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Relationship between tree transpiration and soil properties: Do trees with higher water demand promote formation of soils with higher water retention?

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Abstract: Soil water availability influence plant growth, vegetation, particularly trees, can in turn substantially alter soil properties affecting soil water availability. This study investigates whether tree species with higher transpiration rates promote the development of soils with a higher water-holding capacity using common garden experiment in post-mining heap in northwest Czechia, where several tree species were planted directly into bare overburden. We focused on three monocultures of alder (*Alnus glutinosa*), oak (*Quercus robur*), and spruce (*Picea omorica*). Tree sap flow was measured and used to estimate transpiration at both individual and stand levels. At the same time, soil moisture and water-holding capacity were assessed in each stand. Alder and oak showed similarly high transpiration rates, significantly exceeding those of spruce. The alder stand exhibited the highest average annual soil moisture as well as the highest moisture during the vegetation and dormant season, significantly differing from oak and spruce, while oak soils had a significantly higher moisture than spruce. Water-holding capacity was the highest in oak soils, significantly exceeding that of alder and spruce. These results support the hypothesis that tree species with a higher water demand foster the development of soils with an enhanced water retention capacity.

Keywords: Soil formation; Evapotranspiration; Niche construction; Soil water retention.

1 INTRODUCTION

Water availability is one of the principal environmental factors influencing forest distribution, tree growth, and tree size (Alavi et al., 2002; Brzostek et al., 2014; Gazol et al., 2017; Landsberg and Waring, 2017; Kozlowski, 1982). Conversely, forests can significantly influence soil moisture dynamics through water uptake by vegetation (Martin-Guay et al., 2022) and affect soil hydraulic properties (Jarvis et al., 2013). At broader spatial scales, this uptake may affect local and regional water availability, with important implications for land management and the potential for future afforestation (Hoek van Dijke et al., 2022), which in the end is important not only for the vegetation itself but for the whole ecosystem functioning and water regime on the landscape scale, which in turn is crucial for the wellbeing of human society. Tree water demand may become an even larger issue in the future, as ongoing global warming may cause a shift in the current distribution of precipitation and more persistent rainfall regimes (Francis et al., 2020; Pfleiderer et al., 2019). Besides large-scale climatic change, water availability can also be affected by soil conditions and soil water uptake by plants (Bassett, 1964; Lagergren and Lindroth, 2002; Piedallu et al., 2013).

Trees modify soil properties and this could be viewed as an adaptive strategy affecting water dynamics at site and landscape levels. Individual tree species differ substantially in their water requirements, and water availability plays a critical role in shaping both the presence of particular species and overall forest species composition. It is well known that trees affect soil conditions and this effect is species-specific (Aponte et al., 2013; Binkley and Giardina, 1998; Frouz et al., 2013). According to the adaptive niche construction theory, organisms can modify their habitat to their own advantage (Callahan et al., 2014). In other words, trees promote soil conditions that are beneficial for them (Binkley and Giardina, 1998). This effect is also known as positive intraspecific plant-soil feedback, documented by multiple studies (Kulmatiski et al., 2008). Plant-soil feedback can be mediated by soil biota (e.g., plant symbionts), but also by other soil properties (Frouz, 2024). Particularly in terms of nutrients, it is well known that trees which require more nutrients form litter which decomposes faster and provides fast turnover, which corroborates with a similar plant-soil feedback loop known in plant ecology, where fast-growing plants requiring more nutrients produce litter which decomposes fast and promote a fast nutrient turnover (Cornwell et al., 2008).

There is also extensive evidence in the literature that trees affect various soil hydraulic properties (Cejpek et al., 2013, 2018; Frouz and Kuráž, 2013; Hansson et al., 2011; Jačka et al., 2021; Seiwa et al., 2021), which in the end affect soil water availability (J. Li et al., 2013; Y. Li et al., 2015). Modification of these soil properties is often related to patterns of soil organic matter accumulation and distribution in the soil profile (Frouz and Kuráž, 2013; J. Li et al., 2013; Rawls et al., 2003; Zhao et al., 2022),

which vary between individual tree species (Frouz et al., 2013; Hüblová and Frouz, 2021; Peng et al., 2020; Vesterdal et al., 2002, 2008).

