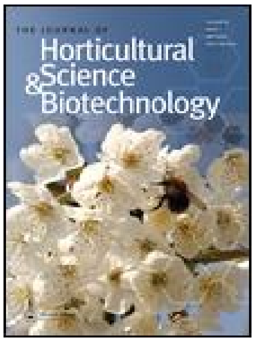

The Journal of Horticultural Science and Biotechnology

ISSN: 1462-0316 (Print) 2380-4084 (Online) Journal homepage: http://www.tandfonline.com/loi/thsb20

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To cite this article: B. Basile, J. Marsal, L.I. Solari, M.T. Tyree, D.R. Bryla & T.M. Dejong (2003) Hydraulic conductance of peach trees grafted on rootstocks with differing size-controlling potentials, The Journal of Horticultural Science and Biotechnology, 78:6, 768-774, DOI: 10.1080/14620316.2003.11511697

To link to this article: http://dx.doi.org/10.1080/14620316.2003.11511697

Journal of Horticultural Science & Biotechnology (2003) **78** (6) 768–774

Hydraulic conductance of peach trees grafted on rootstocks with differing size-controlling potentials

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(Accepted 26 April 2003)

SUMMARY

The objective of this study was to evaluate the hydraulic conductance in various components of peach trees grown on rootstocks with contrasting size-controlling potentials. The experiment was conducted on 'Crimson Lady' peach trees grafted onto two rootstocks: a semi-dwarfing rootstock, K-146-44 (*P. salicina* × *P. persica* hybrid) and a vigorous rootstock, Nemaguard (seed-propagated *Prunus persica* × *P. davidiana* hybrid). Hydraulic conductance of leaves, stems, trunk, graft union, and root system was measured in the scion/rootstocks with a high-pressure flow meter. Total leaf area and dry-matter partitioning into main tree components were also determined. The above and below ground portions of trees grown on Nemaguard rootstock were 393% and 299% larger, respectively, than trees grown on K-146-44 rootstock. Whether trees were grafted on Nemaguard or K-146-44, the root system accounted for most of the resistance to water flow through the tree. When hydraulic conductance was expressed per unit leaf area, trees on K-146-44 rootstock had significantly lower root conductance than trees on Nemaguard rootstock. Rootstocks had no effect on hydraulic conductance through the scion or the graft union. Trees on K-146-44 also partitioned relatively more dry matter to roots and leaves and less to stems than trees on Nemaguard. The results suggest that high root resistance plays a central role in the dwarfing mechanism induced by the size-controlling rootstock.

The dwarfing mechanism of size-controlling rootstocks used for fruit trees is not clearly understood. One theory developed to explain this phenomenon is related to the influence of size-controlling rootstocks on tree water relations (Beakbane, 1956). This hypothesis was supported by the anatomical study of Beakbane and Thompson (1939) who reported that dwarfing rootstocks of apple tend to have roots with fewer and smaller xylem vessels than invigorating rootstocks. In addition, apple trees on dwarfing rootstocks have been reported to have lower midday leaf water potentials (Ψ_{leaf}) (Giulivo and Bergamini, 1982) and stem water potentials (Ψ_{stem}) (Olien and Lakso, 1986) than trees on vigorous rootstocks, but no one has clearly linked this with a size-controlling mechanism. Until recently, even less was known about size-controlling mechanisms in peach because of the lack of availability of suitable dwarfing rootstocks for this species. Since 1986, researchers at the University of California have been evaluating peach rootstocks and have selected promising rootstocks with size-controlling characteristics (Weibel, 1999; DeJong *et al.*, 2001). Peach trees on these rootstocks also have been reported to have lower midday Ψ_{stem} than trees on invigorating rootstocks (Weibel, 1999; Basile *et al.*, 2003). Basile *et al.* (2003) reported a positive correlation between integrated diurnal patterns of Ψ_{stem} and daily stem-extension growth for peach trees on rootstocks with different size control potentials. They documented the effect of decreased water potential on shoot growth in a manner similar to previous works that linked water stress effects with plant growth in annual species (Hsiao, 1973; Boyer, 1985).

