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The impact of forest naturalness and tree species composition on soil organic carbon content in areas with unnatural occurrence of Norway spruce in the Czech Republic

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Abstract: Climate change has increased attention paid in the research to forest soils and tree species composition, in respect to the potential for carbon sequestration. It is known that forest stands are able to store soil organic carbon (SOC), but little is known about the effect of forest naturalness on SOC content. This is important in relation of dying of unnatural spruce stands. It is necessary to determine a suitable composition of tree species which will replace them. This research is based on 248 plots with oak, beech, and spruce stands and mixtures of these species, with measured values of SOC. Our results show that autochthonous and mixed stands, in terms of tree species composition, in the study area had a higher SOC content than allochthonous and pure stands. In addition, it was found that autochthonous oak and beech stands, especially in mixtures, had a higher SOC content than allochthonous spruce stands (monocultures). On the basis of the presented results, it is possible to optimize the future tree species composition of stands in the study area, which currently have an allochthonous representation of spruce, to provide better function of carbon sequestration and resistance to climate change.

Keywords: carbon sequestration; climate change; forest naturalness; forest soil

In terms of climate change and increasing atmospheric CO_2 concentration, it is well known that forest ecosystems, and especially forest soils, are irreplaceable as carbon sinks (Lorenz & Lal 2010; Pan et al. 2011). Many studies confirm that carbon sequestration in soil varies with tree species, type of stand (coniferous vs. deciduous, pure vs. mixed) (Vesterdal et al. 2013; Wiesmeier et al. 2013; Andivia et al. 2016; Kern et al. 2016; Angst et al. 2019), and has an influence on SOC content in the soil. However, insufficient attention has been paid to the influence of forest naturalness on soil organic carbon (SOC) content.

Forests in the Czech Republic, as in much of Europe, underwent significant change in tree species composition during reforestation in the late 18th and early 19th centuries in the fir/beech and beech zones, and also in the oak/beech and oak zones (Klimo et al.

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2000). This includes forest vegetation zones in our study area, where oak and beech occur naturally and dominate in natural tree species composition. Natural tree species composition in these locations was replaced by spruce monocultures in a number of cases. This conversion related to intensive forest management practices and the economic benefits of spruce wood. Spruce monocultures thus became common on sites unsuitable and unnatural for the species (Spiecker et al. 2004; Ammer et al. 2008; Löf et al. 2010), forcing out the site-natural tree species, primarily beech, oak and other broadleaf trees.

The Czech Republic is currently facing a problem of large-scale dying of spruce stands (monocultures) grown on sites unnatural to them. The population of Norway spruce is dying due to a cumulation of negative factors relating to unsuitable conditions for growth and also the onset of the effects of climate change. Therefore, spruce stands grown on unnatural sites and at unnatural altitudes are the most affected, mainly in lower forest vegetation zones (Pretzsch & Ďurský 2002). Allochthonous spruce stands are already dying as premature stands, aged around 40–50 years, and will not live to felling age. Due to the size of the areas on which these allochthonous spruce stands are grown, it is necessary to find suitable composition of tree species which can replace these monocultures, fulfil all the functions of the forest (Hilmers et al. 2020), including carbon sequestration. Many authors focus on determining optimal composition of tree species in forest stands in the context of anticipated climate change and impact, and of carbon sequestration. Some authors agree that mixed stands with major representation of broadleaf tree species will play a very important role in carbon sequestration, especially at lower and mid elevation (Čermák et al. 2004; Hlásny et al. 2011), where spruce stands are currently grown. At the same time, emphasis will also be placed on near-natural tree species composition of stands and natural distribution of tree species, which are considered as potential factors for viability with regard to climate change (Schwab et al. 2022). Forest naturalness is a closely related and also potentially interesting characteristic, in the context of climate change, and especially in terms of carbon sequestration potential.

In this research we hypothesized that: (1) forest naturalness has an influence on SOC content, (2) mixed and pure stands differ in SOC content, (3) main tree species of stand has an influence on SOC content, (4) a more detailed division to type of stands differ in SOC content.

