



RESEARCH PAPER

The effect of root pressurization on water relations, shoot growth, and leaf gas exchange of peach (*Prunus persica*) trees on rootstocks with differing growth potential and hydraulic conductance

Luis I. Solari and Theodore M. DeJong*

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

Received 19 September 2005; Accepted 2 February 2006

Abstract

It is well known that rootstocks can have an effect on the vegetative growth and development of the tree; however, there has been no clear explanation about the physiological mechanism involved in this phenomenon. Evidence indicates that the rootstock effects on tree vegetative growth may be related to hydraulic limitations of the rootstock. The objective of these experiments was to investigate the shoot growth, water potential, and gas exchange of peach trees on different rootstocks in response to manipulations of water relations of trees on rootstocks that differ in root hydraulic conductance. Tree water relations were manipulated by applying different amounts of pneumatic pressure on the root system and then relative shoot extension growth rate, tree transpiration rate, leaf water potential, leaf conductance, leaf transpiration, and net CO₂ exchange rate responses were measured. Root pressurization increased leaf water potential, relative shoot extension growth rate, leaf conductance, leaf transpiration, and net CO₂ exchange rates of trees on both vigorous and dwarfing rootstocks. There was a significant positive linear correlation between applied pneumatic pressure and tree transpiration rate and leaf water potential. Leaf conductance, transpiration rate, and net CO₂ exchange rate as well as relative shoot extension growth rates were also positively correlated with the applied pneumatic pressure on the root system. These relationships were consistent across both vigorous and size-controlling rootstocks, indicating that rootstock hydraulic limitation may be directly involved in the vegetative growth control of peach trees.

Key words: Peach, *Prunus*, root pressurization, rootstock, vegetative growth, water relations.

Introduction

There are several physiological mechanisms that have been proposed to explain the decline in tree growth over time within a species (Ryan and Yoder, 1997). The hydraulic limitation mechanism hypothesis suggests that tree growth is limited by the conductance or resistance of water movement through the soil–plant continuum. The soil–plant hydraulic conductance theoretically determines an operating range for leaf water potential and transpiration rates to preserve the function of the hydraulic system (Tyree and Sperry, 1988). This concept has been experimentally demonstrated by Kolb and Sperry (1999) and Hacke *et al.* (2000). Stomata are regulated to maintain a leaf water potential and transpiration rate within the hydraulic limits of the soil–plant system. Soil–plant hydraulic conductance is positively correlated with stomatal conductance within a species (Saliendra *et al.*, 1995) and among species (Meinzer *et al.*, 1995). Furthermore, experimental manipulations that negatively affect the plant hydraulic system can have negative effects on stomatal conductance (Sperry *et al.*, 1993; Saliendra *et al.*, 1995), limiting transpiration rate (Sperry and Pokman, 1993) and carbon assimilation (Hubbard *et al.*, 2001). This relationship is apparently facilitated by a water potential-mediated regulation of stomatal conductance (Saliendra *et al.*, 1995; Fuchs and Livingston, 1996; Comstock and Mencuccini, 1998). Relative hydraulic conductance decreases with size (Yang and Tyree, 1993) and age (Mencuccini and Grace, 1996).

* To whom correspondence should be addressed. E-mail: tmdejong@ucdavis.edu

© The Author [2006]. Published by Oxford University Press [on behalf of the Society for Experimental Biology]. All rights reserved.

The online version of this article has been published under an Open Access model. Users are entitled to use, reproduce, disseminate, or display the Open Access version of this article for non-commercial purposes provided that: the original authorship is properly and fully attributed; the Journal and the Society for Experimental Biology are attributed as the original place of publication with the correct citation details given; if an article is subsequently reproduced or disseminated not in its entirety but only in part or as a derivative work this must be clearly indicated. For commercial re-use, please contact: journals.permissions@oxfordjournals.org

within a species. More importantly, stomatal conductance and carbon assimilation also tend to decrease with tree age as hydraulic conductance decreases (Yoder *et al.*, 1994; Hubbard *et al.*, 1999). Correspondingly, Tyree *et al.* (1998) reported a good correlation between the hydraulic conductance and growth potentials of different tropical tree species, supporting the hypothesis that hydraulic conductance may constrain the long-term growth potential of trees.

Specific rootstocks can significantly influence the vegetative growth of fruit trees (Rogers and Beakbane, 1957; Lockard and Schneider, 1981; Webster, 1995). Evidence indicates that rootstocks can have an effect on tree vegetative growth by influencing the hormonal balance (Kamboj *et al.*, 1999), mineral nutrition (Jones, 1971), and/or water relations (Olien and Lakso, 1986). It has been argued that the differences in rootstock effects on one or more of these processes account for the observed differences in vegetative growth of trees. Although there have been some improvements in understanding of rootstock effects on tree growth, there is no widely accepted explanation of the underlying physiological mechanism behind this phenomenon (Webster, 2004). Recent research conducted on peach trees with rootstocks that impart different tree growth potentials has shown significant differences in stem water potential (Basile *et al.*, 2003) and leaf carbon assimilation (Solari *et al.*, 2006a) associated with rootstock-induced differences in growth potential. The latter study also evaluated shoot growth responses to manipulations of stem water potential under field conditions. There was a direct positive relationship between stem water potential and shoot growth among peach trees on different rootstocks. Furthermore, differences in rootstock hydraulic conductance were positively related to the relative growth potential that these peach rootstocks imparted to trees growing in field conditions (Solari *et al.*, 2006b). Similar results have been reported for apple rootstocks (Olien and Lakso, 1986; Cohen and Naor, 2002) but the differences in hydraulic conductance have been attributed to the graft unions rather than the rootstocks themselves (Atkinson *et al.*, 2003). It appears therefore that the dwarfing effect of specific peach rootstocks on tree growth may be related to hydraulic limitation of the rootstocks involved. However, no study has related changes in hydraulic conductance to vegetative growth potential among peach trees on different rootstocks.

