Forest Systems
31 (1), e005, 13 pages (2022)
eISSN: 2171-9845
https://doi.org/10.5424/fs/2022311-18824
INIA-CSIC

RESEARCH ARTICLE

OPEN ACCESS

The effect of stand characteristics on soil organic carbon content in spruce and deciduous stands

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Abstract

Aim of study: To determine the effects of stand characteristics, which closely relate to forest management practices, on the soil organic carbon (SOC) content in the organic (O) and surface mineral (A) soil horizons in spruce and deciduous stands, and to show SOC dynamics during the life of production stands.

Area of study: Spruce and deciduous stands located throughout the Czech Republic.

Material and methods: The effects of age, density of stocking and canopy of stand on SOC content in the O and A horizons, and the difference between categories of variables and the trends of SOC were evaluated in spruce and deciduous stands (401 plots) at lower and middle elevations.

Main results: SOC content changed during the life of stands. In spruce stands, a decreasing trend of SOC with stand age was found in the A horizon. In deciduous stands, SOC content was higher overall in the A horizon, fluctuating slightly with stand age, but more balanced during the life of stands. Based on the results, in terms of management of dying spruce stands and carbon sequestration, felling should be carried out in the age group of 81-120 years in spruce stands, whereas in deciduous stands felling should take place in older stands (141 years and more). Density of stocking and canopy of stand had no substantial effect of SOC content.

Research highlights: Deciduous stands have the potential to replace dying spruce stands at lower elevation in terms of carbon sequestration.

Additional key words: forest soil; carbon sequestration; age of stand; density of stocking; canopy of stand; climate change

Abbreviations used: A (surface mineral soil horizon); BD (bulk density); FMI (Forest Management Institute); FVZ (forest vegetation zone); GLM (generalized linear model); O (organic soil horizon); SOC (soil organic carbon); T (thickness of horizon)

Authors' contributions: PHB, MH and BS conceived the idea, drafted the manuscript, structured the article and edited and revised the manuscript. PHB and MH carried out the conception, research design and interpretation of data. PHB conducted data analyses. MH conducted visualization of data. BS conducted critical revision of the manuscript for important intellectual content, provided administrative and funding support and work supervision. VZ ensured and provided input data and work supervision.

Citation: Hanakova-Becvarova, P; Horvath, M; Sarapatka, B; Zouhar, V (2022). The effect of stand characteristics on soil organic carbon content in spruce and deciduous stands. Forest Systems, Volume 31, Issue 1, e005. https://doi.org/10.5424/fs/2022311-18824

Supplementary material (Tables S1 and S2) accompanies the paper on SJAR's website

Received: 07 Sep 2021. **Accepted:** 15 Mar 2022.

Funding: The authors received no specific funding for this work

Competing interests: The authors have declared that no competing interests exist.

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Introduction

The rising concentration of atmospheric CO_2, climate change and its noticeable manifestations are current problems requiring research attention. The impact of climate change has also begun to show in forest ecosystems, which play an important and irreplaceable role as carbon sinks (Lorenz & Lal, 2010). Many studies have focused on a comparison of soil organic carbon (SOC) in different types of stand (Kern *et al.*, 2016; Jonard *et al.*, 2017; Angst *et al.*, 2019). However, insufficient attention has been paid to the effect of stand characteristics such as age of stand, density of stocking or canopy of stand, on SOC content. These stand characteristics are directly influenced by human intervention (forest management practices) carried out in production stands. Age of stand and age structure of stand are shaped and changed by human intervention in production stands, and closely relate to forest management practices, because specific forest management interventions are carried out in stands of a certain age (development stages of stand). Furthermore, density of stocking and canopy of stands are characteristics which are directly influenced by humans via forest management interventions, and which affect the soil environment.