MATERIAL AND METHODS

Description of study area. For our research we used data from 248 monitoring plots from a database of forest typology complied by the Forest Management Institute (FMI) in Brandýs nad Labem between 1956–2004 (Figure 1). The size of selected circular monitoring plots varied in the range of 400 to 500 m^2. Monitoring plots were located within an elevation range of 250–680 m a.s.l., which corresponds to a range of 1^{st}–4^{th} forest vegetation zone (FVZ). The FVZ expresses the relationship of climate, site and species composition of forest community and is usually used for evaluation of the natural zonal area (occurrence) of a given tree species. In this re-

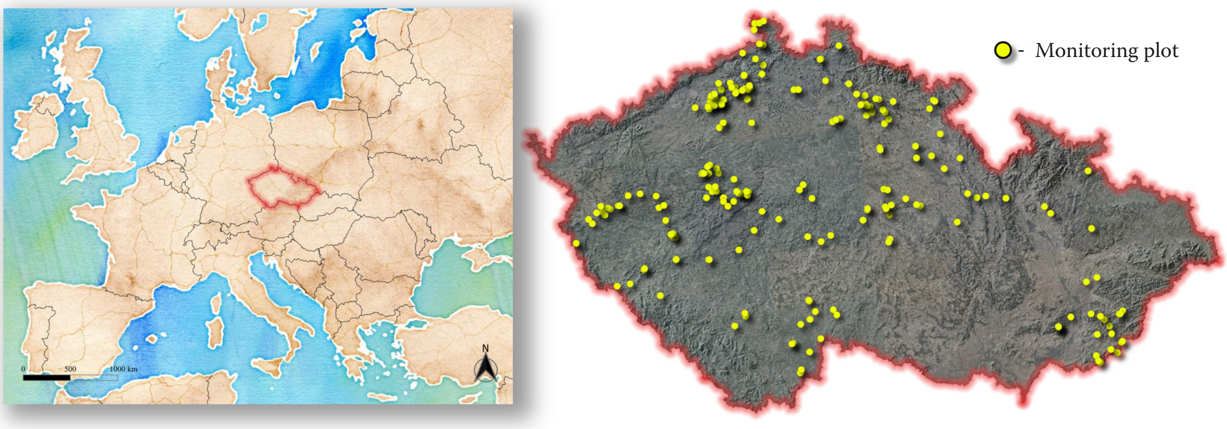

Figure 1. Location of the study area and monitoring plots

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search FVZ is used in relation to regional scenarios for predicted impact of climate change within the Czech Republic by 2030 (Čermák et al. 2004), where changes in distribution and composition of tree species, especially Norway spruce, are stated in individual FVZs. It is predicted that Norway spruce will not be able to survive in lower forest vegetation zones. The locations of our research monitoring plots were selected with respect to areas of allochthonous spruce monocultures. Mean annual air temperature in these locations fluctuates around 7.3 °C (a range of 6.03–8.33 °C) and mean annual precipitation is around 677 mm (a range of 479.6–1129.6 mm) (for more details see Table S1 in Electronic Supplementary Material (ESM)).

According to the World Reference Base (IUSS Working Group WRB 2015), soil conditions on the monitoring plots relate to the soil groups of Cambisols (187 samples), Podzols (6 samples), Stagnosols (17 samples), Luvisols (9 samples), Leptosols (20 samples), Gleysols (1 sample) and Retisols (8 samples). The dominant soil group is Cambisols, the prevalent humus form is moder. The thickness of O horizons ranges from 1 to 35 cm (with a mean of 4 cm), while A horizons range from 1 to 37 cm (with a mean of 9 cm). Both studied soil horizons were represented in all soil pits.