However, little attention has so far been paid to the question of whether modifications of soil hydraulic properties and soil water-holding capacity in particular, are related to the water demand of trees. In this study, we test the hypothesis that trees which need more water (have a higher transpiration rate), produce at the same time soil with a higher ability to store water (have a higher soil moisture).

2 MATERIALS AND METHODS

2.1 Study ares

The studied forest stands are located at the Vintířovská spoil heap, part of the broader Velká Podkrušnohorská spoil heap complex, which lies within the Sokolov lignite mining region in northwestern Czechia. The site is situated at approximately 500–600 meters above sea level, with an average annual temperature of 6.8 °C and annual precipitation of around 650 mm. The substrate consists of slightly alkaline Miocene claystone from the Tertiary period, primarily belonging to the Cypris Formation, which was excavated as overburden during coal mining. Dominant minerals include kaolinite, illite, and montmorillonite, along with quartz and carbonates, often enriched with geogenic organic matter (Frouz et al., 2011; Kříbek et al., 1998). During the mining process, several overlying individual sediment layers with usually have similar properties were extracted and mixed, leading to very uniform material zones spanning several hectares (Frouz et al., 2011). Our research focused on one such uniform area. The material is nutrient-rich, contains a high proportion of clay (about 70%), and after deposition, exhibits a pH between 8 and 9 during early successional stages (Kuráž et al., 2012).

This section of the heap (severa hundred ha) was planted with several tree species, where each species was replanted as a monoculture forest stands, each with an area of about 0.5 to 2 ha, this patchwork of monoculture forest stangs creating a unique opportunity akin to a “common garden experiment” (Frouz et al., 2013). These adjacent patches, laid out in a grid-like or mosaic arrangement, enable comparative analysis of tree performance and soil development under various tree species on nearly identical substrates. Additional information about the site can be found in Frouz et al. (2013) and Jačka et al. (2021).

Three sampling plots were established on the Vintířovská spoil heap. Each plot measured approximately 20 by 50 meters and was predominantly occupied by a single tree species: black alder (*Alnus glutinosa*), pedunculate oak (*Quercus robur*), or Serbian spruce (*Picea omorica*). These species were chosen because their leaf litter varies significantly in quality. As reported by Frouz et al. (2013), the average carbon-to-nitrogen (C/N) ratios of the fallen litter were 24 for alder, 35 for oak, and 52 for spruce. The plots were situated next to each other and shared identical conditions in terms of substrate type and age, having all been planted in 1978. As a result, differences in soil development and properties of the sites can be primarily attributed to the tree species used in reclamation. Soil chemical and physical properties on these sites have been extensively studied in the past. Table 1 summarizes key soil physical and chemical properties based on Frouz et al. (2013) and Jačka et al. (2021).

2.2 Meteorological measurement

Meteorological variables were measured at a station located in an open area about 200 m from the forest stands. The station is equipped with sensors for measuring global radiation (EMS 11S, EMS Brno), air temperature and humidity at a height of 2 m (EMS 33S in an Al60 radiation shield, EMS Brno), and precipitation (Pronamic Pro, Denmark) and soil temperature at depths of 15 and 30 cm. The measured data was used to calculate potential evapotranspiration (Penman 48) and vapor pressure deficit in the manufacturer's application (EMS Brno), where the measured data from the sap flow and soil moisture sensors was also collected, visualized, and archived.

2.3 Measurement of sapflow and tree growth

Sap flow and tree growth measurements were conducted from 2019 to 2023 covering the vegetation seasons of these years. To select trees for sap flow measurements, a census of trees was conducted in the study area. Three sampling plots were established in the study area, each 200 m^2 in size. All trees in these plots were counted and the diameter at breast height (DBH) of all trees was measured. With this overview, five trees of each species were selected for sap flow measurements to cover the range of tree DBH of a particular species. At the same time, trees used for measurement were selected in a way that the closest distance between trees of different species was much shorter than between the most distant tree of the same species, in order to avoid pseudo replication. Properties of selected trees are summarized in Table 2. Sap flow measurements were performed using EMS81 sensors operating according to the principle of the heat balance method (Čermák, 1973; Kučera, 1977), connected in the SDI-12 network to a common GreyBox N2N data logger. For each selected sample, the trunk circumference diameter was simultaneously recorded using DR26 sensors with µm resolution.