Plant water potential is directly related to hydraulic conductivity of water through the soil-plant-air continuum (Kramer and Boyer, 1995). Olien and Lakso (1986) performed indirect estimates of root hydraulic conductivity and suggested that low midday Ψ_{stem} occurring in apple trees on dwarfing rootstocks might be related to low hydraulic conductivity of the root system of these rootstocks, and/or hydraulic conductivity of the graft unions. Hussein and McFarland (1994) reported that, during the development of water stress, sap flow in apple trees on dwarfing rootstock (Mark) decreased faster than in trees on an invigorating rootstock (seedling), but hydraulic conductance was not specifically measured. Syvertsen (1981) also reported that root hydraulic conductivity may be correlated to the growth potential of citrus rootstocks.

Several studies have examined total tree conductance and its components (i.e. roots, stems and leaves) (Roberts, 1977; Tyree *et al.*, 1993; Yang and Tyree, 1994; Tsuda and Tyree, 1997). However, most studies of hydraulic architecture of fruit trees (Olien and Lakso, 1986; Rieger, 1989; Moreshet *et al.*, 1990; Moreshet *et al.*,

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1998; Rieger and Motisi, 1990; Rieger and Duemmel, 1992) focused on estimating the conductance of the root system, but did not analyse the contribution of each organ to total tree conductance. The objective of the present study was to evaluate the hydraulic conductance of different tree organs of peach trees grown on rootstocks with contrasting size-controlling potentials.

MATERIALS AND METHODS

The experiment was carried out at the University of California Kearney Agricultural Center located in Parlier, California, USA. On 16 March 2001, one year old 'Crimson Lady' peach (*Prunus persica* (L.) Batsch) trees on two differing rootstocks were planted in the field in a single row with an east-west orientation. Six trees were on a semi-dwarfing rootstock, K-146-44 (*Prunus salicina* × *P. persica* hybrid), and six trees were on Nemaguard (seed-propagated *Prunus persica* × *P. davidiana* hybrid), a vigorous rootstock commonly used in commercial production. Trees were spaced 6.0 m from an adjacent row and 1.7 m apart in the row and pruned to a single trunk approximately 1 m long at transplanting. Routine horticultural care was provided according to commercial protocol for fruit production. Trees were irrigated to field capacity just prior to measurements.

