Investigation of stem anatomy in relation to hydraulic conductance, vegetative growth and yielding potential of ‘Summit’ cherry trees grafted on different rootstock candidates

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ABSTRACT

Severe climate alterations that seriously challenge fruit production, combined with the demand for healthy, pesticide-free fruits, continuously direct rootstock/cultivar selection towards high adaptable varieties breeding. This study aimed to investigate the rootstocks' influence on the performance of grafted ‘Summit’ cherry trees, including potentially dwarfing *Prunus cerasus*, *Prunus fruticosa* and *Prunus mahaleb* rootstock candidates. Anatomical properties of rootstock and scion stems were investigated to determine variation among different rootstocks and scion-rootstock combinations and to establish the link between trunk hydraulic conductivity, effective tree crown volume and yielding potential. Cross-section anatomical characteristics varied significantly both in rootstock and scion stems, indicating a clear influence of rootstock genotype on grafted sweet cherry trees. It was observed that all investigated cherry rootstock candidates belong to the low-vigorous rootstocks, based on the estimated effective crown volume of grafted trees compared to ‘Gisela 5’, with values ranging from 0.86 to 2.97 m³ in the fifth year after planting. Results showed a statistically significant positive correlation between trunk hydraulic conductivity, effective tree crown volume and yielding potential, with correlation coefficients up to 0.96. Significantly higher effective crown volume and trunk hydraulic conductance of trees grafted on *P. cerasus* compared to the trees on control, as well as highest yielding potential, showed better adaptation of these rootstock candidates in the trial without irrigation implemented. It was found that PC_05_04 rootstock candidate could be considered as the most appropriate choice when raising the high-density sweet cherry plantations, due to assessed parameters of vegetative and generative growth.

Keywords: crown volume, *Prunus*, rootstock selection, semi-arid conditions, size-controlling, sweet cherry

Abbreviations: CSA, cross-section area; k_h , the theoretical axial hydraulic conductance; $k_{h(T)}$, trunk theoretical axial hydraulic conductance; SD, stem diameter; SWA, secondary wood area; SW/SC ratio, secondary wood/secondary cortex ratio; V_e , the effective tree crown volume; VF, vessel frequency; VLA, vessel lumen area; % P, percentage of pith area per stem cross-section; % PD, percentage of periderm area per stem cross-section; % R, percentage of total ray area per stem cross-section; % R_{SW} , percentage of total ray area relative to secondary wood area; % SC, percentage of secondary cortex

INTRODUCTION

Growing demand for healthy, pesticide-free fruits, on the one side, and inevitable climate change, on the other side, impose the need for intensive, continuous

research in the field of rootstock/cultivar selection. To the present day, the significance of adequate rootstock selection for the fruit plantation has been addressed

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area per stem cross-section; % SW, percentage of secondary wood area per stem cross-section; % V, percentage of total vessel area per stem cross-section; % V_{SW} , percentage of total vessel area relative to secondary wood area; % X, percentage of xylem area per stem cross-section; % X_{SW} , percentage of xylem area relative to secondary wood area.

in several research papers (Beckman and Lang, 2002; Webster, 2002b; Nimbolkar et al., 2016; Hrotkó and Rozpara, 2017). Identification of genetic material and understanding of plant properties responsible for the fruit production improvement, as well as the proper selection of rootstock that reduce vegetative growth and increase carbon allocation to reproduction, are considered of great importance (Peschiutta et al., 2013). Rootstocks enrich the cultivar with numerous traits, such as good anchorage, good radial and axial hydraulic conductivity, water use efficiency, soil's pest and disease resistance, improved tolerance to drought and high soil salinity (Gainza et al., 2015a; Ljubojević et al., 2018). In these efforts, new generations of low-vigour-inducing rootstocks, which are being constantly improved through various breeding programmes, represent the key factor. Along with the vigour control, reasons for dwarfing rootstocks utilisation are found in their capability to favourably affect fruit precociousness and productivity rate, despite the need for crop loads to leaf area balancing (Lang, 2000; Whiting et al., 2005). Although the wide range of rootstocks is proven to be size-controlling, the exact mechanism of such control is still unresolved. During the last decades, several studies were conducted to explain how rootstocks affect scion growth and cropping in fruit species (Atkinson and Else, 2001; Webster, 2002a; Gjamovski and Kiprijanovski, 2011; Marra et al., 2013; Tworowski and Fazio, 2016; Yahmed et al., 2016; Bujdosó et al., 2019).

The capacity to transport water throughout a plant can be determined by calculating its hydraulic conductivity, which was proved to be related to the overall tree growth potential (Solari et al., 2006b). In their study on peach trees, Solari et al. (2006a) have found that water status influenced vegetative growth of scions on different rootstocks by directly affecting shoot growth potential and had a significant effect on leaf conductance regulation of gas exchange related to the shoot carbon gain. Tombesi et al. (2010, 2011) concluded that phenotypic differences in xylem anatomical traits, such as dimensions and density of vessels in shoots, trunks and roots of peach trees influence hydraulic conductance capacity. A similar observation was made in the case of sweet cherry trees (Olmstead et al., 2006a; Gonçalves et al., 2007; Zorić et al., 2012) implying that parameters such as vessel frequency (VF), vessel lumen area (VLA), percentage of vessels on wood cross-section and xylem/phloem thickness ratio might be used in the prediction of tree vigour in cherry rootstocks. Jupa et al. (2021) have found larger vessels in rootstock/scion combinations of higher vigour and a positive correlation between mean vessel lumen diameter in roots and annual shoot length, showing that xylem transport efficiency of rootstocks influences the growth vigour

of both apple and pear trees. Cohen and Naor (2002) reported differences regarding water use of apple trees on three rootstocks with different degrees of vigour, while significant variations of xylem vessel features in the leaf of apple grafted onto different rootstocks were found by Hayat et al. (2020).

In addition to the rootstock selection, the selection of scion represents an important part of successful fruit production. If the rootstock is chosen for its ability to grow strong, persistent root systems in the particular soil, scions are selected primarily for the quality and quantity of their fruits (Cohen and Naor, 2002). The effect of rootstock selection on sweet cherry yield and fruit quality was investigated through many studies (Santos et al., 2006; Wociór, 2008; López-Ortega et al., 2016; Dziedzic et al., 2017; Pal et al., 2017; Morandi et al., 2019). Concerning the changing climate that seriously affects fruit growth and yields, rootstocks investigation must be focused on vigour-controlling genotypes with high adaptability to soil water limitations, considering specific pedo-climatic conditions of the area (Ljubojević et al., 2017, 2021). Hajagos and Végvári (2013) stressed the growing interest of fruit producers in rootstock-scion combinations characterised by high water efficiency, relative to the growing number of water-related problems widespread. The study of various types of plant tolerance mechanisms to unfavourable climate conditions, which occurs at different levels of life organisation (molecule, cell, organ and plant), can provide important information for plant breeding purposes (Monneveux and Belhassen, 1996). Therefore, there is an urgent need for experimental trials in conditions without irrigation and with minimal management practices, for examining intrinsic rootstock influences on grafted tree performance. The University of Novi Sad has a rich collection of sour cherry material, collected from the Balkan Peninsula as one of the most valuable centres of genetic diversity (Barać et al., 2014). The capability of autochthonous cherry germplasm to overcome unpredictable environmental circumstances was tested through the use of local *Prunus cerasus* and *Prunus fruticosa* genotypes as potentially dwarfing rootstocks in the previous studies on the stated germplasm (Ljubojević et al., 2013, 2017 and 2018). Thus, there was the necessity to broaden the research and amend the number of surveyed autochthonous genotypes to encompass those already investigated, as well as to investigate and confirm how cherry rootstock candidates affect vegetative and generative growth of grafted 'Summit' cherry trees.

This study aimed to: (1) determine a variation in the rootstock candidates' as well as 'Summit' variety scion stem anatomical properties concerning the effective crown volume of grafted trees; (2) establish the link

between estimated scion crown volume on potentially dwarfing rootstocks and calculated trunk hydraulic conductance; and (3) assess the yielding potential of 'Summit' cherry trees in correlation to the effective tree crown volume and hydraulic conductivity.