2.4 Soil hydrological properties, soil moisture, and root distribution

Soil moisture was monitored using Campbell CS650 sensors installed to a depth of 30 cm, capturing the upper soil profile continuously for a whole year from 2019 to 2024. In each forest stand, three sensors were installed approximately 50 meters apart to cover the area where transpiration measurements were conducted. Sensor data were recorded continuously using separate MicroLog SDI MP data loggers.

To measure soil hydraulic properties, five trenches (70 cm wide and 30 cm deep) were made in each forest stand. Around each trench, three undisturbed soil cores (5 cm in diameter, 100 cm^3 volume) were sampled from a depth of 0-5 cm.

Table 1. Soil properties of different study sites, based on previous studies. Chemical properties based on Frouz et al. (2013), water infiltration based on Jačka et al. (2021).

Parameter	Alder	Oak	Spruce
Soil C content (%)	7.1	5.9	4.6
A horizon thickness (cm)	9.0	5.0	2.0
pH in water	6.6	6.9	7.2
Water infiltration K_s ($m10^{-5}$ s^{-1})	6.9	3.9	1.8

Table 2. Parameters of different tree stands and soil measured in this study.

Parameter	Alder	Oak	Spruce
Stand tree density (tree ha^{-1})	1303±1233	862±65	255±219
Stand average tree DBH (cm)	14.0±7.2	12.6±7.4	14.7±10.0
Sampled tree DBH range (cm)	16.2 – 22.9	15.4 – 27.7	15.3 – 30.9
Sampled tree average DBH (cm)	19.2±2.2a	23.5±5.2b	24.2±5.3b
Sampled tree DBH increase (mm y^{-1})	0.92±0.62b	1.86±0.56a	0.96±0.42b
WDPT 0-5 cm (s)	42±15a	56±41a	230±75b
WDPT 25-30 cm (s)	15±5	9±4	26±2

Statistically homogeneous groups are marked by the same letter (one-way ANOVA, Fisher post hoc test $p<0.05$) if no letters are present no significant difference was found.

Moreover, two undisturbed soil cores were taken from each trench at a depth of 25-30 cm. This resulted in 15 undisturbed soil samples (cores) from a depth of 0-5 cm and 10 samples from a depth of 25-30 cm. At the same sites, three composite disturbed soil samples were taken from the same depths in each forest stand used for a WDPT test, and additional undisturbed cores from depths of 0-5, 5-10, 10-20, and 20-30 cm, yielding three cores for each depth and tree species to study root distribution with depth. To assess volumetric moisture at full water saturation and at field capacity, soil cores were fully saturated in the lab over a two-week period at room temperature by placing them in a tray filled with demineralized water. The cores were submerged in a way that their tops remained exposed to the air, allowing trapped air to escape during saturation. Once saturated, they were weighed and then subjected to a steady suction of –0.33 bar (~pF 2.5) using an Eijkelkamp Sand/Kaolin box to simulate field capacity conditions. This process continued until the samples reached a stable weight. Following, the cores were weighed again and then oven-dried at 105 °C for 48 hours. Field capacity was expressed as volumetric water content, and the degree of saturation was calculated by dividing the volume of water by the total pore space within the sample. The roots were washed, and fine roots (<2 mm) were separated, oven-dried and weighed. Soil water repellency was assessed using the water drop penetration time (WDPT) test, following the procedures described by Kraemer et al. (2019) and Doerr (1998). Summarized, a portion of the soil sample was spread in a Petri dish and oven-dried at 40 °C for 15 hours. Subsequently, a drop of distilled water (58 ± 5 µl) was carefully applied to the soil surface, and the duration required for complete absorption was measured. This procedure was repeated three times per sample.

2.5 Data processing and statistical analysis

The EMS81 measuring system indicates sap flow in kg/hour, only subtraction of the "baseline value" is necessary (Kučera et al., 2020). This task and other calculations were performed using the Mini32 software (EMS Brno). The calculation of vegetation transpiration was performed according to a model describing the average transpiration of all tree samples during a period of unrestricted access to soil water depending on DBH (Kučera et al., 2020). The regression parameters of the relationship between sap flow and DBH were used to calculate the sap flow of all trees, then summarized for the study area and converted to 1 ha (Čermák et al., 2004). This process was performed for all three stands. The calculation was based on 10-minute intervals and converted to hourly, daily, and monthly averages and maximums.