The root pressurization method provides an indirect means of testing the relationship between hydraulic conductance and vegetative growth potential among peach trees on different rootstocks. A pneumatic pressure applied in a chamber raises the hydrostatic pressure across the whole system (Passioura and Munns, 1984). This increases the total water potential throughout the soil-plant system assuming that no substantial increase in water flow occurs through the plant (Passioura and Munns, 1984). However, there is no pneumatic pressure effect on the root water relations because the pressure is equally transmitted

throughout the air and liquid phases in the chamber so the difference between the two phases remains constant (Passioura and Munns, 1984). By contrast, the pneumatic pressure has a significant effect on shoot water relations, altering the turgor pressure component (Passioura and Munns, 1984). The present study used the root pressurization method to test the hypothesis that rootstock hydraulic limitations can account for the differences in vegetative growth potential in peach trees. The objective was to investigate the shoot growth, water potential, and leaf gas exchange responses of peach trees on different rootstocks under changing pneumatic pressure conditions of the root system. This was achieved by temporarily subjecting the rootstocks to differing amounts of pneumatic pressure, thus overcoming the differences in root hydraulic conductance between rootstocks.

Materials and methods

One-year-old peach trees (*Prunus persica* L. Batsch, cv. O'Henry) grafted on two rootstocks were grown at the Controlled Environment Facility, University of California, Davis. The rootstocks used for this experiment were previously documented to impart a low (*Prunus salicina* Lindl. × *Prunus persica* L. Batsch hybrid, cv. K146-43) and high (*Prunus persica* L. Batsch × *Prunus davidiana* hybrid, cv. Nemaguard) vegetative growth potential (Weibel *et al.*, 2003). The environmental conditions in the controlled environment room were set at 14 h of light at 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ PPFD, 25/20 °C air temperature, and 50/80% relative humidity during the light and dark periods, respectively. The three trees of each rootstock were pruned to ~0.2 m above the graft union, weighed, and planted in 40 l steel pressure chambers (wine fermentors; Webb *et al.*, 1966) in February 2004. The soil medium consisted of 50% by volume of Turface fritted clay (Profile Products LLC, Buffalo Grove, USA) and 50% by volume of Pro-Mix BX peat moss (Premier Tech Ltd, Quebec, Canada) amended with 0.5 kg per tree of 18-6-12 Multicote fertilizer (N-P-K; Schultz Co., Bridgeton, USA). The trees were irrigated once a day to maintain the soil medium near maximum water-holding capacity. Each pressurization experiment involved two trees and six pressures, and pressurization experiments were repeated three times over a period of 1 month. The experiments were conducted on a total of three trees per rootstock and each rootstock was exposed to pressurization treatments twice.

The pressure chambers consisted of steel cylindrical containers with flanges to attach a round steel plate with a welded coupler in the centre. The trunk of the dormant tree went through the coupler, two steel washers, and a threaded steel clamping device at the time of planting. The steel plate was bolted to the container flanges separated by a rubber gasket to ensure a pressure seal. Pressure chambers with trees grafted on the same rootstock were interconnected in series to a compressed air cylinder through an IR4000 series high-pressure regulator (Parker Hannifin Corp, Veriflow Division, Richmond, USA). On each measurement day a pressure seal was formed around the tree trunk by inserting a silicone rubber grommet between the washers and compressing it with the threaded steel clamping device. Pressure gauges, relief valves, check valves, and caps were also installed at this time. Different levels of pneumatic pressure (none, 0.2, 0.3, 0.4, 0.5, and 0.6 MPa) were applied on the root system over several days and physiological responses were measured at each pressure. The root system was initially pressurized using an air compressor and then a compressed air cylinder was opened to maintain the pneumatic pressure constant at each level for 6 h.

Experimental measurements were made during May. Shoot extension was measured on one shoot of each tree with a linear voltage displacement transducer (Transtek Co., Hartford, USA) during a root pressurization period. The shoot tip was attached to a fine copper wire with clear adhesive tape. The free end of the wire went through two eye screws and then was connected to the core of a linear voltage displacement transducer. The first and second eye screws were true to the shoot tip and the linear voltage displacement transducer, respectively, so that the shoot extension was equal to the displacement of the core. The relative shoot extension rate (*RSER*) was calculated as:

$$RSER = (L_2 - L_1) / [L_1(T_2 - T_1)]$$

where L_2 and L_1 are the shoot lengths at times, T_2 and T_1 , and the relative shoot extension rate has units of $\text{m m}^{-1} \text{h}^{-1}$. The average relative shoot extension growth rate was calculated by plotting the shoot extension against time and then fitting an exponential function once the shoot extension rate reached the 'steady state' during a root pressurization period.

Tree transpiration rate was gravimetrically measured with an ES100L digital scale (Ohaus Corp., Pine Brook, USA) during the last hour of a root pressurization period. Leaf water potential was also measured at this time on two fully mature, well-exposed leaves for each tree using the pressure chamber method (Scholander *et al.*, 1965). The excised leaves of the selected shoots were pressurized with a 3005-model pressure chamber (Soil Moisture Equipment, Santa Barbara, USA). Leaf water potential was also measured at the end of the dark period and assumed to be in equilibrium with the soil water potential.

Leaf gas exchange measurements were conducted on five fully mature and well-exposed leaves with an LI-6400 infrared gas analyser (Li-Cor Inc., Lincoln, USA) during the last hour of a root pressurization period. Reference concentration of CO_2 inside the leaf chamber was controlled at $400 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$. The PPFD, reference air temperature, and relative humidity inside the leaf chamber were set at $1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ PPFD, 25°C , and 50%, respectively. The soil respiration rate was measured by sampling the air inside the chamber during the last hour of a root pressurization period. CO_2 concentration in the samples was determined with a Horiba infrared gas analyser (Horiba Instruments Inc., Irvine, USA).