MATERIALS AND METHODS

Plant material and growth conditions

The trial was carried out in Rimski Šančevi, at the experimental farm of the Faculty of Agriculture, University of Novi Sad, in northern Serbia (45°20' N and 19°50' E, altitude 80 m above sea level). The climate of this area is temperate continental, with extremely warm summers and cold winters. During the experimental years 2017–2020, mean annual temperatures were 12.6 °C, 13.2 °C, 13.4 °C and 12.8 °C, with annual precipitation sums of 513 mm, 718 mm, 632 mm and 733 mm, respectively. Seven ungrafted rootstocks were investigated during the 4 years, including five cheery rootstocks belonging to *P. fruticosa* (Pall.) and *P. cerasus* (L.) ecovar. 'Oblačinska', one 'Mahaleb' (*Prunus mahaleb*) genotype PM_09_01 and 'Gisela 5' were used as a control rootstock (Table 1). Concomitantly, the investigation included mid- to late-maturing sweet cherry cultivar Summit grafted on the same rootstocks. *P. cerasus* genotypes were PC_05_04 and PC_02_01/4, while European ground cherry (*P. fruticosa*) genotypes were PF_02_16, PF_01_01 and PF_04_09. Trees were planted in autumn 2015, with a planting distance 4 m × 2 m. All investigated plants were equally managed, in conditions without irrigation and with minimal herbicide usage. The trial was located on flat terrain exposed to the cold winds, without a frost protection strategy implemented. The trees were not pruned during the experiment.

Stem anatomical measurements

One year after orchard establishment, in 2016, an initial anatomical characterisation of rootstocks and scion stems was conducted. Both ungrafted rootstock mother trees, as well as grafted 'Summit' trees, were cut back to 10 cm to obtain appropriate cross-sections. Anatomical measurements were performed on seven ungrafted rootstocks and the same seven rootstocks – 'Summit' scion combinations. During the winter dormancy period (November 2016), 1-year-old main stems were collected

from five replicate plants per rootstock/rootstock-scion combination (five samples per variety). To preserve the structure of plant tissues, samples were fixed in 60% ethanol, with the addition of 10% of glycerin. Before cross-section preparation, plant material was immersed in 50% glacial acetic acid for 1–2 days, to soften stems and facilitate sectioning. Cross-sections were obtained using a hand microtome and examined under a Motic Digital BA310 biological light microscope with a built-in digital camera. Images of cross-sections were taken at 40× and 400× magnifications and measurements were performed using the image analysing system Motic Images Plus 2.0; Motic China Group Co., Ltd. Cross-sections were obtained from the third to fifth internode region (approximately the middle) of 1-year-old stems, 1.5–6.5 mm in diameter, as described by Ljubojević et al. (2021). On each stem cross-section, anatomical characteristics were investigated on four radial segments, 90° apart. Anatomical analyses included both total cross-section and secondary wood measurements. Pith radius, secondary wood outer radius, secondary cortex outer radius and periderm outer radius, which is equal to the stem radius, were measured to calculate stem diameter (SD, mm), cross-section area (CSA, mm²), areas and the percentage of the pith (% P), secondary wood (% SW), secondary cortex (% SC) and periderm (% PD), relative to the total CSA. Stem cross-section was considered a regular circle as indicated by Hajagos and Végvári (2013). Secondary wood/secondary cortex ratio (SW/SC ratio) was calculated for all investigated stems, by dividing the secondary wood area (SWA) with the area of the secondary cortex. At higher magnification, 1–2 visual fields were selected for measurement on each radial segment, depending on the stem thickness. The number and lumen areas of all vessels captured in the field of vision were measured, to calculate average VLA (μm²) and VF (number of vessels per mm²). Total vessel and ray areas, as well as xylem area per each visual field, were measured and calculated and their percentages relative to CSA and SWA were determined. For further hydraulic conductance (k_h) calculation, vessel diameters (VD, μm) were determined from the VLA values [$VLA = (VD/2)^2\pi$], by assuming the vessels were circular. Based on their lumen area, vessels were classified into three classes: I – VLA <300 μm²; II – VLA in the range 300–700 μm²; and III – VLA >700 μm². The number of vessels per class was expressed as a percentage of the total number of vessels (100%).

Trunk hydraulic conductivity calculation ($k_{h(T)}$)

During the 4 consecutive years, trunk cross-section measurements of grafted sweet cherry trees were conducted. Small segments of the trunk were cut out carefully using a wood chisel, 10 cm above the graft union. Each year, samples were taken out from the different radial segments of the trunk, so as not to disturb the tree growth in the following years as a result of harming the plant tissues. Sampling was carried out in

Table 1. List of investigated *Prunus* sp. genotypes.

Accession name	Species, interspecific hybrid
PC_02_01/4	<i>Prunus cerasus</i> ecovar. Oblačinska
PC_05_04	<i>Prunus cerasus</i> ecovar. Oblačinska
PF_01_01	<i>Prunus fruticosa</i>
PF_02_16	<i>Prunus fruticosa</i>
PF_04_09	<i>Prunus fruticosa</i>
PM_09_01	<i>Prunus mahaleb</i>
Gisela 5	<i>Prunus cerasus</i> × <i>Prunus canescens</i>

the winter dormancy period (December), on five replicate plants per scion-rootstock combination. Obtained trunk segments were preliminarily screened for VLAs and frequency, to ensure the accuracy of the determined vessel size ranges and calculations based on entire stem cross-sections sampled in 2016. Trunk diameter 10 cm above grafting point (mm) and trunk CSA (mm²) were measured and calculated. Knowing those values, trunk SWA (mm²) was calculated by measuring the periderm and secondary wood ring thickness and calculating the secondary wood inner and outer radius.

Based on the initial anatomical characterisation in the first year after tree planting, the theoretical axial hydraulic conductance (k_h) per mm² of the stem was determined. The theoretical axial hydraulic conductance of stems was calculated according to the expression given by Tyree and Ewers (1991), based on Hagen-Poiseuille's law:

$$k_h = \frac{\pi \cdot \rho}{128 \cdot \eta} \sum_{i=1}^n d_i^4$$

where d was the diameter of the vessels in meters, ρ was the fluid density (assumed to be 10³ kg · m⁻³ for water at 20 °C) and η was the viscosity (assumed to be 1.002 × 10⁻⁹ · s for water at 20°C).

Total trunk theoretical axial hydraulic conductance ($k_{h(T)}$) was calculated from the stem k_h per mm² and trunk SWA values. Because trunk tissues represent the last barrier to the plant water transport from the roots to the plant's upper parts, trunk k_h was obtained rather than rootstock k_h .

Tree crown volume measurements

Between 2017 and 2020, the investigated plants of all seven scion-rootstock combinations were measured to estimate the effective tree crown volume (V_e) for each tree. Crown height (cm) and crown diameter (cm) measurements were used in the tree crown volume calculation, according to the formula given by Changok (2007):

$$CD^2 \times CH \times \text{crown shape index} = \text{tree crown volume}$$

where CD was crown diameter and CH was crown height. A crown shape index was assigned to every plant as described by the same author.

Yielding potential estimation

In the period 2019–2021, during the flowering time, the total number of flowers per tree was determined. The manual counting was carried out on three plants per scion-rootstock combination and the average number per tree was calculated. The year 2018 was excluded from the analysis, due to the very scarce number of flowers per tree (the very first year of fruit occurrence).

Data analysis

The obtained data were statistically processed by analysis of variance and correlation analysis, using STATISTICA 14 software (Tibco, USA). The significance of differences between mean values was determined using Duncan's multiple range tests with the confidence of $p \leq 0.05$.

RESULTS

Cross-section anatomical characteristics of rootstock stems

Among the investigated ungrafted rootstocks, significant differences in rootstock stem anatomical properties were observed (Table 2). Regarding SD and CSA, significant variation was found between and within species. Among species, PM_09_01 and the control rootstock 'Gisela 5' had the greatest SD, while *P. cerasus* genotypes had significantly thicker stems in comparison with *P. fruticosa* genotypes. SD in *P. cerasus* genotypes was within the range of 2.65–2.88 mm, while rootstock stems of *P. fruticosa* genotypes varied from 1.61 mm to 2.12 mm. The percentage of secondary wood was lower than % SC in all *P. cerasus* and *P. fruticosa* genotypes and did not differ significantly among the two species. On contrary, in both PM_09_01 and 'Gisela 5', % SW was higher than % SC, reaching 44.94 and 43.77%,

Table 2. Rootstock stem anatomical characteristics for seven investigated candidate genotypes.

