



Proposed pre-selection method for identification of dwarfing peach rootstocks based on rapid shoot xylem vessel analysis



Claudio H. Bruckner^{a,*}, Theodore M. DeJong^{b,1}

^a Departamento de Fitotecnia, Universidade Federal de Viçosa, Viçosa, MG 36570-000, Brazil

^b Department of Plant Science, University of California Davis, One Shields Ave., Davis, CA 95616, USA

ARTICLE INFO

Article history:

Received 15 August 2013

Received in revised form

11 November 2013

Accepted 14 November 2013

Keywords:

Rootstock selection

Tree vigor

Xylem anatomy

Selection method

Rootstock breeding

ABSTRACT

The association between a genotype's dwarfing ability and a genetic, physiological, or anatomical trait would be of great value for selecting dwarf rootstocks at an early stage of development. Dwarfing peach rootstocks have been associated with decreased hydraulic conductance due to smaller xylem vessel diameters compared to invigorating rootstock genotypes. We evaluated tentative anatomical criteria for selecting dwarfing peach rootstocks based on measurements of the diameter of the largest xylem vessels and the number of xylem vessels surrounding the largest vessels in cross sections of shoots. Epicormic and proleptic shoots were collected from trees of the standard, invigorating 'Nemaguard' peach rootstock and a series of dwarfing rootstocks: 'Controller 9.5'™ (HBOK 50), 'Controller 9'™ (P30-135), 'Controller 8'™ (HBOK 10), 'Controller 7'™ (HBOK 32), 'Controller 6'™ (HBOK 27) and 'Controller 5'™ (K146-43). Transverse sections were cut from 2, 3, and 4 mm diameter stems of proleptic shoots and from 4, 5, and 6 mm diameter stems of epicormic shoots. The samples were fresh sectioned to a thickness of about 150 µm, stained with Toluidin-Blue-O and photographed on a light microscope. The largest xylem vessel was visually identified in each microscopic view field, and the surrounding circle of vessels with a diameter of ~164 micrometers were counted. Rootstock genotype, shoot diameter, and the interactions between rootstock × shoot diameter significantly affected the diameters of the largest vessels of both proleptic and epicormic shoots. Most of the evaluations of the largest vessel diameter were able to distinguish the lowest vigor rootstock from the vigorous, but the intermediate vigor rootstocks were not clearly distinguished by this criterion. The less vigorous rootstocks showed a tendency for having more vessels. The larger vessel diameters in more vigorous rootstocks appeared to be related with fewer vessels. For rootstock screening purposes epicormic shoots appeared to be better for evaluation than proleptic shoots. Young, vigorous seedlings are in the vegetative phase of plant growth, and probably more similar to epicormic shoots than to proleptic oneshoots that are physiologically more related to fruit bearing than to rapid vegetative growth. We propose that the evaluation of the largest vessel of a microscopic view field associated with the number of vessels around the largest vessel, measured on 5 mm vigorous shoots would be useful as a criterion for selecting dwarfing peach rootstock genotypes.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Dwarf fruit trees are trees that normally do not reach the characteristic size of the species or related species. For pomology, the term dwarf tree is applied to trees that grow smaller than normal due to artificial means such as selection of dwarf genotypes, specific training and/or pruning procedures or through grafting on dwarfing rootstocks (Ingels et al., 2002). Dwarf fruit trees are developed to increase productivity, fruit quality, and reduce costs associated

with pruning, fruit thinning, and harvesting in high density planting systems (Muleo et al., 2011; Tanasescu et al., 2013). Dwarf or semi-dwarf genotypes have been developed in species such as apples (Looney and Lane, 1984; Laurens, 1998), cashews (Moura et al., 2001) and peaches (Hansche, 1989; Hu and Scorza, 2009; Scorza et al., 2002; Gradziel and Beres, 1993).

Dwarfing apple rootstocks were developed early in the last century and are used in commercial practice all over the world (Atkinson and Else, 2005; Blanco et al., 2008; Jensen et al., 2010; Czynczyk and Bielicki, 2012; Piestrzeniewicz et al., 2013; Tomala and Slowinska, 2006). Though with less commercial success, dwarfing rootstocks have been obtained for avocado (Barriento-Priego et al., 1992), cherry (Ystaas and Frøynes, 1996; Charlot et al., 2005; Moghadam and Khalighi, 2007), peach (Glenn and Scorza, 1992; DeJong et al., 2004) and plum (Jänes and Pae, 2003).

* Corresponding author. Tel.: +55 31 3899 1344; fax: +55 31 38992641.

