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The nature and way of root adaptation of juvenile woody plants *Sorbus* and *Pyrus* to drought

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Abstract The functional root traits of *Pyrus pyraster* (L.) Burgsd. and *Sorbus domestica* L. during early growth stages were evaluated. The aim of the study was to identify the functional traits of root systems that determine the adaptability of these woody species to drought conditions. The experiment was carried out under the controlled environment of a growth chamber. The root systems were analyzed using WinRhizo software. Several functional root traits were identified, including specific root length, root surface area, root length, root volume, root-to-shoot mass ratio (R:S), fine root ($\phi < 2$ mm) volume, coarse root ($\phi > 2$ mm) volume, and fine-to-coarse root volume ratio (F/C). In drought, *P. pyraster* maintained the absorptive root surface unchanged, when increased the volume of the fine root fraction. The different strategy of adaptation to drought has been confirmed for *S. domestica*, which accumulated more dry mass in the root system in comparison to aboveground organs (significant increase of R:S ratio). The functional root traits analyzed here were species-dependent. The key functional traits that indicate the responses of studied tree taxa to drought conditions include root thickening, F/C, and R:S. Increased values of these parameters indicate the investment of the plant towards root extension. A higher proportion of fine roots increases the absorbing surface of the root system, thereby promoting water uptake from the soil.

Keywords Root traits · Growth · Plant responses · Trees · Seedlings

Introduction

Drought is one of the environmental stresses affecting integrity of the plant body and significantly limiting the physiological activity of the plants. At present, it is considered to be the most significant stressor from the global point of view, which can occur locally, but has substantial impact ever large territory.

Plant phenotypic plasticity in response to environmental factors is expressed by the morpho-physio-phenological traits which impact the fitness of individual species (Violle et al. 2007). According to Freschet et al. (2013), the plasticity of functional traits is a major component of the plant adjustment to environmental stresses. Plant functional traits are the mediators in regulating effects of changes in abiotic site conditions on ecosystem functioning and have potential to describe how communities respond to environmental gradients (Bu et al. 2019).

The functional traits of aboveground organs are relatively well described for trees (Hajek et al. 2016; Petruzzelis et al. 2017; Bu et al. 2019). The functional root traits are much less identified, although many of

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them are important characteristics of the species resistance to drought.

Research activities have focused on studying mechanisms of resistance and functional features of underground and aboveground plant organs that respond to drought. The key traits studied include the size and weight of the root systems of these plants (Comas et al. 2013), which are expressed as an allometric relationship between the root and shoot dry masses (root to shoot mass ratio, R:S). Several researchers (Ryser and Lambers 1995; Mokany et al. 2006; Brassard et al. 2011) have indicated that the mass relationship between roots and aboveground organs can be used to estimate the size and functionality of the root system. Additionally, Pretzsch et al. (2012) and Modrzyński et al. (2015) reported that dry mass ratios do not reflect the plastic adaptation of plants to stress conditions that may cause changes in plant structure, tissue thickness, and organs; the authors highlight the importance of studies focusing on root morphology, especially the specific root length (SRL). Roots are important organs for plants' adaptation to drought, but knowledge of root length or weight is no longer sufficient for understanding the plasticity of their nature.

Although studies have confirmed that drought affects the structure and growth of both coarse and fine roots (Kozlowski and Pallardy 2002; Rühr et al. 2009; Olmo et al. 2014), the physiological responses of woody plant roots to drought remain unclear. The development of new methods and techniques improves the identification of root parameters; this is evidenced by experiments on minirhizotrons (Meier and Leuschner 2007; Coleman and Aubrey 2018), determination of electrical conductivity in roots (Aubrecht et al. 2006), soil core analyses (Středa et al. 2014), and image analysis of the roots using the WinRhizo software (Bauhus and Messier 1999; Augé et al. 2003; Paganová and Jureková 2014). These methods confirm the measurable functional traits of roots that can be correlated with the efficacy of plants to acquire resources and survive under unfavorable conditions (Diaz et al. 2004; Cornelissen et al. 2003; Hodgson et al. 2011; Masarovičová et al. 2015).

Some authors (Fitter 2002; Nardini et al. 2002; Westoby and Wright 2006) have also proposed morphological functional traits in root. The key morphological traits are those that influence total root length and surface area of root systems, including root diameter, root tissue density, SRL, and specific surface area (SSA). Root diameter and tissue density control the length and surface area of root systems for a given biomass of the root system (Fitter 2002; Ostonen et al. 2007); thus, SRL has been established as an indicator of environmental changes. In a study investigating seedling growth of 10 temperate tree species, Modrzyński et al. (2015) showed the importance of studying root morphology, especially SRL, in relation to shade tolerance during early ontogeny. Tachibana and Ohta (2012) examined root surface area as a parameter that can affect water and nutrient uptake by plants.