The species composition of forest stands in the Czech Republic has changed through history, as it has changed throughout central Europe (Klimo *et al.*, 2000). Especially at middle and lower elevation, natural deciduous stands were replaced by spruce stands. Thus, spruce stands were very often grown on unsuitable sites (*e.g.* on desiccant sites or waterlogged sites) and unnatural sites at lower elevation (around 250 m. a.s.l.), but also at medium elevation, where the spruce is outside its ecological optimum range (around 600-900 m. a.s.l.) and natural occurrence (around 500 m. a.s.l.). As predicted in regional scenarios for the impact of climate change on the Czech Republic by 2030 (Čermák *et al.*, 2004) and also based on the statements of other authors (Hanewinkel *et al.*, 2013; Pardos *et al.*, 2021), Norway spruce will be unable to survive at lower elevation (primarily up to 400 m a.s.l.). However, the predicted impact of climate change is already beginning to show (Pajtík *et al.*, 2018). Norway spruce stands grown primarily at lower elevation are already dying as premature stands, at around 80 years of age, but also as 40-50-year old stands, in poor health, often attacked by biological agents (insect pests, pathogens) (Holuša *et al.*, 2018) and in some cases they will not survive to felling age. These stands will have to be replaced with stands of suitable tree species composition for these positions. Based on the results of many studies (Błońska *et al.*, 2018; López-Marcos *et al.*, 2018), it is known that deciduous, mixed stands are considered appropriate in terms of carbon sequestration. But the SOC content is not known in any particular age of stand, density of stocking, and canopy of stand and little is known about SOC dynamics during the life of the production stands.

The objective of this study was to determine the effects of stand characteristics, which closely relate to forest management practices (human interventions), on SOC content in the organic (O) and surface mineral (A) soil horizons in spruce and deciduous stands and to show the dynamics of SOC content during the life of stands. We hypothesized that: 1) stand characteristic - age of stand, density of stocking, canopy of stand, have an influence on SOC content, especially in the A horizon; 2) SOC content changes during the life of the stands; 3) deciduous stands have a higher SOC content than spruce stands, primarily in the A horizon, in comparable site conditions; and 4) deciduous stands sequester more SOC than spruce stands in the research elevation range, especially in locations where there is intensive dying of spruce (lower elevations).

Material and methods

Description of study area

This research made use of a database of forest typology compiled by the Forest Management Institute (FMI). The research monitoring plots were established between 1953 and 2004. The size of the selected circular monitoring plots varied in the range of 400-500 m^2. The database contains information about soil conditions, including content of SOC, species composition of forest stands and stand characteristics.

The analysed samples were obtained from monitoring plots throughout the Czech Republic (Fig. 1). Mean annual air temperature in these locations fluctuates around 7.1°C (a range of 5.53-8.33°C) and mean annual precipitation is around 710 mm (a range of 479.6-1129.6 mm). Monitoring plots were located within an elevation range of 250-650 m a.s.l. (low and middle positions). The elevation range corresponds to a range of 1^{st}-6^{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 research, the FVZ is used in relation to predicted impact of climate change, according to regional scenarios for the Czech Republic in 2030 (Čermák *et al.*, 2004). This prediction discusses changes in distribution and composition of tree species in individual FVZs. It is predicted that Norway spruce will not be able to survive in lower forest vegetation zones (especially in 1^{st}-3^{rd} FVZ), *i.e.* in unnatural sites and unsuitable conditions for spruce. The locations of our research monitoring plots were selected with respect to areas of non-natural spruce monocultures and areas of natural occurrence of deciduous stands.

The soil conditions of research monitoring plots vary. They represent the soil groups of Cambisols, Stagnosols, Podzols, Leptosols, Retisols, Gleysols, Luvisols and Fluvisols (according to the World Reference Base – WRB, 2014). The absolute dominant soil group is Cambisols (274 samples). Soil groups are stated in descending order, from the most common, and other soil groups are represented in the order of dozens of samples. The prevalent humus form is moder. The thickness of the O horizon ranges from 1 to 35 cm (with a mean of 5 cm), while the A horizon ranges from 3 to 65 cm (with a mean of 14 cm).

Soil sampling, determination of soil organic carbon (SOC)

Soil samples were taken only once, during the growing season. They were taken from the O horizon, which included

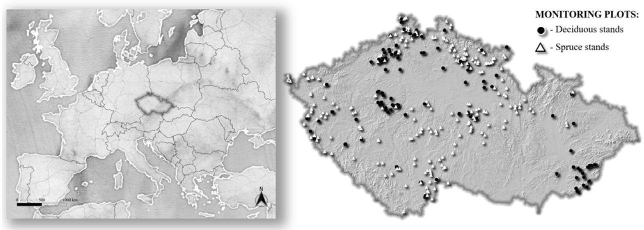

Figure 1. Location of the study area and monitoring plots.

all three layers − OL (litter), OF (fragmented) and OH (humus) −, and from the A horizon in each soil pit. Each soil pit was established in the central part of the monitoring plot. One soil pit was established on each monitoring plot, and the O and the A soil horizons were distinguished by an FMI field specialist with relevant experience of pedology, on site at the time when the soil pits were made and when the soil samples were taken, according to appropriate and current internal methodology at the time (between 1953 and 2004). The depth (thickness) of soil horizons (O and A) was subsequently measured (in cm) for each soil sample (in each soil pit). Soil samples from both studied soil horizons were analysed in the soil science laboratory at FMI in Brandýs nad Labem. All soil samples were homogenized and subsequently analysed separately for the O and A horizons.