Genotype	SD (mm)	CSA (mm ²)	% P	% SW	% SC	% PD	SW/SC ratio	% V	% R	% X
PC_02_01/4	2.65 d	5.57 d	15.78 a	23.89 e	51.75 a	8.58 d	0.47 e	3.91 de	2.45 d	17.53 d
PC_05_04	2.88 c	6.57 c	9.72 c	37.87 b	42.83 bc	9.59 c	0.90 c	4.29 cd	4.09 c	29.49 a
PF_01_01	2.11 e	3.50 e	9.53 c	27.71 d	51.20 a	11.56 ab	0.55 e	4.68 c	2.24 d	20.79 c
PF_02_16	1.61 f	2.06 f	6.39 e	37.05 b	44.19 b	12.37 a	0.85 c	4.01 cde	2.18 d	30.86 a
PF_04_09	2.12 e	3.56 e	11.40 b	32.03 c	45.27 b	11.31 b	0.71 d	3.52 e	2.75 d	25.76 b
PM_09_01	3.92 a	12.09 a	8.93 cd	44.94 a	38.44 d	7.69 e	1.19 a	8.52 a	6.75 a	29.67 a
Gisela 5	3.12 b	7.67 b	7.91 d	43.77 a	41.09 c	7.23 e	1.08 b	7.64 b	5.92 b	30.21 a
Mean	2.63	5.86	9.95	35.32	44.97	9.76	0.82	5.22	3.77	26.33

Mean values designated with the same letter were not significantly different according to Duncan's test ($p \leq 0.05$).

CSA, cross-section area (mm²); % P, percentage of pith area per stem cross-section; % PD, percentage of periderm area per stem cross-section; % SW, percentage of SWA per stem cross-section; SWA, secondary wood area; % SC, percentage of secondary cortex area per stem cross-section; SD, stem diameter (mm); SW/SC ratio, secondary wood/secondary cortex ratio; % V, percentage of total vessel area per stem cross-section; % R, percentage of total ray area per stem cross-section; % X, percentage of xylem area per stem cross-section.

respectively. Such tissue distribution was reflected in a significantly lower SW/SC ratio in analysed sour and ground cherry genotypes, in comparison to 'Gisela 5' and PM_09_01 that reached values of 1.08 and 1.19, respectively. *P. fruticosa* genotypes showed greater % PD than *P. cerasus* genotypes, with the highest value of 12.37% in PF_02_16. Total vessel area percentages (% V) were significantly higher in rootstock stems of PM_09_01 and the control than in *P. cerasus* and *P. fruticosa* genotypes, whose % V varied from 3.52% to 4.68%. The CSA was significantly positively correlated with % V ($r = 0.85$, as shown in Table S1 in Supplementary Materials). Ray area percentages (% R) were also higher in PM_09_01 and 'Gisela 5' compared to other genotypes. Xylem portions (% X) varied between and within species, ranging from 17.53% to 29.49% in *P. cerasus*, and 20.79–30.86% in *P. fruticosa* genotypes.

Cross-section anatomical characteristics of scion stems

Scion stems of a variety 'Summit' grafted on different rootstock candidates showed significant differences regarding examined anatomical features (Table 3). SD varied between trees grafted on rootstock candidates belonging to different species, with higher average values when grafted on *P. cerasus* (reaching up to 6.28 mm). Concerning % P, significant variation was found between scion stems on *P. cerasus* and *P. fruticosa* rootstock candidates, with higher pith portions of 14.73–16.92% in scion stems on *P. cerasus*. In general, % SW and % SC were higher on *P. fruticosa* than on *P. cerasus* rootstock candidates (reaching average values of 34.3 and 47.79%, respectively), due to notably higher percentage of pith area in *P. cerasus*. For all scion-rootstock combinations, SW/SC ratio has shown that secondary cortex portions were higher than portions of secondary wood in scion stems, with 13% difference on average. CSA was significantly negatively correlated with % SC in scion stems ($r = -0.93$; Table S2

in Supplementary Materials). No rootstock species-related pattern was observed concerning % V, while regarding % R the highest values were found in scion stems of trees grafted on *P. fruticosa* (7.54–8.93%). A significant positive correlation of CSA was found with the % V ($r = 0.92$; Table S2 in Supplementary Materials). Both % R and % X was significantly higher in scion stems in comparison with rootstock stems. Scion stems on all investigated rootstock candidates had a lower % X, when compared to the control. In general, scion stems were approximately 2-fold thicker than rootstock stems. According to the mean values, portions of the secondary wood, as well as the secondary cortex, were similar in both rootstock and scion stems, accompanied by higher % P and lower % PD values in scions.

Secondary wood features in rootstock and scion stems

Within the secondary wood ring, differences between genotypes were determined, both for the rootstock plants and grafted 'Summit' trees (Tables 4 and 5, Figure 1). SWA varied from 0.78 mm² to 5.42 mm² in rootstock stems; in scion stems values fell within a range of 6.48–10.66 mm². Regarding rootstock stem analysis, SWA followed CSA values, resulting in the highest SWA observed in PM_09_01. Rootstock stems of *P. cerasus* genotypes had higher SWA than *P. fruticosa* genotypes, with average values of 1.93 and 0.97 mm², respectively. The percentage of vessels in secondary wood (% V_{sw}) differ significantly between *P. cerasus* and *P. fruticosa* genotypes as well as within species, while the highest % V_{sw} was found in *P. mahaleb* genotype and the control (up to 18.99% in PM_09_01). Genotypes belonging to *P. cerasus* formed one homogenous group with ray portions of >10%, while the lowest values were found in three *P. fruticosa* genotypes (ranging from 5.89% to 8.54%). Consequently, the average percentage of xylem in secondary wood (% X_{sw}) was higher in *P. fruticosa* genotypes compared to *P. cerasus* and *P. mahaleb*

Table 3. 'Summit' scion stem anatomical characteristics on different rootstock candidates and 'Gisela 5' control rootstock.

Summit/Rootstock candidate	SD (mm)	CSA (mm ²)	% P	% SW	% SC	% PD	SW/SC ratio	% V	% R	% X
PC_02_01/4	6.28 a	31.31 a	16.92 a	33.58 abc	44.21 d	5.30 c	0.76 ab	5.47 a	6.95 bc	21.15 b
PC_05_04	5.75 bc	26.16 bc	14.73 b	31.05 c	47.64 bc	6.58 b	0.66 c	4.91 abc	6.77 bc	19.37 b
PF_01_01	5.02 d	19.91 d	11.15 cd	32.46 bc	49.82 a	6.58 b	0.66 c	4.17 c	7.81 b	20.48 b
PF_02_16	5.46 c	23.78 c	10.42 d	34.40 ab	48.87 ab	6.30 b	0.71 bc	4.55 bc	8.93 a	20.92 b
PF_04_09	5.90 abc	27.48 abc	12.63 c	36.14 a	44.68 d	6.55 b	0.81 a	5.49 a	7.54 b	23.11 a
PM_09_01	5.87 abc	27.99 ab	15.06 b	32.25 bc	46.12 cd	6.57 b	0.71 bc	5.17 ab	6.23 c	20.84 b
Gisela 5	5.97 ab	28.24 ab	11.10 cd	36.01 a	45.37 d	7.52 a	0.80 a	4.99 abc	7.77 b	23.26 a
Mean	5.75	26.41	13.14	33.70	46.67	6.49	0.73	4.96	7.43	21.31

Mean values designated with the same letter were not significantly different according to Duncan's test ($p \leq 0.05$).

CSA, cross-section area (mm²); % P, percentage of pith area per stem cross-section; % PD, percentage of periderm area per stem cross-section; % SW, percentage of SWA per stem cross-section; SWA, secondary wood area; % SC, percentage of secondary cortex area per stem cross-section; SD, stem diameter (mm); SW/SC ratio, secondary wood/secondary cortex ratio; % V, percentage of total vessel area per stem cross-section; % R, percentage of total ray area per stem cross-section; % X, percentage of xylem area per stem cross-section.

Table 4. Secondary wood anatomical properties in rootstock stems.

