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Phenotyping vigour control capacity of new peach rootstocks by xylem vessel analysis

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ABSTRACT

In peach, xylem anatomical characteristics have been shown to be related to vigour of selected rootstocks. The goal of this research was to determine if xylem characteristics of a new set of rootstocks that exhibit a range of size-controlling potential and have a different genetic background from previously examined material would also exhibit similar differences in xylem characteristics. If so, then anatomical analysis of xylem may be a useful means of predicting the vigour control capacity of selected peach rootstock genotypes. Samples of xylem tissue were taken from roots, trunks and shoots of four new rootstocks that were derived from a genetic cross between 'Harrow Blood' and 'Okinawa' peaches and compared with tissue from 'Nemaguard', a vigorous control. Xylem samples were sectioned and analysed by optical microscope. The number and dimensions of vessels in recently developed xylem of each rootstock were measured and compared. The more dwarfing rootstocks had fewer large vessels and more small vessels than the more vigorous rootstocks. Weighted mean vessel diameter (W_m) and calculated hydraulic conductance (K_h) differed among rootstocks: more vigorous rootstocks had higher K_h and W_m than dwarfing rootstocks. Rootstock xylem vessel dimensions varied in relation to the vigour they imparted to a common scion cultivar ('O'Henry'). After the 'Nemaguard' control, 'HBOK 50' was the most vigorous rootstock followed by 'HBOK 10', 'HBOK 32' and 'HBOK 27', respectively. Thus, as was seen in previous research with a separate set of rootstocks, the vigour-control capacity of this new series of peach rootstocks was strongly related to their xylem hydraulic characteristics and it appears likely that it would be possible to use xylem anatomical characteristics of shoots or roots of young trees to pre-select for size-controlling potential in a rootstock development program.

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1. Introduction

The use of composite trees is an old and common practice in commercial orchards. It allows for control of scion vigour, a decrease in the incidence and/or impact of specific soil pests and diseases and can induce early production (Webster, 2004). Almost all commercial peach orchards consist of trees propagated on rootstocks.

The main vigour control mechanism for a series of peach rootstocks has been linked to differences in stem water potential among trees on different rootstocks (Solari et al., 2006b) and a similar linkage between tree water relations and dwarfing has been proposed for apple rootstocks (Cohen and Naor, 2002; Atkinson et al., 2003). Patterns of stem water potential occurring during the afternoon hours can strongly influence shoot growth rates in the field

(Berman and DeJong, 1997) and Basile et al. (2003) found a strong correlation between stem water potential and shoot growth over a day and over a growing season in trees growing on rootstocks that imparted a range of vigour with a common scion cultivar (Weibel et al., 2003). Basile et al. (2003) also found that tree vegetative growth on different rootstocks was related to cumulative water potential differences experienced during the first half of a growing season. Subsequently it was demonstrated that differences in stem water potential are causally related to differences in relative shoot growth rates among peach trees on different rootstocks (Solari et al., 2006a). Stem water potential is strongly influenced by stem hydraulic conductance (Tyree and Sperry, 1988). In peach rootstocks, measured differences in rootstock hydraulic conductance described by Solari et al. (2006b) have been also related to xylem vessel characteristics: the more dwarfing rootstocks had smaller mean xylem vessel diameters (Tombesi et al., 2010a). Thus, it appears that the number and diameter of xylem vessels may be a significant rootstock characteristic that influences scion vigour, considering their potential effects on the hydraulic conductivity and its linkage to shoot growth. This might also explain some of

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the morphological differences among scions of apple on M9 (dwarfing) and M 106 (vigorous) rootstocks described by Seleznyova et al. (2008). However, it has been shown that dwarfing peach rootstocks do not substantially influence scion xylem characteristics (Tombesi et al., 2010b).