SOC was determined by means of the chromo-sulfuric compound oxidation method (wet method), which was accompanied by titration of Mohr's salt and later with hydroquinone (Walkley & Black, 1934; Zbíral *et al.*, 2011). SOC values were calculated for both studied horizons, according to Eq. (1):

$$SOC = T \times BD \times SOC\,(\%) \qquad (1)$$

where SOC is soil organic carbon content in Mg C ha^{-1}; T is the thickness of horizon (cm); BD is the bulk density (g cm^{-1}); and SOC (%) is the percentage of SOC (Marek *et al.*, 2011). Values of bulk density were part of the methodology according to Marek *et al.* (2011) and were determined during physical analysis of soils.

Stand description

The dataset for this research included 401 stands. Based on the percentage of the main tree species (Macků, 2012), these stands were divided into two groups: spruce stands and deciduous stands. Spruce stands are stands with 50-100% representation of Norway spruce (*Picea abies* L. H. Karst.); Norway spruce is the main tree species of these stands. Deciduous stands are stands with 50-100% representation of deciduous tree species, whereas the main tree species of stands are pedunculate oak (*Quercus robur* L.) and European beech (*Fagus sylvatica* L.). Both of the groups of stands also comprised of based, admixed and interspersed tree species, such as Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Mill.), silver fir (*Abies alba* Mill.), white poplar (*Populus alba* L.), black alder (*Alnus glutinosa* L. Gaertner) and European ash (*Fraxinus excelsior* L.), in addition to the main tree species.

The stands included in this research are production forests with applied forest management practices. Each stand goes through certain growth developmental stages, in which specific forest management practices are conducted and which closely relate to age of stand. The age of research stands was in the range of 12-185 years. Stand age was categorized in age groups: 10-60 years, 61-80 years, 81-120 years, 121-140 years and 141 and more years. These age groups were based on growth developmental stages (described in detail in Table S1 [suppl]), which reflect the applied forest management practices and silvicultural measures, and with respect to a sufficient number of samples (stands) at individual groups. Therefore, the individual age groups are not of the same length.

Density of stocking expresses a relative stand density rate and serves as an indicator of the growth conditions of the stand. It is expressed as a ratio of the real stand basal area and tabular stand basal area. This is a categorical variable, which may reach values in the range of 0.1-1.0. Density of stocking must not fall below a value of 0.7 in production forests, according to forest law. Density of stocking of tree layer in this research is in the range of 0.7-1.0.

The canopy (canopy cover percentage) expresses the mutual touch (contact) and interweaving of tree branches. The canopy directly relates to density of stocking; with increasing density of stocking the canopy increases. Canopy is expressed as a percentage. The values of canopy in research stands were in the range of 50-100%.

Statistical analysis

The dataset comprised of 401 samples. This input dataset was divided into two groups: spruce stands (252 samples) and deciduous stands (149 samples) and statistical analysis was conducted separately in the O and the A soil horizons and separately for spruce stands and deciduous stands. Subsequently their comparison was made.

Statistical analysis was conducted in STATISTICA software version 13 (TIBCO Software Inc. Palo Alto, CA, USA). Descriptive statistics, especially median, mean, variance, interquartile and non-outlier range, were used to describe the dataset and for the purpose of displaying results in figures. Detailed values of individual variables are stated in Table S2 [suppl].

Firstly, data and residual normality were verified by the Shapiro-Wilk test ($p>0.05$). The data normality, and especially the residual normality condition, for dependent variables was not met. In order to perform further statistical analysis, an appropriate transformation (Box-Cox-transformation) for values of SOC (Mg C ha^{-1}) in both soil horizons for both groups of stands was conducted. The homogeneity of variance was tested by Levene's test.

Correlation analysis of the transformed data was performed to obtain information about the relationships and dependencies between selected variables (SOC content, age of stand, density of stocking, canopy and elevation). Correlation matrix was performed at levels of significance $p<0.05$ by means of Pearson´s correlation coefficient (r).