In the present study, the functional root traits of juvenile woody plants grown under conditions of water scarcity were evaluated. The key traits for the growth of root biomass were determined on the basis of their functional importance. The plant species included in this study were *Pyrus pyraster* (L.) Burgsd. and *Sorbus domestica* L. The variability of root traits within and between the two species was also evaluated in response to drought.

S. domestica and *P. pyraster* are members of the autochthonous flora in Central Europe. Both taxa appear in stands that undergo frequent changes in water balance and high temperatures (Paganová and Jureková 2011); therefore, they are expected to present good adaptability to drought conditions.

S. domestica and *P. pyraster* are light-demanding woody plants that reach a height of 15–20 m in a forest canopy of 30 m. More often, they grow as solitary trees in open landscapes. *S. domestica* prefers warm and temperate climate and can tolerate low soil moisture content. However, a constant supply of water is important for its successful growth (Májovský 1992). The root system of *S. domestica* is capable of receiving water from a depth of several meters (Kausch 2000). Conditions of wet stands, such as those in valleys around watercourses and in waterlogged areas with high levels of groundwater (Hrdoušek et al. 2014), are not suitable for this plant species.

P. pyraster has a wider ecological amplitude than *S. domestica*. Wild pear grows in cold climates in mountainous areas, where it can be found at altitudes up to 1400 m. This taxon grows on almost all soil types, except for extremely acidic soil. The tap root system permits successful growth on very dry soils. Due to the high light demands, *P. pyraster* occurs in rather extreme or marginal site conditions, where competition with other tree species is weakened (Milner 2011).

Materials and methods

Experimental design and timeline

The experimental plants were grown from seeds collected from original locations (Table 1) in Slovakia. Their environmental conditions represent common habitats of the two taxa.

The seeds were extracted from fruits immediately after harvest. They were cleaned and stored for a short time, and then passed through cold stratification with temperatures ranging from − 5 °C to +5 °C. The seeds were germinated in pots with a peat-based growth substrate.

The experiment was carried out under the controlled environment of a growth chamber. Young plants (1-year-old seedlings) of *P. pyraster* and *S. domestica* were grown and maintained in two variants of a differential water regime. There were analyzed 10 plants per taxon and regime.

In the phenological growth stage, "expanded cotyledon" seedlings were placed in root boxes with a fertilized peat-based growth substrate (20% black peat, 80% white peat moss, 0–5 mm fraction, pH of 5.5–6.5, enriched with nutrients 1.0 kg m^{-3} NPK in a ratio of 14:16:18). The retractable front wall of the metal boxes enabled careful extraction of roots for analysis, as well as detailed study of the root growth and root fractions (Paganová and Jureková 2012, 2014). The volume of a root box for one seedling was 1.15 L.

The size of root boxes was carefully considered, because the biomass of experimental plants can be affected by size of the pots, as it is documented in the literature (Poorter et al. 2012). In the beginning of experiment the plant biomass, that is present at a given volume of rooting space (BVR) was calculated. The fresh weight of a seedling was 0.2 g for *P. pyraster* and 0.3 g for *S. domestica*. In the beginning of experiment, the calculated BVR based on total plant biomass present in the volume of 1.15 L was 0.17 g L^{-1} for *P. pyraster* and 0.26 g L^{-1} for *S. domestica*. These values correspond with suggested plant biomass to pot volume ratio < 1 (Poorter et al. 2012).

After 15-day acclimatization, the plants were maintained under differential water regimes for 150 days from April to September in the growth chamber (PolEko KK1450). The photoperiod of the growth chamber was set to a long light period (LP) of 14 h light/10 h dark; the irradiation density on the surface of the uppermost leaves was 202.5 μmol m^{-2} s^{-1}. Air humidity was maintained within a range of 63–67%, while the temperature was maintained at 24 °C during the light period and at 14 °C during the dark period.

Differential water regimes were established in two variants: drought (40% water as per the weight of the fully saturated growth substrate) and control (60% water as per the weight of the fully saturated growth substrate). The water content in the growth substrate was calculated on the basis of wet weight (Trautmann and Richard 1996).

$$\mathrm{Mn} = \frac{(\mathrm{Ww}{-}\mathrm{Wd})}{\mathrm{Ww}} \times 100$$

M_n moisture content (%) of material *n*
W_w wet weight of the sample
W_d weight of the sample after drying

Differential water regimes were maintained by regularly weighing the root boxes on Kern SD digital scales (max = 8000 g, standard deviation = 0.05 g) at 2-day intervals.

The water potential of leaf tissues was determined using leaves at the middle parts of the experimental plants (*S. domestica*, fourth macroblast leaf; *P. pyraster*, sixth macroblast leaf). The leaf samples were taken from four plants growing in each of the two water regime variants. Measurements were performed in triplicates for each

Table 1 Climatic–geographic description of the original stands of woody plants (Lapin et al. 2002)

Taxon	Location	Altitude (m)	Exposure	TI. (°C)	TVII. (°C)	Precipitation (mm)	Type	Subtype
P. pyraster	Tŕnie	540	S	− 3	18	750	MW	W6
S. domestica	Kosihovce	250	S-SE	− 2	19	600	W	W4

TI. the average temperature in January; *TVII.* the average temperature in July; *W* warm region; *W4* warm, moderately dry, with mild winter; *MW* moderately warm region; *W6* moderately warm, humid, highland climate plant. The leaf surface was not treated before sampling and measurement.