Hydraulic measurements were made on each tree in June, subsequent to the pressurization experiments. The high pressure flow method was used to measure the hydraulic resistance (inverse of conductance) of the peach trees (Tyree *et al.*, 1993, 1994). The high pressure flow method involves quasi-steady- and/or transient-state measurements. The hydraulic resistance from quasi-steady ($R_{\text{quasi-steady state}}$) and transient ($R_{\text{transient state}}$) state measurements were calculated as:

$$R_{\text{quasi-steady state}} = P/F$$

$$R_{\text{transient state}} = dP/dF$$

where P is applied water pressure, F is the water flow rate, and the hydraulic resistance has units MPa s kg^{-1} . For these measurements, the scion was cut above the graft union, connected to the high pressure flow meter (Dynamax Inc., Houston, USA) and immersed in a large sink of deionized water. The water temperature in the sink was determined with a Fluke 2190A/Y2001 thermocouple digital thermometer (Fluke Corp., Everett, USA). 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- and transient-state measurements. Subsequently, a wood segment that included the graft union was cut off from the rootstock. The steel containers with the roots

were filled with deionized water and the rootstock was connected to a high-pressure flow meter instrument. 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 quasi-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} , $R_{\text{rootstock}}$, and $R_{\text{wood segment}}$ are the scion, rootstock, and wood segment hydraulic resistance, respectively. For the sake of clarity, resistance data were converted to conductance ($1/\text{resistance}$) and expressed as leaf specific hydraulic conductance to normalize for differences in tree size.

The biomass of the tree was separated into leaves, stems, trunk, root shank, and extension roots at the end of the hydraulic measurements. The total leaf area was measured with an LI-3100 area meter (Li-Cor Inc.). The fresh biomass was dried in a forced-air oven at 60°C for at least 2 weeks to determine dry weight. Tree absolute growth rate (*AGR*) was calculated as:

$$AGR = (W_2 - W_1) / (T_2 - T_1)$$

where W_2 and W_1 are the tree dry weights at the end of growing season (T_2) and time of planting (T_1). The tree absolute growth rate was expressed as kg d^{-1} . Tree relative growth rate (*RGR*) was calculated as:

$$RGR = [\log_e(W_2) - \log_e(W_1)] / (T_2 - T_1)$$

The tree relative growth rate was expressed as $\text{kg kg}^{-1} \text{d}^{-1}$. The net assimilation rate (*NAR*) was calculated as:

$$NAR = RGR/LAR$$

where leaf area ratio (*LAR*) is the leaf area per unit tree dry weight. The net assimilation rate was expressed as $\text{kg m}^{-2} \text{d}^{-1}$.

Statistical analyses of the data were made with SAS statistical software (SAS Institute, Cary, USA). Analysis of variance was used to test the rootstock effect on dry matter production, distribution, and growth of the trees. Analysis of variance was also used to test the rootstock effect on the scion, rootstock, and tree hydraulic conductance. The mean separation between the rootstocks was carried out with a 0.05 level of significance by the Tukey pair-wise comparison test. Non-linear regression analysis was used to test the rootstock effect on the relative shoot extension rate pattern. Multiple linear regression analysis was used to evaluate the relationships between applied pneumatic pressure, water potential, shoot growth, soil respiration, and leaf gas exchange variables of trees on different rootstocks.

Results

The leaf water potential and tree transpiration rate were positively correlated with the applied pneumatic pressure on the root system ($P < 0.0001$ and 0.0001). Trees grafted on Nemaguard had higher mean leaf water potentials ($P < 0.0001$) and tree transpiration rates ($P < 0.0001$) than trees on K146-43 (Fig. 1). There were no significant interaction effects between rootstock and applied pneumatic pressure on leaf water potential but there were on tree transpiration rate ($P = 0.0024$). Leaf water potential at the end of the dark period (assumed to reflect soil water potential) was not significantly different among trees on different rootstocks (data not shown).

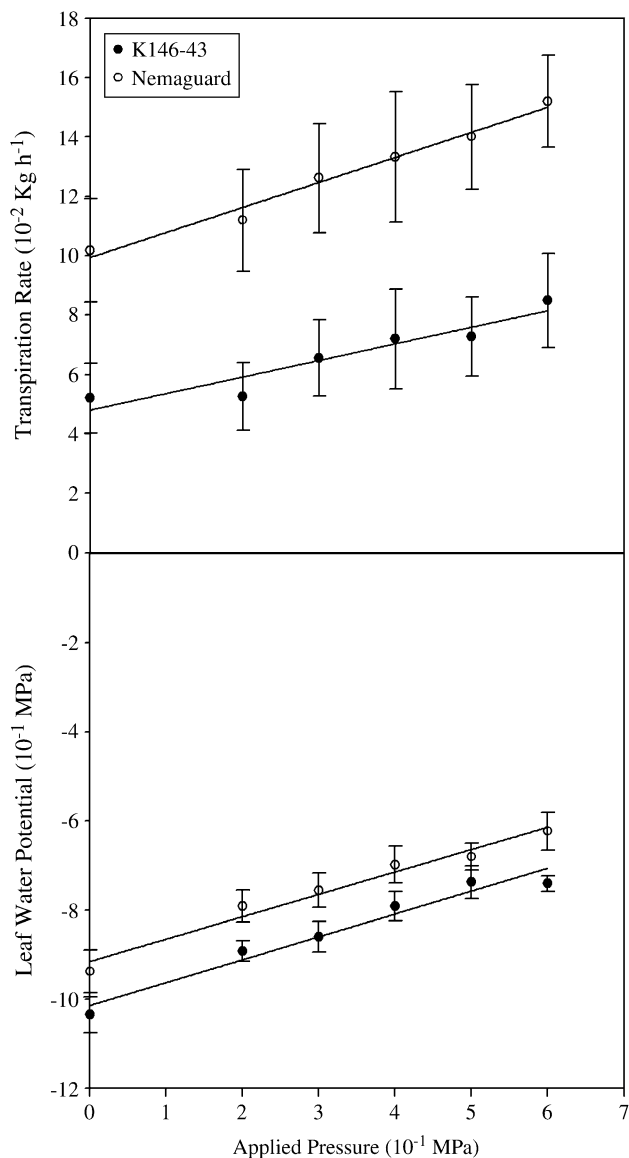


Fig. 1. Relationships between applied pneumatic pressure, tree transpiration rate, and leaf water potential of 1-year-old peach trees on Nemaguard and K146-43 rootstocks. Individual points represent data values from the mean of three trees \pm standard error bar ($n=36$). Lines represent the fitted simple linear regression for each rootstock. Upper panel: $y_{\text{Nemaguard}}=0.84x+9.95$, $r^2=0.98$; $y_{\text{K146-43}}=0.48x+5.58$, $r^2=0.89$. Lower panel: $y_{\text{Nemaguard}}=0.50x-9.15$, $r^2=0.97$; $y_{\text{K146-43}}=0.51x-10.14$, $r^2=0.96$.