Subsequently, Generalized Linear Model (GLM) was used for clarification of relations and influences of categorical variables (age groups, density of stocking, canopy) on the dependent quantitative variable (SOC in the O and the A horizons) and also for clarification of trends of SOC for spruce and deciduous stands. Statistical differences between categories were tested by the Scheffe's test.

The one-way analysis of variance (ANOVA) was used to determine the influence of group of stand (type of stand) on SOC content (transformed values) and Scheffe's test was used to find statistical differences in SOC content between groups (spruce stands vs. deciduous stands) in both studied soil horizons.

The t-test was used to find significant differences and to compare SOC content in individual categories of age groups, density of stocking, canopy of stand and FVZs between spruce and deciduous stands, separately in each of studied horizons. All tests were performed at 5% level of significance.

Results

Spruce stands

The correlation analysis performed on the spruce stands dataset (Table 1) showed a significant positive correlation between content of SOC in the O horizon and age of stand (r=0.24; p<0.05). In the A horizon, a negative correlation between SOC content and age of stand (r =-0.15; p<0.05) and a positive correlation between SOC content and elevation (r=0.15; p<0.05) were proven. These stated correlations were weak but significant. Other variables did not show significant correlation.

For more detailed results, GLM was used. Outputs from GLM showed that age of stand has an influence on SOC content in the O horizon (p=0.0002). A significant increasing trend in SOC content in the O horizon was proven (p=0.0003) and a significant difference was found between age groups of 10-60 years and 121-140 years (Fig 2a). The lowest SOC content (with a median of 10.38 Mg C ha^{-1}) in the O horizon was detected in the 10-60 year age groups, and the highest SOC content was found in the 141 and more years age group (with a median of 24.99 Mg C ha^{-1}) (Fig. 2a). In the A horizon an influence of age of stands on SOC content was also proven (p=0.02). In contrast with the O horizon, a significant decreasing trend in SOC content in the A horizon was detected with a slight deviation in the 121-140 year age group (Fig. 2a). The highest SOC content in the A horizon was found in the 10-60 year age group (with a median of 27.75 Mg C ha^{-1}), and the lowest in the 141 and more years age group (with a median of 15.39 Mg C ha^{-1}) (Fig. 2a). Differences in SOC content in the A horizon between age groups were not significant.

Table 1. Correlation matrix of studied variables with the Pearson correlation coefficients (r) at levels of significance p < 0.05 for spruce and deciduous stands in studied soil horizons, given separately.

Variable	Spruce stands		Deciduous stands	
	SOC in the O horizon	SOC in the A horizon	SOC in the O horizon	SOC in the A horizon
Age of stand	r= 0.24	r= –0.15	r= 0.19	ns
Density of stocking	ns	ns	ns	ns
Canopy	ns	ns	r= 0.22	ns
Elevation	ns	r= 0.15	r= 0.20	ns

SOC: soil organic carbon. ns = non-significant

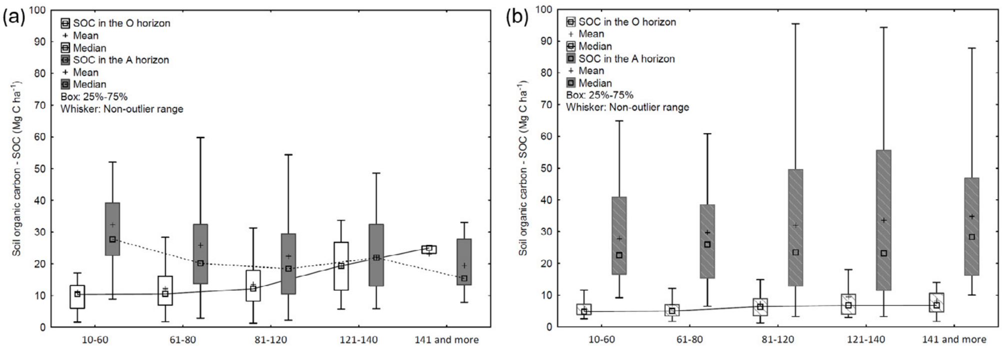

Figure 2. Comparison and trends in SOC content, in the O and A horizons in individual age groups, between spruce stands (a) and deciduous stands (b).

For other variables relating to stands, such as density of stocking and canopy, no effect on SOC content in both studied horizons was proven. Although the density of stocking did not show significant relation to SOC content, a higher SOC content in the A horizon was noticeable at lower levels of density of stocking (Fig. 3a). The figures for canopy of stand did not show any trend in SOC content, they fluctuated considerably in both horizons (Fig. 4a).