E-mail addresses: bruckner@ufv.br, claudio.bruckner@gmail.com
(C.H. Bruckner), tmdejong@ucdavis.edu (T.M. DeJong).

¹ Tel: +1 530 752 1843.

Peach rootstocks have been developed with the aim of controlling tree vigor and increasing productivity, fruit quality, and tree survival (Reighard and Loret, 2008). The germplasm used to the development are peach and related *Prunus* species. Several released rootstocks are intergeneric hybrids (Salesses et al., 1998; Moreno and Cambra, 2004; Felipe, 2009; Pinochet, 2009; DeJong et al., 2011; Legal et al., 2012). The main selected traits are easy clonal propagation, graft compatibility, adaptation to heavy, saline and calcareous soil condition, cold hardiness, waterlogging, tolerance to iron chlorosis, nematodes, root fungal diseases, and orchard replanting (Reighard and Loret, 2008). The selection of rootstocks with dwarfing effect is an important goal for breeding purposes while it reduces cost and increases the productivity and fruit quality (Reighard and Loret, 2008). Cousins (2005) consider the improvement of rootstocks slower than the improvement of scion varieties because the test requirements, the novel functions, and first tests procedures need to be understood to expand selection criteria.

Rootstock breeding programs are long term research endeavors that involve the choice of potential parents with dwarfing genes, hybridization cycles, preliminary evaluation and selection for desired rootstock traits, evaluation of scion test genotypes grafted on the potential rootstocks, evaluation of orchard behavior in preliminary field trials, and scion-rootstock production trials with the promising rootstocks (Gruppe, 1985). Field evaluations of dwarfing rootstocks are expensive and time and space consuming; involving field experiments with plants composed of specific scion and rootstock combinations. This makes the initial screening and ability to discard inferior genotypes at an early stage in the process very important (Johnson et al., 2001). The dwarfing effect of a rootstock genotype is one of the traits that must be evaluated in composite trees, and an association between a genotype's dwarfing ability with a genetic, physiological or anatomical trait would be of great value for breeding purposes.

Studies of genetic markers associated with the dwarfing ability of rootstocks have been presented for apple (Rusholme Pilcher et al., 2008; Celton et al., 2009), *Poncirus trifoliata* as a *Citrus* rootstock (Cheng and Roose, 1995), and pear (Wang et al., 2011). However the physiological basis of rootstock dwarfing is not well recognized. There are probably different physiological processes affecting growth rate and tree size associated with specific rootstocks. Apple dwarf rootstocks were found to have less sap flow under water stress conditions (Hussein and McFarland, 1994; Cohen and Naor, 2002). In peach rootstocks, the dwarfing characteristics have been associated with less hydraulic conductance due to smaller xylem vessel diameters (Tombesi et al., 2010; Tombesi et al., 2011). Tombesi et al. (2011) pointed out that the anatomical measurements of xylem vessels might be useful for predicting rootstock vigor in rootstock breeding programs. However, to apply anatomical measures as a selection tool, it is necessary to specify anatomical traits that are easy to identify and measure. To be feasible for evaluating large populations, such measurements need to be simple, objective and quickly done. Ideally, the methods should be able to be carried out on young plants before they are planted into field trials.

The objective of this work was to evaluate tentative anatomical criteria for selecting dwarfing peach rootstocks. In this study we focused on measurements of the diameter of the largest xylem vessel and the number of xylem vessels around the largest vessel found in a microscopic field view of cross sections of epicormic and proleptic shoots of specific diameters.

2. Material and methods

Epicormic and proleptic peach shoots were collected from virus free rootstock genotypes growing in the Foundation Plant Services

foundation blocks at the University of California, Davis. The rootstocks evaluated included vigorous standard 'Nemaguard' and the following dwarfing rootstocks: 'Controller 9.5'™ (HBOK 50), 'Controller 9'™ (P30-135), 'Controller 8'™ (HBOK 10), 'Controller 7'™ (HBOK 32), 'Controller 6'™ (HBOK 27) and 'Controller 5'™ (K146-43), which impart respectively, about 50–95% of the vigor of trees on Nemaguard to normal scion cultivars (DeJong et al., 2013). These dwarfing rootstocks were developed by the Plant Sciences Department of the University of California, Davis and the USDA ARS Station in Parlier, CA.