Genotype	SWA (mm ²)	% V _{sw}	% R _{sw}	% X _{sw}	VLA (μm ²)	VF (N · mm ⁻²)
PC_02_01/4	1.33 d	16.26 b	10.27 c	73.46 d	264.65 c	614.56 b
PC_05_04	2.54 c	11.68 c	10.74 c	77.58 c	332.20 b	355.40 d
PF_01_01	0.97 ef	16.85 b	8.28 d	74.87 d	241.58 c	708.91 a
PF_02_16	0.78 f	10.77 c	5.89 e	83.34 a	211.81 d	520.20 c
PF_04_09	1.15 de	11.03 c	8.54 d	80.43 b	215.48 d	511.40 c
PM_09_01	5.42 a	18.99 a	15.11 a	65.90 f	492.45 a	387.79 d
Gisela 5	3.39 b	17.59 ab	13.55 b	68.86 e	334.65 b	556.68 bc
Mean	2.22	14.74	10.34	74.92	298.97	522.14

Mean values designated with the same letter were not significantly different according to Duncan's test ($p \leq 0.05$).

SWA, secondary wood area (mm²); % V_{sw}, percentage of total vessel area relative to SWA; % R_{sw}, percentage of total ray area relative to SWA; % X_{sw}, percentage of xylem area relative to SWA; VLA, vessel lumen area (μm²); VF, vessel frequency (number of vessels per mm²).

Table 5. Secondary wood anatomical properties in scion stems.

Summit/Rootstock candidate	SWA (mm ²)	% V _{sw}	% R _{sw}	% X _{sw}	VLA (μm ²)	VF (N · mm ⁻²)
PC_02_01/4	10.66 a	16.18 a	20.67 cd	63.15 abc	368.44 a	456.36 b
PC_05_04	8.15 bc	15.71 a	21.95 bc	62.34 bc	390.55 a	436.23 b
PF_01_01	6.48 c	12.77 c	24.17 ab	63.06 abc	232.84 c	545.37 a
PF_02_16	8.30 bc	13.19 c	26.00 a	60.80 c	248.22 c	549.14 a
PF_04_09	9.94 ab	15.17 ab	20.91 cd	63.93 abc	292.43 b	529.33 a
PM_09_01	9.74 ab	15.41 ab	18.86 d	65.73 a	370.34 a	445.66 b
Gisela 5	10.28 ab	13.92 bc	21.61 bcd	64.47 ab	304.73 b	471.77 b
Mean	9.08	14.62	22.03	63.35	315.36	490.55

Mean values designated with the same letter were not significantly different according to Duncan's test ($p \leq 0.05$).

SWA, secondary wood area (mm²); % V_{sw}, percentage of total vessel area relative to the SWA; % R_{sw}, percentage of total ray area relative to the SWA; % X_{sw}, percentage of xylem area relative to SWA; VLA, vessel lumen area (μm²); VF, vessel frequency (number of vessels per mm²).

rootstock candidates, as well as when compared to control.

Concerning investigated scion-rootstock combinations, maximal % V_{sw} was achieved in trees grafted on *P. cerasus* rootstock candidates (15.95%, on average while the average % V_{sw} in scion stems on *P. fruticosa* was lowest (13.71%). The percentage of rays in secondary wood was approximately 2-fold higher in scion stems compared to rootstock stems, reaching up to the average value of 22.03%. Such partitioning resulted in the lower % X_{sw} in scion stems that accounted for about 63.35% of total SWA, on average.

Average VLAs in rootstock and scion stems significantly varied between and within species. In rootstocks, VLA was significantly positively correlated with stem CSA ($r = 0.98$) and %V ($r = 0.86$; Table S1 in Supplementary Materials). Generally, in *P. cerasus* and *P. fruticosa* genotypes, lower VLA values were found compared to *P. mahaleb* genotype and the control. Between species, VLA in *P. cerasus* was higher than in *P. fruticosa* genotypes, with variation from 264.65 μm² to 332.20 μm² in the former and from 211.81 μm² to 241.58 μm² in the latter. The size of the CSA was not significantly correlated with VF, both in rootstock and scion stems (Tables S1 and S2 in Supplementary Materials). Regarding the average VF in rootstock stems relative to rootstock species, a greater number of vessels was found in those genotypes that had lower VLA values. Thus, VF in *P. fruticosa* genotypes was 16%

higher than average VF in *P. cerasus*. Consequently, *P. mahaleb* genotype, which was characterised with the highest VLA, had the lowest VF – about 33% lower than in *P. fruticosa*, which had 580.17 vessels per mm² on average. In scion stems a significant negative correlation between VLA and VF was found ($r = -0.95$; Table S2 in Supplementary Materials). Generally, scion stems were characterised by larger average VLA and lower VF values in comparison to the rootstock stems. On average, scion stems on *P. cerasus* and *P. fruticosa* recorded the VLA increase and VF decline when compared to rootstock stems of the same genotypes, with the lower average VLA of 257.83 μm² and the greater VF in scion stems on *P. fruticosa* rootstock candidates, counting 541.28 vessels per mm² in average. In scions, % V_{sw} was significantly positively correlated with VLA ($r = 0.91$) but negatively correlated with VF ($r = -0.77$; Table S2 in Supplementary Materials). In comparison to the control, scion stems on *P. cerasus* and *P. mahaleb* rootstock candidates had significantly larger vessels, ranging from 368.44 μm² to 390.55 μm², while VF was similar according to Duncan's multiple range tests.

Portions of vessels per size category are shown in Figure 2. Between rootstock candidates, two patterns of vessel distribution considering categories I and II were observed (Figure 2A). All cherry genotypes had a higher percentage of vessels <300 μm² in comparison with the percentage of vessels belonging to group II. In *P. cerasus* genotypes, portions of smallest vessels were

Figure 1. Rootstock influence on VLA in rootstock candidates and grafted 'Summit' cherry trees: (A) PC_02_01/4 rootstock candidate; (B) 'Summit'/PC_02_01/4 scion-rootstock combination; (C) PF_02_16 rootstock candidate; (D) 'Summit'/PF_02_16 scion-rootstock combination. VLA, vessel lumen area.

Figure 2. Percentages of vessels per size category in the secondary wood of (A) rootstock stems and (B) scion stems of grafted sweet cherry trees. Mean values designated with the same letter were not significantly different according to Duncan's test ($p \leq 0.05$).

52.37% in PC_05_04 and 63.30% in PC_02_01/4, while in *P. fruticosa* genotypes group I percentages varied from 71.57% in PF_01_01 to particularly high 79.98% in PF_02_16. Consequently, the lowest percentages of vessels from group II were observed in *P. fruticosa* genotypes, ranging from 19.87% to 27.91%. The second

pattern regarding vessel distribution was observed in PM_09_01 rootstock stems, where the highest number of vessels belonged to class II (58.07%) while small and large vessels were similarly present. 'Gisela 5' was characterised by the higher number of vessels sized within the range of 300–700 µm² (50.23%), but vessels

from class I were also highly present in the rootstock stem secondary wood (46.27%). The share of vessels $>700 \mu\text{m}^2$ in the total number of vessels was lowest in all investigated rootstocks. Percentage of largest vessels varied from 0.14% in PF_02_16 to 18.67% in PM_09_01.

Among scion stems, portions of vessels with different VLA did not match strictly patterns observed in rootstock candidates (Figure 2B). Concerning vessel affiliation to different size categories in scion stems of trees grafted on *P. fruticosa* genotypes where lowest V_e was observed, the highest percentage of vessels $<300 \mu\text{m}^2$ (60.08–73.56%), lowest portions of medium vessels (25.22–36.55%) and extremely low percentage of vessels $>700 \mu\text{m}^2$ (1.16–3.37%) were found. On the contrary, ‘Summit’ trees of highest V_e grafted on *P. cerasus* genotypes, had a similar percentage of small ($<300 \mu\text{m}^2$) and medium vessels ($300\text{--}700 \mu\text{m}^2$) in their scion stems, as well as a higher percentage of large vessels ($>700 \mu\text{m}^2$) compared to the previous group of trees, reaching 8.64% for PC_02_01/4 and 12.61% for PC_05_04. In contrast with the vessel categories’ percentages in rootstock stems, PM_09_01 and ‘Gisela 5’ values in scion stems showed larger portions of vessels $<300 \mu\text{m}^2$ (47.68 and 58.91%, respectively),

while vessels within a group III had the smallest share for both rootstocks (10.55% and 4.23%, respectively).