General linear models (GLM) with tree species, year, and tree DBH were used to compare the sap flow and transpiration of individual trees. For this comparison, monthly values of sap flow and transpiration were used. For the sap flow, these monthly data were based either on daily means or on daily maxima.

Two-way ANOVA was used to compare soil moisture at saturation and water field capacity, using tree species and soil depth as factors. Likewise, soil moisture was compared by means of two-way ANOVA using season (vegetation season vs dormant season) and tree species as factors. Similarly, root biomass and WDPT at various depths were compared by means of two-way ANOVA using tree species and depth as factors. In addition to two-way ANOVAs, one-way ANOVA was used to compare the above-mentioned parameters between tree species at a specific depth or in a particular season. One-way ANOVA was also used to compare transpiration of whole forest stands obtained in various years. All computations were performed using Statistica 13.0.

3 RESULSTS

When maximum daily values were considered, alder had a significantly higher sap flow than oak, which had a significantly higher sap flow than spruce (Fig. 1a, Table 3). However, comparing mean daily values, alder and oak sap flows were significantly higher than those of spruce, without a significant difference between oak and alder (Fig. 1b, Table 3). Consequently, total annual transpiration of alder and oak was significantly higher than that of spruce without a significant difference between the first two species (Figs 1c, 1d). Both sap flow and transpiration of individual trees were also affected by tree DBH (Fig. 2, Table 3) and varied between individual years (Table 3).

Root biomass was the highest in the 0-5 and 5-10 cm surface layers, and significantly lower in deeper layers. This pattern was similar for all species, without any significant difference between species, nor any significant interactions between soil depth and species (Fig. 3, Table 3).

There was no significant difference in soil moisture during water saturation between either tree species or particular depths (Fig. 4a, Table 3). The significantly highest moisture at field capacity was found in oak, followed by alder, for which it was significantly lower than for oak but significantly higher than for spruce, which had the lowest moisture at water field capacity (Fig. 4b, Table 3). This pattern applied to the topsoil layer as well as to both layers pooled. However, when the deeper layer was evaluated separately, no significant difference was found between the tree species. Soil moisture in alder was significantly higher than in oak, which was higher than that of spruce (Fig. 4d, Table 3). These differences hold for the vegetation season as well as for the measurements outside the vegetation season. Soil moisture during the vegetation season was significantly lower than outside the vegetation season (Table 3).

WDPT differed significantly between forest stands as well as soil depths. WDPT was higher in the surface layer than in the deeper soil layer (Table 2). Spruce soil showed a significantly

higher WDPT than oak and alder soils, without significant differences between them. This was true for both layers evaluated together as well as for the surface layers separately (Table 2). When the deeper soil layer was evaluated separately, no differences in WDPT were found between tree stands (Table 2), which is also the reason for the significant interaction between soil depth and tree species found with two-way ANOVA (Table 3).

4 DISCUSSION

4.1 Relationship between sap flow and water retention

The results show that forest stands with species that have a high transpiration (such as alder and oak) also store most water in the form of soil moisture. This confirms our hypothesis that trees promote the formation of soil that satisfies their need for water (Fig. 5). This idea is supported by an earlier observation by Cejpek et al. (2018) made in the same area who found that reclaimed alder plantations have a higher water storage than unreclaimed sites dominated by birch, willow, and aspen. Cejpek et al. (2018) suggested that higher soil water storage of alder sites may be compensated by higher transpiration of alder stands indicated by other studies conducted at the same location (Bujalský et al., 2018).