Transverse sections of shoots of three diameters were made after the shoots developed secondary tissue. Proleptic shoot sections were cut from 2, 3, and 4 mm diameter proleptic shoots, and epicormic shoot sections were cut from epicormic shoots (water sprouts) that were 4, 5, and 6 mm in diameter. Shoot tissue samples smaller than these diameters did not have fully formed secondary xylem tissue. The samples of each diameter were fresh sectioned at a thickness of about 150 µm to obtain a cross section of each sample, with eight replications. The cross sections were stained with Toluidin-Blue-O (O'Brien et al., 1964) and photographed with an image capture software DEI-750D (Optronics, Goleta, CA, USA), connected to a camera model Lei 750 (Leica, Wetzlar, Germany), mounted on a light microscope (Nikon Eclipse E 600, Nikon, Tokyo Japan).

In each microscopic view field with a diameter of 163.75 µm the largest xylem vessel was visually identified, and the surrounding vessels formed a circle within the view field. The maximum and minimum diameter of the largest vessel was measured. The mean diameter was calculated by the average between the largest and the smallest diameters. The vessels surrounding the largest vessels were counted except on samples from the thinner shoot diameters, i.e., 3 mm on proleptic and 4 mm on epicormic shoots because these shoots had xylem tissue layers smaller than a circle corresponding to 163.75 µm.

The data from proleptic and epicormic shoots were analyzed separately as completely randomized factorial experiments, with 7 treatments corresponding to the rootstock factor and two or three treatments for the diameter factor. The data were submitted to analysis of variance, and the treatments were presented as means with standard errors (S.E.).

3. Results and discussion

3.1. Diameter of the largest xylem vessel

According to the analysis of variance, the evaluations of proleptic shoots revealed rootstock effects, shoot diameter effects, and an interaction between rootstock and shoot diameter (Table 1), at the 1% level of probability. Similarly, the analysis of variance of epicormic shoots revealed rootstocks effects, shoot diameter effects, and an interaction between rootstocks and shoot diameters (Table 2), at the 1% level of probability; except for the interaction between rootstocks and shoot diameters for the largest vessel diameter, which was significant at the 5% level of probability. The means and standard errors of the diameters of the largest vessel are presented on Table 3 (proleptic shoots) and Table 4 (epicormic shoots).

The analysis of variance F-test of the diameter of the largest vessel was significant (Tables 1 and 2) for rootstock, shoot diameter, and the interaction between rootstock x shoot diameter for proleptic shoots and also for epicormic shoots. Thus the shoot diameter affected the diameter of the largest vessel. Consequently, it was necessary to standardize the shoot diameter for evaluations Table 4.

The Controller series of peach rootstocks was developed at the University of California, Davis in collaboration with USDA ARS

Table 1

Mean squares of larger (A), shorter (B), and mean (C) diameter of the largest xylem vessel of proleptic shoots.

Source	Degree of freedom	Mean square		
		A	B	C
Rootstock	6	202.1232 ^a	88.9501 ^a	124.0896 ^a
Diameter	2	566.8901 ^a	740.9071 ^a	642.6585 ^a
Interaction between rootstock and shoot diameter	12	86.9006 ^a	40.6727 ^a	54.0980 ^a
Error	147	24.2441	11.4127	12.1589
Total	167			
CV%	13.27	12.76	10.97	

^a F-test significant (1%).**Table 2**

Mean squares of larger (A), shorter (B), and mean (C) diameter of the largest xylem vessel of epicormic shoots.

Source	Degree of freedom	Mean square		
		A	B	C
Rootstock	6	424.4175 ^b	132.7712 ^b	255.1282 ^b
Diameter	2	1121.3012 ^b	535.5816 ^b	801.4358 ^b
Interaction between rootstock and shoot diameter	12	66.9384 ^a	78.8106 ^b	63.4243 ^b
Error	147	36.7924	19.1445	18.3269
Total	167			
CV%	12.88	12.68	10.49	

^a F-test significant (5%).^b F-test significant (1%).**Table 3**Average larger (A), smaller (B), and mean (C) diameters of the largest xylem vessel of proleptic shoots (μm) according to rootstock and shoot diameter.