The CSA was significantly negatively correlated with the percentage of vessels under $300 \mu\text{m}^2$, both in rootstock ($r = -0.99$) and scion ($r = -0.79$) stems (correlation coefficients are shown in Tables S1 and S2 in Supplementary Materials). In rootstocks, portions of vessels belonging to the groups II and III were in a significant positive correlation with stem size (correlation coefficients were 0.96 and 0.91, respectively), while in scions significant positive correlation was found with the percentage of medium-sized vessels ($r = 0.89$). Significant correlations of VF were found in scion stems with vessels percentage from I ($r = 0.93$), II ($r = -0.87$) and III ($r = -0.93$) size class.

Effective tree crown volume (vegetative trait) and potential yielding (generative trait) relation to trunk hydraulic conductivity ($k_{h(T)}$)

Results showed a statistically significant correlation between V_e , $k_{h(T)}$ and yielding potential of grafted trees, with the highest alteration from the correlation curve recorded for trees grafted on PM_09_01 and ‘Gisela 5’ (Figure 3). Effective tree crown volume of sweet

Figure 3. Diagrams of correlations between: (A) V_e and $k_{h(T)}$ in 2019; (B) V_e and $k_{h(T)}$ in 2020; (C) V_e and yielding potential in 2019; (D) $k_{h(T)}$ and yielding potential in 2020.

Table 6. Effective tree crown volume and trunk hydraulic conductivity of ‘Summit’ trees in 2017–2020.

Effective tree crown volume (m ³)				
Rootstock	2017	2018	2019	2020
PC_02_01/4	0.47 a	1.29 a	2.47 a	2.97 a
PC_05_04	0.24 b	0.78 bc	1.85 ab	2.41 ab
PF_01_01	0.11 c	0.39 cd	0.91 cd	1.21 cd
PF_02_16	0.05 c	0.24 d	0.47 d	0.86 d
PF_04_09	0.06 c	0.41 cd	0.64 d	1.10 cd
PM_09_01	0.08 c	0.36 d	0.84 cd	1.29 cd
Gisela 5	0.23 b	1.09 ab	1.45 bc	1.97 bc
Mean	0.18	0.65	1.21	1.65
Trunk hydraulic conductivity (10 ⁻⁴ kg · m · MPa ⁻¹ · s ⁻¹)				
Rootstock	2017	2018	2019	2020
PC_02_01/4	10.31 a	24.21 a	38.25 a	51.07 a
PC_05_04	8.82 a	21.64 a	33.30 a	37.90 b
PF_01_01	1.73 c	3.63 d	6.90 c	10.58 d
PF_02_16	1.67 c	4.88 cd	7.88 c	8.59 d
PF_04_09	2.30 c	5.27 cd	10.02 c	15.99 d
PM_09_01	5.17 b	12.06 b	22.40 b	27.97 bc
Gisela 5	4.49 b	8.66 bc	13.27 c	17.97 cd
Mean	4.93	11.48	18.86	24.29

Mean values designated with the same letter were not significantly different according to Duncan's test ($p \leq 0.05$).

cherry ‘Summit’ trees was strongly influenced by the rootstock selected for grafting (Table 6). Relative to the V_c of trees grafted on control (100%), the estimated V_c in the first experimental year was lower for trees grafted on the following rootstock candidates: PF_02_16 (22%), PF_04_09 (26%), PF_01_01 (48%) and PM_09_01 (35%). ‘Summit’ trees on *P. cerasus* rootstock candidates had higher V_c in comparison with the control trees, reaching 104% on PC_05_04 and 204% on PC_02_01/4, of V_c value achieved on control. During the 4 years, trees grafted on PC_02_01/4 had the highest crown volume values, from 0.47 m³ in the first year of measuring to 2.97 m³ in 2020. Trees grafted on *P. fruticosa* genotypes showed lower V_c than on *P. cerasus* genotypes, with crown volumes within the range of 0.86–1.37 m³ in the fifth year after planting. Although trees on ‘Gisela 5’ achieved similar values as trees on PC_05_04 in 2017 (0.23 m³ and 0.24 m³, respectively) and had higher V_c in the following year, during 2019 and 2020 this genotype influenced higher crown volumes in comparison with the control. Trees with lower V_c determined in previous years obtained higher percentages in 2020 in comparison with trees grafted on ‘Gisela 5’, with an estimated 44% (PF_02_16), 56% (PF_04_09), 61% (PF_01_01) and 65% increase (PM_09_01), while *P. cerasus* rootstock candidates induced values of 122% and 151% of V_c achieved on ‘Gisela 5’ (PC_05_04 and PC_02_01/4, respectively). Sweet cherry trees on PM_09_01 had lower V_c than ‘Gisela 5’ during all experimental years, reaching 0.08 m³ in 2017 and 1.29 m³ in 2020.

Trunk calculated hydraulic conductivity varied among grafted trees, with maximal calculated values

on *P. cerasus* genotypes and minimal values on *P. fruticosa* genotypes during the 4 consecutive years. In 2017 trunk k_h values on PC_05_04 and PC_02_01/4 were approximately 3-fold higher than $k_{h(T)}$ achieved on *P. fruticosa* genotypes, and about 2-fold higher compared to PM_09_01 and the control. During 2017–2020 maximal values were found on PC_02_01/4, reaching maximal $51.07 \times 10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1}$ in 2020. Results obtained in 2020 varied from $8.59 \times 10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1}$ in trees on PF_02_16 to previously listed highest value on PC_02_01/4 genotype, where control rootstock influenced 2.5-fold lower trunk conductance than *P. cerasus* genotypes and 1.5-fold higher $k_{h(T)}$ when compared to *P. fruticosa* genotypes. The third highest value in the last year of measuring was found in trees grafted on PM_09_01 ($27.97 \times 10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1}$), pointing to the approximately 1.5-fold greater $k_{h(T)}$ in comparison to control, during the 4 consecutive years. Trees grafted on *P. cerasus* genotypes had significantly higher $k_{h(T)}$ compared to trees on other rootstock candidates, with about 4-fold and 1.5-fold higher values than trees on *P. fruticosa* and *P. mahaleb* in 2020, respectively.

The effective tree crown volumes in the years 2017, 2019 and 2020 were significantly positively correlated with $k_{h(T)}$ for the same years (coefficients of correlation were 0.86, 0.86 and 0.89, respectively, as shown in Table S3 in Supplementary Materials).

There were significant differences in the number of flowers per tree determined in trees grafted on differing rootstocks (Figure 4). In 2019, *P. cerasus* genotypes PC_05_04 and PC_02_01/4 induced the highest flowering of sweet cherry trees, forming a homogenous group with 723.76 and 741.59 flowers per tree, respectively. Plants grafted on control rootstock ‘Gisela 5’ counted 614 flowers per tree, while those grafted on PM_09_01 counted 282.89 flowers. *P. fruticosa* genotypes were characterised with only 25.68 to 43.60 flowers per tree. In comparison with 2019, the number of flowers in 2020 increased by 23% on PC_05_04 and 38% on PC_02_01/4, 6–15 times on *P. fruticosa* rootstock candidates, 50% on PM_09_01 and only 12% on control. Values from 2020 and 2021 showed that *P. cerasus* genotypes PC_05_04 and PC_02_01/4 achieved the highest numbers of flowers per tree, reaching up to 889.60 and 1023.40 flowers per tree in 2020 and 1,112.18 and 1,083.69 flowers per tree in 2021, respectively. In 2021, the largest increase in the number of flowers per tree compared to the previous year was noted on trees on *P. fruticosa* rootstock candidates (1.7- to 3.3-fold higher) and on PM_09_01 (2.6-fold higher). Yielding potential on *P. cerasus* rootstock candidates and control was raised by 25%, 8% and 44% (PC_05_04, PC_02_01/4 and ‘Gisela 5’, respectively), which led to a similar number of flowers on *P. fruticosa* and control rootstock, as well as on PC_02_01/4 and PM_09_01. Trees grafted on PF_02_16, PF_01_01 and PF_04_09 achieved the lowest yielding potential, counting 791.72,

Figure 4. Yielding potential of seven scion-rootstock combinations in three consecutive years. Mean values designated with the same letter were not significantly different according to Duncan's test ($p \leq 0.05$).

919.05 and 918.90 flowers per plant, respectively. A significant positive correlation of yielding potential was found with the V_c and $k_{h(T)}$ values in 2019 and 2020 (correlation coefficients varied between 0.84 and 0.96; Table S3 in Supplementary Materials).

