Peach Tree Vigor Is a Function of Rootstock Xylem Anatomy and Hydraulic Conductance

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Abstract

Recently we have demonstrated that there are anatomical differences between dwarfing and vigorous peach rootstocks. These differences in xylem anatomy have been linked to the vigour control capacity of the specific rootstocks. Previously we showed that dwarfing peach rootstocks generally have lower mid-day stem water potentials and that this limits shoot growth during the most active period for vegetative growth. The key factor affecting shoot growth appears to be stem hydraulic conductance which is strongly influenced by xylem vessel diameters. Weighted mean xylem vessel diameters are smaller in dwarfing rootstock genotypes than in vigorous ones. Thus it appears that xylem vessel diameter is a genetically controlled, phenotypic trait that is the primary factor that determines the size-controlling capacity of graft-compatible peach rootstocks. This paper will summarize the physiological and anatomical evidence for this hypothesis that provides a mechanistic basis for understanding the size-controlling phenomenon associated with graft-compatible peach rootstocks. This mechanistic explanation of the size-controlling phenomenon provides researchers with a useful means to screen for size-controlling genotypes in rootstock development programs. Furthermore it may be the basis for the future investigation of vigour-related phenomena in other fruit tree species.

INTRODUCTION

Composite trees, formed by a scion grafted onto a rootstock, are commonly used in commercial fruit orchards. The use of rootstocks can increase tolerance to pests and disease, increase scion performance in particular edaphic conditions, induce early production and control scion vigour (Webster, 1995). Tree vigour control can accommodate higher density plantings, reduce growing costs and lead to increased yields.

Two series of new peach rootstocks that provide a wide range of vigour controlling capacity have recently been developed at the University of California, Davis (Tables 1 and 2). The development of these rootstocks led to studies of the physiological mechanism involved in controlling scion vigour in graft-compatible peach rootstocks. Weibel et al. (2003) reported that dwarfing rootstocks reduced both shoot length as well as the number of shoots per tree while the number of internodes per shoot was not generally affected by rootstock vigour. Basile et al. (2003) reported that shoot growth of trees on dwarfing rootstocks was correlated with differences in seasonal patterns of stem water potential. Subsequently, Solari et al. (2006a) confirmed that trees on dwarfing rootstocks had lower midday stem water potential values than trees on vigorous rootstocks. Stem water potential is closely related to hydraulic conductance (Tyree and Sperry, 1988) and in another paper Solari et al. (2006b) reported that dwarfing rootstocks had lower leaf-specific hydraulic conductance than a vigorous rootstock. In a subsequent study Solari and DeJong (2006) documented that shoot growth could be manipulated by manipulating stem water potential in trees with dwarfing and vigorous rootstocks, thus confirming the links between stem water potential, stem hydraulic conductance and shoot growth rates.

This series of studies led to an investigation of the physiological basis for the reductions of hydraulic conductance in dwarfing rootstocks. Axial hydraulic conductance in plants is a function of the anatomical characteristics of xylem. Xylem vessel diameters are especially important because of the Hagen-Poisseuille law which states that the hydraulic conductance of a tube is a function of the diameter of the tube raised to the fourth power (Vercambre et al., 2002). Therefore, we investigated if differences in rootstock-induced tree vigour were related to differences in mean xylem vessel diameters of a range of rootstock genotypes (Tombesi et al., 2010a). Furthermore, we tested if the vigour of a rootstock had any influence on the xylem characteristics of the scion and if differences in xylem anatomy could explain the partial vigour reductions obtained when a dwarfing rootstock genotypes was used as an inter-stem (Tombesi et al., 2010b). Finally we tested if anatomical screening of the xylem of rootstock genotypes could be used as a tool for selection of new dwarfing rootstocks in peach (Tombesi et al., 2011)