Rootstock	Shoot diameter: 2 mm			Shoot diameter: 3 mm			Shoot diameter: 4 mm		
	A	B	C	A	B	C	A	B	C
Nemaguard	41.24 ± 1.16 ^a	25.58 ± 1.21	27.65 ± 0.95	41.24 ± 1.04	29.03 ± 0.84	35.14 ± 0.59	44.93 ± 1.43	32.72 ± 1.09	38.82 ± 1.20
Controller 9.5 (HBOK 50)	32.72 ± 1.43	22.81 ± 1.04	32.26 ± 1.21	37.79 ± 1.35	24.88 ± 1.10	31.34 ± 1.14	43.09 ± 2.36	34.56 ± 1.90	38.82 ± 1.82
Controller 9 (P30-135)	31.57 ± 1.57	22.58 ± 1.54	32.03 ± 1.48	37.10 ± 2.01	24.88 ± 1.44	30.99 ± 1.37	35.71 ± 1.43	28.80 ± 1.04	32.26 ± 1.21
Controller 8 (HBOK 10)	32.26 ± 0.84	23.04 ± 0.85	28.92 ± 0.80	41.01 ± 1.38	27.42 ± 1.45	34.22 ± 1.05	44.01 ± 2.86	32.03 ± 1.15	38.02 ± 1.89
Controller 7 (HBOK 32)	33.87 ± 2.01	20.97 ± 1.44	30.99 ± 1.37	35.02 ± 2.87	24.19 ± 1.76	29.61 ± 2.23	36.18 ± 2.31	25.35 ± 1.09	30.76 ± 1.34
Controller 6 (HBOK 27)	27.65 ± 0.73	20.74 ± 1.51	27.07 ± 0.76	35.02 ± 1.05	29.49 ± 0.85	32.26 ± 0.60	41.71 ± 1.20	32.03 ± 1.25	36.87 ± 0.92
Controller 5 (K146-43)	35.71 ± 1.70	23.96 ± 0.70	29.84 ± 0.97	38.48 ± 1.57	25.58 ± 1.54	32.03 ± 1.48	32.72 ± 0.84	25.12 ± 0.85	28.92 ± 0.80

^a mean ± S.E.**Table 4**Average larger (A), smaller (B), and mean (C) diameters of the largest xylem vessel of epicormic shoots (μm) according to rootstock and shoot diameter.

Rootstock	Shoot diameter: 4 mm			Shoot diameter: 5 mm			Shoot diameter: 6 mm		
	A	B	C	A	B	C	A	B	C
Nemaguard	42.86 ± 2.41 ^a	28.57 ± 1.30	35.71 ± 1.43	58.53 ± 2.76	40.55 ± 1.78	49.54 ± 1.91	56.68 ± 1.34	43.55 ± 2.03	50.12 ± 1.38
Controller 9.5 (HBOK 50)	40.32 ± 1.45	31.80 ± 1.38	36.06 ± 1.09	47.00 ± 1.91	35.02 ± 1.30	41.01 ± 1.26	47.47 ± 1.43	33.64 ± 1.19	40.55 ± 1.06
Controller 9 (P30-135)	38.48 ± 1.18	28.80 ± 2.00	33.64 ± 1.35	43.55 ± 1.87	33.41 ± 2.75	38.48 ± 1.90	45.62 ± 1.70	32.95 ± 1.50	39.29 ± 1.40
Controller 8 (HBOK 10)	44.70 ± 2.30	33.87 ± 1.56	39.29 ± 1.52	51.84 ± 1.28	39.40 ± 0.92	45.62 ± 0.72	51.61 ± 4.12	36.87 ± 1.44	44.24 ± 2.60
Controller 7 (HBOK 32)	51.61 ± 0.78	34.33 ± 1.39	42.97 ± 1.04	49.08 ± 0.77	33.64 ± 1.59	41.36 ± 0.79	54.84 ± 2.53	41.24 ± 1.87	48.04 ± 1.97
Controller 6 (HBOK 27)	38.02 ± 2.95	28.34 ± 0.92	33.18 ± 1.38	49.77 ± 1.39	37.79 ± 1.35	43.78 ± 1.28	48.85 ± 3.67	34.10 ± 1.84	41.47 ± 2.51
Controller 5 (K146-43)	37.79 ± 1.39	31.11 ± 1.32	34.45 ± 1.10	43.78 ± 1.62	30.41 ± 0.92	37.10 ± 1.00	46.54 ± 2.36	35.02 ± 0.70	40.78 ± 1.41

^a mean ± S.E.

Table 5

Mean squares of number of xylem vessels around the larger vessel in proleptic and epicormic shoots.