The water potential of the leaf tissues (Ψ_{wl}) was determined by psychrometric measurement performed by Wescor (model Psypro, EliTech Incc, Logan, UT, USA) using a C-52 sample chamber at an ambient temperature of 24 °C. Data were analyzed by multifactor analysis of variance (ANOVA) to detect significant factors (water regime/taxon) influencing water potential. They were not subject to further analysis, and only provided information on the physiological state of the aboveground organs.

At the end of the experimental period, the root system of seedlings was manually extracted from the growth substrate by washing in a water bath, while carefully preserving the entire root structure. In both variants with different levels of the growth substrate saturation, 10 plants were analyzed for each taxon.

Root system parameters measured

The WinRhizo REG 2009 system (Regent Instruments, Canada, SK0410192) was used for analytical processing of the plant root system. Image analysis of the root system allowed the evaluation of root morphology, topology, and architecture, using washed and growth substrate-free roots.

The following parameters were measured: root length (mm), root surface area (mm^2), root volume (mm^3), average root diameter (mm), and the volume of particular root fractions (mm^3). After assessment of the qualitative and quantitative parameters of the root system, its dry weight was determined by drying at 105 °C. The relative values of dry matter and water content were calculated, as well as SRL and other functional traits: R:S and fine-to-coarse root volume ratio (F/C).

Interspecific differences and the effect of different levels of growth substrate saturation on selected root parameters were calculated: length, surface, volume, diameter, and dry weight. The SRL, which represents the ratio between root length and root weight, was calculated from the basic data.

The ratio of the volume of fine and coarse roots was also evaluated. In the analysis, the volume of fine roots ($\phi < 2$ mm) and the volume of coarse roots ($\phi > 2$ mm) were quantified to calculate the F/C ratio.

Statistical analysis

Mathematical and statistical data analysis was performed using the Statgraphics Centurion XVII software (StatPoint Technologies, USA, XVII (license number: S7B0-D10A-57C0-P00S-20P1).

The data obtained from direct measurements (using WinRhizo software) were checked for normality (Shapiro-Wilk's test at significance level $\alpha = 0.001$) and homogeneity (Leven's test at significance level, $\alpha = 0.05$). Grubbs' test was used to detect and remove single outliers in the experimental data set. Data for analyzed parameters were normally distributed and met the assumption of homogeneity. A log transformation was applied in the data set "volume of coarse roots" to restore symmetry of the data.

Multifactor analysis of variance (ANOVA) was used to assess differences in root parameters of *P. pyraster* and *S. domestica* grown in the two variants with different levels of growth substrate saturation (drought and control) to identify interspecific differences in root system development and to obtain information on the effect of drought on underground organs of the woody plants. The obtained data were evaluated by one-way ANOVA to assess the effects of differential water regimes on root growth. The differences in functional traits and root parameters were evaluated by post hoc analysis with Tukey HSD test at significance levels of 0.05 and 0.01.

The relationship between root dry mass and volume of fine and coarse root fractions was evaluated by regression analysis.

Results

Growth substrate saturation and taxon significantly influenced the water potential of experimental plants. The results of the Tukey HSD test, and the average values for leaf water content in *P. pyraster* and *S. domestica* grown in the two water regime variants are shown in Table 2.

The water potential of leaf tissues was species-dependent, and was significantly lower in *S. domestica* compared with *P. pyraster*. In the control, Ψ_{wl} was − 2.83 MPa and in the drought group, Ψ_{wl} was − 3.37 MPa. Significantly low values of leaf water content (54% in control and 53% in drought) were recorded in *S. domestica*. The water potential of *P. pyraster* leaf tissues was also affected by drought ($\Psi_{\mathrm{wl}} = -2.25$ MPa) compared with the control ($\Psi_{\mathrm{wl}} = -1.83$ MPa).

Table 2 A two-way ANOVA analysis of the measured water potential of leaf tissues (Ψ_{wl}) and the leaf water content (LWC) in the pot experiment with *P. pyraster and S. domestica* seedlings, comparing the effects of taxon (T), drought treatment (R), and interaction between them (T*R). Significant differences ($P < 0.05$) are marked in italics. The multiple comparison of means was performed using 95% Tukey HSD. Data are the mean values ± SD (n = 12). Mean values followed by a different letters differ significantly

Parameter	*P-value*	*P. pyraster*		*S. domestica*	
	T/R/T*R	Control	Drought	Control	Drought
Ψ_{wl} (MPa)	*0.00/0.01*/0.95	− 1.83 (± 0.34) a	− 2.25 (± 0.48) b	− 2.83 (± 0.71) c	− 3.37 (± 0.71) d
LWC (%)	*0.00*/0.07/0.55	58.03 (± 2.85) a	55.88 (± 1.55) ab	54.15 (± 0.63) c	53.00 (± 1.14) d

These data helped to document the different properties of the two species studied under conditions of differential water regimes (control and drought). The low values of Ψ_{wl} are related to the water content of the leaves (LWC) and can be indicative of the potential capacity of plants to uptake available water.