Hydraulic resistance measurements were done on 2–7 August 2001 using a high-pressure flow meter (HPFM) (Dynamax Inc., Houston, Texas, USA). The HPFM is described in detail in Tyree *et al.* (1995) and has been used for measuring hydraulic resistance of leaves, stems, and roots by others (Tyree *et al.*, 1993; Tyree *et al.*, 1995; Yang and Tyree, 1994). To avoid the potential effect of diurnal periodicity in root hydraulic resistance in the rootstocks (Tyree and Zimmermann, 2002), measurements were made on two trees per day (one per rootstock) between 1100 hours and 1400 hours. Trees were cut off 5 cm above the graft union. Once cut, the scion was connected to the HPFM and perfused with degassed water until the leaves were completely infiltrated with water and a quasi-steady-state condition was reached (i.e. when values of pressure (P) and flow rate (F) were stable). Trees were covered with a plastic tarpaulin and water was sprayed under the tarpaulin during measurements to minimize transpiration and facilitate the reaching of the quasi-steady-state condition. Hydraulic resistance of the scion was calculated as $R_s = P/F$ according to the Ohm's law analogue. A transient measurement (described in Tyree *et al.*, 1995) and a second quasi-steady-state measurement were also done and R_S measurements were averaged. During the second quasi-steady-state condition, leaves were removed from the scion. When the system reached a new quasi-steady-state condition, hydraulic resistance of the scion without leaves, $R_{S\text{-}L}$, was calculated. Hydraulic resistance of the leaves, R_L, was calculated by substracting R_{S-L} from R_S. New stem growth from the current season was also removed to measure hydraulic resistance of the trunk, R_T. Hydraulic resistance of the new stems, R_{St}, was calculated by subtracting R_T from $R_{S\text{-}L}$. Immediately after measurement of scion hydraulic resistance the HPFM was connected to the root system (5 cm above the graft union) and hydraulic resistance of the root system (rootstock) plus the graft union, R_{R+G}, was estimated from transient measurements as described by Tyree *et al.* (1995). Root hydraulic resistance was not measured during quasi-steady-state conditions because the disadvantage of measuring root hydraulic resistance with the HPFM is that the direction of the flow is opposite to the normal direction of transpiration. During quasi-steady-state measurements of root hydraulic resistance, the reversed flow pushes solutes backward toward the root tips and solutes are concentrated by reverse osmosis (Tyree *et al.*, 1994; Tyree *et al.*, 1995). The solute concentration occurring during quasi-steady-state measurements can cause errors in the estimation of root hydraulic resistance (Tyree *et al.*, 1994), whereas rapid measurements (transient measurements) minimize the change in solute and provide good estimates of root hydraulic resistance (Tyree *et al.*, 1995). Five or six consecutive transient measurements were taken for each root system and averaged. Finally, the base of the trunk was cut off 5 cm below the graft union and quasi-steady-state measurements were made to calculate hydraulic resistance of the graft union, R_G. Hydraulic resistance of the root system (rootstock), R_r, was calculated by subtracting R_G from R_{R+G}. Hydraulic resistance of the entire tree, R_{tree}, was calculated as the sum of R_S, R_G and R_R. Hydraulic conductance of the scion, the graft union, the root system (rootstock) and the entire tree were calculated as the inverse of R_S, R_G, R_R and R_{tree}, respectively.

When HPFM measurements were completed on each day, a Li-COR 3200 leaf area meter (Li-COR, Lincoln, Nebraska, USA) was used to measure total leaf area, A_L, of each tree. Cross-sectional area of the trunk was calculated by measuring its circumference 5 cm above the graft union. Leaves, shoots, and trunks were dried at 60°C for at least one week and then weighed. On 8 August 2001 the trees were excavated with a backhoe keeping the roots from individual trees as intact as possible. After the main root mass was removed, a 1.5 × 1.5 × 0.75 m volume of soil was excavated and sifted through for root pieces. The roots were hydraulically separated from soil and subsequently oven-dried and weighed. Weather information (temperature, relative humidity, and net solar radiation) collected during the experiment was downloaded from a nearby CIMIS (California Irrigation Management Information System) weather station located less than 1 km from the site.

Hydraulic conductances, leaf areas and dry weights of each rootstock were compared using one-way analysis of variance (ANOVA) with SPSS software (SPSS Inc., Chicago, Massachusetts). Relationships between leaf area and hydraulic conductance were developed using a linear regression model.

RESULTS

Weather conditions

The weather was very consistent during the six days of field measurements. Mean air temperature, relative humidity, and net solar radiation calculated between 1100 hours and 1400 hours during the six days of the experiment were 29.9 ± 0.5°C, 45.8 ± 1.9%, and 524.3 ± 8.8 W m^{-2}, respectively.

TABLE I

Total scion dry weight (including the graft union), root dry weight, leaf area, shoot length, and trunk cross-sectional area of 'Crimson Lady' peach trees on Nemaguard and K-146-44 rootstock. Values represent the mean of six trees ± the standard error of the mean

Rootstock	Scion dry weight (g)	Root dry weight (g)	Leaf area (m^2)	Shoot length (m)	Trunk cross-sectional area (cm^2)
Nemaguard	411.0 ± 72.3	119.1 ± 12.1	2.01 ± 0.40	24.27 ± 5.33	4.05 ± 0.77
K-146-44	104.5 ± 13.3	39.8 ± 4.0	0.55 ± 0.06	5.64 ± 0.68	0.90 ± 0.10
Probability[z]	0.002	0.0001	0.0051	0.0061	0.0022

[z] According to a one-way ANOVA.