Source	Degree of freedom	Mean square	
		Proleptic shoots (3 and 4 mm)	Epicormic shoots (5 and 6 mm)
Rootstock	6	19.6012 ^b	30.7440 ^b
Diameter	1	270.3214 ^b	9.7232 ^b
Interaction between rootstock and shoot diameter	6	23.9048 ^b	2.9107 ^a
Error	98	4.7934	2.4860
Total	111		
CV%	22.83	25.04	

^a F-test significant (5%).^b F-test significant (1%).

researchers at Parlier, CA and were named according to the vigor the impart to scion cultivars in relation to Nemaguard rootstock, the standard peach rootstock used in California. Thus, scions on Controller 5 exhibit approximately 50% of the vigor of scions on Nemaguard; Controller 6, 60% etc.

Most of the evaluations of the largest vessel diameter taken at specific shoot diameters were able to distinguish the lowest vigor rootstock Controller 5 from the vigorous Nemaguard in epicormic as well as in proleptic shoots, but the intermediate vigor rootstocks were not clearly distinguished by this criterion.

The rootstock Controller 9 had similar vessel diameters as Controller 5 even the two rootstocks impart different vigor. Probably there is a genetic influence of their origin over this trait since these two rootstocks have the same interspecific origin *P. persica* x *P. salicina*. Among the HBOK series, which had the same parents ('Harrow Blood' and 'Okinawa') there was not a good association of vigor and the diameter of the largest xylem vessel.

3.2. Number of xylem vessels around the largest xylem vessel

As the xylem layers were narrower than the diameter of the view circle in the smaller diameter shoots, the numbers of vessels around the largest vessel were counted only on proleptic shoots with diameters of 3 and 4 mm and epicormic shoots of 5 and 6 mm. The analysis of variance of the number of xylem vessels around the largest xylem vessels showed an effect of rootstock, shoot diameter and interactions between rootstock and shoot diameter. For proleptic shoots the effects were significant at the 1% level of probability. For epicormic shoots the effect of rootstock and shoot diameter were significant at 1% but at 5% for the interactions between rootstock and shoot diameter (Table 5). The mean numbers of vessels around the largest vessel are presented in Table 6.

The evaluation of the average number of xylem vessels around the largest vessel showed a tendency for the less vigorous rootstocks to have more vessels. The presence of larger mean vessel diameters in more vigorous rootstocks (Tombesi et al., 2010, 2011) is related with a lower number of smaller vessels. This hypothesis was not confirmed by the 4 mm proleptic shoot evaluations, but

was relatively consistent in the other shoots evaluated. The highly vigorous Nemaguard could be distinguished from the less vigorous Controller 5 based on the 5 mm proleptic shoot evaluation but also based on the 5 and 6 mm epicormic shoot evaluations. The two interspecific *Prunus persica* x *Prunus salicina* rootstocks Controller 5 and Controller 9 were not considered similar according to this criterion, although Controller 9 was more similar to Controller 5 than to the other intermediate rootstocks.

When considering the HBOK series separately, there was no consistent association between less vigor and more vessels around the largest vessel in proleptic shoots, but this association was observed in epicormic shoots.

When applying the number of vessels around the larger vessel of epicormic shoots with 5 mm diameter as a selection criterion, the rootstocks could be selected as dwarf or semi-dwarf compared to Nemaguard according to the adopted selection intensity. Samples of the microscopic field views of epicormic shoots with 5 mm diameter are shown in Fig. 1. As shown in Table 7, when using a selection criterion equal to the number of vessels of Nemaguard plus 10% all dwarfing rootstocks except for Controller 9.5 would be selected as potentially dwarfing. By using a selection criterion of vessel numbers 20% greater than Nemaguard only the Controller 5 and 6 rootstocks would be selected. Using a criterion of 15% greater than Nemaguard, Controller 9 would be included, but not Controller 7 and 8, apparently reflecting the interspecific hybrid origin (*P. persica* x *P. salicina*) of Controller 9 compared to the intraspecific hybrid origin of Controller 7 and 8.

Even if not exact, the association among number of vessels around the largest vessel with the dwarfing ability of the rootstocks may be useful as pre-selection method, reducing the number of genotypes required to be evaluated in the further selection phases of a rootstock breeding program. This could significantly reduce the field space, labor, and consequently the costs of improving dwarfing peach rootstocks.

Ideally, pre-selection of rootstocks would be made in young seedlings. Shoots of young seedlings are probably more similar to epicormic shoots than to proleptic shoots, considering their vigor and juvenile growth stage. Based on these experiments,

Table 6

Average number of xylem vessels around the largest xylem vessel in proleptic and epicormic shoots according to rootstock and shoot diameter.