DISCUSSION

The results presented above indicate that there is a great variation and significant potential for the selection of size-controlling productive rootstocks. Cross-section anatomical characteristics varied significantly both in rootstock and scion stems, indicating a clear influence of rootstock genotype on grafted sweet cherry trees. Since investigated stems were of the same age, sampled from the same part of the plant and grown in the same environmental setting, SDs are presumed to be strongly genetically dependent as previously noted for eucalyptus (Bartholomé et al., 2020). High heritability and genetic control of anatomical traits and water use efficiency was previously noted by Lauri et al. (2011) as well as Lopez et al. (2017). Lesser variation in CSA was observed in scion stems in comparison with the rootstock stems, indicating that to some extent scion retains its scion-specific cambial activity. Due to secondary thickening in rootstock stems, the production of new xylem elements significantly increased. The same was observed in scion stems. Comparing stem cross-section anatomical characteristics and secondary wood properties of ungrafted and grafted rootstocks, trees have generally shown the absence of statistically significant correlation (Tables S4 and S5 in Supplementary Materials). This is in accordance with the findings of a study by Ljubojević et al. (2013), which suggested that the anatomical mechanism of vigour control is defined by the genetic

basis of both rootstock and scion, characterised by their specific features that remain unchanged in the coexistence after grafting.

Previous studies have shown that sweet cherry low-vigorous rootstocks had larger VF but smaller VD than invigorating ones (Olmstead et al., 2006a; Gonçalves et al., 2007). Regarding VLA values in the rootstock stems, the smallest VLA and relatively high number of vessels were found in the cherry rootstock candidates that induce the smallest V_c of 'Summit' trees. However, the largest VLA was found in the stems of PM_09_01 rootstock, which did not induce the highest V_c of grafted trees, while in PC_02_01/4, which influenced the highest tree crown growth, relatively small VLA and high VF were found. These results are in accordance with the previously noted strong genetic dependence of investigated cross-section anatomical properties (Ljubojević et al., 2021). In contrast with rootstock stems, VLA and VF in scion stems were strongly negatively correlated, where an increase in VLA led to a decline in VF. For scion stems of trees grafted on *P. cerasus* and *P. fruticosa* rootstock candidates, our observations are that in trees with higher V_c , larger vessels and lower VF were found, whereas in stems of trees characterised with lower V_c , smaller vessels and higher VF were noticed. Compared to the results for 'Summit' cheery trees obtained by Ljubojević et al. (2013), investigated rootstock candidates in this study seem to alter VLA without compromising VF.

A significantly lower xylem/phloem thickness ratio in stems of dwarfed trees than in invigorating ones was found by Gonçalves et al. (2007). In the present study, observed SW/SC ratio in the rootstock stems had shown a higher portion of secondary cortex on stem cross-section of all *P. cerasus* and *P. fruticosa* rootstock

candidates. In rootstock stems of PM_09_01 and 'Gisela 5', small differences between the percentage of secondary wood and secondary cortex were noted, with a greater percentage of the former. However, estimated V_e of 'Summit' trees did not show higher growth on PM_09_01 despite the assumption that a higher percentage of xylem tissue induces higher vegetative growth, which presumably resulted from hydraulic conductance correction in the graft union and reduced water flow from roots to upper tree parts (Olmstead et al., 2006b). Higher SW/SC ratio in 'Gisela 5' rootstock stems, in comparison with cherry rootstocks' stems, might imply lower tree crown volume when grafted on these rootstock candidates. Although all investigated scion/rootstock combinations were exposed to water deficit due to lack of irrigation in the semi-arid conditions, symptoms of water stress were most obvious in trees grafted on 'Gisela 5' (flagging and/or cupped leaves during the drought have been observed). Thus, higher V_e of trees on *P. cerasus* rootstock candidates in comparison with control trees could be due to higher susceptibility of trees on 'Gisela 5' to water scarcity during the drought events, which might have resulted in suppressed tree growth. Since 'Gisela 5' is considered as low-vigour inducing (Lang, 2000), our results showed that all investigated rootstock candidates are potentially dwarfing.

A statistically significant positive correlation of V_e with $k_{h(T)}$ acknowledges water uptake and movement through the plant as an important factor of tree growth (Tombesi et al., 2010). Species influence induced differences in hydraulic conductance of 'Summit' trees grafted on different rootstocks, further affecting the vegetative and generative traits of scion/rootstock combinations. Along with the trunk cross-sectional area characteristics (embedded in the calculation of $k_{h(T)}$), secondary wood properties provide the necessary data about $k_{h(T)}$, which is considered a vital part of the plant growth regulation (Tombesi et al., 2011). Nonetheless, climate factors and environmental conditions in which plants are grown must be included in the analysis. Compact tree growth and low vigour of grafted sweet cherry trees, as well as high yield and fruit quality, are indicators of compatibility and adequate rootstock selection (Gainza et al., 2015b). However, the same plant might perform surprisingly poorly when planted under certain conditions, while able to thrive in an alternative condition. Sweet cherry trees grafted on 'Gisela 5' have shown good performance when irrigated (Pal et al., 2017), but the same was not observed under the drought (Vercammen, 2004). In our study, significantly higher V_e and $k_{h(T)}$ of trees grafted on *P. cerasus*, in comparison with the trees on 'Gisela 5', showed better adaptation of these rootstock candidates in the trial without irrigation implemented.

Fruit development is strongly influenced by climate changes (Salama et al., 2021; Vanalli et al., 2021). Rising temperatures in this century can induce the

earlier beginning of cherry blossom, which increases the vulnerability of buds to spring frosts (Chmielewski et al., 2018). Such climate conditions, complemented with an inadequate schedule of precipitation and high-temperature fluctuations, can severely reduce yields and cause high financial losses to sweet cherry producers. Although a total of fruits harvested represents a real indicator of production efficiency, in some years it cannot be obtained. As the alternative, the number of flowers per tree could be assessed as the preliminary yielding potential in different scion/rootstocks combinations, since the degree of fruit set and yield largely depends on the abundance of flowering (Radović et al., 2020). Trees on dwarfing rootstocks usually produce an increased number and quality of floral buds, which is probably linked to the earlier cessation of shoot extension growth in the summer that redirects trees' assimilates and nutrients towards the production of floral buds (Webster, 2002b). Our results showed a positive correlation of potential yielding with the estimated V_e and $k_{h(T)}$. 'Summit' trees characterised by the lowest V_e had the lowest number of flowers per tree, while trees with the highest values of V_e produced more flowers, corroborating adaptability assumptions. Since V_e values' calculation proved the dwarfing character of all investigated rootstocks, the focus was set on the selection of rootstock with the highest yielding potential, rather than on vigour versus number of flowers assessment. During the first 2 years, trees grafted on *P. cerasus* rootstock candidates produced a higher number of flowers in comparison with trees on *P. fruticosa* and PM_09_01, as well as on control rootstock. The abundance of flowers was notably higher on *P. cerasus* rootstock candidates, which might be due to earlier fruiting phase entering. It was noted that trees on PM_09_01 had a similar number of flowers as trees on *P. fruticosa* in 2020, with the expectation of significantly higher flower abundance in the following years, since *P. mahaleb* does not induce high fertility in the first years of fruiting (Lang, 2000). It was observed that the highest number of flowers per tree on PC_05_04 and PC_02_01/4 have resulted from the increased length of fruiting branches in comparison with the branches of trees on 'Gisela 5', which induced the earlier shoot cessation in control trees (Prassinis et al., 2009).

CONCLUSIONS

Scarcity of water resources worldwide and numerous environmental changes lead to a shift in the breeding goals towards both productive and adaptive rootstock selection. It was found that all investigated cherry rootstock candidates belong to the low-vigorous rootstocks based on the estimated V_e of grafted trees in relation to the trees on dwarfing control rootstock 'Gisela 5'. Trees on *P. cerasus* rootstock candidates showed good performance in the conditions without irrigation, with the highest yielding potential measured. Although *P. fruticosa* rootstock candidates induced the

highest yearly increase in the number of flowers per ‘Summit’ tree during the 3 consecutive years, observed yielding potential did not meet the precociousness criterion. Similarly, *P. mahaleb* rootstock influenced the sufficiently good performance of grafted trees, but during the 2 initial years of fruit-bearing failed to produce a high number of flowers. Regarding calculated V_c of grafted ‘Summit’ trees, $k_{h(T)}$ and determined yielding potential, PC_05_04 rootstock candidate could be considered as the most appropriate choice when raising the high-density sweet cherry plantations. Doubtless, ‘Summit’ variety on both PC_05_04 and PC_02_01/4 rootstock candidates showed better performance than on ‘Gisela 5’, due to higher tolerance to variable environmental conditions without compromising potential fruit set. Exceptionally high correlation coefficients between 4-year measurements of ‘Summit’ trees’ crown volumes and hydraulic conductivity calculations based on the initial anatomical stem measurements (confirmed yearly on small trunk segments obtained by wood chisel) imply that conducted method could be used in the forthcoming rootstock breeding programmes.