MATERIALS AND METHODS

Plant Material

In the first experiment, a comparison of the xylem characteristics and theoretical hydraulic conductance of dwarfing vs. vigorous rootstocks, a series of three rootstocks representing a range of vigour (‘Nemaguard’ vigorous, ‘P30-135’ semi-vigorous, ‘K146-43’dwarfing) were used. In a second experiment the xylem characteristics of four new rootstocks (‘HBOK 27, 32, 10 and 50’), representing a similar range of vigour as in the first experiment, were analyzed and compared with those on the standard vigorous rootstock ‘Nemaguard. Root and trunk samples were obtained from trees planted in 2002 and 2003 (for the first and second experiment, respectively) at the Kearney Agricultural Center of the University of California (Parlier, CA) and trained to a perpendicular V system (DeJong et al., 1995). Shoots were also sampled from rootstock “mother” trees of both rootstock series planted in 2002, on the campus of the University of California, Davis. For the inter-stem experiment five trees were used. In each tree ‘Nemaguard’ was used as the rootstock, ‘K146-43’ as the inter-stem, and ‘O’Henry’ as the scion. These trees were planted at the UC Kearney Agricultural Center (Parlier, CA) in 2004 and were also trained to a perpendicular V.

Sample Analysis

Root, trunk and shoot xylem tissue samples taken in May were fresh sectioned with a manual microtome at 150 µm of thickness to obtain two cross-sections from each field sample. The sections were stained with Toluedine-Blue-O to increase visual contrast. Photographs of the cross-sections were taken with a camera (Model Lei 750, Leica, Wetzlar, Germany) mounted on a light microscope (Eclipse E 600, Nikon, Tokyo, Japan). Images were then acquired with DEI-750D software (Optronics, Goleta, CA, USA). Vessels were measured and counted in frequency classes, as described by Solla and Gil (2002), using a computer graphics program (GIMP, freeware; www.gimp.org) to paste a ruled grid at the same magnification onto photographs of vessels. The frequency classes were established at intervals of 30 µm for trunk and root vessels, and at 15 µm for shoot vessels.

Theoretical hydraulic conductance (k_h; kg m MPa^{-1} s^{-1}) was calculated with the modified Hagen-Poisseuille law described by Tyree and Ewers (1991). A weighted mean (Wm) diameter was calculated as described by Tombesi et al. (2010a). Statistical analyses of the data were performed with SAS statistical software (SAS Institute, Cary, NC, USA). Treatments were analysed by one-way ANOVA with significance level set at 0.05. Means were separated by Tukey’s w-procedure at P=0.05 (Sokal and Rohlf, 1969).

RESULTS

'Nemaguard' had the largest weighted mean xylem vessel diameter (W_m) and highest theoretical hydraulic conductance (K_h) in all three organs compared to 'P30-135' and 'K146-43', respectively (Fig. 1). The same scion grafted on different rootstocks had very similar W_m and K_h values (Table 3). Rootstock xylem vessel W_m and K_h varied significantly: 'Nemaguard' had the largest W_m and K_h followed by 'P30-135' and 'K 146-43', respectively.

As with the rootstocks in the first experiment the four newly-selected HBOK rootstocks had a range of hydraulic conductance in all the three organs that reflected their relative rootstock vigour (Table 2, Fig. 2). 'Nemaguard', the vigorous standard, had the highest theoretical hydraulic conductance followed by 'HBOK 50', 'HBOK 10', 'HBOK 32' and 'HBOK 27', respectively.

Theoretical hydraulic conductance also varied among genotypes in the inter-stem trees. The inter-stem, 'K146-43', had the lowest theoretical hydraulic conductance; 'Nemaguard', the rootstock, and 'O'Henry', the scion, had K_h values that were similar to each other and higher than the inter-stem (Fig. 3).