The leaf conductance, transpiration and net CO_2 exchange rates were also positively correlated with the applied pneumatic pressure on the root system ($P=0.0001$, 0.0001 , and 0.004 , respectively). Trees grafted on Nemaguard had a higher mean leaf conductance ($P=0.0473$), net CO_2 exchange ($P=0.0578$), and transpiration rates ($P=0.0212$) than trees on K146-43 (Fig. 2). There was no significant interaction effect between rootstock and applied pneumatic pressure on these measurements.

Trees grafted on Nemaguard had higher mean relative shoot extension rates ($P < 0.0001$) than trees on K146-43

(Fig. 3). The relative shoot extension rates were also positively correlated with the applied pneumatic pressure on the root system ($P < 0.0001$). However there was no significant interaction effect between the rootstock and applied pneumatic pressure on relative shoot extension rates (Fig. 4).

Scion and rootstock hydraulic conductance per unit leaf area were significantly different among trees on different rootstocks ($P=0.0015$ and 0.003 , respectively; Fig. 5). Trees on K146-43 had the highest mean scion hydraulic conductance per unit leaf area, whereas trees on Nemaguard had the highest mean rootstock hydraulic conductance per unit leaf area. Overall, trees on Nemaguard had a higher mean tree hydraulic conductance unit leaf area ($P=0.0462$) than trees on K146-43 (Fig. 5).

The tree dry weight was not significantly different among trees on different rootstocks at the time of planting (Table 1). However, trees grafted on Nemaguard had a higher mean final tree dry weight than trees grafted on K146-43 ($P=0.0037$). The significant differences in final tree dry weights were only related to significant differences in final scion dry weights ($P=0.0013$) and, consequently, Nemaguard had the highest mean final scion to rootstock dry weight ratio ($P=0.0018$; Table 1).

Trees on Nemaguard had higher mean absolute and relative growth rates ($P=0.0018$ and 0.0148 , respectively) than trees on K146-43 (Table 2). Trees grafted on Nemaguard also had the highest mean net assimilation rate and leaf area ratio ($P=0.0378$ and 0.0163 , respectively; Table 2). Conversely, trees grafted on K146-43 had a higher mean soil/root respiration rate than trees on Nemaguard ($P=0.0320$; Fig. 6).

Discussion

As expected, root pressurization had a significant influence on the tree water relations. Leaf water potential was directly proportional to applied pneumatic pressure on the root system (Fig. 1). The rootstocks also had a significant effect on leaf water potential confirming previous studies (Basile *et al.*, 2003; Solari *et al.*, 2006a). However, the leaf water potential response to root pressurization was independent of the rootstock. The leaf water potential rise was not equivalent to the applied pneumatic pressure on the root system contrary to what was reported by Passioura and Munns (1984). For instance, a 0.6 MPa increase in applied pressure to the Nemaguard trees might have been expected to result in an increase in leaf water potential from -0.9 to -0.3 MPa if transpiration and hydraulic conductance remained unchanged. But since transpiration also increased by $\sim 50\%$ there was an apparent increase in the water potential gradient within the plant and a measured leaf water potential of about -0.6 MPa after pressurization. Thus a transient increase in leaf water potential following root pressurization was reduced by an increase in the