Soil sampling, determination of soil organic carbon. Soil samples were taken from the organic soil horizon (O horizon), which included all three layers – OL (litter), OF (fragmented) and OH (humus), and from the surface mineral soil horizon (A horizon) in soil pits. Each soil pit was established in the central parts of the monitoring plot. For this reason, the soil samples taken are considered representative. One soil pit was established on each monitoring plot, and the O and the A soil horizons were distinguished by a field FMI specialist with relevant experience of pedology, according to appropriate and current internal methodology at the time. Soil samples from both studied soil horizons were homogenized and subsequently analyzed in the soil science laboratory at FMI in Brandýs nad Labem.

For determination of SOC, the chromo-sulfuric compound oxidation method (wet method) was used, which was accompanied by titration of Mohr's salt and later with hydroquinone (Walkley & Black 1934; Zbíral et al. 2011). SOC stock were calculated for both studied horizons, according to this formula Marek et al. (2011):

$$SOC = T \times BD \times SOC\ (\%) \tag{1}$$

where:

SOC – soil organic carbon content (t/ha);
T – the thickness of horizon (cm);
BD – the bulk density (g/cm);
SOC (%) – percentage of soil organic carbon.

Values of bulk density were part of the methodology according to Marek et al. (2011) and were determined as part of the physical analysis of soils.

Stand description. Forest management practices were applied in all studied stands. All monitoring plots had been forest-covered for several generations. A dataset of 248 investigated plots includes type of stand, based on the percentage of the main tree species (Macků 2012) – Norway spruce (*Picea abies* L.H. Karst.), Pedunculate oak (*Quercus robur* L.) and European beech (*Fagus sylvatica* L.), as described in more detail in Table 1. Within mixed stands, admixed and interspersed tree species are also represented, such as Scots pine, White poplar, European ash, European larch and Silver fir, in addition to the main tree species. The age of the studied stands ranges from 15–185 years, but the average is 96 years. Mature stands predominate.

Definition of degree of naturalness (forest naturalness). Concerning naturalness, forest typology was used when setting the degree of naturalness of forest stands. This was based on comparison of actual species composition at the level of potential natural vegetation by the FMI method. The natural tree species composition is derived from the model composition for classification units (forest sites type) of the FMI Typological System (Macků 2012). Forest sites type is based on a part of forest including all original geobiocenosis with homogenous ecological or growth conditions and with explicit amplitude of potential autochthonous and allochthonous tree species production (Macků 2012). The forest type is characterized by a dominant species combination of phytocenosis, soil properties, habitat and potential yield class of the tree species.

The degree of naturalness is a categorical variable and it may reach values in the range of 0–6. Individual degrees of naturalness are described in Table 2. Such a detailed division would require a larger number of samples (stands). Therefore, the degree of naturalness was amalgamated into two groups: mostly autochthonous vegetation (stands) – with a degree of naturalness of 4–6, and mostly allochthonous vegetation (stands) – with a degree of naturalness

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Table 1. Description of studied types of stands

Abbreviation of type of stand	Forest naturalness	Main tree species	Representation of main tree species	Representation of other tree species	Mixture type	No. of samples
AL SP 91–100%	AL – allochthonous	SP – Norway spruce	pure (91–100%)	–	pure	91
AU OAK 91–100%	AU – autochthonous	OAK – Pedunculate oak	pure (91–100%)	–	pure	94
AU OAK 71–90%	AU – autochthonous	OAK – Pedunculate oak	dominant (71–90%)	interspersed (up to 10%)	mixed	
AU OAK 31–70%	AU – autochthonous	OAK – Pedunculate oak	major and basic (31–70%)	admixed (up to 30%) and interspersed (up to 10%)	mixed	
AU BE 91–100%	AU – autochthonous	BE – European beech	pure (91–100%)	–	pure	63
AU BE 71–90%	AU – autochthonous	BE – European beech	dominant (71–90%)	interspersed (up to 10%)	mixed	
AU BE 31–70%	AU – autochthonous	BE – European beech	major and basic (31–70%)	admixed (up to 30%) and interspersed (up to 10%)	mixed	

of 0–3, for the sake of simplification. This simplified division of forest naturalness into 2 groups is used in all analyzes, and is then interpreted throughout the article.