ACKNOWLEDGEMENTS

The authors would like to express their gratitude to Dragan Kereši, for a great amount of assistance with the field investigation and data collection during the experimental years. The study was supported by prestigious national awards ‘Startup for science’ (raised by Philip Morris Company and the centre for leadership development); ‘For Women in Science’ (raised by L’Oreal, UNESCO and Serbian Ministry of Education and Science); and ‘Dr. Zoran Đinđić’ (raised by the University of Novi Sad, Serbia).

FUNDING

This research was funded by the Ministry of Education and Science, the Republic of Serbia, as one of the research topics in the project ‘Selection of sweet and sour cherry dwarfing rootstocks and development of intensive cultivation technology based on sustainable agriculture principles’, evidence number TR 31038.

AUTHOR CONTRIBUTIONS

M. LJ. was responsible for conceptualisation and experimental design. T. N. performed the experimental work. M. LJ. and T. N. conducted the investigation and data analysis. T. N. wrote the original draft. M. LJ. was responsible for manuscript reviewing and editing. J. O. was responsible for visualisation. V. O. and G. B. provided and managed resources for the research conduction. V. O. supervised the research and manuscript preparation.

CONFLICT OF INTEREST

All authors declare that no conflict of interest exists.

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Received: June 8, 2021; accepted: July 29, 2021

SUPPLEMENTARY MATERIALS

Table S1. Correlation coefficients between rootstocks' stem anatomical characteristics in 2016 (underlined values were statistically significant at $p < 0.05$).

	SD (mm)	CSA (mm ²)	% P	% SW	% SC	% PD	SW/ SC ratio	% V	% R	% X	SWA (mm ²)	% V _{SW}	% R _{SW}	% X _{SW}	VLA (μm ²)	VF (N · mm ⁻²)	% of vessels <300 μm ²	% of vessels 300– 700 μm ²	% of vessels >700 μm ²
SD (mm)	1.00																		
CSA (mm ²)	<u>0.99</u>	1.00																	
% P	0.06	-0.01	1.00																
% SW	0.57	0.62	-0.72	1.00															
% SC	-0.58	-0.64	0.62	-0.97	1.00														
% PD	-0.90	-0.86	-0.20	-0.44	0.42	1.00													
SW/SC ratio	0.64	0.69	-0.66	<u>0.99</u>	-0.98	-0.49	1.00												
% V	<u>0.82</u>	<u>0.85</u>	-0.38	<u>0.77</u>	-0.68	-0.74	<u>0.79</u>	1.00											
% R	<u>0.91</u>	<u>0.92</u>	-0.31	<u>0.84</u>	-0.82	-0.81	<u>0.88</u>	<u>0.93</u>	1.00										
% X	0.22	0.28	-0.82	<u>0.91</u>	-0.91	-0.09	<u>0.88</u>	0.44	0.55	1.00									
SWA (mm ²)	<u>0.95</u>	<u>0.98</u>	-0.22	<u>0.77</u>	-0.77	-0.79	<u>0.83</u>	<u>0.91</u>	<u>0.97</u>	0.47	1.00								
% V _{SW}	0.69	0.68	0.12	0.18	-0.07	-0.70	0.22	<u>0.77</u>	0.58	-0.23	0.61	1.00							
% R _{SW}	<u>0.98</u>	<u>0.96</u>	0.04	0.59	-0.58	-0.94	0.65	<u>0.86</u>	<u>0.93</u>	0.23	<u>0.93</u>	0.73	1.00						
% X _{SW}	-0.89	-0.88	-0.09	-0.40	0.34	<u>0.88</u>	-0.46	-0.87	-0.80	0.01	-0.82	-0.94	-0.92	1.00					
VLA (μm ²)	<u>0.95</u>	<u>0.98</u>	-0.15	0.68	-0.69	-0.76	0.75	<u>0.86</u>	<u>0.91</u>	0.37	<u>0.98</u>	0.63	<u>0.91</u>	-0.82	1.00				
VF (N · mm ⁻²)	-0.50	-0.54	0.25	-0.67	<u>0.79</u>	0.28	-0.70	-0.28	-0.56	-0.70	-0.60	0.24	-0.41	0.07	-0.59	1.00			
% of vessels <300 μm ²	-0.98	-0.99	0.10	-0.67	0.65	<u>0.85</u>	-0.73	-0.88	-0.93	-0.33	-0.98	-0.69	-0.95	<u>0.88</u>	-0.99	0.53	1.00		
% of vessels 300–700 μm ²	<u>0.97</u>	<u>0.96</u>	-0.04	0.62	-0.59	-0.92	0.67	<u>0.85</u>	<u>0.92</u>	0.28	<u>0.93</u>	0.71	<u>0.97</u>	-0.90	<u>0.93</u>	-0.46	-0.98	1.00	
% of vessels >700 μm ²	<u>0.85</u>	<u>0.91</u>	-0.21	0.67	-0.70	-0.58	0.74	<u>0.80</u>	<u>0.83</u>	0.40	<u>0.93</u>	0.54	<u>0.78</u>	-0.71	<u>0.96</u>	-0.61	-0.90	0.79	1.00

CSA, cross-section area (mm²); % P, percentage of pith area per stem cross-section; % SW, percentage of SWA per stem cross-section; SD, stem diameter (mm); % SC, percentage of secondary cortex area per stem cross-section; % PD, percentage of periderm area per stem cross-section; SW/SC ratio, secondary wood/secondary cortex ratio; % V, percentage of total vessel area per stem cross-section; % R, percentage of total ray area per stem cross-section; % X, percentage of xylem area per stem cross-section; SWA, secondary wood area (mm²); % V_{SW}, percentage of total vessel area relative to SWA; % R_{SW}, percentage of total ray area relative to SWA; % X_{SW}, percentage of xylem area relative to SWA; VLA, vessel lumen area (μm²); VF, vessel frequency (number of vessels per mm²).

Table S2. Correlation coefficients between scions' stem anatomical characteristics in 2016 (underlined values were statistically significant at $p < 0.05$).