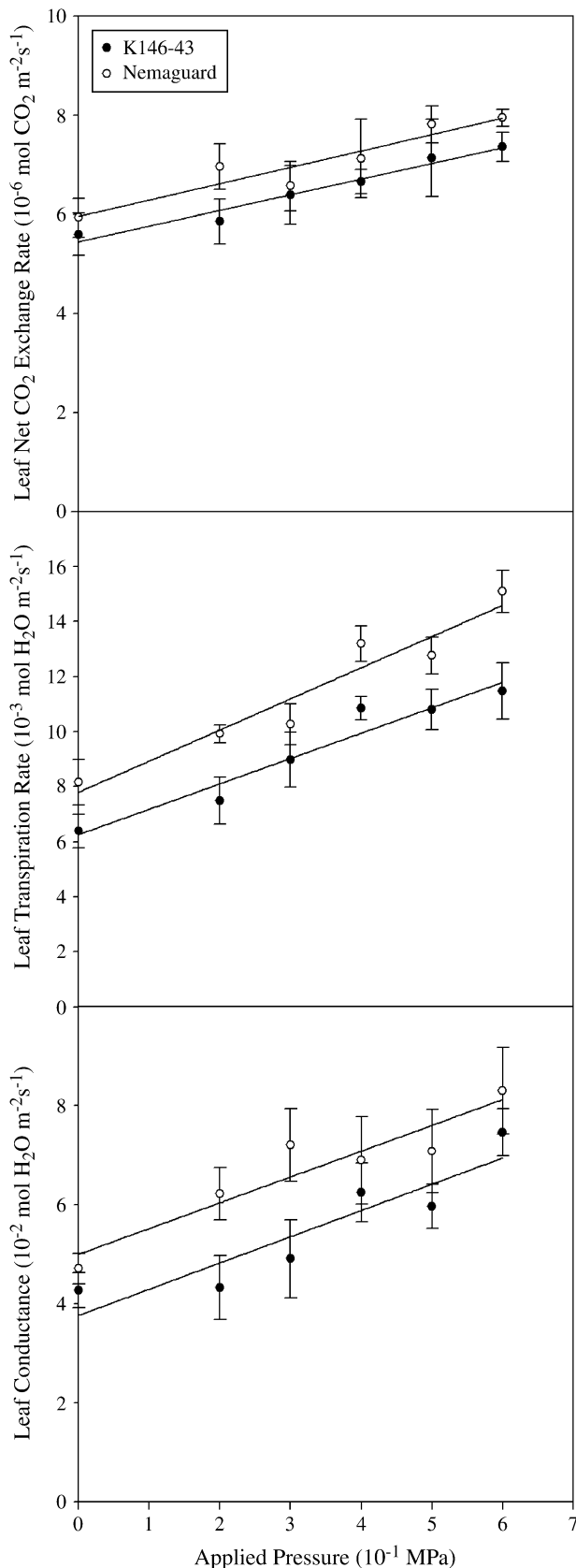


Fig. 2. Relationships between applied pneumatic pressure, leaf net CO_2 exchange rate, transpiration rate, and conductance of 1-year-old peach

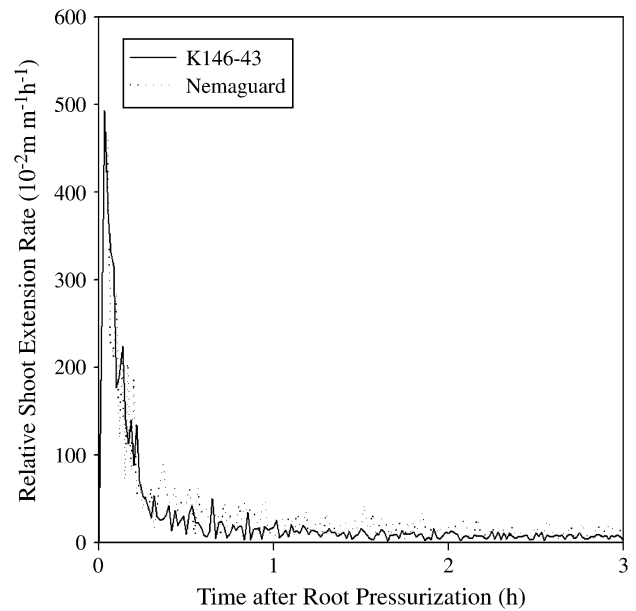


Fig. 3. Relative shoot extension rate pattern of 1-year-old peach trees on Nemaguard and K146-43 rootstocks during root pressurization. Lines represent the mean relative shoot extension rate for all the levels of applied pneumatic pressure for each rootstock.

transpiration rate of the trees (Fig. 1), and this corresponded to a measured increase in leaf conductance (Fig. 2). Tree transpiration rate was directly proportional to the applied pneumatic pressure on the root system but the slope of the relationship differed between rootstocks (Fig. 1). The different rootstock effects on tree transpiration rate response to root pressurization may suggest differences in hydraulic conductance among trees on the two rootstocks. Previous studies have also used the root pressurization technique to drive changes in plant water status (Saliendra *et al.*, 1995; Fuchs and Livingston, 1996; Comstock and Mencuccini, 1998). These studies demonstrated that leaf water potential acts as a feedback mechanism that can regulate stomatal conductance. The present study supports those reports and also shows that leaf transpiration and net CO_2 exchange rates increased linearly with the applied pneumatic pressure on the root system (Fig. 2). Solari *et al.* (2006a) presented similar results in the field when the water potential of peach trees on the same rootstocks was manipulated by partially covering the tree canopies. After covering the canopy there was an increase in stem water potential, leaf conductance, transpiration, and net CO_2 exchange rates. These results clearly indicate the physical

trees on Nemaguard and K146-43 rootstocks. Individual points represent data values from the mean of three trees \pm standard error bar ($n=36$). Lines represent the fitted simple linear regression for each rootstock. Upper panel: $y_{\text{Nemaguard}}=0.33x+5.95$, $r^2=0.88$; $y_{\text{K146-43}}=0.32x+5.44$, $r^2=0.96$. Centre panel: $y_{\text{Nemaguard}}=1.13x+7.80$, $r^2=0.92$; $y_{\text{K146-43}}=0.92x+6.26$, $r^2=0.94$. Lower panel: $y_{\text{Nemaguard}}=0.52x+5.00$, $r^2=0.88$; $y_{\text{K146-43}}=0.53x+3.77$, $r^2=0.83$.

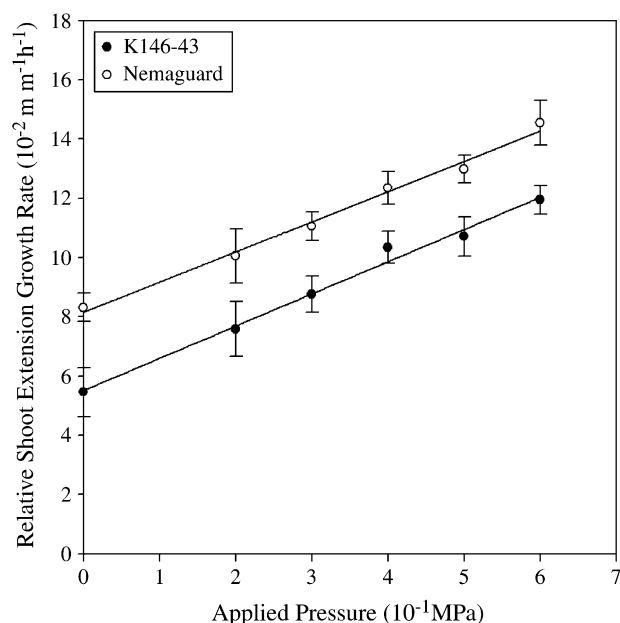


Fig. 4. Relationship between applied pneumatic pressure and relative shoot extension growth rate during the steady-state condition of 1-year-old peach trees on Nemaguard and K146-43 rootstocks. Individual points represent data values from the mean of three trees \pm standard error bar ($n=36$). Line represents the fitted simple linear regression for each rootstock. $y_{\text{Nemaguard}}=1.02x+8.14$, $r^2=0.99$; $y_{\text{K146-43}}=1.09x+5.51$, $r^2=0.99$.

aspects of the control of water movement through the soil-plant system. These physical principles have been used to explain patterns of water use with respect to soil and atmosphere environments and differences in species and cultivars (Sperry, 2000), and now this paper demonstrates the same principles with regard to the differences in rootstocks of compound fruit trees.