Statistical analysis. Descriptive statistics, especially median, variance and interquartile range, were used to describe the dataset. Data normality was verified by a Shapiro-Wilk test. The data normality condition was not met for values of SOC (t/ha) in both soil horizons. Therefore, the log-transformation was conducted.

The existence of influence of selected categorical variables on the dependent quantitative variable (SOC) and statistical differences were tested using analysis of variance (ANOVA) and Duncan's multiple comparison test. All tests were performed at 5% level of significance.

Statistical analysis was conducted in STATISTICA software Version 13 (TIBCO Software Inc. Palo Alto, USA).

RESULTS

O – organic soil horizon. Analysis of variance (ANOVA) proved significant influence of forest naturalness on SOC content ($F = 43.34$; $P < 0.001$). Significant difference between naturalness groups 0–3 and 4–6 was detected, whereas a higher SOC content was found in group 0–3 with a median of 10.40 t per ha. In group 4–6 a median value of SOC was only 5.65 t/ha (Figure 2).

In addition to forest naturalness, the influence of mixture type (pure vs. mixed stands) on SOC content ($F = 15.77$; $P < 0.001$) and significant differ-

Table 2. Description of degrees of naturalness established by Forest Management Institute in Brandýs nad Labem

Degree	Designation	Description	Naturalness category	No. of samples
0	unsuitable	introduced tree species	allochthonous	91
1	very low	mostly unsuitable composition		
2	low	rather unsuitable composition		
3	medial	culture forest – appropriate composition		
4	high	mostly natural composition	autochthonous	157
5	very high	near natural composition		
6	exceptional	natural composition		

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ence between pure and mixed stands were proven. In pure stands, a higher SOC content was detected, with a median of 8.85 t/ha, whereas in mixed stands the median value was only 5.33 t/ha (Figure 3A).

The influence of main tree species (beech, oak, spruce) in stands on SOC content was also proven ($F = 21.68$; $P < 0.001$). Significant differences were detected between beech and spruce ($P < 0.001$) and between oak and spruce ($P < 0.001$) stands. Beech and oak stands did not differ significantly ($P > 0.05$) in SOC content. The significantly highest SOC content was found in spruce stands, with a median of 10.40 t/ha. On the other hand, the lowest SOC content was detected in beech stands, with a median of 5.43 t/ha (Figure 3B).

Based on the findings mentioned above, stands were divided into types of stand. The influence of type of stand on SOC content was proven ($F = 8.07$; $P < 0.001$). A significant difference in SOC content between types of stand was also detected. It can be stated that all types of stand differed significantly from AL SP 91–100% in SOC content. When oak types of stand were compared with AL SP 91–100% stands, it was noticeable that the highest SOC content was demonstrated in AL SP 91–100%, with a median of 10.40 t/ha (Figure 4A). No significant differences in SOC content were found between oak types of stand (Table 3), although SOC content decreases with increasing percentage representation of oak. When beech types of stand were compared with AL SP 91–100% stands, it was also proven that the highest SOC content was demonstrated in AL SP 91–100% (Figure 4B). The second highest content of SOC (after AL SP 91–100% stands) was detected in AU BE 91–100% stands, with a median of 6.58 t/ha (Figure 4B). In beech types of stand significant difference was found in SOC content between AU BE 91–100% and AU BE 71–90% stands (Table 4).

A – surface mineral horizon. As in the O horizon a significant influence of forest naturalness on SOC content was also proven in the A horizon ($F = 27.34$; $P < 0.001$) and a significant difference ($P < 0.001$) was detected between naturalness groups 0–3 and 4–6. Significantly higher content of SOC was detected in the 4–6 group with a median of 30.61 t/ha, while in the 0–3 group the median value was only 19.07 t/ha (Figure 2). It is an opposite trend to that in the O horizon.

