J. Marsal, L.I. Solari, M.T. Tyree, D.R. Bryla and T.M. DeJong. 2003b. Hydraulic conductance of peach trees grafted on rootstocks with differing size-controlling potentials. J. Hortic. Sci. Biotechnol. 78: 768–774.
- Beakbane, A.B. 1956. Possible mechanism of rootstock effect. Ann. Appl. Biol. 44:517–521.
- Berman, M.E. and T.M. DeJong. 1997. Diurnal patterns of stem extension growth in peach (*Prunus persica*): temperature and fluctuations in water status determine growth rate. Physiol. Plant. 100: 361–370.
- Brouwer, R. 1962. Distribution of dry matter in the plant. Neth. J. Agric. Sci. 10:361–376.
- Cohen, S. and A. Naor. 2002. The effect of three rootstocks on water use, canopy conductance and hydraulic parameters of apple trees and predicting canopy from hydraulic conductances. Plant Cell Environ. 25:17–28.

- Hubbard, R.M., M.G. Ryan, V. Stiller and J.S. Sperry. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. 2001. *Plant Cell Environ.* 24: 113–121.
- Jones, O.P. 1971. Effect of rootstock and interstock on the xylem sap composition in apple trees: effects on nitrogen, phosphorus and potassium content. *Ann. Bot.* 35:825–836.
- Jones, O.P. 1974. Xylem sap composition in apple trees: effect of the graft union. *Ann. Bot.* 38:463–467.
- Jones, H.G. and R.A. Sutherland. 1991. Stomatal control of xylem embolism. *Plant Cell Environ.* 14:607–612.
- Kamboj, J.S., G. Browning, J.D. Quinlan, P.S. Blake and D.A. Baker. 1997. Polar transport of [3H]-IAA in apical shoot segments of different apple rootstocks. *J. Hortic. Sci.* 72:773–780.
- Kamboj, J.S., P.S. Blake, J.D. Quinlan and D.A. Baker. 1999. Identification and quantification by GC-MS of zeatin and zeatin riboside in xylem sap from rootstock and scion of grafted apple trees. *Plant Growth Regul.* 28:199–205.
- Koch, G.W., S.C. Sillett, G.M. Jennings and S.D. Davis. 2004. The limits to tree height. *Nature* 428:851–854.
- Kolb, K.J. and J.S. Sperry. 1999. Transport constraints on water use by the great basin shrub, *Artemisia tridentata*. *Plant Cell Environ.* 22:925–935.
- Lockard, R.G. and G.W. Schneider. 1981. Stock and scion growth relationship and the dwarfing mechanism in apple. *Hortic. Rev.* 2:315–375.
- Olien, W.C. and A.N. Lakso. 1986. Effect of rootstock on apple (*Malus domestica*) tree water relations. *Physiol. Plant.* 67: 421–430.
- Rieger, M. 1989. Pressure and transpiration induced flow methods for estimating hydraulic resistance in peach. *Hortscience* 24:648–650.
- Rogers, W.S. and A.B. Beakbane. 1957. Stock and scion relations. *Annu. Rev. Plant Physiol.* 8:217–236.
- Running, S.W. 1980. Field estimates of root and xylem resistances in *Pinus contorta* using root excision. *J. Exp. Bot.* 31:555–569.
- Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. *Bioscience* 47:235–242.
- Solari, L.I., S. Johnson and T.M. DeJong. 2006. Relationship of water status to vegetative growth and leaf gas exchange of peach (*Prunus persica*) trees on different rootstocks. *Tree Physiol.* 26:1333–1341.
- Soumelidou, K., N.H. Battey, P. John and J.R. Barnett. 1994. The anatomy of the developing bud union and its relationship to dwarfing in apple. *Ann. Bot.* 74:605–611.
- Sperry, J.S. and W.T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betulia occidentalis*. *Plant Cell Environ.* 16:279–287.
- Sperry, J.S., N.N. Alder and S.E. Eastlack. 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *J. Exp. Bot.* 44:1075–1082.
- Steinberg, S.L., J.C. Miller and M.J. McFarland. 1990. Dry matter partitioning and vegetative growth of young peach trees under water stress. *Aust. J. Plant Physiol.* 17:23–36.
- Tsuda, M. and M.T. Tyree. 1997. Whole plant hydraulic resistance and vulnerability segmentation in *Acer saccharinum*. *Tree Physiol.* 17:351–357.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol.* 88:574–580.
- Tyree, M.T., B. Sinclair, P. Liu and A. Granier. 1993. Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flow meter. *Ann. Sci. For.* 50:417–423.
- Tyree, M.T., S. Yang, P. Cruziat and B. Sinclair. 1994. Novel methods of measuring hydraulic conductivity of tree root systems and interpretation using AMAIZED: a maize-root dynamic model for water and solute transport. *Plant Physiol.* 104:189–199.
- Tyree, M.T., V. Velez and J.W. Dalling. 1998. Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. *Oecologia* 114:293–298.
- Webster, A.D. 1995. Rootstock and interstock effects on deciduous fruit tree vigour, precocity, and yield productivity. *N.Z. J. Crop Hortic. Sci.* 23:373–382.
- Weibel, A., R.S. Johnson and T.M. DeJong. 2003. Comparative vegetative growth responses of two peach cultivars grown on size-controlling versus standard rootstocks. *J. Am. Soc. Hortic. Sci.* 128: 463–471.
- Woodruff, D.R., B.J. Bond and F.C. Meinzer. 2004. Does turgor limit growth in tall trees? *Plant Cell Environ.* 27:229–236.