DISCUSSION

Axial hydraulic conductance in plant stems is influenced by several anatomical factors such as xylem vessel length, shape and inclination, and cross-sectional diameter. Of these, vessel diameter appears to be one of the most important (Tyree and Zimmermann, 2002). Theoretical hydraulic conductance can be easy estimated by the Hagen-Poisseuelle law (Tyree and Ewers, 1991). It determines the physical limit of hydraulic conductance of xylem. Comparisons of calculated theoretical hydraulic conductance of two sets of rootstocks corresponded with their respective capacity to control the vigour of a vigorous scion cultivar in field-grown trees. The more dwarfing rootstocks generally had smaller vessels than vigorous rootstocks and correspondingly lower theoretical hydraulic conductance (Figs. 1 and 2). The differences in theoretical hydraulic conductance between 'K146-43 ' and 'Nemaguard' rootstocks correspond with the empirically measured differences in hydraulic conductance previously reported for the same rootstocks (Solari et al., 2006b).

Measurement of xylem vessel characteristics may be a useful means for early identification of genotypes with size-controlling potential in rootstock breeding programs since similar patterns of correspondence between rootstock vigour and xylem characteristics were observed for both series of peach rootstocks used in this study. Since differentiating xylem characteristics that were apparent in young roots and shoots it may be possible to screen rootstocks for size-controlling characteristics in one- or two year-old seedlings.

The third experiment involving a dwarfing rootstock genotype used as an inter-stem indicates that the mechanism involved in the inter-stem effect on tree vigour probably involves a similar mechanism as with rootstocks. In the case of inter-stems, a dwarfing genotype can apparently act to restriction of water flow (Fig. 3) and thus reduce tree growth. This could partly explain the results reported by Parry and Rogers (1972) and DiVaio et al. (2009) who observed that increasing the length of the dwarfing genotype inter-stems increased their vigour control capacity.

In summary, anatomical analysis of size-controlling rootstocks in comparison with their vigorous counterparts indicates a clear mechanism that can account for their size-controlling behaviour that is consistent with a large body of accumulated research on the same, or similar, peach rootstocks. This research indicates that normally vigorous scion cultivars growing on dwarfing rootstocks have reduced shoot growth and numbers of vigorous shoots than the same scion cultivars growing on vigour inducing rootstocks. Reductions in shoot growth are related to decreased mid-day stem water potentials. Decreased mid-day stem water potentials are related to decreased measured root hydraulic conductance. Decreased measured root hydraulic conductance appears to be related to xylem vessel characteristics and decreased theoretical xylem hydraulic conductance.

However rootstocks do not strongly influence scion xylem characteristics and thus factors that limit tree axial hydraulic conductance primarily reside in the root and the rootstock shank. A dwarfing genotype used as an inter-stem appears to cause a restriction of hydraulic conductance because of its xylem vessel characteristics and this restriction also appears to be primarily caused by the inter-stem. This research was limited only to fully graft-compatible peach rootstocks. There are reports that similar factors may govern the behaviour of cherry trees on specific dwarfing rootstocks (Goncalves et al., 2007; Olmstead et al., 2006) however graft compatibility factors may be involved in the dwarfing mechanism of size-controlling rootstocks in other fruit tree species.

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Tables

Table 1. Trunk circumference (cm) after twelve growing seasons of trees with two different scion cultivars (‘Loadel’ and ‘Flavorcrest’) two training systems (Open Vase and KAC-V) and three rootstocks (‘Nemaguard’ (standard), ‘P30-135’ (semi-dwarfing), ‘K146-43’ (dwarfing)). Each value is the mean ± SE of five trees (*n*=5). Means with different lower-case letters are significantly different at P<0.05 (Tukey’s test).

Rootstock	Loadel		Flavorcrest	
	Open Vase	KAC-V	Open Vase	KAC-V
Nemaguard	78.1±0.68 a	54.6±0.96 a	90.2±1.97 a	62.6±1.17 a
P30-135	72.2±2.11 b	52.6±2.21 a	86.3±2.59 a	63.4±3.75 a
K146-43	53.0±0.36 d	38.1±1.69 c	61.7±1.18 c	41.6±0.39 c

Table 2. Trunk cross sectional area (cm^2) and winter pruning weights (kg/tree) after four growing seasons of four newly selected ‘HBOK’ rootstocks in comparison with the standard ‘Nemaguard’. Each value is the mean ± SE of five trees (*n*=5). Means with different lower-case letters are significantly different at P<0. 05 (Tukey’s test).