Tree size and dry-matter partitioning

Peach trees grown on Nemaguard rootstock were significantly larger than trees on the size-controlling rootstock, K-146-44 (Table I). Overall, Nemaguard had 393% more dry mass above ground and 299% dry mass below ground than K-146-44. Trees on Nemaguard also had significantly more leaf area, shoot length, and trunk cross-sectional area than trees on K-146-44 (Table I). Leaf area of trees on K-146-44 ranged between 0.31 m^2 and 0.68 m^2, whereas trees on Nemaguard had leaf areas between 0.83 m^2 and 3.6 m^2.

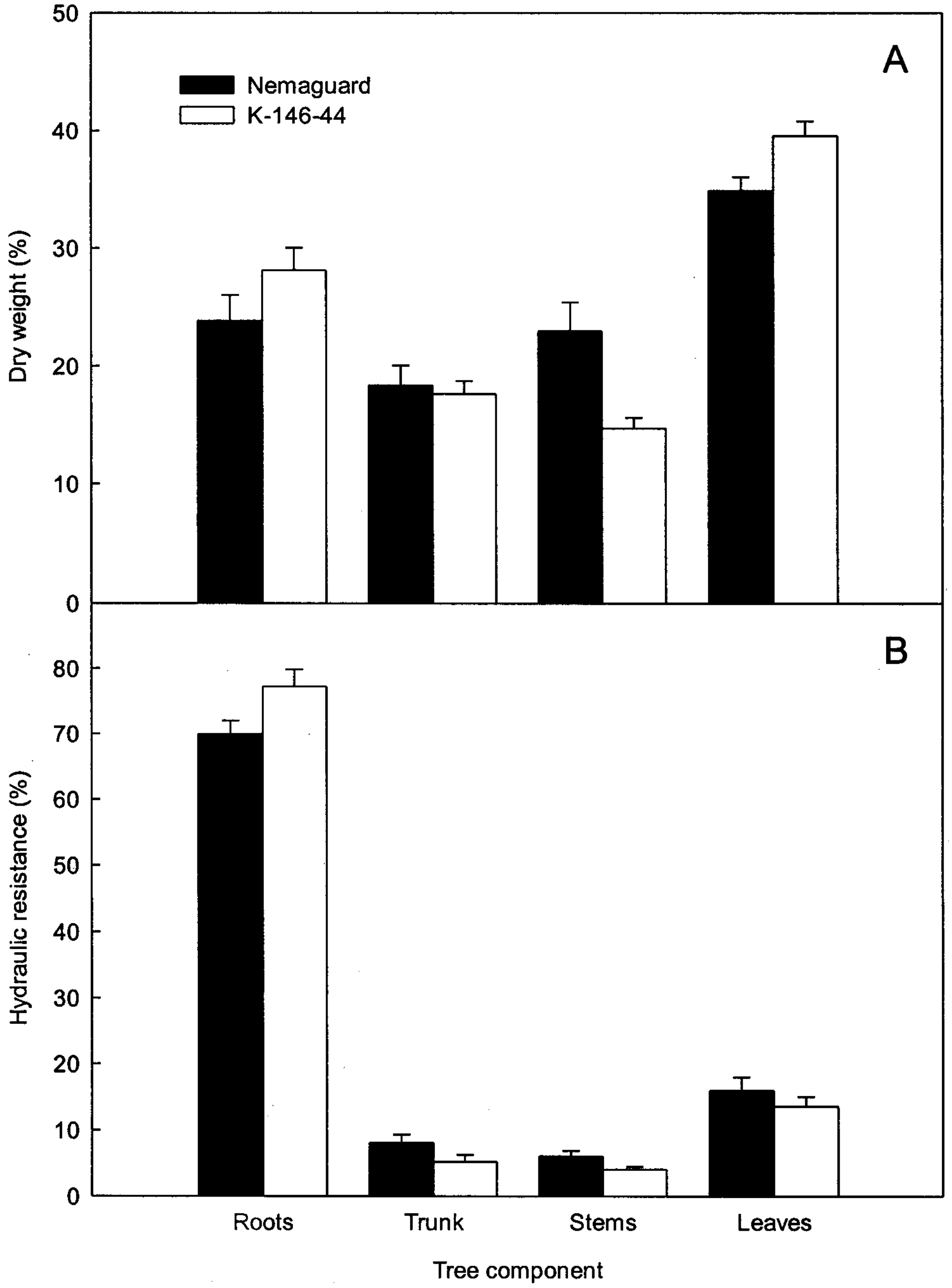

FIG. 1

Percent contribution of roots, trunk (including the graft union), stems and leaves to total tree (A) dry mass and (B) hydraulic resistance (inverse of hydraulic conductance) in Crimson Lady peach trees on K-146-44 and Nemaguard rootstock. Each measurement represents the mean of six trees on K-146-44 and Nemaguard rootstock. Each measurement represents the mean of six trees and error bars represent 1 standard error.

TABLE II

Equations, determination coefficients (R^2) and significance of the regression models relating total leaf area (A_L) to hydraulic conductance of the scion (K_S), the graft union (K_G), the root system (K_R), and the entire tree (K_{tree}) of 'Crimson Lady' peach trees on Nemaguard and K-146-44 rootstock. Each regression was performed on data from six trees

Rootstock	Dependent Variable	Model	R^2	Probability
Nemaguard	K_s	$K_s = 2.68 \times 10^{-4} A_L - 1.21 \times 10^{-4}$	0.94	0.0015
	KG	$K_G = 2.47 \times 10^{-3} A_L - 7.23 \times 10^{-4}$	0.64	0.0561
	K_R	$K_R = 6.56 \times 10^{-5} A_L + 1.64 \times 10^{-5}$	0.93	0.0021
	K_{tree}	$K_{tree} = 5.23 \times 10^{-5} A_L - 1.94 \times 10^{-}7$	0.96	0.0006