The development of new cultivars for tree fruit industries is a slow and costly process because of the long generation times characteristic of tree fruit species and the expense of growing and maintaining seedling trees in experimental orchards while field evaluations are being conducted (Sykes, 2002). The development of new rootstocks is even more arduous and costly because each new seedling produced from hybridizations must be grafted with one or more scion cultivars and then grown at spacings suitable for gauging the performance of the grafted trees. This is particularly the case when selecting for size-controlling rootstocks because tree growth and ultimate size is a function of many factors including; tree spacing, crop load and orchard management (Chalmers et al., 1981). A peach rootstock development program at UC Davis has recently identified a series of new peach rootstocks of common ancestry ('Harrow Blood' peach × 'Okinawa' peach) that display a range of size-controlling potential when used with standard, commercial peach scion cultivars. The commercial potential of these rootstocks appears promising and details of their horticultural performance will be presented elsewhere.

As stated above, previous research with a specific set of peach rootstocks developed in an earlier rootstock development effort (Tombesi et al., 2010a) resulted in the identification of mean xylem vessel diameter as a genetically related phenotypic trait associated with peach rootstock vigour that was expressed in the roots and stems of rootstock genotypes. That set of size-controlling rootstocks was developed with inter-specific hybrids of peach (*Prunus persica*) and Japanese plum (*Prunus salicina*) or other more complex crosses (open pollinated seedlings of *P. persica* × *Prunus davidiana*) (Brooks and Olmo, 1961; DeJong et al., 2005). However the relationship between mean xylem vessel diameter and rootstock vigour has not been tested in other peach rootstocks. The goal of the present work was to determine if the same relationships between rootstock vigour and xylem vessels characteristics described by Tombesi et al. (2010a) for 'Nemaguard', 'P30-135' and 'K146-43' are characteristics of the new series of 'Harrow Blood' × 'Okinawa' peach rootstocks ('HBOK 50', 'HBOK 10', 'HBOK 32' and 'HBOK 27') currently being evaluated in field tests. If the relationships between xylem vessel characteristics and vigour characteristics imparted to the scion by the rootstocks are consistent, then, in the future, it may be possible to screen germplasm for rootstock dwarfing potential by examining the xylem vessel characteristics of young seedlings.

2. Materials and methods

Plant material was sampled from an experimental orchard located at the University of California Kearney Agricultural Center, Parlier, CA. The series of new rootstocks used in this study were derived from a controlled cross between 'Harrow Blood' and 'Okinawa' peach trees. Trees in the experimental orchard were developed by clonally propagating four rootstock selections that exhibited a range of rootstock vigour ('HBOK 50' (medium high vigour), 'HBOK 10' (medium vigour), 'HBOK 32' (medium-low vigour) and 'HBOK 27' (low vigour)) and bud-grafting 'O'Henry' peach on them as a scion cultivar. 'O'Henry' peach trees on seedling 'Nemaguard' rootstock growing in the same block were used as the standard for comparing the vigour characteristics of the new selected rootstocks.

The 'Nemaguard', 'HBOK 50', 'HBOK 10', and 'HBOK 32' trees used in this study were 7 years old, trained to a perpendicular V

(DeJong et al., 1995) and received horticultural care characteristic of commercial orchards. The 'HBOK 27' trees were one year younger but planted in the same block and received the same care. During May 2009 three woody root segments of ~5.5 mm diameter were sampled from each of the five trees on each rootstock. Root samples were collected from a distance of about 20 cm from the base of the trunk and from three different positions around the base of each tree. During the same period samples of trunk xylem tissue (~1.5 cm long × 0.5 cm wide × 0.25 cm deep) were extracted from the rootstock trunk below the graft union using a wood chisel. A few days later, shoot samples were collected from the same rootstock genotypes that were grown as grafted trees on 'Nemaguard' rootstock for the purpose of growing shoots for vegetative propagation, in the experimental orchards of the University of California Davis campus in Davis, CA. All of these trees were heavily pruned each year to generate numerous vigorous shoots that could be harvested for vegetative propagation. Three shoots with a basal diameter of ~4.5 mm were collected from each of the five trees per rootstock. All samples were immediately placed on ice in plastic bags and then stored at 0 °C until sectioned.