The root pressurization also had a significant influence on the pattern of shoot growth. The applied pneumatic pressure initially caused a dramatic increase in relative shoot extension rate (Fig. 3). This initial extension surge cannot be entirely attributed to an elastic expansion since this process was not entirely reversible after the pneumatic pressure was released on the root system. Thereafter, the relative shoot extension rate decreased, probably related to adjustments in cell wall properties (Green *et al.*, 1971). The decrease in relative shoot extension rate was the same for trees on both rootstocks. The shoot extension rate eventually returned to a steady-state condition (Fig. 3). Passioura and Munns (2000) reported similar growth patterns when pneumatic pressure was applied on other plant species that exhibited elastic and inelastic responses in leaf extension during root pressurization. Similar responses have also been observed in response to sudden environmental changes in light (Christ, 1978), relative humidity (Shackel *et al.*, 1987; Serpe and Matthews, 2000), and soil water potential (Acevedo *et al.*, 1971; Serpe and Matthews, 1992).

However, the relative 'steady-state' shoot extension rates of the pressurized trees in the present study clearly differed

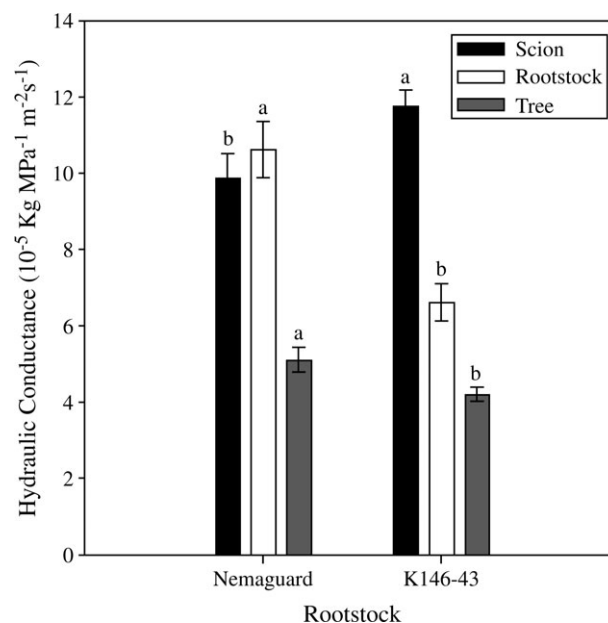


Fig. 5. Scion, rootstock and tree hydraulic conductance per unit leaf area of 1-year-old peach trees on Nemaguard and K146-43 rootstocks. Individual bar values represent the mean of three trees \pm standard error bar ($n=6$). Values not connected by the same letter are significantly different among rootstocks with a 0.05 level of significance according to Tukey's mean comparison test.

from the non-pressurized trees (Fig. 4). These resultant relative shoot extension rates were directly proportional to the applied pneumatic pressure on the root system. More importantly, the rootstocks did not have significant differential effects on this relationship despite their inherent differences in relative shoot extension growth rates (Solari *et al.*, 2006a). The differences in relative shoot extension rate between pressurized and non-pressurized trees presumably involved a persistent adjustment in growth-inducing water potential gradients (Nonami and Boyer, 1993; Nonami *et al.*, 1997) expressed as turgor pressure (Serpe and Matthews, 1992; Hsiao *et al.*, 1998) contrary to the proposed complete self-stabilization growth concept (Green and Cummins, 1974; Passioura and Fry, 1992; Zhu and Boyer, 1992).

The present study confirms the influence that specific peach rootstocks have on the hydraulic conductance of the tree. The rootstocks had a significant effect on tree hydraulic conductance (Fig. 5). These differences in tree hydraulic conductance were associated with significant differences in rootstock hydraulic conductance. This result is consistent with previous studies on the same peach rootstocks (Solari *et al.*, 2006b). However, the scion in this study also showed significant differences in hydraulic conductance partially counteracting the effect of the rootstock. It is difficult to explain the differences in scion conductance since they were the same genotype, except to note that the hydraulic conductance of the scion and root of the trees on Nemaguard were relatively balanced, while

Table 1. Initial and final tree dry weight, final scion and rootstock dry weight, and scion to rootstock dry weight ratio of 1-year-old peach trees on Nemaguard, and K146-43 rootstocks

Individual values represent the mean of three trees \pm standard error ($n=6$). Values not followed by the same letter are significantly different with a 0.05 level of significance according to Tukey's mean comparison test.

Rootstock	Initial 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	0.08 ± 0.01 a	0.41 ± 0.02 a	0.32 ± 0.02 a	0.09 ± 0.01 a	3.55 ± 0.28 a
K146-43	0.08 ± 0.01 a	0.26 ± 0.02 b	0.17 ± 0.02 b	0.08 ± 0.01 a	2.12 ± 0.07 b

Table 2. Absolute and relative growth rate, leaf area ratio and net assimilation rate of 1-year-old peach trees on Nemaguard and K146-43 rootstocks

Individual values represent the mean of three trees \pm standard error ($n=6$). Values not followed by the same letter are significantly different with a 0.05 level of significance according to Tukey's mean comparison test.