The outcome of this study is a nice example of plant-soil feedback driven by modification of the soil environment by plants, which feeds back on altering conditions for plant growth (Frouz, 2024). It is generally known that trees depend on soil conditions while at the same time trees modify the soil in which they grow (Binkley and Giardina, 1998). The effect of trees on soil properties has been demonstrated in many studies (Aponte et al., 2013; Binkley and Giardina, 1998; Frouz et al., 2013). The feedback loop is well explored for nutrients. It has been demonstrated that trees which require more nutrients produce litter with a higher nutrient content, which decomposes faster, allowing faster nutrient return (Aponte et al., 2013). This is in agreement with the general relationship between nutrient demand and nutrient return showing that faster growing plants produce easily decomposable litter, which returns nutrients faster (Cornwell et al., 2008). Many studies also demonstrate a substantial effect of trees on soil carbon storage (Hüblová and Frouz, 2021; Peng et al., 2020; Vesterdal et al., 2002, 2008). There are also numerous studies showing that tree species and soil carbon storage affect soil hydraulic properties such as soil moisture, infiltration and water retention (Frouz and Kuráž, 2013; Jačka et al., 2021; J. Li et al., 2013; Seiwa et al., 2021). There is thus enough evidence that trees affect soil hydraulic properties in various ways, directly or indirectly via their effect on carbon storage and bioturbation (Frouz and Kuráž, 2013; Jačka et al., 2021; J. Li et al., 2013; Rawls et al., 2003; Seiwa et al., 2021; Zhao et al., 2022), and water availability is an important factor affecting tree growth (Bassett, 1964; Piedallu et al., 2013).

Despite that, the feedback loop between water demand by trees and water storage in the soil formed by those trees, as demonstrated in this study, is underexplored. Nevertheless, there can be a potential link here between water storage and nutrient cycling, as the trees that provide easily decomposable litter with faster nutrient turnover are also likely to support carbon accumulation in mineral soil, while trees producing less decomposable litter tend to accumulate more organic matter in overlying soil horizons (Vindušková and Frouz, 2013). As elaborated in detail below, accumulation of organic matter in mineral soil is likely to promote soil water storage in the soil (Rawls et al., 2003). On the other hand, organic matter in the forest floor, namely that of coniferous species, may often be water-repellent and reduce water infiltration and consequently the overall amount of water in the soil (Jačka et al., 2021; Kim et al., 2014; Neris et al. 2013). This is supported by earlier reports indicating larger water storage in broadleaf species compared to conifers (Frouz and Kuráž, 2013; Kim et al., 2014).

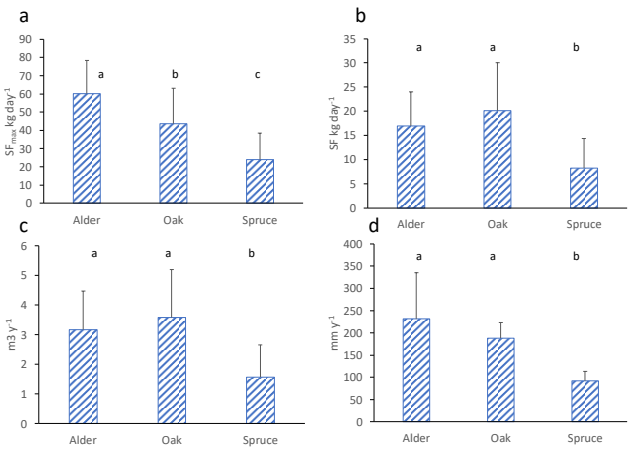


Fig. 1. Tree water use characteristics (±SD, n=5): a) maximum daily sap flow in a year, b) average daily suction flow, c) annual transpiration per tree, d) annual transpiration of forest stand. Statistically homogeneous groups of trees are marked by the same letter based on GLM considering tree DBH and year (a-c), or based on one-way ANOVA, d), in both cases using the Fisher post hoc test ($p<0.05$).

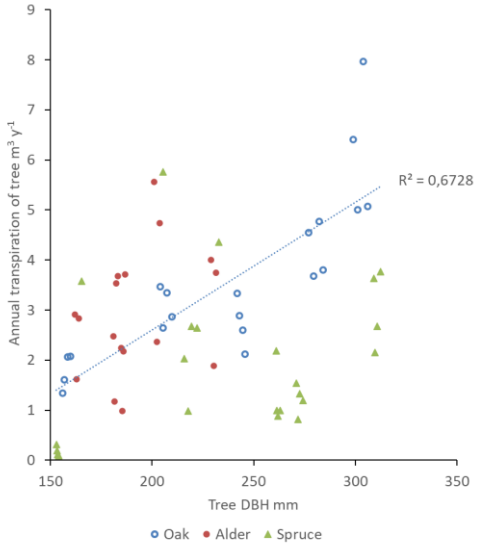


Fig. 2. Relationship between annual transpiration of trees and tree diameter at breast height (DBH). For each tree species, data from five trees and four years were used. Only the regression line associated with a significant regression coefficient is shown.