Samples were fresh sectioned with a manual microtome at 150 µm of thickness to obtain two cross-sections from each field sample. The cross-sections were stained with Toluidin-Blue-O to increase the visual contrast. Photographs of the cross-sections were taken with a camera model Lei 750 (Leica, Wetzlar, Germany) mounted on a light microscope (Nikon Eclipse E 600, Nikon, Tokyo, Japan). Images were then acquired with DEI-750D software (Optronics, Goleta, CA, USA). Three photographs were taken from each cross-section slide; the first one covered a visual field of 1.83 mm² in order to measure the thickness of xylem tissue, the other two were taken at a greater magnification and they took in account 0.217 mm² of xylem tissue. The two photographs were used to calculate the vessel density and dimensions from two randomly selected view fields of xylem tissue.

Vessels were measured and counted in frequency classes, as described by Solla and Gil (2002) using a computer graphics program (The Gimp, freeware; www.gimp.org) to paste a ruled grid at the same magnification onto photographs of vessels. The frequency classes for trunk and root vessels were established in intervals of 30 µm and 15 µm for shoot vessels, respectively.

Theoretical hydraulic conductance (k_h) (kg m MPa⁻¹ s⁻¹) was calculated with the modified Hagen–Poiseuille's law described by Tyree and Ewers (1991):

$$k_h = \left(\frac{\pi \rho}{128 \eta} \right) \sum_{i=1}^n (d_i^4)$$

where d is the radius of the vessel in meters, ρ is the fluid density (assumed to be 1000 kg × m⁻³ or equal to that of water at 20 °C) and η is the viscosity (assumed to be 1 × 10⁻⁹ MPa s, or equal to that of water at 20 °C). Weighted mean (Wm) vessel diameters of each genotype were calculated as described previously by Tombesi et al. (2010a).

Statistical analyses of the data were performed with SAS statistical software (SAS Institute, Cary, NC). Treatments were analysed by one-way ANOVA model with significance level set at 0.05. Means were separated by Tukey's w-procedure at $P=0.05$ (Sokal and Rohlf, 1969). For measurements in shoots and roots, two randomly chosen visual fields from each of two sections of each of three shoots and roots were determined for each of the five trees to calculate a grand mean with $n=5$. For trunk values, the grand mean values ($n=5$) were calculated using data from two randomly chosen visual fields of each of the four sections from each of the five trees.

Table 1

Trunk cross sectional area (cm²) of 5-year-old trees and winter pruning weights (kg) after the fifth year in the orchard.

Rootstock	Trunk cross sectional area (cm ²)	Winter pruning weight (kg)
'Nemaguard'	128.8 ± 5.72a	9.25 ± 0.73a
'HBOK 50'	107.7 ± 5.13b	7.39 ± 1.26ab
'HBOK 10'	71.9 ± 6.77c	5.68 ± 1.11bc
'HBOK 32'	67.5 ± 3.76c	4.34 ± 0.72c
'HBOK 27'	50.3 ± 5.71d	2.80 ± 0.13d

* Means ± s.e. of five trees (n=5). Means with different lower-case letters are significantly different at P=0.05 (Tukey's test).