Rootstock	Absolute growth rate (10^{-3} kg d $^{-1}$)	Relative growth rate (10^{-3} kg kg $^{-1}$ d $^{-1}$)	Leaf area ratio (m 2 kg $^{-1}$)	Net assimilation rate (10^{-3} kg m $^{-2}$ d $^{-1}$)
Nemaguard	2.87 ± 0.17 a	15.20 ± 0.88 a	5.90 ± 0.29 a	2.58 ± 0.17 a
K146-43	1.78 ± 0.11 b	11.50 ± 0.70 b	4.63 ± 0.25 b	2.48 ± 0.24 b

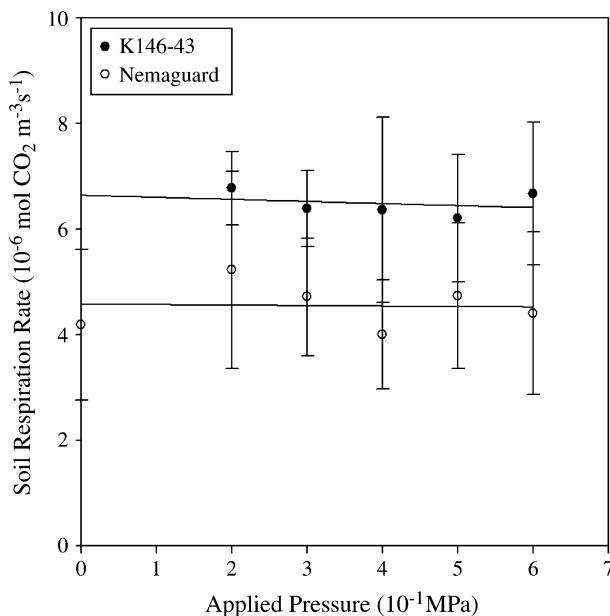


Fig. 6. Relationship between applied pneumatic pressure and soil respiration rate of 1-year-old peach trees on Nemaguard and K146-43 rootstocks. Individual points represent data values from the mean of three trees \pm standard error bar ($n=36$). Lines represent the fitted simple linear regression for each rootstock. $y_{\text{Nemaguard}} = -0.09x + 4.57$, $r^2 = 0.002$; $y_{\text{K146-43}} = -0.39x + 6.63$, $r^2 = 0.007$.

the conductances of the two were clearly unbalanced in the trees on K146-43. It may be that the scion response to decreased relative conductance in the rootstock was to increase its relative conductance.

The differences in tree hydraulic conductance among rootstocks were overcome by applying differing amounts of pneumatic pressure on the root system. This process

simulated changes in tree hydraulic conductance considering the biophysics of water movement. The root pressurization improved the tree water status which had a positive effect on shoot growth in agreement with Berman and DeJong (1997) and carbon assimilation similar to previous field studies (Solari *et al.*, 2006a). In the long term, the rootstock-related differences in tree water status had a pronounced effect on dry matter distribution (Table 1), similar to what has been reported previously (Steinberg *et al.*, 1989), and the overall vegetative growth of the tree. These effects on the tree dry matter production, distribution, and growth are consistent with the physiological responses to root pressurization and indicate that the hydraulic limitation mechanism can account for differences in vegetative growth potential in peach trees (Tables 1, 2). Additionally, the fact that the two rootstocks had the same root dry weight, while having substantially different apparent root/soil respiration rates, suggests that the rootstocks differed in specific root respiration rates (Fig. 6). This, in turn, may also have affected the total tree relative growth and net assimilation rates (Table 2). More comparative research needs to be done to clarify the potential role of differences in root respiration rates among these vigorous and size-controlling peach rootstocks. In the meantime, this study clearly documents that there is a direct relationship between tree hydraulic conductance and peach relative shoot extension growth rate; and this, as well as previous research (Solari *et al.*, 2006b), indicates that rootstock hydraulic conductance differs among the peach rootstocks examined. Thus there is clear evidence that rootstock hydraulic conductance is at least one physiological mechanism involved in the size-controlling potential of selected peach rootstocks.

Acknowledgements

We would like to thank Drs Albert Fischer, Bruce Lampinen, Kenneth Shackel, and Mark Matthews for the use of their equipment and laboratories. We are grateful to Mr Manuel Solari for his invaluable assistance during measurements and Mr Dennis Lewis and William Slater at the UC Davis Controlled Environment Facility for their assistance with the controlled environment room.