	SD (mm)	CSA (mm ²)	% P	% SW	% SC	% PD	SW/ SC ratio	% V	% R	% X	SWA (mm ²)	% V _{SW}	% R _{SW}	% X _{SW}	VLA (μm ²)	VF (N · mm ⁻²)	% of vessels <300 μm ²	% of vessels 300– 700 μm ²	% of vessels >700 μm ²
SD (mm)	1.00																		
CSA (mm ²)	<u>1.00</u>	1.00																	
% P	0.66	0.69	1.00																
% SW	0.28	0.25	-0.45	1.00															
% SC	-0.94	-0.93	-0.55	-0.47	1.00														
% PD	-0.25	-0.27	-0.62	0.27	0.16	1.00													
SW/SC ratio	0.67	0.65	0.00	<u>0.88</u>	-0.83	0.10	1.00												
% V	<u>0.92</u>	<u>0.92</u>	0.65	0.33	-0.95	-0.28	0.72	1.00											
% R	-0.48	-0.50	-0.83	0.51	0.44	0.15	0.07	-0.52	1.00										
% X	0.37	0.35	-0.33	<u>0.95</u>	-0.60	0.38	<u>0.92</u>	0.43	0.26	1.00									
SWA (mm ²)	<u>0.95</u>	<u>0.95</u>	0.46	0.51	-0.95	-0.12	<u>0.83</u>	<u>0.90</u>	-0.33	0.60	1.00								
% V _{SW}	<u>0.81</u>	<u>0.82</u>	<u>0.92</u>	-0.21	-0.73	-0.44	0.26	<u>0.85</u>	-0.78	-0.09	0.64	1.00							
% R _{SW}	-0.71	-0.73	-0.71	0.05	<u>0.76</u>	0.03	-0.39	-0.77	<u>0.88</u>	-0.21	-0.67	-0.78	1.00						
% X _{SW}	0.38	0.41	0.31	0.10	-0.54	0.32	0.37	0.45	-0.67	0.40	0.48	0.33	-0.85	1.00					
VLA (μm ²)	0.72	0.73	<u>0.87</u>	-0.43	-0.54	-0.24	0.02	0.64	-0.85	-0.28	0.51	<u>0.91</u>	-0.75	0.36	1.00				
VF (N · mm ⁻²)	-0.66	-0.68	-0.76	0.42	0.48	0.04	0.00	-0.51	<u>0.82</u>	0.23	-0.48	-0.77	0.73	-0.45	-0.95	1.00			
% of vessels <300 μm ²	-0.79	-0.80	-0.91	0.35	0.62	0.32	-0.11	-0.71	<u>0.82</u>	0.22	-0.58	-0.94	0.75	-0.34	-0.99	<u>0.93</u>	1.00		
% of vessels 300–700 μm ²	<u>0.89</u>	<u>0.89</u>	<u>0.90</u>	-0.19	-0.74	-0.38	0.28	<u>0.81</u>	-0.74	-0.07	0.71	<u>0.96</u>	-0.76	0.34	<u>0.95</u>	-0.87	-0.98	1.00	
% of vessels >700 μm ²	0.54	0.56	<u>0.84</u>	-0.60	-0.35	-0.20	-0.19	0.47	-0.87	-0.45	0.31	<u>0.83</u>	-0.68	0.32	<u>0.97</u>	-0.93	-0.94	<u>0.85</u>	1.00

CSA, cross-section area (mm²); % P, percentage of pith area per stem cross-section; % SW, percentage of SWA per stem cross-section; % SC, percentage of secondary cortex area per stem cross-section; % PD, percentage of periderm area per stem cross-section; SD, stem diameter (mm); SW/SC ratio, secondary wood/secondary cortex ratio; % V, percentage of total vessel area per stem cross-section; % R, percentage of total ray area per stem cross-section; % X, percentage of xylem area per stem cross-section; SWA, secondary wood area (mm²); % V_{SW}, percentage of total vessel area relative to SWA; % R_{SW}, percentage of total ray area relative to SWA; % X_{SW}, percentage of xylem area relative to SWA; VLA, vessel lumen area (μm²); VF, vessel frequency (number of vessels per mm²).

Table S3. Correlation coefficients between calculated effective tree crown volumes, trunk hydraulic conductivity and potential yielding in 2017–2021 (underlined values were statistically significant at $p < 0.05$).

	V_e (mm ³) in 2017	V_e (mm ³) in 2018	V_e (mm ³) in 2019	V_e (mm ³) in 2020	$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2017	$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2018	$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2019	$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2020	Number of flowers · tree ⁻¹ in 2019	Number of flowers · tree ⁻¹ in 2020	Number of flowers · tree ⁻¹ in 2021
V_e (mm ³) in 2017	1.00										
V_e (mm ³) in 2018	<u>0.93</u>	1.00									
V_e (mm ³) in 2019	<u>0.97</u>	<u>0.91</u>	1.00								
V_e (mm ³) in 2020	<u>0.96</u>	<u>0.92</u>	<u>1.00</u>	1.00							
$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2017	<u>0.86</u>	<u>0.76</u>	<u>0.93</u>	<u>0.94</u>	1.00						
$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2018	<u>0.83</u>	0.70	<u>0.89</u>	<u>0.91</u>	<u>0.99</u>	1.00					
$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2019	<u>0.80</u>	0.66	<u>0.86</u>	<u>0.88</u>	<u>0.99</u>	<u>0.99</u>	1.00				
$k_{h(T)} (10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1})$ in 2020	<u>0.84</u>	0.71	<u>0.89</u>	<u>0.89</u>	<u>0.98</u>	<u>0.98</u>	<u>0.99</u>	1.00			
Number of flowers · tree ⁻¹ in 2019	<u>0.85</u>	<u>0.89</u>	<u>0.91</u>	<u>0.94</u>	<u>0.91</u>	<u>0.87</u>	<u>0.84</u>	<u>0.82</u>	1.00		
Number of flowers · tree ⁻¹ in 2020	<u>0.90</u>	<u>0.89</u>	<u>0.95</u>	<u>0.96</u>	<u>0.91</u>	<u>0.88</u>	<u>0.85</u>	<u>0.87</u>	<u>0.90</u>	1.00	
Number of flowers · tree ⁻¹ in 2021	0.61	0.58	0.73	0.75	<u>0.85</u>	<u>0.82</u>	<u>0.85</u>	<u>0.84</u>	<u>0.79</u>	0.75	1.00

V_e effective tree crown volume (mm³), $k_{h(T)}$ trunk hydraulic conductivity ($10^{-4} \text{ kg} \cdot \text{m} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1}$).

Table S4. Correlation coefficients between cross-section anatomical characteristics of rootstocks’ and scions’ stems in 2016 (underlined values were statistically significant at $p < 0.05$).

Rootstock/Scion	SD (mm)	CSA (mm ²)	% P	% SW	% SC	% PD	SW/SC ratio	% V	% R	% X
SD (mm)	0.47	0.51	0.53	−0.30	−0.41	0.24	0.04	0.38	<u>−0.83</u>	−0.03
CSA (mm ²)	0.43	0.47	0.49	−0.31	−0.36	0.24	0.01	0.35	<u>−0.79</u>	−0.05
% P	0.56	0.56	<u>0.76</u>	−0.05	−0.60	−0.72	0.28	0.61	−0.47	0.01
% SW	0.08	0.09	−0.22	0.03	0.01	0.72	0.03	−0.01	−0.13	0.13
% SC	−0.19	−0.20	0.10	−0.04	0.11	−0.62	−0.10	−0.16	0.23	−0.14
% PD	−0.67	−0.69	−0.50	0.05	0.59	−0.21	−0.29	−0.48	0.66	−0.18
SW/SC ratio	0.14	0.15	−0.13	0.00	−0.05	0.67	0.04	0.06	−0.22	0.11
% V	0.15	0.19	0.01	−0.04	−0.14	0.55	0.06	0.03	−0.39	0.18
% R	0.34	0.37	0.17	−0.08	−0.29	0.57	0.12	0.24	−0.55	0.15
% X	−0.06	−0.07	−0.40	0.09	0.17	0.67	−0.02	−0.11	0.15	0.07

CSA, cross-section area (mm²); % P, percentage of pith area per stem cross-section; % SW, percentage of SWA per stem cross-section; SWA, secondary wood area; SD, stem diameter (mm); % SC, percentage of secondary cortex area per stem cross-section; % PD, percentage of periderm area per stem cross-section; SW/SC ratio, secondary wood/secondary cortex ratio; % V, percentage of total vessel area per stem cross-section; % R, percentage of total ray area per stem cross-section; % X, percentage of xylem area per stem cross-section.

Table S5. Correlation coefficients between secondary wood anatomical characteristics of rootstocks’ and scions’ stems in 2016 (underlined values were statistically significant at $p < 0.05$).

Rootstock/Scion	SWA (mm ²)	% V_{SW}	% R_{SW}	% X_{SW}	VLA (μm ²)	VF (N · mm ⁻²)
SWA (mm ²)	0.35	0.33	−0.69	<u>0.76</u>	0.57	−0.70
% V_{SW}	0.19	0.00	−0.48	0.72	0.18	−0.38
% R_{SW}	0.49	0.44	<u>−0.81</u>	<u>0.85</u>	0.64	<u>−0.79</u>
% X_{SW}	−0.36	−0.23	0.68	<u>−0.84</u>	−0.43	0.62
VLA (μm ²)	0.26	0.38	−0.68	0.71	0.63	−0.74
VF (N · mm ⁻²)	−0.22	−0.53	0.40	−0.16	−0.66	0.58

SWA, secondary wood area (mm²); % V_{SW} , percentage of total vessel area relative to SWA; % R_{SW} , percentage of total ray area relative to SWA; % X_{SW} , percentage of xylem area relative to SWA; VLA, vessel lumen area (μm²); VF, vessel frequency (number of vessels per mm²).