In addition to stand characteristics, the effect of elevation (categorized according to FVZs) on SOC content was also observed. In the O horizon, the effect of FVZ on SOC content (p=0.0003) and significant differences between 3rd FVZ and 6th FVZ, and between 4th FVZ and 6th FVZ were found. Although the increasing trend in SOC content in the O horizon from 3rd to 6th FVZ was noticeable in Fig. 5a, this trend was not statistically significant. In the A horizon, the effect of FVZ on SOC content was also proven (p=0.0194), in addition a significant increasing trend in SOC content was found (p=0.0182), but the differences between FVZs were not significant (Fig. 5a).

Deciduous stands

Correlation analysis was also performed on the deciduous stand dataset (Table 1). In the O horizon, significant positive correlations between SOC content and the following variables were proven: age of stand (r=0.19; p<0.05), canopy (r=0.22; p<0.05) and elevation (r=0.20; p<0.05). These correlations were rather weak, but significant. In the A horizon, no significant correlation was proven.

Outputs from GLM for deciduous stands showed that age of stand had an influence on SOC content in the O horizon and a significant increasing trend in SOC content was found (p=0.0197) (Fig. 2b). The highest median values of SOC content were detected in the 121-140 year age group (with a median of 6.76 Mg C ha^{-1}) and the 141 and more years age group (with a median of 6.77 Mg C ha^{-1}). The lowest SOC content was found in the 10-60 year age group (with a median of 4.79 Mg C ha^{-1}) (Fig. 2b). However, the differences between age groups were not significant. In the A horizon the effect of age of stand on SOC content was not significant. The medians of SOC content in the A horizon fluctuating slightly with the age of stands (age groups), and some of age groups had considerable scatters.

Density of stocking had no significant effect on SOC content in either studied horizon. However, an increasing trend in SOC content in the O horizon, and a contrasting decreasing trend in SOC content in the A horizon, are evident in Fig. 3b.

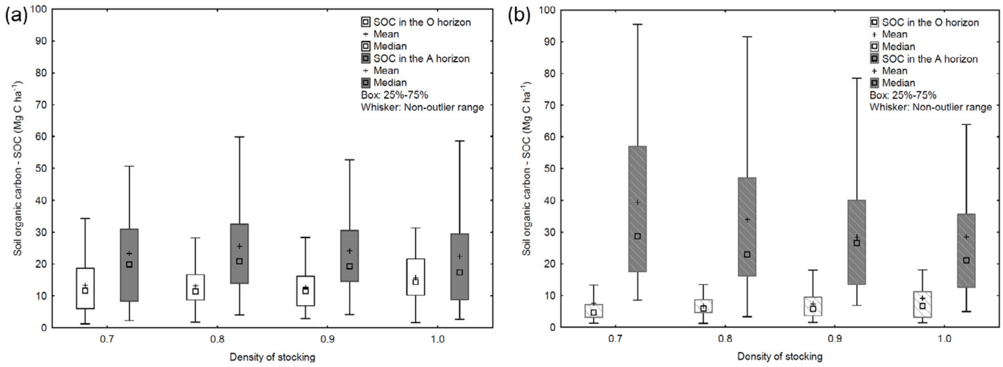

Figure 3. Comparison of SOC content, in the O and A horizons for individual levels of density of stocking of stands, between spruce stands (a) and deciduous stands (b).

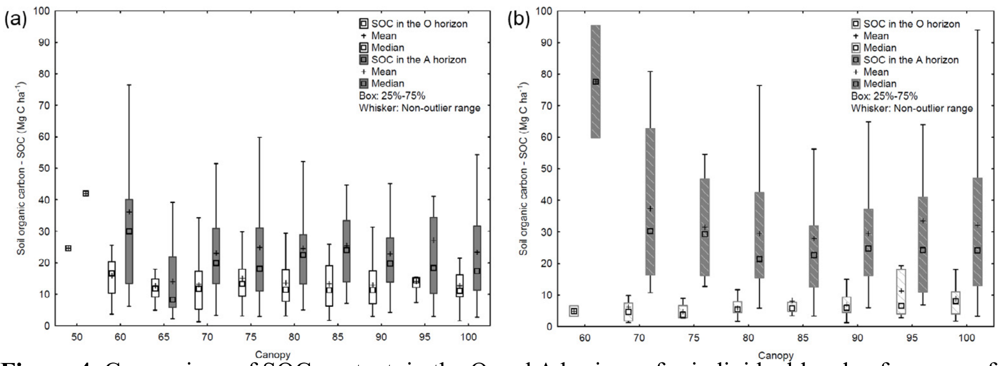

Figure 4. Comparison of SOC content, in the O and A horizons for individual levels of canopy of stands, between spruce stands (a) and deciduous stands (b).