K-146-44	K_S	$K_S = 1.79 \times 10^{-4} A_L + 2.77 \times 10^{-5}$	0.34	0.2268
	K_G	$K_G = 2.67 \times 10^{-3} A_L - 2.90 \times 10^{-4}$	0.71	0.0345
	K_R	$K_R = 2.49 \times 10^{-5} A_L + 1.73 \times 10^{-5}$	0.59	0.0735
	K_{tree}	$K_{tree} = 2.29 \times 10^{-5} A_L + 1.12 \times 10^{-5}$	0.89	0.0050

Dry-matter partitioning also differed significantly between rootstocks (Figure 1A). For example, trees on K-146-44 partitioned significantly ($P \leq 0.05$) more dry matter to production of roots (23.8 ± 2.2%) than trees on Nemaguard (28.1 ± 1.9%) (Figure 1A). K-146-44 also partitioned significantly more dry matter to leaves ($P \leq 0.05$). On the other hand, trees on Nemaguard partitioned significantly more dry matter to the production of stems ($P \leq 0.01$) than trees on K-146-44 (Figure 1A). The proportion of dry matter in the trunk of the scion was not significantly different between rootstocks (Figure 1A). Rootstock did not significantly influence the ratio of root dry weight to total leaf area (K-146-44: 74.8 ± 8.8 g m^{-2}; Nemaguard: 67.2 ± 9.2 g m^{-2} (P 0.20)).

Hydraulic resistance/conductance

The resistance to water flow through trees on K-146-44 rootstock ($4.26 \times 10^4 \pm 0.28 \times 10^4$ MPa s kg^{-1}) was nearly four-fold higher than hydraulic resistance through trees on Nemaguard rootstock ($1.15 \times 10^4 \pm 0.21 \times 10^4$ MPa s kg^{-1}). Most of the hydraulic resistance occurred in the root system of both rootstocks (Figure 1B). Root resistance accounted for 70% of the total tree resistance in Nemaguard and 77% of the total resistance in K-146-44. Hydraulic resistance in the trunk, stems, or leaves never accounted for more than 22% of the total resistance in any of the trees measured.