Table 3. Output of different statistical tests for values depicted in Figs 1-4 and Table 2, p-values and number of replicates are shown.

Parameter / Factor	Species	Depth	Interaction	n	Test
Root biomass	ns	<0.0001	ns	36	2wANOVA
Moisture at saturation	ns	ns	ns	75	2wANOVA
Moisture at FC	<0.0001	ns	ns	75	2wANOVA
WDPT	0.0079	0.0021	0.0207	18	2wANOVA
	Species	**Season**	**Interaction**		
Soil moisture	0.0050	<0.0001	ns	118	2wANOVA
	Species	**DBH**	**Year**		
SFmax	<0.0001	<0.0001	ns	48	GLM
SF	<0.0001	<0.0001	0.0002	48	GLM
Tree transpiration	<0.0001	<0.0001	0.0049	48	GLM
Tree radial increment (growth)	<0.0001	ns	ns	48	GLM
Stand transpiration	0.0300	-	-	12	1wANOVA
Tree DBH	ns	-	-	90	1wANOVA
Tree radial increment (growth)	<0.0001	-	-	48	1wANOVA
Tree density	ns	-	-	4	1wANOVA
Moisture at saturation 0-5 cm	ns	-	-	45	1wANOVA
Moisture at saturation 25-30 cm	ns	-	-	30	1wANOVA
Moisture at WFC 0-5 cm	0.0003	-	-	45	1wANOVA
Moisture at WFC 25-30cm	ns	-	-	30	1wANOVA
WDPT 0-5cm	0.0321	-	-	9	1wANOVA
WDPT 25-30cm	ns	-	-	9	1wANOVA

p-values higher than 0.05 are labeled "ns". 2wANOVA – two-way ANOVA, 1wANOVA – one-way ANOVA, GLM – FC – water field capacity, SF – sap flow based on daily means, SFmax – sap flow based on daily maxima, DBH – diameter at breast height, WDPT – water drop penetration time.

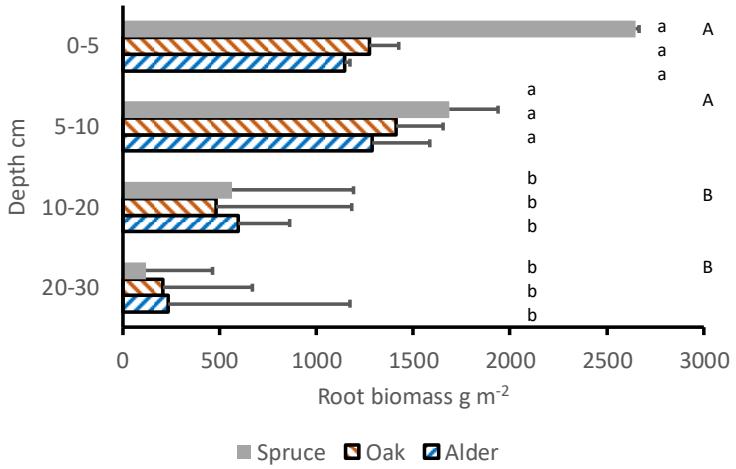


Fig. 3. Distribution of root biomass (±SD, n=5) of spruce, oak and alder with depth. Homogeneous groups are marked by the same letter; large letters mark the effect of a tree stand for both depths based on two-way ANOVA, small letters mark differences between particular depths based on one-way ANOVA. In both cases, the Fisher test ($p<0.05$) was applied. No statistically significant differences between tree species were found (Table 3).

4.2 Factors affecting soil water retention differences between species

As already mentioned, our study shows that the amount of water retained in soil differs under particular tree species, being the highest in species that have a high-water demand. In agreement with other studies (Cejpek et al., 2013, 2018; Martin-Guay et al., 2022), our results also show that water consumption during the vegetation season significantly reduces soil moisture. This means that tree species with a high-water demand may exhibit an even greater effective retention capacity than indicated by simple moisture differences measured in the field, as these soils maintain a relatively high moisture despite substantial water removal by the trees.

A large soil water storage partly corresponds with a higher water field capacity, which is higher for broadleaf species than

for conifers (Fig. 4b). A high retention capacity may correspond with the higher soil carbon content found under broadleaf species compared to conifers (Table 1), as several previous studies show that an increasing amount of soil organic matter increases the soil water-holding capacity (Frouz and Kuráž, 2013; J. Li et al., 2013; Rawls et al., 2003; Seiwa et al., 2021).