Rootstock	Proleptic		Epicormic	
	Shoot diameter		Shoot diameter	
	4 mm	5 mm	5 mm	6 mm
Nemaguard	12.88 ± 0.81 ^a	5.50 ± 0.27	5.25 ± 0.84	4.25 ± 0.62
Controller 9.5 (HBOK 50)	12.13 ± 0.74	8.25 ± 0.59	5.50 ± 0.42	5.13 ± 0.30
Controller 9 (P30-135)	8.63 ± 0.78	8.38 ± 0.60	6.25 ± 0.45	6.50 ± 0.42
Controller 8 (HBOK 10)	9.25 ± 0.73	8.13 ± 0.85	5.75 ± 0.37	6.00 ± 0.63
Controller 7 (HBOK 32)	12.13 ± 1.06	7.63 ± 1.05	6.00 ± 0.38	5.88 ± 0.40
Controller 6 (HBOK 27)	10.63 ± 0.94	7.38 ± 0.18	7.25 ± 0.56	6.25 ± 0.65
Controller 5 (K146-43)	12.38 ± 0.98	11.00 ± 0.65	10.13 ± 0.85	8.00 ± 0.57

^a μm ± S.E.

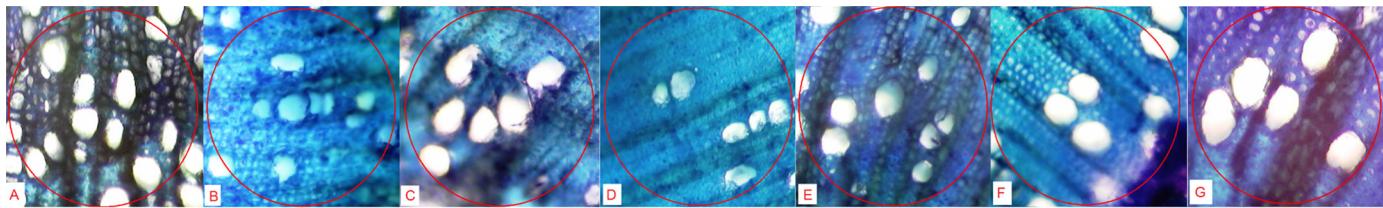


Fig. 1. Microscopic view fields of transverse sections of 5 mm diameter epicormic shoots [A–Controller 5 (K146-43), B–Controller 6 (HBOK 27), C–Controller 7 (HBOK 32), D–Controller 8 (HBOK 10), E–Controller 9 (P30-135), F–Controller 9.5 (HBOK 50), G–Nemaguard], evidencing the xylem vessels in a circle of 163.75 μm diameters.

Table 7
Rootstocks selected as dwarf according to the number of vessels around the largest vessel over the number of vessels of Nemaguard evaluated on 5 mm epicormic shoots.

Rootstock	Number	Vessels over Nemaguard		
		10% (>5.77)	15% (>6.03)	20% (>6.30)
Nemaguard	5.25 ± 0.84			
Controller 9.5 (HBOK 50)	5.50 ± 0.42	S ^a	S ^a	
Controller 9 (P30-135)	6.25 ± 0.45	S ^a		
Controller 8 (HBOK 10)	5.75 ± 0.37	S ^a		
Controller 7 (HBOK 32)	6.00 ± 0.38	S ^a		
Controller 6 (HBOK 27)	7.25 ± 0.56	S ^a	S ^a	S ^a
Controller 5 (K146-43)	10.13 ± 0.85	S ^a	S ^a	S ^a

^a S: selected.

pre-selection should be possible after choosing a specific shoot diameter, 5 or 6 mm and then visualizing the largest vessels in a microscopic view of a cross section of a stem and counting the number of vessels around the largest vessel in a circle of a specific diameter. The plants with a number higher than the number of vessels in Nemaguard would be selected if selecting for size-controlling rootstocks is an objective of the program. The percentage difference over the number of vessels in the tissue of Nemaguard would depend on the intensity of the dwarfism desired.

In the future, we plan to conduct a validation study of this procedure in a new population of peach rootstock seedlings that is segregating for the dwarfing characteristic.

Acknowledgements

We thank Foundation Plant Services at the University of California, Davis for the plant samples, and CNPq - Conselho nacional de Desenvolvimento Científico e Tecnológico, Brazil for the scholarship supported to the first author.