References

- Acevedo E, Hsiao TC, Henderson DW. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. *Plant Physiology* **48**, 631–636.
- Atkinson CJ, Else MA, Taylor L, Dover CJ. 2003. Root and stem hydraulic conductivity as determinants of growth potential in grafted trees of apple (*Malus pumila* Mill.). *Journal of Experimental Botany* **54**, 1221–1229.
- Basile B, Marsal J, DeJong TM. 2003. Daily shoot extension growth of peach trees growing on rootstocks that reduce scion growth to daily dynamics of stem water potential. *Tree Physiology* **23**, 695–704.
- Berman ME, DeJong TM. 1997. Diurnal patterns of stem extension growth in peach (*Prunus persica*): temperature and fluctuations in water status determine growth rate. *Physiologia Plantarum* **100**, 361–370.
- Christ RA. 1978. The elongation rate of wheat leaves. 2. Effect of sudden light change on the elongation rate. *Journal of Experimental Botany* **50**, 1393–1401.
- Cohen S, Naor A. 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 and Environment* **25**, 17–28.
- Comstock JP, Mencuccini M. 1998. Control of stomatal conductance by leaf water potential in *Hymenoclea salsola* (T. & G.), a desert subshrub. *Plant, Cell and Environment* **21**, 1029–1038.
- Fuchs E, Livingston N. 1996. Hydraulic control of stomatal conductance in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Alder (*Alnus rubra* Bong) seedlings. *Plant, Cell and Environment* **19**, 1091–1098.
- Green PB, Cummins WR. 1974. Growth rate and turgor pressure: auxin effect studied with an automated apparatus for single coleoptiles. *Plant Physiology* **54**, 863–869.
- Green PB, Erickson RO, Buggy J. 1971. Metabolic and physical control of cell elongation rate. *Plant Physiology* **47**, 423–430.
- Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schafer KVR, Oren R. 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* **124**, 495–505.
- Hsiao TC, Frensch J, Rojas-Lara BA. 1998. The pressure-jump technique shows maize leaf growth to be enhanced by increase in turgor only when water status is not too high. *Plant, Cell and Environment* **21**, 33–42.
- Hubbard RM, Bond BJ, Ryan MG. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology* **111**, 413–417.
- Hubbard RM, Ryan MG, Stiller V, Sperry JS. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant, Cell and Environment* **24**, 113–121.
- Jones OP. 1971. Effect of rootstock and interstock on the xylem sap composition in apple trees: effects on nitrogen, phosphorus and potassium content. *Annals of Botany* **35**, 825–836.
- Kamboj JS, Blake PS, Quinlan JD, Baker DA. 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 Regulation* **28**, 199–205.
- Kolb KJ, Sperry JS. 1999. Transport constraints on water use by the great basin shrub, *Artemisia tridentata*. *Plant, Cell and Environment* **22**, 925–935.
- Lockard RG, Schneider GW. 1981. Stock and scion growth relationship and the dwarfing mechanism in apple. *Horticultural Reviews* **2**, 315–375.
- Meinzer FC, Goldstein G, Jackson P, Holbrook NM, Butierrez MV, Cavelier J. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic conductance properties. *Oecologia* **101**, 514–522.
- Mencuccini M, Grace J. 1996. Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. *Plant, Cell and Environment* **19**, 939–948.
- Nonami H, Boyer JS. 1993. Direct demonstration of a growth-induced water potential gradient. *Plant Physiology* **102**, 13–19.
- Nonami H, Wu Y, Boyer JS. 1997. Decreased growth-induced water potential. *Plant Physiology* **114**, 501–509.
- Olien WC, Lakso AN. 1986. Effect of rootstock on apple (*Malus domestica*) tree water relations. *Physiologia Plantarum* **67**, 421–430.
- Passioura JB, Fry SC. 1992. Turgor and cell expansion: beyond the Lockhart equation. *Australian Journal of Plant Physiology* **19**, 565–576.
- Passioura JB, Munns R. 1984. Hydraulic resistance of plants. II. Effects of rooting medium, and time of day, in barley and lupin. *Australian Journal of Plant Physiology* **12**, 455–461.
- Passioura JB, Munns R. 2000. Rapid environmental changes that affect leaf water status induce transient surges or pauses in leaf expansion rate. *Australian Journal of Plant Physiology* **27**, 941–948.
- Rogers WS, Beakbane AB. 1957. Stock and scion relations. *Annual Review of Plant Physiology* **8**, 217–236.
- Ryan MG, Yoder BJ. 1997. Hydraulic limits to tree height and tree growth. *Bioscience* **47**, 235–242.
- Saliendra NZ, Sperry JS, Comstock JP. 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance and soil drought in *Betula occidentalis*. *Planta* **196**, 357–366.
- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA. 1965. Sap pressure in vascular plants. *Science* **148**, 339–346.
- Shackel KA, Matthews MA, Morrison JC. 1987. Dynamic relation between expansion and cellular turgor in growing grape (*Vitis vinifera* L.) leaves. *Plant Physiology* **84**, 1166–1171.
- Serpe MD, Matthews MA. 1992. Rapid changes in cell wall yielding of elongating *Begonia argenteo-guttata* L. leaves in response to changes in plant water status. *Plant Physiology* **100**, 1852–1857.
- Serpe MD, Matthews MA. 2000. Turgor and cell yielding in dicot leaf growth in response to changes in relative humidity. *Australian Journal of Plant Physiology* **27**, 1131–1140.
- Solari LI, Johnson S, DeJong TM. 2006a. The relationship of water status to vegetative growth and leaf gas exchange of peach (*Prunus persica*) trees on different rootstocks. *Tree Physiology* (in press).
- Solari LI, Johnson S, DeJong TM. 2006b. Hydraulic conductance characteristics of peach (*Prunus persica*) trees on different rootstocks are associated with differences in biomass production, distribution and growth rates. *Tree Physiology* (in press).
- Sperry JS. 2000. Hydraulic constraints on plant gas exchange. *Agricultural and Forest Meteorology* **104**, 13–23.
- Sperry JS, Alder NN, Eastlack SE. 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *Journal of Experimental Botany* **44**, 1075–1082.

- Sperry JS, Pokman WT. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* **16**, 279–287.
- Steinberg SL, McFarland MJ, Miller JC. 1989. Effect of water stress on stomatal conductance and leaf water relations of leaves along current-year branches of peach. *Australian Journal of Plant Physiology* **16**, 549–560.
- Tyree MT, Sinclair B, Liu P, Granier A. 1993. Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flow meter. *Annales des Sciences Forestières* **50**, 417–423.
- Tyree MT, Sperry JS. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiology* **88**, 574–580.
- Tyree MT, Velez V, Dalling JW. 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.
- Tyree MT, Yang S, Cruiziat P, Sinclair B. 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 Physiology* **104**, 189–199.
- Webb AD, Richard EK, Galetto WG. 1966. Volatile components of sherry wine. II. Isolation and identification of *N*-(2-phenethyl) acetamide and *N*-isoamylacetamide. *American Journal of Enology and Viticulture* **17**, 1–10.
- Webster AD. 1995. Rootstock and interstock effects on deciduous fruit tree vigour, precocity, and yield productivity. *New Zealand Journal of Crop and Horticultural Science* **23**, 373–382.
- Webster AD. 2004. Vigour mechanisms in dwarfing rootstocks for temperate fruit trees. *Acta Horticulturae* **658**, 29–41.
- Weibel A, Johnson RS, DeJong TM. 2003. Comparative vegetative growth responses of two peach cultivars grown on size-controlling versus standard rootstocks. *Journal of the American Society for Horticultural Science* **128**, 463–471.
- Yang S, Tyree MT. 1993. Hydraulic resistance in the shoots of *Acer saccharum* and its influence on leaf water potential and transpiration. *Tree Physiology* **12**, 231–242.
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufman MR. 1994. Evidence of reduced photosynthetic rates in old trees. *Forest Science* **40**, 513–527.
- Zhu GL, Boyer JS. 1992. Enlargement in *Chara* studied with a turgor clamp: growth rate is not determined by turgor. *Plant Physiology* **100**, 445–453.