The root system of 1-year-old seedlings was analyzed by the WinRhizo software, which allowed the root length and root diameter to be directly measured, and the root surface area and volume of analyzed plants to be calculated.

Effect of drought on the basic root parameters of *P. pyraster* and *S. domestica*

The results of ANOVA for most of the scanned root parameters allowed us to reject the null hypothesis regarding the mean values. Significant differences between *P. pyraster* and *S. domestica* were identified in root length, root surface area, root system volume, specific root length, and parameters expressing the volume of fine and coarse root fractions. The null hypothesis was adopted for average root diameter and the fine-to-coarse root volume ratio (Table 3). A significant effect of reduced water content in the growth substrate was found for all root parameters within the complex set of experimental plants.

Quantitative data analyses were performed, including multiple comparisons of means using Tukey's honestly significant difference (HSD) procedure (Table 3). *S. domestica* formed a longer and bulkier root apparatus with more than twice the surface area of that from *P. pyraster*. Differences in the examined parameters were almost twofold between the studied tree species.

Table 3 A two-way ANOVA analysis of all parameters measured in the pot experiment with *P. pyraster* and *S. domestica* seedlings, comparing the effects of taxon (T), drought treatment (R), and interaction between them (T*R). Significant differences ($P < 0.05$) are marked in italics. The multiple comparison of means (n = 20) was performed using 95% Tukey HSD. Mean values followed by a different letters differ significantly

Parameter	*P* value (T/R/T*R)	*P. pyraster*	*S. domestica*
Root length (mm)	*0.00/0.00/0.00*	5673.68 (± 1455.89) a	9893.31 (± 4964.18) b
Specific root length (mm mg^{-1})	*0.00/0.00*/0.93	6.93 (± 2.49) b	5.09 (± 1.27) a
Root surface area (mm^2)	*0.00/0.00/0.00*	9244.13 (± 2598.83) a	19,133.10 (± 9957.75) b
Root volume (mm^3)	*0.00/0.00/0.00*	3224.17 (± 988.69) a	7414.33 (± 4361.70) b
Average root diameter (mm)	0.74/*0.00/0.00*	0.82 (± 0.28) a	0.80 (± 0.11) a
Fine root volume (mm^3)	*0.00/0.00/0.00*	1274.21 (± 469.56) a	2837.84 (± 1403.69) b
Volume of coarse roots (mm^3)	*0.00/0.00/0.00*	2416.50 (± 1529.59) a	4658.66 (± 3056.60) b
Fine-to-coarse root ratio	0.93/*0.00*/0.33	0.73 (± 0.45) a	0.73 (± 0.34) a
Dry weight of root (mg)	*0.00/0.00/0.00*	854.07 (± 268.92) a	2113.65 (± 1252.38) b
Dry weight of shoot (mg)	*0.00/0.00/0.00*	1424.62 (± 825.66) a	2295.65 (± 1604.64) b
Root to shoot mass ratio	*0.00/0.00*/0.34	0.76 (± 0.32) a	1.03 (± 0.26) b
Water content in roots (%)	*0.00/0.01/0.04*	63.34 (± 2.47) a	58.64 (± 2.88) b

However, no differences were found in the average root diameter. The parameter is calculated as the average thickness of all root system fractions. Basic comparison in the ANOVA model revealed that the average root diameter was influenced by a lack of water (Table 3).

The null hypothesis was adopted for the root parameters of *P. pyraster*—root length, SRL, root surface area, root volume, fine root volume, dry weight of root, as well as the water content in roots (Table 4). The lack of water had a non-significant effect on the abovementioned root parameters. Growth of the *P. pyraster* root system remained balanced even with low water saturation of the growth substrate, as documented by the multiple comparisons of means using Tukey test (Table 5). In the drought variant, the total volume of *P. pyraster* roots, and fine root volume were not significantly different compared with that of the control. Lack of water affected the mean root diameter. The color of thickened roots was visibly altered, from white to brown.

The interspecific differences in root response to drought

Under drought conditions, several parameters of the *S. domestica* root system were reduced (Table 5); the root length decreased by 63%, the root surface area by 61%, and the root volume by 67%. Conversely, a 38% increase was observed in the SRL.