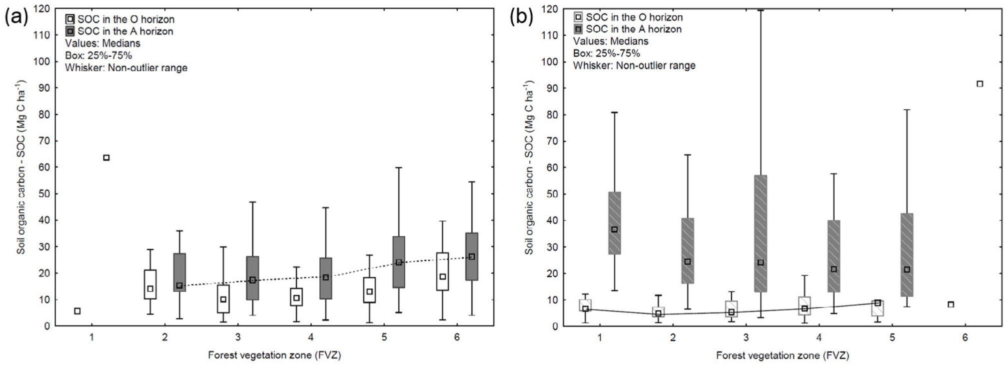

Figure 5. Comparison and trends in SOC content, in the O and A horizons in forest vegetation zones (FVZs) represented in the study area, between spruce stands (a) and deciduous stands (b).

The effect of canopy on SOC content (p=0.0065), and an increasing trend of SOC content in the O horizon, were further demonstrated. In Fig. 4b, it is evident that a higher SOC content was detected in stands with a higher percentage of canopy. In the A horizon the effect of canopy on SOC content was not significant, but in Fig. 4b there are noticeably higher medians of SOC content at lower percentage of canopy.

Besides stand characteristics, the effect of elevation on SOC was tested. It was proven that elevation relates with SOC content in the O horizon, a significant increasing trend in SOC content was found (p=0.0167) (Fig. 5b). Differences in SOC content between FVZs were not significant. In the A horizon, no effect of elevation on SOC content was proven and no differences between FVZs were found. However, it is noticeable that a higher SOC content was detected in lower FVZs, and a slightly decreasing trend in SOC content is indicated (Fig. 5b).

Comparison of spruce stands and deciduous stands

In general, significant differences in SOC content in both soil horizons were proven (p<0.05). A significantly higher SOC content (with a median of 11.97 Mg C ha^{-1}) in the O horizon was detected in spruce stands ($F_{1,39}$=89.45; p=0.0000). In contrast, a significantly higher SOC content (with a median of 24.41 Mg C ha^{-1}) in the A horizon was found in deciduous stands ($F_{1,39}$=11.86; p=0.0007) (Fig. 6).

When SOC content was compared in age groups, a significant increasing trend in SOC content was evident for both groups of stands (spruce and deciduous) in the O horizon, while the medians of all age groups in spruce stands are higher than the medians of deciduous stands (Figs. 2a and 2b). Significant differences in SOC content were proven between spruce and deciduous stands in age groups of 10-60 years (p=0.0061), 61-80 years (p=0.0000), 81-120 years (p=0.0000), 121-140 years (p=0.0004) and 141 and more years (p=0.0008) (Table 2). In the A horizon, there is a significantly decreasing trend in SOC content in spruce stands with the variance in age group of 121-140 years, whereas in deciduous stands this trend is not evident. Significant difference in SOC content in the A horizon was proven between spruce and deciduous stands only in the 81-120 year age group (p=0.0074) (Table 2). In deciduous stands, SOC content fluctuated slightly within age groups, but overall SOC content is more balanced throughout the life of stands than in spruce stands.