Hydraulic conductance in trees on both rootstocks was positively correlated with total leaf area (Table II). Leaf area was also significantly correlated with the hydraulic conductance of the scion (K_S) and root system (K_R) of trees on Nemaguard and to the hydraulic conductance of the graft union of trees on K-146-44 (Table II). When hydraulic conductance was expressed per unit leaf area (leaf-specific hydraulic conductance) as shown in Table III, K_R/A_L (leaf-specific hydraulic conductance of the root system) was significantly higher in Nemaguard than in K-146-44. The rootstocks, however, did not significantly affect leaf-specific hydraulic conductance in the scion (K_S/A_L) or at the graft union (K_G/A_L). Leaf specific hydraulic conductance of the root system plus graft union (K_{R+G}/A_L) of trees on Nemaguard ($7.35 \times 10^{-5} \pm 5.11 \times 10^{-6}$ kg s^{-1} MPa^{-1} m^{-2}) was significantly ($P \leq 0.005$) higher than for trees on K-146-44 ($5.70 \times 10^{-5} \pm 5.02 \times 10^{-6}$ kg s^{-1} MPa^{-1} m^{-2}). Table III also illustrates that K_G does not limit K_{tree} in trees on these rootstocks.

DISCUSSION

Hydraulic resistance was highest in the roots and root resistance was higher in K-146-44 than in Nemaguard

The root system accounted for 67–77% of the total amount of hydraulic resistance in 'Crimson Lady' peach trees whether trees were grafted to a vigorous rootstock, Nemaguard, or to a size-controlling rootstock, K-146-44. Rieger (1989) similarly found that root systems of non-grafted Nemaguard peach trees accounted for most of the hydraulic resistance measured. They demonstrated using two methods to estimate hydraulic resistance, a transpiration induced flow method and a pressure induced flow method, that 73–90% of total resistance in the tree could be accounted for in the roots. In other species, studies on the relative contribution of tree root and canopy to total hydraulic resistance have produced contrasting results. As occurred in the present study, several studies indicate that hydraulic resistance to water flow is higher in the roots than in the above ground part of the tree (Olien and Lakso, 1986; Rieger, 1989; Tsuda and Tyree, 1997). Other studies indicate that the magnitude of root and canopy resistance is similar (Roberts, 1977; Moreshet *et al.*, 1990). Still others have reported that root hydraulic resistance is lower than aboveground resistance (Hellkvist *et al.*, 1974). Variability among plant species in their vascular tissue may account for the fact that some species have the highest amount of hydraulic resistance belowground while others have more resistance aboveground.

In the present study, leaf-specific hydraulic conductance of the root system (K_R/A_L) was significantly lower in the size-controlling rootstock than in the vigorous

TABLE III

Leaf-specific hydraulic conductance of the scion, the graft union, the root system (measured below the graft union), and the entire tree of Crimson Lady peach trees on Nemaguard and K-146-44 rootstock. Values represent the mean of six trees

	Leaf-specific hydraulic conductance (kg s^{-1} MPa^{-1} m^{-2})			
Rootstock	Scion	Graft union	Root system	Entire tree
Nemaguard	2.00×10^{-4}	2.14×10^{-3}	7.64×10^{-5}	5.32×10^{-5}
K-146-44	2.32×10^{-4}	2.11×10^{-3}	5.88×10^{-5}	4.49×10^{-5}
Probability[z]	0.328	0.932	0.041	0.095

[z] According to a one-way ANOVA.