Table 4 One-way ANOVA analysis for all parameters of 1-year-old seedlings of *P. pyraster and S. domestica* under conditions of differential water regime. Significant differences ($P < 0.05$) are marked in italics

Parameter	*P. pyraster*	*S. domestica*
Root length (mm)	0.8591	*0.0000*
Specific root length (mm mg^{-1})	0.1246	*0.0017*
Root surface (mm^2)	0.9966	*0.0000*
Root volume (mm^3)	0.2445	*0.0000*
Average root diameter (mm)	*0.0000*	0.0521
Fine root volume (mm^3)	0.1752	*0.0000*
Volume of coarse roots (mm^3)	*0.0211*	*0.0000*
Fine-to-coarse root ratio	*0.0081*	*0.0440*
Dry weight of root (mg)	0.1022	*0.0000*
Dry weight of shoot (mg)	*0.0000*	*0.0000*
Root to shoot mass ratio	*0.0005*	*0.0053*
Water content in roots (%)	0.5759	*0.0010*

Significant interspecific differences were observed in traits of the underground organs. Compared with *P. pyraster*, *S. domestica* had a larger root system in the juvenile stage of growth, as documented by a detailed analysis (Table 3). Water scarcity had a significant negative effect on this taxon, as shown by a marked decrease in the accumulation of mass in the underground organs and by a significant reduction in root length, volume, and surface. The SRL of *S. domestica* was significantly lower than that of *P. pyraster* (Table 5).

The volume of fine root classes ($\phi < 2$ mm) and the effect of water scarcity on this parameter were further analyzed for both species. *S. domestica* had a significantly higher root volume for both fine and coarse root classes in the control variant compared with *P. pyraster* (Table 5). However, this taxon responded to water scarcity with a marked decrease in the accumulation of root mass, which resulted in a significant decrease in root volume in fine root classes with a diameter up to 2.00 mm and in coarse root classes (Table 5).

The lack of water had no negative effect on the volume of fine roots ($\phi < 2.00$ mm) in *P. pyraster* (Table 5). However, the volume of coarse roots under conditions of water scarcity was reduced by half. In this context, the F/C ratio was also analyzed. The influence of growth substrate saturation was evident for the studied taxa in the volume of different root classes. Under drought conditions, both *P. pyraster* and *S. domestica* had significantly higher proportions of fine roots in their root systems, demonstrated by an increase in the F/C ratio (Table 5).

The results (Table 3) revealed significant differences between the studied taxa and variants with different levels of growth substrate saturation. Under conditions of sufficient water supply, *P. pyraster* distributed more dry matter to the aboveground organs (shoots and leaves) than to the root system. The mean R:S ratio for *P. pyraster* was 0.54 (Table 5). Under conditions of water scarcity, the mean value of the parameter increased significantly to 0.97, which demonstrated a more even distribution of biomass between the aboveground and underground organs. *S. domestica* had a similar model of dry matter distribution, although its root system accumulated significantly more dry matter (R:S ratio = 0.88) compared with the root system of *P. pyraster*. Under drought conditions, *S. domestica* preferably invested dry matter in underground organs (R:S ratio = 1.18).

Table 5 Parameters of *P. pyraster* and *S. domestica* seedlings based on the level of growth substrate saturation (control/drought). Data are the means ± SD (n = 20). The multiple comparison of means was performed using 95% Tukey HSD. Mean values followed by a different letters differ significantly

Parameter	*P. pyraster*		*S. domestica*	
	Control	Drought	Control	Drought
Root length (mm)	5733.88 (± 1643.55) a	5613.48 (± 1328.70) a	13,776.30 (± 2678.52) b	5120.80 (± 1964,78) a
Specific root length (mm mg^{-1})	6.07(± 2.34) a	7.79 ± (2.43) a	4.28 (± 0.70) a	5.90 (± 1.20) b
Root surface area (mm^2)	9246.74 (± 2993.89) a	9241.53 (± 2301.05) a	27,442.80 (± 5507.32) b	10,823.30 (± 5054.88) a
Root volume (mm^3)	3534.80 (± 1175.80) a	2975.66 (± 785.31) a	11,146.60 (± 2633.84) b	3682.02 (± 1506.55) a
Average root diameter (mm)	0.60 (± 0.10) a	1.04 (± 0.23) b	0.76 (± 0.09) a	0.85 (± 0.11) a
Fine root volume (mm^3)	1091.14 (± 446.74) a	1388.24 (± 465.95) a	3966.45 (± 834.15) b	1709.40 (± 795.78) a
Volume of coarse roots (mm^3)	3151.56 (± 1103.05) b	1587.42 (± 600.25) a	7180.19 (± 2161.90) b	2137.13 (± 959.54) a
Fine-to-coarse root ratio	0.46 (± 0.26) a	0.98 (± 0.38) b	0.58 (± 0.16) a	0.88 (± 0.40) b
Dry weight of root (mg)	960.70 (± 320.21) a	758.10 (± 178.60) a	3246.90 (± 548.41) b	980.40 (± 395.61) a
Dry weight of shoot (mg)	2057.33 (± 727.89) b	791.90 (± 140.48) a	3773.70 (± 739.97) b	817.60 (± 183.12) a
Root to shoot mass ratio	0.54 (± 0.18) a	0.98 (± 0.27) b	0.88 (± 0.16) a	1.18 (± 0.25) b
Water content in roots (%)	63.66 (± 2.04) a	63.02 (± 2.91) a	60.51 (± 1.94) b	56.71 (± 2.39) a