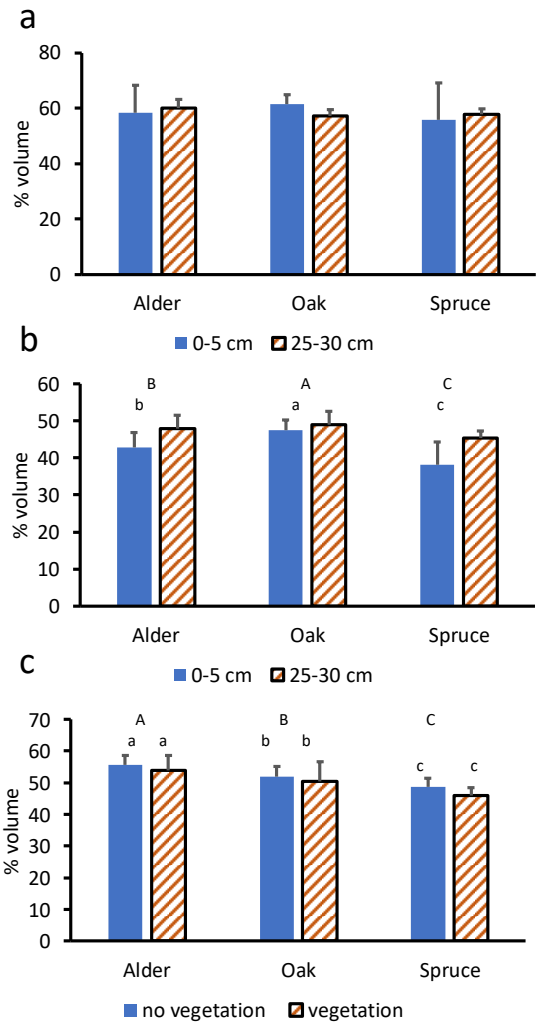


Fig. 4. Soil volumetric moisture a) at soil saturation, and b) at water field capacity based on laboratory measurements of samples from depths of 0-5 cm and 25-30 cm, and c) field-measured average seasonal soil moisture at a depth of 0-30 cm, no vegetation means no vegetation season, vegetation means vegetation season. Mean and sd are given, homogeneous groups are marked by the same letter; large letters mark the effect of a tree stand for both depth or season based on two-way ANOVA, small letters mark differences between particular depths or seasons based on one-way ANOVA. In both cases, the Fisher test ($p<0.05$) was applied.

However, the field capacity of oak soil is significantly higher than that of alder, but the soil under alder stores more water than that under oak. This also holds outside the growing season, when the amount of water cannot be influenced by water uptake by trees. This suggests that also other factors besides difference in field capacity may be responsible for the higher soil moisture at the alder site. We propose that this may be a significantly higher water infiltration at the alder site compared to both the oak and spruce site (Table 1, Fig. 5), as shown in the study by Jačka et al. (2021), conducted at the same sites. Jačka et al. (2021), with a dye experiment, also observed that water at the spruce site has a tendency to be retained in the organic topsoil (especially in the fermentation layer) rather than to be infiltrated deeper into the mineral soil. As a consequence, fast shallow subsurface runoff may be enhanced (Ritsema and Dekker, 1995).

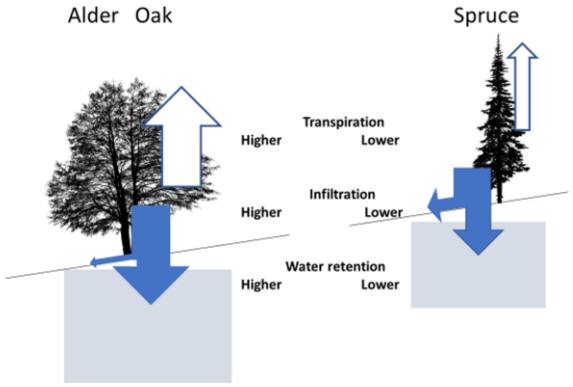


Fig. 5. Conceptual scheme summarizing the major differences in tree transpiration and key soil properties that determine the soil water storage capacity under broadleaf and coniferous tree species in this study.