Rootstock	Trunk sectional area (cm^2)	Winter pruning weight (kg/tree)
Nemaguard	128.8 ± 5.72 a	9.25 ± 0.73 a
HBOK 50	107.7 ± 5.13 b	7.39 ± 0.26 ab
HBOK 10	71.9 ± 6.77 c	5.68 ± 1.11 bc
HBOK 32	67.5 ± 3.76 c	4.34 ± 0.72 c
HBOK 27	50.3 ± 5.71 d	2.80 ± 0.13 d

Table 3. Weighted mean vessel diameter (W_m (µm)) and theoretical hydraulic conductance (k_h (kg m MPa^{-1} s^{-1} 10^{-5})) of rootstock-scion combinations used in the first experiment. Each value is the mean ± SE of five trees (*n*=5). Means with different lower-case letters are significantly different at P<0. 05 (Tukey's test).

	O'Henry on Nemaguard		O'Henry on P30-135		O'Henry on K146-43	
	Rootstock	Scion	Rootstock	Scion	Rootstock	Scion
W_m	62.1±3.31 a	55.5±5.63 a	42.4±1.55 b	54.4±2.83 a	26.6±1.13 c	49.4±5.38 a
K_h	1.91±0.10 a	1.54±0.17 a	0.69±0.05 b	1.82±0.12 a	0.41±0.04 c	1.55±0.27 a

Figures

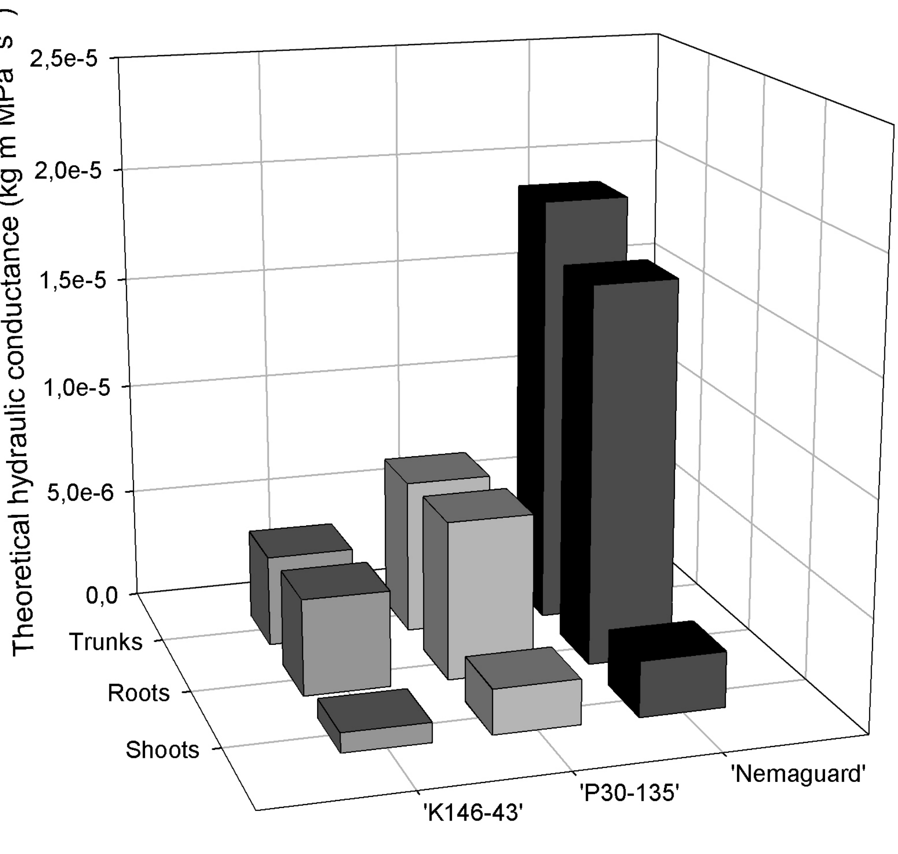

Fig. 1. Calculated axial hydraulic conductance per visual microscopic field in shoots, trunks and roots of 'Nemaguard', 'P30-135' and 'K146-43' rootstock genotypes.