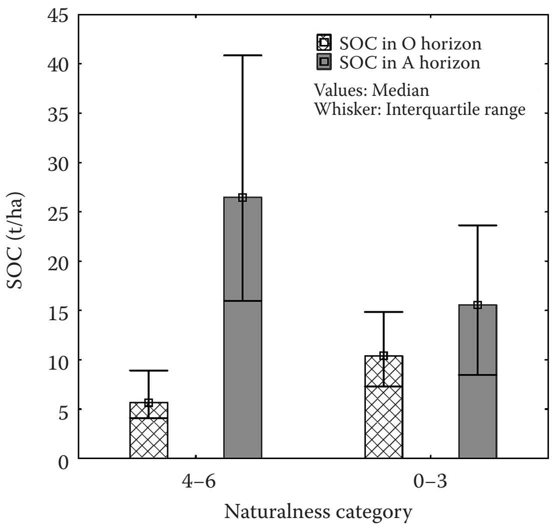

Figure 2. Variation of soil organic carbon (SOC) content in the O – organic and A – surface mineral soil horizons in relation to naturalness category

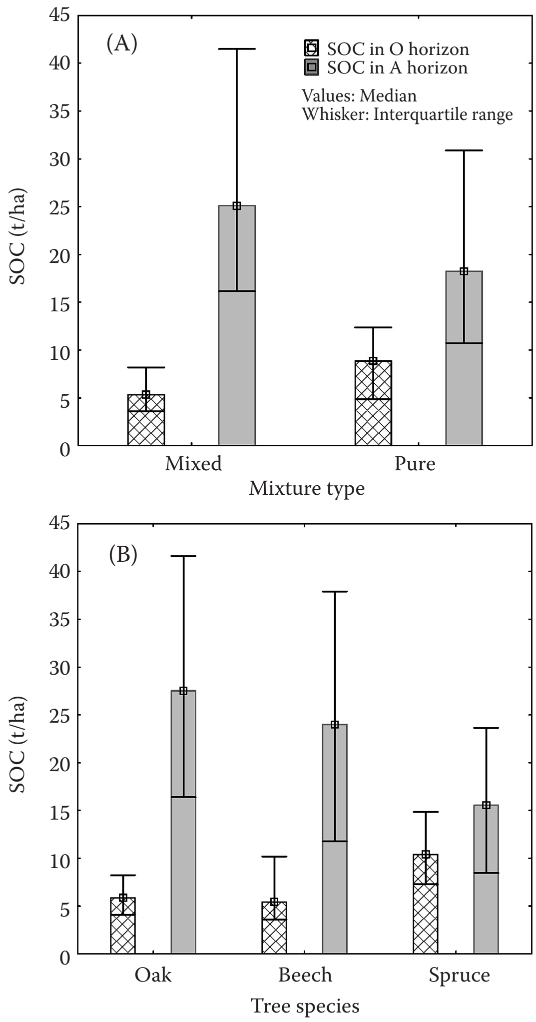

Figure 3. Variation of soil organic carbon (SOC) content in the O – organic and A – surface mineral soil horizons in relation to mixture type (A) and main tree species of stands (B)