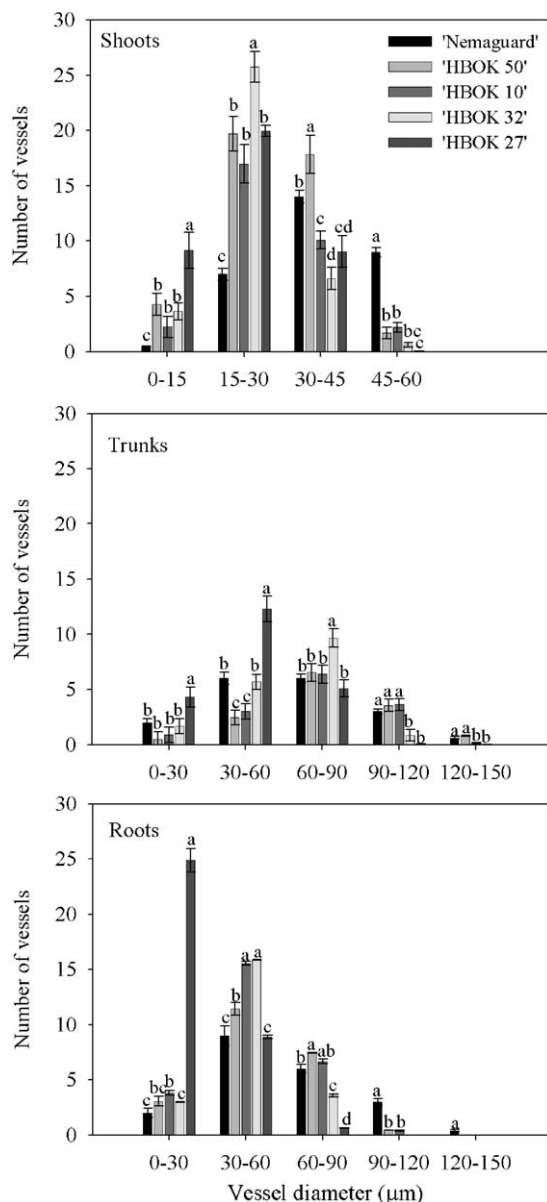


Fig. 1. Frequency distributions of xylem vessel sizes per visual field in shoots, trunks and roots of 'Nemaguard', 'HBOK 50', 'HBOK 10', 'HBOK 32' and 'HBOK 27' rootstock genotypes. For shoots and roots each value is the mean ± s.e. of two visual fields from two sections per three shoots or roots from each of five trees (n=5). For trunks each value is the mean ± s.e. of two visual fields from four sections of one sample from each of five trees (n=5). Means with different lower-case letters are significantly different at P=0.05 (Tukey's test).

3. Results

The scion growth on the four new rootstocks evaluated in this study ranged from ~40 to 90% of the growth of scions on the standard 'Nemaguard' rootstock growing on the same plots (Table 1) 'HBOK 27' was the most dwarfing rootstock with a reduction of trunk cross sectional area in 5-year-old trees of about the 60% compared to trees on 'Nemaguard' followed by 'HBOK 32', 'HBOK 10' and 'HBOK 50' with reductions of 47.56%, 44.17% and 16.37%. Similar trends were apparent in winter pruning weights after 5 years of growth in the orchard.

Vessel diameters varied among rootstock genotypes in all three organ tissues. In general the more size-controlling rootstocks had more vessels in the smaller size classes while the more vigorous rootstocks had more vessels in the larger size classes (Fig. 1). For instance, 'HBOK 27' shoots had the largest number of vessels in the 0–15 μm class while the other four rootstocks had significantly fewer but there were no significant differences among them. 'HBOK 32' had the most vessels in the 15–30 μm class while the other rootstocks had fewer vessels of this diameter. 'HBOK 50' had the largest number of vessels in the 30–45 μm size class while 'Nemaguard' had the most vessels in the 45–60 μm class.

In trunks 'HBOK 27' had the largest number of vessels in the 0–30 and 30–60 μm classes. 'HBOK 32' had significantly fewer vessels in the 30–60 μm class than 'HBOK 27' but significantly more vessels than 'HBOK 10' and 'HBOK 50' that had the lowest number of vessels without significant differences between themselves. 'HBOK 32' had the most vessels in the 60–90 μm class. In 90–120 μm class 'Nemaguard', 'HBOK 50' and 'HBOK 10' had more vessels than 'HBOK 32' and 'HBOK 27'. 'Nemaguard' and 'HBOK 50' had the most vessels in the 120–150 μm class followed by 'HBOK 10'. No vessels of this diameter were found in 'HBOK 32' and 'HBOK 27' trunks.

The differences among genotypes were most pronounced in roots. 'HBOK 27' had a very large number of vessels in the 0–30 μm size class while 'HBOK 10' and 'HBOK 32' had the most vessels in the 30–60 μm size class. 'HBOK 50' and 'HBOK 10' had the most vessels in the 60–90 μm size class while 'Nemaguard' had the most in the 90–120 μm size class. 'Nemaguard' was the only rootstock with vessels in the 120–150 μm size class.

Weighted mean vessel diameter (Wm) values of 'Nemaguard' shoots were the highest, followed by 'HBOK 50' and 'HBOK 10'.