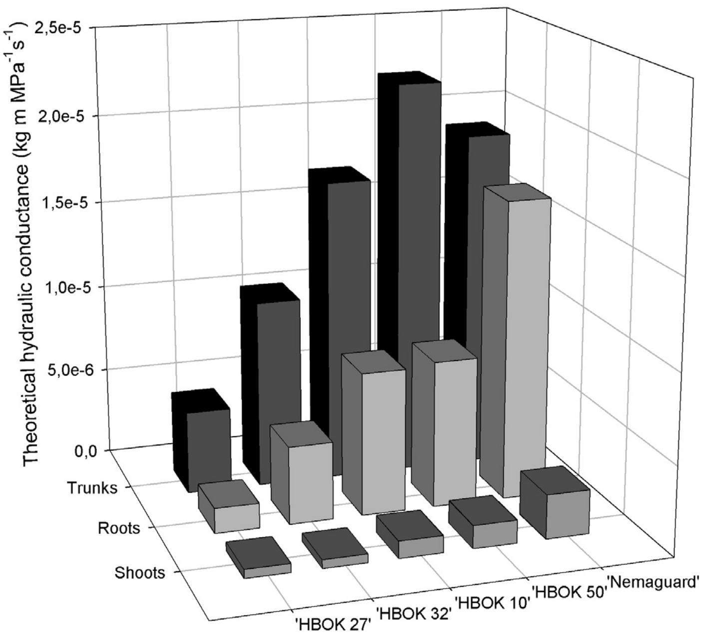

Fig. 2. Calculated axial hydraulic conductance per visual microscopic field in shoots, trunks and roots of ‘Nemaguard’, ‘HBOK 50’, ‘HBOK 10’, ‘HBOK 32’ and ‘HBOK 27’ rootstock genotypes.

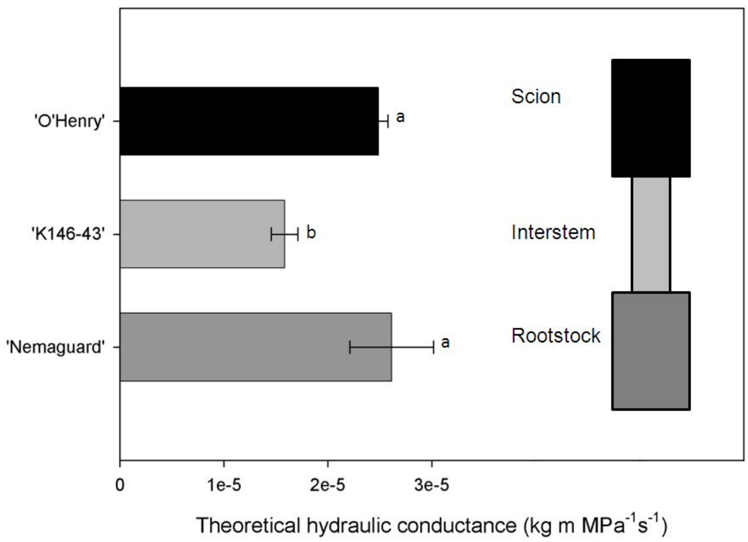

Fig. 3. Calculated axial hydraulic conductance (kg m MPa^{-1} s^{-1}) per visual microscopic field in stem pieces of inter-stem trees with a ‘Nemaguard’ rootstock, a ‘K146-43’ inter-stem and an ‘O’Henry’ scion.