rootstock. But leaf-specific hydraulic conductances of the scion (K_S/A_L) and of the graft union (K_G/A_L) were not significantly different between trees grafted on Nemaguard and K-146-44. These results raise the question of whether root hydraulic resistance is the main mechanism causing reduced growth by size-controlling rootstocks. Cohen and Naor (2002) also reported that apple trees on the dwarfing rootstock M:9 had lower leaf-specific hydraulic conductance (relative to the soil to stem and the soil to leaf pathways) than apple trees on the vigorous rootstock MM.106. But they did not specifically assign this difference to the leaf-specific hydraulic conductance of root system. Other authors suggested that the dwarfing mechanism induced by apple (Olien and Lakso, 1986) and citrus (Syvertsen, 1981) rootstocks may be related to hydraulic resistance of the root system and/or of the graft union. The graft union has been suggested to affect tree water relations in apple trees on dwarfing rootstock (Atkinson *et al.*, 2001). These affects may be due to morphological and developmental anomalies of the vascular system at the graft union (Simons and Chu, 1984; Ussahatanonta and Simons, 1988; Soumelidou *et al.*, 1994; Salvatierra *et al.*, 1998). Thus, in dwarfed apple trees, the graft union may cause significant resistance to water flow from the root system to the canopy. Although the present study did not examine morphological features of the xylem vessels at the graft union, the graft union had little effect on water flow through the trunks of the vigorous and size-controlling rootstocks. Rootstocks can also affect scion characteristics of fruit trees (Tubbs, 1973a; Tubbs 1973b; Tubbs, 1980; Rom and Carlson, 1987). However, we found no evidence that the rootstocks influenced hydraulic conductance of the scion of 'Crimson Lady' peach. This result agrees with those reported by Olien and Lakso (1986) who scaled scion conductance by different tree size-related parameters (trunk circumference, trunk cross-sectional area and estimated total leaf area) and concluded that apple rootstocks with differing vigour did not affect hydraulic conductivity in the scion.

Hydraulic conductance increases with tree size

In both rootstocks, hydraulic conductance of the whole tree, as well as individual components of the tree including the root system, the scion, and the graft union, linearly increased with total leaf area. A positive correlation between hydraulic conductance and tree size was expected to occur (Tyree *et al.*, 1998). For this reason it is always necessary to normalize hydraulic conductance measurements for plant size. Tyree *et al.* (1998) compared different ways of scaling root and shoot hydraulic conductance to take tree size differences into account. They suggested that scaling both root and shoot conductance by dividing by total leaf area is particularly appropriate when investigating physiological relationships in plants. The physiological justification of scaling hydraulic conductance by total leaf area (leaf-specific hydraulic conductance) can be explained by the Ohm's law analogue (Tyree *et al.*, 1998).

Potential effects of hydraulic conductance of the rootstocks on plant water relations and growth

In a previous study, Basile *et al.* (2003) reported that peach trees on K-146-43 (a size-controlling rootstock very similar to K-146-44) had different diurnal patterns of Ψ_{stem} compared with trees on Nemaguard. Furthermore, differences in integrated diurnal Ψ_{stem} were strongly correlated with differences in daily stem extension growth rates induced by the two rootstocks. The importance of hydraulic conductance on plant water potential can be illustrated using the Ohm's law analogue as described by Kramer and Boyer (1995). According to this analogy and to the assumptions made by Tyree *et al.* (1998) we can assume that:

$$\Psi_{leaf} \cong -[1/(K_S/A_L) + 1/(K_G/A_L) + 1/(K_R/A_L)]E \quad (1)$$

where Ψ_{leaf} is the leaf water potential (MPa), K_S, K_G and K_R are the hydraulic conductance (kg s^{-1} MPa^{-1}) of the scion, graft union and root system (rootstock), respectively, and E is the average evaporative flux density (kg m^2). K_S/A_L, K_g/A_L and K_r/A_L are the leaf-specific hydraulic conductance of the scion, graft union and root system (rootstock), respectively. Similarly, Ψ_{stem} can be expressed as follows:

$$\Psi_{stem} \cong -[1/(K_{S-L}/A_L) + 1/(K_G/A_L) + 1/(K_R/A_L)]E \quad (2)$$

where K_{S-L} is the hydraulic conductance of the scion without leaves and K_{S-L}/A_L is the leaf-specific hydraulic conductance of the scion without leaves. If stem extension is maximized when afternoon Ψ_{stem} recovery is greatest (Basile *et al.*, 2003), equation 2 explains the advantage of high leaf-specific hydraulic conductance in the root system (K_R/A_L), the graft union (K_G/A_L) and the trunk and stems (K_{S-L}/A_L), for increasing shoot growth.