References

- Atkinson, C., Else, M.A., 2005. Enhancing harvest index in temperate fruit tree crops through the use of dwarfing rootstocks. In: Proceedings of the International Workshop on Cocoa Breeding for Improved Production Systems, Accra, Ghana, October 19–21, 2003, pp. 118–131.
- Barrientos-Priego, A.F., Sanchez-Colín, S., Aguilar-Melchor, J.J., López-Jimenez, A., 1992. Selection of Avocado Dwarfing Rootstocks. In: Proceedings of the Second World Avocado Congress, pp. 515–520.
- Blanco, A., Mata, A.P., Lasaosa, A., Val, J., 2008. The P16 rootstock inhibits the growth but enhances the fruit quality of 'Jonagored' apples when grown under warm summer conditions. *Span. J. Agric. Res.* 6, 412–421.
- Celton, J.M., Tustin, D.S., Chagné, D., Gardiner, S.E., 2009. Construction of a dense genetic linkage map for apple rootstocks using SSRs developed from Malus ESTs and *Pyrus* genomic sequences. *Tree Genet. Genomes* 5, 93–107.
- Charlot, G., Edin, M., Flochay, F., Soing, P., Boland, C., 2005. Tabel Edabriz: a dwarf rootstock for intensive cherry orchards. *Acta Hort.* 667, 217–221.
- Cheng, F.S.H., Roose, M.L., 1995. Origin and inheritance of dwarfing by the citrus rootstock *Poncirus trifoliata* 'Flying-Dragon'. *J. Amer. Soc. Hort. Sci.* 120, 286–291.
- 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 conductance. *Plant Cell Environ.* 25, 17–28.
- Cousins, P., 2005. Rootstock breeding: an analysis of intractability. *Hort. Sci.* 40, 1945–1946.
- Czynczyc, A., Bielicki, P., 2012. Eleven year evaluation of American (Geneva) and polish rootstocks with 'Golden Delicious Reinders' apple in Poland. *J. Fruit Ornam. Plant Res.* 20, 11–21.
- DeJong, T.M., Grace, L., Almehdi, A., Johnson, R.S., Day, K.R., 2013. Performance and physiology of the Controller™ series of peach rootstocks. *Acta Hort.*, In press.
- DeJong, T.M., Johnson, R.S., Day, K.R., 2011. Controller 5, Controller 9 and Hiawatha peach rootstocks: their performance and physiology. *Acta Hort.* 903, 221–228.
- DeJong, T.M., Johnson, R.S., Doyle, J.F., Basile, B., Marsal, J., Ramming, D., Bryla, D., 2004. Growth, yield and physiological behavior of size-controlling peach rootstocks developed in California. *Acta Hortic.* 658, 449–455.
- Felipe, A.J., 2009. 'Greepac', a new peach hybrid rootstock adapted to mediterranean conditions. *Hort. Sci.* 44, 1456–1457.
- Glenn, D.M., Scorza, R., 1992. Reciprocal grafts of standard and dwarf peach alter dry-matter partitioning and root physiology. *Hort. Sci.* 27, 241–243.
- Gradziel, T.M., Beres, W., 1993. Semidwarf growth habit in clingstone peach with desirable tree and fruit qualities. *Hort. Sci.* 28, 1045–1047.
- Gruppe, W., 1985. An overview of the cherry rootstock breeding program at Giessen 1965–1984. *Acta Hortic.* 169, 189–198.
- Hansche, P.E., 1989. Three brachytic dwarf peach cultivars: Valley Gem, Valley Red, and Valley Sun. *Hort. Sci.* 24, 707–709.
- Hu, D., Scorza, R., 2009. Analysis of the 'A72' peach tree growth habit and its inheritance in progeny obtained from crosses of 'A72' with columnar peach trees. *J. Amer. Soc. Hort. Sci.* 134, 236–243.
- Hussein, I.A., McFarland, M.J., 1994. Rootstock-induced differences in sap flow of 'Granny Smith' apple. *Hort. Sci.* 29, 1120–1123.
- Ingels, C., Jeisel, P.M., Unruh, C.L., 2002. *Fruit Trees: Training and Pruning Deciduous Trees*. Publication 8057 ANR Communication University of California.
- Jänes, H., Pae, A., 2003. First results of a dwarfing plum rootstocks trial. *Agron. Res.* 1, 37–44.
- Jensen, P.J., Makalowska, I., Altman, N., Fazio, G., Praul, C., Maximova, S.N., Crassweller, R.M., Travis, J.W., McNellis, T.W., 2010. Rootstock-regulated gene expression patterns in apple tree scions. *Tree Genet. Genomes* 6, 57–72.
- Johnson, W.C., Aldwinckle, H.S., Cummins, J.N., Forsline, P.L., Holleran, H., Norelli, T.J., Robinson, L.T.L., 2001. The new USDA-ARS/Cornell University apple rootstock breeding and evaluation program. *Acta Hort.* 557, 35–40.
- Laurens, F., 1998. Review of the current apple breeding programmes in the world: objectives for scion cultivar improvement. *Acta Hort.* 484, 163–170.
- Legal, P., Pinochet, J., Moreno, M.A., Martinez, J.J., 2012. *Prunus* hybrid rootstocks for flat peach. *Sci. Agric.* 69, 13–18.
- Looney, N.E., Lane, W.D., 1984. Spur-type growth mutants of McIntosh apple: a review of their genetics, physiology and field performance. *Acta Hort.* 146, 1984.
- Moghadam, E.G., Khalighi, A., 2007. Relationship between vigor of Iranian *Prunus mahaleb* L. selected dwarf rootstocks and some morphological characters. *Sci. Hort.* 111, 209–212.
- Moreno, M.A., Cambra, R., 2004. 'Adarcias': an almond x peach hybrid rootstock. *Hort. Sci.* 29, 925.
- Moura, C.F.H., Alves, R.E., Innecco, R., Filgueiras, H.A.C., Mosca, J.L., Pinto, S.A.A., 2001. Physical characteristics of cashew apples for fresh fruit. *Rev. Bras. Frutic.* 23, 537–540.
- Muleo, R., Intrieri, M.C., Iacona, C., Maggi, E., Loretto, F., 2011. Peach rootstocks inducing different vigour reflect genomic, physiological and morphological diversity in roots. *Acta Hort.* 903, 113–120.
- O'Brien, T.P., Feder, N., McCully, M.E., 1964. Polychromatic staining of plant cell walls by Toluidine Blue O. *Protoplasma* 59, 368–373.
- Piestrzeniewicz, C., Sadowski, A., Dziuban, R., Odziemkowski, S., Wrona, D., 2013. Results of ten-year rootstock testing with apple cultivar Rubin on fertile soil. *Hort. Sci.* 40, 31–36.