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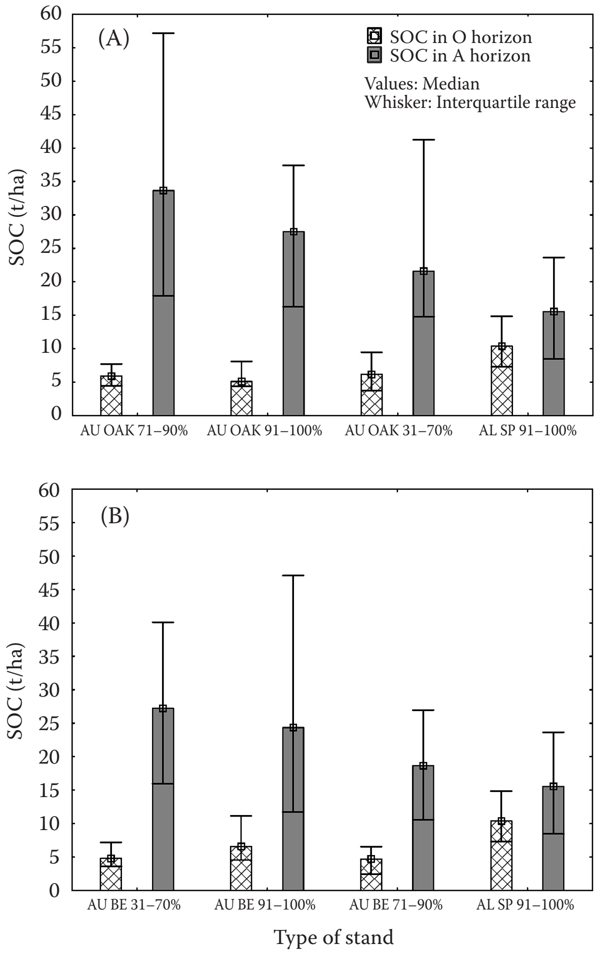

Figure 4. Comparisons of soil organic carbon (SOC) content in the O – organic and A – surface mineral soil horizons for oak and spruce (A) and beech and spruce (B) types of stand
For explanation of stand types abbreviations see Table 1

Also, in the A horizon, the influence of mixture type (pure × mixed) on SOC content was proven ($F = 7.44$; $P < 0.007$). Significant difference between pure and mixed stands was demonstrated. A higher content of SOC was detected in mixed stands, with a median of 31.02 t/ha, than in pure stands, with a median of 23.95 t/ha (Figure 3A). This is also an opposite trend to that in the O horizon.

Besides the aforementioned, a significant influence of tree species (beech, oak, spruce) on SOC content was also evident, with significant differences between beech and spruce ($P < 0.001$) and between oak and spruce ($P < 0.001$) stands. Beech and oak stands did not differ significantly ($P > 0.05$) in SOC content, as in the O horizon. The significantly highest content of SOC was detected in oak stands (median value 32.04 t/ha), and the lowest in spruce stands (median value 19.07 t/ha) (Figure 3B).

As in the O horizon, a significant influence of type of stand on SOC content ($F = 5.90$; $P < 0.001$) with significant differences proven between them in the A horizon. When oak types of stand were compared with AL SP 91–100% stands, it was found that all oak types of stand differ significantly from AL SP 91–100% stands (Table 3). The highest content of SOC was detected in AU OAK 71–90% stands, with a median of 33.63 t/ha (Figure 4A). On the other hand, the lowest content of SOC in this comparison was found in AL SP 91–100% stands, with a median of 15.55 t/ha. This trend is opposite to that in the O horizon. When beech types of stand were compared with AL SP 91–100% stands, significant difference was proven only between AU BE 91–100% stands and AL SP

Table 3. Significant differences in soil organic carbon (SOC) content between oak types of stand and spruce type of stand in the O – organic and A – surface mineral soil horizons according to Duncan's multiple comparison test

Abbreviation of type of stand	AL SP 91–100%	AU OAK 91–100%	AU OAK 71–90%	AU OAK 31–70%
O horizon (SOC; $P < 0.05$)				
AL SP 91–100%	–	0.000057	0.000367	0.000335
AU OAK 91–100%	0.000057	–	ns	ns
AU OAK 71–90%	0.000367	ns	–	ns
AU OAK 31–70%	0.000335	ns	ns	–
A horizon (SOC; $P < 0.05$)				
AL SP 91–100%	–	0.002865	0.000008	0.005654
AU OAK 91–100%	0.002865	–	ns	ns
AU OAK 71–90%	0.000008	ns	–	ns
AU OAK 31–70%	0.005654	ns	ns	–

For explanation of stand types abbreviations see Table 1; ns – non-significant

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Table 4. Significant differences in soil organic carbon (SOC) content between beech types of stand and spruce type of stand in the O – organic and A – surface mineral soil horizons according to Duncan's multiple comparison test