In drought, *P. pyraster* maintained the absorptive root surface unchanged, when increased the volume of the fine root fraction (Table 5). The different strategy of adaptation to drought has been confirmed for *S. domestica*, which accumulated more dry mass in the root system in comparison to aboveground organs (significant increase of R: S ratio).

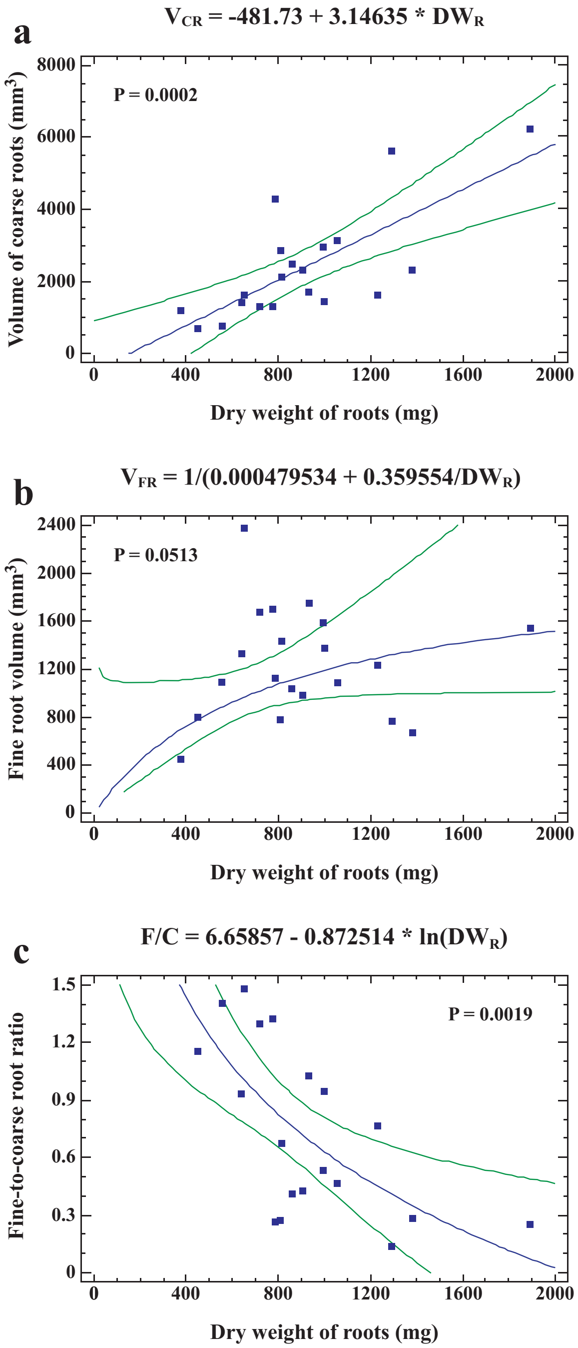
Associations between the volume of root fractions and dry weight of roots

It is difficult to interpret species' plastic reactions to drought, especially when species exhibit multiple and different responses to the studied factors. It is necessary to identify the functional significance of a particular trait in the physiological expression, such as growth. The volume of the coarse root fraction (V_{CR}) for *P. pyraster* was significantly correlated (r = 0.74, P = 0.002) with root dry matter (DW_R) (Fig. 1a). A moderately strong positive correlation was found between the fine root volume (V_{FR}) and root dry matter (r = 0.44, P = 0.0513) (Fig. 1b). However, there was a moderately strong negative correlation between the F/C ratio and DW_R (r = − 0.66, P = 0.0019). This relationship revealed that a decrease in the dry weight of *P. pyraster* roots was accompanied by a significant increase in the fine root fraction (Fig. 1c); however, the coarse root fraction was negatively affected by drought.

A strong positive correlation was found between the fine root volume and root dry matter (r = 0.92, P < 0.0001) of *S. domestica*, and between the volume of coarse roots (r = 0.91, P < 0.0001) and DW_R. (Fig. 2a, b). The relationships between the abovementioned root traits were highly significant and closely correlated. However, the F/C ratio was not significantly correlated with DW_R (r = − 0.41, P = 0.0707) (Fig. 2c). These results suggest that, compared to *Pyrus*, *Sorbus* plants failed to effectively distribute dry matter between fine and coarse root fractions under drought conditions.