Density of stocking had no significant effect on SOC content in either studied horizon in both groups of stands. However, in the O horizon, there was a noticeable increasing trend in SOC content, the highest SOC content was detected in full density of stocking in both groups of stands (Fig. 3a and 3b). In the spruce stands, there were also higher median values of SOC content in the O horizon in all categories of density of stocking than in deciduous stands. Significant differences in SOC content between spruce and deciduous stands were proven at stocking densities of 0.7 (p=0.0011), 0.8 (p=0.0000), 0.9 (p=0.0000) and 1.0 (p=0.0000) (Table 3). In the A horizon, a higher SOC content was apparent at lower than full density of stocking in both groups of stands (Fig. 3a

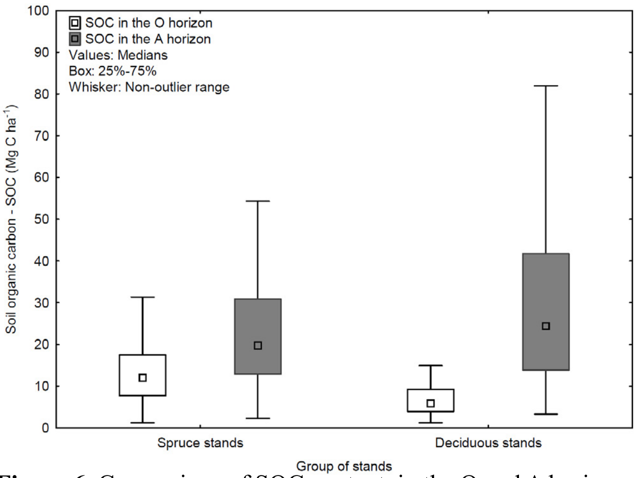

Figure 6. Comparison of SOC content, in the O and A horizons, between spruce stands and deciduous stands.

Table 2. Significant differences (*p*-values) in soil organic carbon (SOC) content, in the O and the A horizons in individual age groups, between spruce and deciduous stands, according to t-test.

		Significant differences in SOC content in the O horizon					
		Spruce stands					
	Age group	**10-60**	**61-80**	**81-120**	**121-140**	**141 and more**	**N (252)**
Deciduous stands	**10-60**	p=0.0061	–	–	–	–	15
	61-80	–	p=0.0000	–	–	–	32
	81-120	–	–	p=0.0000	–	–	58
	121-140	–	–	–	p=0.0004	–	20
	141 and more	–	–	–	–	p=0.0008	24
	N (149)	21	67	144	15	5	--
		Significant differences in SOC content in the A horizon					
		Spruce stands					
	Age group	**10-60**	**61-80**	**81-120**	**121-140**	**141 and more**	**N (252)**
Deciduous	**10-60**	ns	–	–	–	–	15
	61-80	–	ns	–	–	–	32
	81-120	–	–	p=0.0074	–	–	58
	121-140	–	–	–	ns	–	20
	141 and more	–	–	–	–	ns	24
	N (149)	21	67	144	15	5	--

N = number of samples. ns = non-significant; $p < 0.05$. – not statistically evaluated

Table 3. Significant differences (*p*-values) in SOC content, in the O and A horizons for individual levels of density of stocking, between spruce and deciduous stands, according to t-test.

		Significant differences in SOC content in the O horizon				
		Spruce stands				
	Density of stocking	**0.7**	**0.8**	**0.9**	**1.0**	**N (252)**
Deciduous stands	**0.7**	p=0.0011	–	–	–	21
	0.8	–	p=0.0000	–	–	49
	0.9	–	–	p=0.0000	–	52
	1.0	–	–	–	p=0.0000	27
	N (149)	54	73	77	48	--
		Significant differences in SOC content in the A horizon				
		Spruce stands				
	Density of stocking	**0.7**	**0.8**	**0.9**	**1.0**	**N (252)**
Deciduous stands	**0.7**	p=0.0040	–	–	–	21
	0.8	–	ns	–	–	49
	0.9	–	–	ns	–	52
	1.0	–	–	–	ns	27
	N (149)	54	73	77	48	--

N = number of samples. ns = non-significant; $p < 0.05$. – not statistically evaluated and 3b). A significant difference in SOC content between spruce and deciduous stands was proven only in density of stocking 0.7 (p=0.0040).

The canopy of stands had no effect on SOC content in either studied horizon in spruce stands and no trend is evident. However, all median values of SOC content in the O horizon in spruce stands were higher, overall, than median values of SOC content in the O horizon in deciduous stands (Fig. 4a and 4b). In contrast, overall higher median values of SOC content were noticeable in deciduous stands in the A horizon (but with higher scatters) than in the spruce stands. Comparison of SOC content (significant differences) at certain levels of canopy of stand between spruce and deciduous stands was not conducted, because knowledge of the existence of a trend in SOC content and the effect of canopy on SOC content in the studied horizons had greater explanatory value in this research.