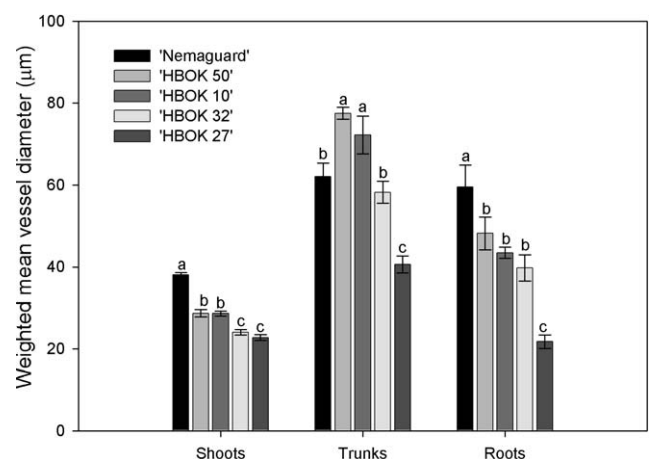


Fig. 2. Weighted mean xylem vessel diameters in shoots, trunks and roots of 'Nemaguard', 'HBOK 50', 'HBOK 10', 'HBOK 32' and 'HBOK 27' rootstock genotypes. For shoots and roots each value is the mean ± s.e. of two visual fields from two sections per three shoots or roots from each of five trees (n=5). For trunks each value is the mean ± s.e. of two visual fields from four sections of one sample from each of five trees (n=5). Means with different lower-case letters are significantly different at P=0.05 (Tukey's test).

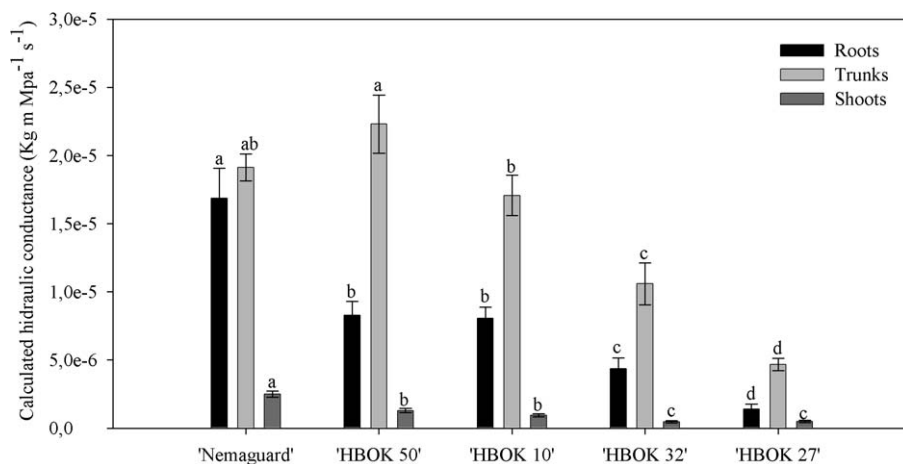


Fig. 3. Calculated axial hydraulic conductance per visual field in shoots, trunks and roots of 'Nemaguard', 'HBOK 50', 'HBOK 10', 'HBOK 32' and 'HBOK 27' rootstock genotypes. For shoots and roots each value is the mean \pm s.e. of two visual fields from two sections per three shoots or roots from each of five trees ($n=5$). For trunks each value is the mean \pm s.e. of two visual fields from four sections of one sample from each of five trees ($n=5$). Means with different lowercase letters are significantly different at $P=0.05$ (Tukey's test).

'HBOK 32' and 'HBOK 27' shoots had the lowest Wm (Fig. 2). Similar trends were seen in Wm of trunks and roots except that 'Nemaguard' trunks had lower Wm than 'HBOK 50' and 'HBOK 10'.

Roots of 'Nemaguard' had the highest calculated hydraulic conductance followed by 'HBOK 50', 'HBOK 10', 'HBOK 32' and 'HBOK 27', respectively (Fig. 3). In trunks 'HBOK 50' and 'Nemaguard' had the highest calculated conductance followed by 'HBOK 10', 'HBOK 32' and 'HBOK 27', respectively. In shoots 'Nemaguard' had the highest calculated conductance followed by 'HBOK 50', 'HBOK 10', 'HBOK 32' and 'HBOK 27', respectively.