We believe that the high-water repellency of the spruce soil surface layer of may contribute to this phenomenon. We therefore suggest that differences in water infiltration, which determine the amount of water that enters the soil, are an important factor contributing to the overall higher soil moisture in broadleaf trees and especially in alder observed in this study. In addition to differences in soil properties, also other three traits may reduce water input in the soil under spruce (Kuželková et al., 2024; Oulehle et al., 2021). Spruce as an evergreen tree has a much higher water interception, its soil being able to retain up to 20% of the annual precipitation (Oulehle et al., 2021) in addition to the higher interception crown architecture of spruce also support lower stemflow of water in comparison to broadleaf tree species, which may again reduce water input into the soil (Kuželková et al., 2024). This combination of tree morphological traits and soil modification is responsible for the lower soil water storage under spruce.

Earlier studies conducted on the same sites also show that higher soil organic matter content, a higher field capacity as well as higher water infiltration are strongly affected by soil fauna, namely earthworm bioturbation (Frouz et al., 2006, 2013; Frouz and Kuráž, 2013; Jačka et al., 2021). Earthworm bioturbation incorporates soil organic matter into the soil, promotes formation of soil aggregates, and creates microbial biomass, which increases soil organic matter content and field capacity (Frouz et al., 2006, 2013; Frouz and Kuráž, 2013). In addition, aggregate formation and burrowing by soil fauna increase macroporosity which promotes infiltration (Jačka et al., 2021). This suggests that, at least at the sites used in our study, the effect of trees on soil hydraulic properties is mediated by soil fauna.

4.3 Sapflow differences between species

Our observation that the sap flow of spruce was lower than the sap flow of broadleaf species (Figs 1a, 1b) agrees with the observation by other authors suggesting that conifers have a lower sap flow than broadleaf trees (Huang et al., 2012; Peters et al., 2010). The overall annual transpiration of individual oak trees observed in our study was about ten times lower than that observed for mature oak trees in a lowland floodplain forest (Čermák et al., 1982). This difference could be attributed to the

fact that the trees in the lowland forest were an order of magnitude larger, but some limitation by water availability at our site is also a possibility. The overall transpiration of alder is similar to that of oak, which may be surprising, as alder is generally assumed to be more water-demanding than oak. However, in our study one can also see that the daily maxima of transpiration were significantly higher for alder compared to oak. This suggests that alder transpires more in suitable conditions when water is easily available, but once water availability decreases, alder transpiration drops.

4.4 Limitations of the study and practical implications

Our study was conducted on a limited number of trees and expanding this exercise to a larger set of trees is an important task for future research. An interesting question to answer is how much this is relationships between water demand and soil water storage capacity differ between certain categories or functional groups of trees, such as broadleaves and conifers. Apart from a larger number of tree species, also a larger variation in soil conditions is needed. At our study sites, soil was developing de novo under the influence of particular tree species and consequently, the effect of individual species was very pronounced. In a real landscape, soil may be the outcome of not only the present vegetation but also the previous history of soil development.

However, if proven right, this concept may have many theoretical and practical applications. The most important ecological application is that trees naturally growing at a particular site will support the formation of soil that will store a sufficient amount of water that the trees need. From that, one can derive a practical application that supporting locally adapted species may improve water provisioning for trees and consequently increase forest resilience and vice versa. The observed changes in soil water storage represent a legacy of tree growth on soil development over time (Frouz, 2024). This means that for example afforestation, i.e. planting trees in non-forested soil, may over time affect the soil, leading to improvement (Cejpek et al., 2013) but also deterioration (Šurda et al., 2021) of soil properties that contribute to soil water storage. More research is needed to turn this into more detailed recommendations but choosing trees which belong to so-called reconstruction vegetation, i.e., trees which would likely naturally grow in such situations may good approach to achieve that soil that will be formed in given spot will be in equilibrium with water supply and tree needs.

4 CONCLUSIONS

Our study showed that tree species with a higher water demand represented by a higher sap flow and high transpiration produce soil that has a higher ability to retain water. On the contrary, trees with a lower water demand produced soils with a lower water storage. Higher water storage corresponded with higher accumulation of organic matter in mineral soil and higher infiltration. These effects could be potentially enhanced by interaction with soil biota, namely higher earthworm activity under the more water-demanding broadleaf trees. Moreover, also other tree traits affecting interception and stem flow may strengthen this pattern.

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