Discussion

Studies investigating the effect of drought on long-lived trees have focused primarily on responses of aboveground organs; much less attention has been paid to the root systems. Several studies in the literature have focused on the importance of root system tolerance or adaptation to drought. However, data on the depth of roots or their density are no longer sufficient. In the present study, we investigated interspecies differences in the root traits of *S. domestica* and *P. pyraster* in the juvenile growth stage, especially root length and root volume. The selected root parameters were already presented in the earlier work Paganová and Jureková (2017). The results are comparable with findings of

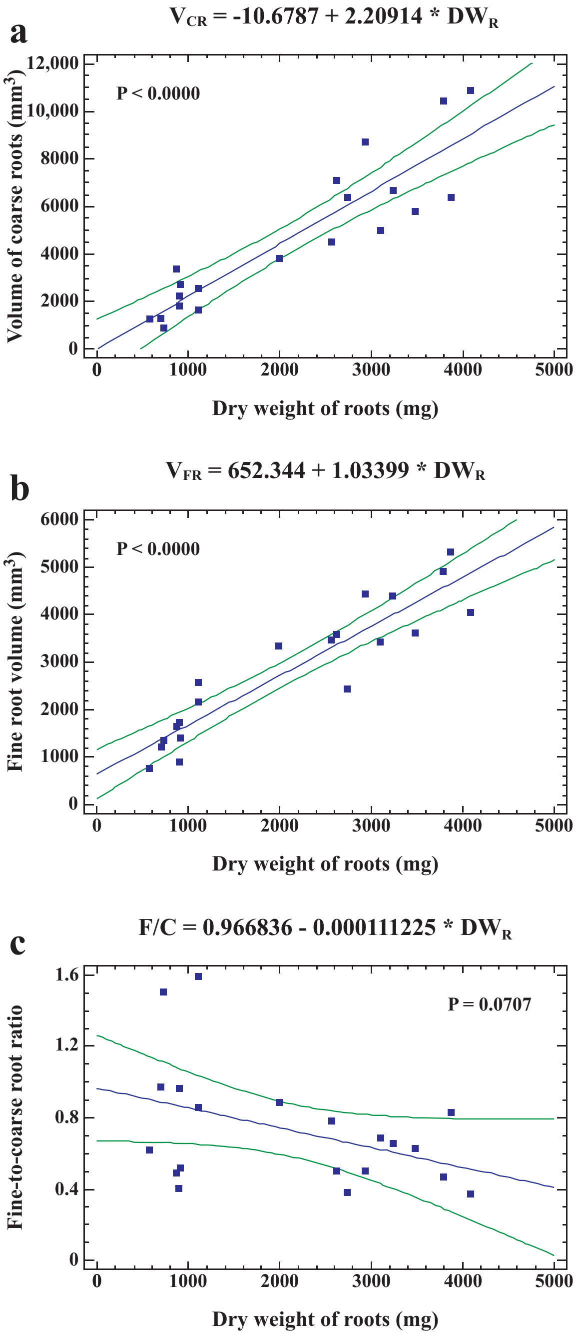


a $V_{CR} = -481.73 + 3.14635 * DW_R$

b $V_{FR} = 1/(0.000479534 + 0.359554/DW_R)$

c $F/C = 6.65857 - 0.872514 * \ln(DW_R)$

Fig. 1 Relationship between the volume of the root fractions and dry matter of the root system of *P. pyraster* (**a**), where volume of coarse roots (V_{CR}) and the dry weight of roots (DW_R) were significantly correlated ($r = 0.74$). **b** There was a non-significant correlation between the fine root volume (V_{FR}) and DW_R. **c** There was a moderately strong negative correlation ($r = -0.66$) between fine-to-coarse root ratio (F/C) and DW_R. Decrease in dry weight of roots was accompanied by a significant increase in the fine root fraction (**c**), while coarse root fraction was negatively affected by drought (**a**)



a $V_{CR} = -10.6787 + 2.20914 * DW_R$

b $V_{FR} = 652.344 + 1.03399 * DW_R$

c $F/C = 0.966836 - 0.000111225 * DW_R$

Fig. 2 Relationship between the volume of the root fractions and dry matter of the root system of *S. domestica* (**a**), where volume of coarse roots (V_{CR}) and dry weight of roots (DW_R) were significantly correlated ($r = 0.92$). **b** There was a significantly strong correlation between the fine root volume (V_{FR}) and DW_R ($r = 0.91$). **c** There was a non-significant correlation between the fine-to-coarse root ratio (F/C) and DW_R ($r = -0.42$). Volume of the fine and coarse root fractions was strongly correlated with changes in the dry weight of roots (**a, b**). The distribution of dry matter for fine root fractions was not effective in conditions of drought, while these conditions affected dry matter of roots (**c**)

Davies and Bacon (2003) and Manes et al. (2006), who observed a decrease in the root volume and root length of broadleaved tree species under drought stress.