Abbreviation of type of stand	AL SP 91–100%	AU BE 91–100%	AU BE 71–90%	AU BE 31–70%
O horizon (SOC; $P < 0.05$)				
AL SP 91–100%	–	0.044032	0.000031	0.004125
AU BE 91–100%	0.044032	–	0.026978	ns
AU BE 71–90%	0.000031	0.026978	–	ns
AU BE 31–70%	0.004125	ns	ns	–
A horizon (SOC; $P < 0.05$)				
AL SP 91–100%	–	0.042505	ns	ns
AU BE 91–100%	0.042505	–	ns	ns
AU BE 71–90%	ns	ns	–	ns
AU BE 31–70%	ns	ns	ns	–

For explanation of stand types abbreviations see Table 1; ns – non-significant

91–100% stands (Table 4), although a decreasing trend in SOC content is noticeable in the following order: AU BE 31–70% > AU BE 91–100% > AU BE 71–90% > AL SP 91–100% stands. Differences between beech types of stand were not significant. The highest content of SOC in beech types of stand was detected in AU BE 31–70% stands, with a median value of 21.23 t/ha (Figure 4B). On the other hand, the lowest content of SOC in this comparison was found in AL SP 91–100% stands, as well as in oak types of stand.

DISCUSSION

Although many stands are not autochthonous in their species composition or on a certain site, almost no attention has been paid to the influence of forest naturalness on SOC content. Based on our results, it is possible to state that forest naturalness has an influence on SOC content in the study area. It was found that autochthonous stands have a higher SOC content than allochthonous stands in the A horizon (Figure 2). The opposite was found for the O horizon. It is possible to explain this by the difference in decomposition processes. Autochthonous stands are primarily broadleaf stands in the study area, and conditions for decomposition processes are optimal, decomposition is relatively rapid. This can relate to higher biological diversity and activity in the soil (Prescott 2002; Augusto et al. 2015). It is known that earthworms enable the transport of carbon from forest floor to mineral soil through bioturbation (Devliegher & Verstraete 1997; Reich et al. 2005; Frouz et al. 2009). In addition, it can be assumed that SOC is in permanent turnover as part of soil organic matter, and its sequestration is limited in the O horizon (Vesterdal et al. 2012). Allochthonous stands are primarily coniferous (spruce) in the study area, and conditions for decomposition processes are unsuitable. Decomposition is slower due to a considerable amount of litterfall (Hobbie et al. 2006). Therefore, SOC content in the O horizon is higher here, and only a small amount of SOC is transported to the A horizon (Mareschal et al. 2010; Lorenz & Sören 2019). Many studies (Jandl et al. 2007; Frouz et al. 2009; Rumpel & Kögel-Knabner 2011; Vesterdal et al. 2013) agree that carbon (SOC) should preferably be stored in deeper soil horizons, because the organic horizon is more vulnerable and more influenced by disturbance (e.g., cutting, fires, erosion), abiotic factors and also decomposition processes. Overall, the organic horizon is not suitable for long-term and stable carbon storage. Therefore, our research was focused primarily on SOC in the mineral horizon.

It was further found that mixed stands have a higher SOC content in the A horizon than pure stands (Figure 3A), which has also been proven by a number of authors (Andivia et al. 2016; Kern et al. 2016; Błońska et al. 2018; López-Marcos et al. 2018). This probably relates to the root system and litterfall (Finér et al. 2007), as it is known that deciduous stands have greater root biomass, thanks to which they have greater root litter as C input to the mineral soil horizon and can induce a greater accumulation of carbon (Andivia et al. 2016). The opposite trend was found in the O horizon (Figure 3A). This closely

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relates to a considerable amount of litterfall and slower decomposition. Based on these results, it is possible to state that mixed stands are more suitable for carbon sequestration than pure stands in the study area, because they store more SOC in the A horizon. However, it is necessary to bear in mind, that it is not possible to state that mixed stands, in general, are the most suitable in terms of carbon sequestration, because it is known that Norway spruce stands, especially in higher altitudes, can sequester a large amount of SOC (Kern et al. 2016; Bojko & Kabala 2017; Jonard et al. 2017; Bečvářová et al. 2018).