4. Discussion

Previous research has shown that differences in hydraulic conductance are physiologically linked to differences in vigour among different peach rootstock genotypes (Basile et al., 2003; Solari et al., 2006a,b,c) and that differences in measured hydraulic conductance are associated with differences in xylem characteristics among those same rootstocks (Tombesi et al., 2010a). The present study documents that there are similar relationships between rootstock vigour and xylem anatomy characteristics in a new set of size-controlling peach rootstocks.

This study focused on four new size-controlling rootstocks whose vigour ranged from 40 to 83% of the vigorous 'Nemaguard' control (Fig. 1, Table 1). The two more dwarfing rootstocks ('HBOK 27' and 'HBOK 32') tended to have smaller vessels and a lower numbers of large vessels than the two more vigorous ones ('HBOK 10 and 50'). Thus Wm values for 'HBOK 32' and 'HBOK 27' were lower than for 'HBOK 10' and 'HBOK 50'. The different anatomical characteristics caused a reduction in the theoretical calculated hydraulic conductance that was related to dimension of vessels according to the Hagen–Poiseuille law (Tyree and Ewers, 1991). In the four 'HBOK' rootstocks the calculated hydraulic conductance of each organ reflected differences in vigour of a common scion cultivar grown on these four rootstocks in the order of vigour. Of the new rootstock selections 'HBOK 50' was the most vigorous followed by 'HBOK 10', 'HBOK 32' and 'HBOK 27', respectively. The 'Nemaguard' control trees were the most vigorous and had the highest Wm and theoretical hydraulic conductance of shoots and roots. However the greater tree vigour of 'Nemaguard' trees relative to the more vigorous 'HBOK' rootstocks was not consistently reflected in the trunk xylem characteristics. It is difficult to explain this deviation from the pattern of xylem characteristics observed in the roots and the stems except that it is possible that the trunk growth of these trees

may have decreased as the trees filled their allotted space in the orchard and thus their trunk xylem characteristics also changed.

5. Conclusions

Since the differences in rootstock genotype vigour were consistently reflected in roots and young current-year shoots of the rootstock genotypes it appears that it may be possible to screen for size-controlling peach rootstock genotypes in a rootstock seedling population by quick examination of xylem anatomy of shoots from seedlings. However the xylem anatomy of roots appeared to provide more resolution for differentiating the potential vigour differences among genotypes. Thus an even more intriguing possibility would be to attempt to use the differences in xylem anatomical root phenotypes to develop molecular markers for identifying size-controlling phenotypes in a peach rootstock breeding program. Previously one of the primary difficulties in developing such molecular markers was the inability to identify clear phenotypes associated with the dwarfing mechanism (Chaparro et al., 1994; Venkatachalam et al., 2004).

It would also be interesting to determine if it may be possible to select for rootstock vigour in other fruit tree species in which vigour is related to similar anatomical differences in xylem tissue as reported here for peach. It has been hypothesized that the size-controlling behaviour of some rootstocks may involve partial scion/rootstock incompatibilities (Basile and DeJong, 2007). Obviously, screening procedures based on xylem anatomical characteristics discussed in this study would probably not be appropriate for selecting such rootstocks. The rootstocks involved in the present study were 100% *P. persica*, had smooth graft unions and showed no signs of scion/rootstock partial incompatibility. Xylem anatomical characteristics have also been related to tree vigour of olive (Tombesi et al., unpublished) and cherry (Goncalves et al., 2007; Olmstead et al., 2006) trees. While some studies with apple have implicated that differences in water relations or that hydraulic conductance may be mechanistically involved in the size-controlling behaviour of selected rootstocks (Olien and Lakso, 1986; Cohen and Naor, 2002; Atkinson et al., 2003) other factors are also probably involved (Basile and DeJong, 2007; Webster, 2004). Interestingly, hydraulic conductance may be involved in rootstock related control of vigour in kiwifruit however in this case the differences in hydraulic conductance are more related to phenological timing of the development of the xylem rather than anatomical characteristics of the xylem (Clearwater et al., 2007).

If it is possible to select for rootstock vigour by analyzing the xylem anatomy of either shoots or roots of one- or two-year-old trees it could speed up the development of new size-controlling fruit tree rootstocks by more than a decade. Furthermore, if the anatomical characteristics of root xylem can be linked to genetic markers even greater speed and efficiencies could be gained.

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