In the complex set of experimental plants, reduced water content in the growth substrate had a significant effect on all evaluated root traits. Drought affects the structure and growth of coarse and fine roots, and their functions (Kozlowski and Pallardy 2002; Brunner et al. 2015). In the present study, we observed that drought affected coarse root production, as well as fine root production. This is an interesting finding; in relation to the response of woody plants under drought conditions, the formation of coarser roots and the effect of drought on the functionality of the thinnest roots have been previously investigated (Davies and Bacon 2003).

The reduction in *S. domestica* root volume in the drought variant versus the control was marked (− 57 %). In *P. pyraster*, the volume of fine roots ($\phi < 2.00$ mm) was not affected by the lack of water. However, had a significant influence on the increased average root diameter (+ 73%) in *P. pyraster*. Thickened roots changed from white to brown. Thickening and hardening of roots in ornamental plants exposed to water stress have been described by Franco et al. (2006). Drought induced formation and deposition of suberin in the cell walls (Vandeleur et al. 2009; Moura et al. 2010), which is the element that changes the root diameter, water content in roots, and water-use efficiency. The suberinization of roots minimizes water losses to the soil during conditions of water deficit (Steudle 2000). The results also implied that, even under conditions of water scarcity in the growth substrate, the water content in the roots of *Pyrus* did not decrease and did not change significantly.

Studies on the root system of woody plants here also focused on the ratio of the root dry mass to the dry mass of aboveground organs (R:S). It is well documented in the literature that woody plants adapted to drought have a higher R:S ratio and a deeper root system than those of species growing in humid soils (Kozlowski and Pallardy 2002; Hartmann 2011). Sultan and Bazzaz (1993) studied the *Polygonum persicaria* genotype and showed that under conditions of moderate drought, the R:S ratio increased by 70%, and by 100% under conditions of strong drought. The traits of adaptation have been described as “plastic adjustment.” The results obtained in the present study also imply that experimental juvenile woody plants have their own strategy of distributing dry mass into the aboveground and underground organs. Redistribution of dry matter is species-dependent. Compared to *Pyrus*, *Sorbus* accumulated more dry mass in the root than in the shoot; however, the increase in the R:S ratio was greater in *Pyrus* than in *Sorbus*. Comas et al. (2013) did not consider the R:S ratio to reflect the plants’ response to water scarcity. They reported that the most frequent growth and morphological response of woody plants to drought is a reduction in the biomass in fine roots. Similarly, Brunner et al. (2015) reported that the R:S ratio tends to increase under drought conditions, while the biomass of fine roots is often reduced as a consequence of reduced transpiration. The results of the present study show that under drought conditions, *P. pyraster* increased its R:S ratio and the volume of its fine roots maintained unchanged. The reduction in volume was related to coarse roots. When adapting to drought, *S. domestica* exhibited a significant reduction in the growth and volume of both fine and coarse roots.

Based on the present data, *Pyrus* and *Sorbus* present two strategies of adaptation to drought, which were described in more detail by Verslues et al. (2006). *P. pyraster* demonstrates tolerance to dehydration (root thickening), while *S. domestica* avoids stress (reduced growth). *S. domestica* can prevent water loss by stomatal closure, and over the longer term, by restricting shoot growth leading to an increased R: S ratio. Under conditions of severe drought, *S. domestica* avoids stress by early leaf dropping. According to a study by Kunz et al. (2016), the response of transpiration and stomatal conductance to drought in *S. domestica* might indicate an isohydric strategy.

Comparison of functional root traits in the studied species revealed a significant species response. Under drought conditions, *S. domestica* significantly decreased the root length, root surface, and root volume. The lack of water did not affect the abovementioned root traits in *P. pyraster*. This taxon maintained balanced growth of the root system under conditions of low water saturation. This has been well documented in other species by Kozlowski and Pallardy (2002), Mokany et al. (2006), and Markestejin and Poorter (2009).

Conclusion

The results of *P. pyraster* and *S. domestica* roots grown under drought conditions indicate that the functional root traits are species-dependent and reflect the reaction of specific tree taxa to water scarcity. The present data indicate (1) *Pyrus* has adapted to drought via root thickening, increasing the ratio of fine roots. *Pyrus* maintains balanced absorptive root surface and water content in its roots, even under conditions of reduced water content in the substrate. (2) The different strategy of adaptation to drought has been confirmed for *Sorbus* and documented by the significant increase of R: S parameter. When adapting to drought, *Sorbus* had significantly reduced growth and the water content in its roots also decreased. (3) Based on the present data, *Pyrus* and *Sorbus* present two strategies of adaptation to drought. *P. pyraster* demonstrates tolerance to dehydration (root thickening), while *S. domestica* avoids stress (reduced growth) by restricting shoot growth leading to an increased R: S ratio.

Knowledge on root functional traits enhances understanding of adaptive phenotypic plasticity and contributes to a better understanding of resource (water) management at the level of plant root systems

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ZJ wrote the first draft of the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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