In our research an increasing trend of SOC in spruce < beech < oak tree species was proven in the A horizon (Figure 3B). This result is interesting, because many studies agree that spruce stands have a higher stock of SOC in the mineral soil horizon than beech stands (Gurmesa et al. 2013; Andivia et al. 2016). This could relate to forest naturalness, because these spruce stands are allochthonous (unsuitable elevation and sites). On the other hand, there are studies which confirm our results (Vesterdal et al. 2008; Frouz et al. 2009; Mareschal et al. 2010). This is often in relation to the root biomass. According to Finér et al. (2007), fine root biomass is greater under beech than under conifers. Root systems of spruce have a preference especially for forest floors (Puhe 2003). Likewise the diversity, abundance and activity of earthworms, which are known for their incorporation of material from forest floor into deeper soil horizons (Devliegher & Verstraete 1997), is lower in spruce stands than in beech or oak stands (Schelfhout 2010). In the O horizon, an almost opposite trend of SOC was detected for beech ≤ oak < spruce tree species, compared with the A horizon (Figure 3B). Similar results were found in other studies (Frouz et al. 2009; Gurmesa et al. 2013; Andivia et al. 2016). These findings are not groundbreaking, confirming some results of other authors, but they are important for the study area, because they provide information about SOC content in the studied horizons under stands with different main tree species. Oak stands (autochthonous stands in our study area) which have a higher SOC content in the A horizon than spruce stands (allochthonous stands in our study area), are more able to perform function of carbon sequestration.

In addition to the above, when comparing autochthonous oak stands with allochthonous spruce stands (monocultures) it was found that all oak types of stand have a higher SOC content in the A horizon than spruce stands (Figure 4A), whereas oak stands with admixed other tree species (AU OAK 71–90%) have the highest SOC content of all oak types of stand. Pretzsch et al. (2013) discusses the benefits of growing oak in mixtures, specifically with beech, one of the benefits is that forests from these species are considered more tolerant to climatic effects and are expected to become important mixture under climate change. This is important when considering suitable stands to replace dying spruce stands in the context of carbon sequestration and climate change.

Similar results were achieved when autochthonous beech stands were compared with allochthonous spruce monocultures (AL SP 91–100%). Beech stands with basic and major representation of beech (AU BE 31–70%) have the highest SOC content in the A horizon in this comparison (Figure 4B). In beech stands, it was also proven that a mix of beech and other tree species is more suitable in term of carbon sequestration.

A substantial output of this research is the fact that mixed stands are more suitable for long-term and stable carbon sequestration than pure stands in the study area. It is also considered a key finding that autochthonous stands of oak and beech, are able to replace the dying allochthonous spruce stands, and can perform a better function of carbon sequestration in a same time.

CONCLUSION

Our results show that forest naturalness (autochthonous oak and beech vs. allochthonous spruce stands), mixture type (mixed vs. pure stands), individual tree species, and in a more detailed breakdown also type of stand had an influence on SOC content. In terms of long-term and stable carbon sequestration, more attention during research was paid to the surface mineral horizon than the organic horizon.

Overall, from this research it is possible to state, that autochthonous and mixed stands in the study area (in a range of 1^{st}–4^{th} forest vegetation zones) had a higher SOC content than allochthonous and pure stands, and are considered to be more suitable for carbon sequestration. A key finding is also the fact that autochthonous oak and beech stands, primarily in mixtures, are able to replace dying allochthonous spruce stands (monocultures) in the study area, while also providing better function of carbon sequestration and showing better resistance to climate change. These results can have practical application for silviculture practice and can contribute to the creation of adaptive strategies in the context of climate change.

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