- Pinochet, J., 2009. 'Felinem', 'Garnem' and 'Monegro', almond x peach hybrid rootstocks. *Hort. Sci.* 44, 196–197.
- Reighard, G.L., Loretto, F., 2008. Rootstock development. In: Layne, D.R., Bassi, D. (Eds.), *The Peach: Botany, Production and Uses*. CABI, Oxfordshire, pp. 193–220.
- Rusholme Pilcher, R.L., Celton, J.M., Gardiner, S.E., Tustin, D.S., 2008. Genetic markers linked to the dwarfing trait of apple rootstock 'Malling 9'. *J. Amer. Soc. Hort. Sci.* 133, 100–106.
- Salesses, G., Dirlewanger, E., Bonnet, A., Lecouls, A.C., Esmenjaud, D., 1998. Interspecific hybridization and rootstock breeding for peach. *Acta Hort.* 465, 209–217.
- Scorza, R., Bassi, D., Liverani, A., 2002. Genetic interactions of pillar (columnar), compact, and dwarf peach tree genotypes. *J. Amer. Soc. Hort. Sci.* 127, 254–261.
- Tanasescu, N., Mladin, G.H., Sumedrea, D., Marin, F.C., Popescu, C., 2013. Preliminary results on growth and fruiting of trees, grafted on the Romanian vegetative rootstock 'IP-C-7' and German vegetative rootstock 'Gisela 5', in an intensive sweet cherry orchard. *Acta Hort.* 981, 361–366.
- Tomala, K., Slowinska, I., 2006. The effect of rootstocks on the physiological status and storage ability of 'Elise' apples. *Latv. J. Agron.* 9, 162–166.
- Tombesi, S., Almehdi, A., DeJong, T.M., 2011. Phenotyping vigour control capacity of new peach rootstocks by xylem vessel analysis. *Sci. Hort.* 127, 353–357.
- Tombesi, S., Johnson, R.S., Day, K.R., DeJong, T.M., 2010. Relationships between xylem vessel characteristics, calculated axial hydraulic conductance and size-controlling capacity of peach rootstocks. *Ann. Bot.* 105, 327–331.
- Wang, C., Tian, Y., Buck, E.J., Gardiner, S.E., Dai, H., Jia, Y., 2011. Genetic mapping of *PcDw* determining pear dwarf trait. *J. Amer. Soc. Hort. Sci.* 136, 48–53.
- Ystaas, J., Frøynes, O., 1996. Evaluation of size-controlling rootstocks for 'Stella' and 'Ulster' sweet cherries. *Acta Hort.* 410, 197–204.