When measuring Ψ_{stem} on leaves borne by stems located just above the graft union as suggested by McCutcham and Shackel (1992) equation 2 can be expressed as:

$$\Psi_{stem} \cong -[1/(K_H/A_L) + 1/(K_G/A_L)]E \quad (3)$$

or

$$\Psi_{stem} \cong -[1/(K_{R+G}/A_L)]E \quad (4)$$

where K_{R+G} is the hydraulic conductance of the root system (rootstock) plus the graft union and K_{R+G}/A_L is the leaf-specific hydraulic conductance of the root system (rootstock) plus the graft union.

In well watered soils, leaf-specific hydraulic conductance of the rootstock (plus the graft union) and average evaporative flux density are the most important terms affecting Ψ_{stem} near the trunk base. In the present study, leaf-specific conductance of the root system (K_R/A_L) and leaf-specific conductance of the root system plus the graft union (K_{R+G}/A_L) of trees on K-146-44 were 23% and 22% lower than trees on Nemaguard, respectively. If trees on Nemaguard and K-146-44 had similar average evaporative flux density (E), a reduction in leaf-specific hydraulic conductance of the root system plus the graft union (K_{R+G}/A_L), as was found in the present study, would decrease Ψ_{stem}. Indeed, Basile *et al.* (2003) found that trees on K-146-43 had 26% lower Ψ_{stem} (measured at solar noon on stems located just above the graft union) than trees on Nemaguard. These results agree with those found by Olien and Lakso (1986) who reported that Ψ_{stem} values were also lower in apple trees on dwarfing rootstocks than trees on more vigorous rootstocks.

Effect of size-controlling rootstocks on dry-matter partitioning

Dry-matter partitioning among roots, stem and leaves differed between 'Crimson Lady' trees on Nemaguard and K-146-44 rootstocks. In general, trees on the size controlling rootstock partitioned more dry matter to roots and leaves, and less dry matter to stems, than trees on the vigorous rootstock. This result agrees with previous results found by DeJong and Doyle (1984) who reported that six year old dwarf peach trees partitioned more dry matter to leaves and to small branches with reduced internodes than to large wood compared to standard peach trees of the same age. Furthermore, Glenn and Scorza (1992) reported that one year old dwarf peach trees had a tendency to allocate more dry matter to leaves than to stems compared with a standard phenotype. Caruso *et al.* (1997) also found that seasonal dry-matter partitioning differed among 'Flordaprince' peach trees on various rootstocks.

The higher root hydraulic resistance of trees on K-146-44 compared with trees on Nemaguard may be related to intrinsic characteristics of K-146-44 root system and/or to insufficient expansion of its root system (effecting water supply) compared with total leaf area (affecting water demand). In the present experiment, trees on K-146-44 partitioned more dry matter to roots on a total tree percent basis than trees on Nemaguard, but rootstock did not significantly affect root dry mass to total tree leaf area ratio. For these reasons it is likely that the differences in root leaf-specific hydraulic conductance between trees on K-146-44 and Nemaguard are related to intrinsic characteristics of the K-146-44 rootstock. In apples, for instance, Beakbane and Thompson (1939) reported that dwarfing had fewer and smaller xylem vessels than vigorous rootstocks. K-146-44 may compensate for lower root hydraulic conductance by producing relatively larger root systems than Nemaguard. Higher partitioning of carbohydrates to the roots may reduce carbohydrate availability for shoot growth, and hence, contribute to the dwarfing effect.

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