When SOC was compared in the elevation gradient (categorized according to FVZs), there were apparent increasing trends in SOC content in the O horizon in both groups of stands, and in deciduous stands this trend was significant (Fig. 5a and 5b). Significant differences in SOC content were proven between spruce and deciduous stands in the 2^{nd} FVZ (p=0.0000), 3^{rd} FVZ (p=0.0072), 4^{th} FVZ (p=0.0015), and 5^{th} FVZ (p=0.0022) (Table 4). In the A horizon, the opposite trend to the O horizon was evident. In spruce stands, there was a significant increasing trend in SOC content, whereas in deciduous stands there was a noticeable decreasing trend in SOC content (Figs. 5a and 5b). Significant differences in SOC content between spruce and deciduous stands were only proven in the 3^{rd} FVZ (p=0.0234).

Discussion

In the introductory part of the discussion, we would like to address the issue of carbon determination and SOC recalculation. In this research we worked with organic carbon determined by the Walkley & Black (1934) method. Many authors state that oxidation of carbon is incomplete, with a mean recovery of 76% (Walkley & Black, 1934). Therefore, several correction factors were proposed and introduced. The correction factor for individual soils can vary between 1.16 and 1.59 (Nelson & Sommers, 1982), whereas a correction factor of 1.3 is very often used. It is difficult to choose a suitable correction factor, especially on forest soils, because true factors vary greatly between and within soils because of differences in the nature of organic matter according to soil depth and vegetation type (Grewal *et al.*, 1991), and also depending on soil parent material (Gillman *et al.*, 1986). Krishan *et al.* (2009) point out that when SOC content is evaluated from several study

Table 4. Significant differences (p-values) in SOC content, in the O and A horizons for represented forest vegetation zones (FVZs), between spruce and deciduous stands, according to t-test.

		Significant differences in SOC content in the O horizon					
		Spruce stands					
	FVZ	**1**	**2**	**3**	**4**	**5**	**6**
Deciduous stands	**1**	ns	–	–	–	–	–
	2	–	p=0.0000	–	–	–	–
	3	–	–	p=0.0072	–	–	–
	4	–	–	–	p=0.0015	–	–
	5	–	–	–	–	p=0.0022	–
	6	–	–	–	–	–	ns
		Significant differences in SOC content in the A horizon					
		Spruce stands					
	FVZ	**1**	**2**	**3**	**4**	**5**	**6**
Deciduous stands	**1**	ns	–	–	–	–	–
	2	–	ns	–	–	–	–
	3	–	–	p=0.0234	–	–	–
	4	–	–	–	ns	–	–
	5	–	–	–	–	ns	–
	6	–	–	–	–	–	ns

ns = non-significant; p < 0.05. – not statistically evaluated areas, different correction factors can ideally be used, but this makes research very difficult. Due to the diversity of our study plots (stands) and their substrates, and also in relation to the lengthy timespan (from 1953 to 2004) of analysis conducted, we decided not to apply the correction factor (similar to Cao *et al.*, 2019, and others).

The effect of many different variables on SOC in various types of stand has already been studied (Jonard *et al.*, 2017; Angst *et al.*, 2019; Yao *et al.*, 2019; Devi, 2021). However, little attention has been paid to the relationship to SOC of stand characteristic such as age of stand (some age classes were studied in Nitsch *et al.*, 2018; Cao *et al.*, 2019; Hou *et al.*, 2019), density of stocking and canopy of stand (Noh *et al.*, 2013; Na *et al.*, 2021). There has been very little research focusing on the dynamics of SOC throughout the life of stands (Chen & Shrestha, 2012). Some studies confirm that these stand characteristics, which relate to developmental stages of forest stands, are very important not only in terms of carbon sequestration, but also in diversity-structure-productivity relationships in forest stands (Dieler *et al.*, 2017; Zeller & Pretzsch, 2019).

This research studied the impact of stand characteristics (age of stand, density of stocking and canopy of stand) which are directly influenced by human intervention through forest management practices in production stands, on SOC content. Due to the difficulty of obtaining detailed information about individual management interventions conducted in each of 401 stands between 1953-2004, we tried to find out, through the selected stand characteristics, the indirect influence of management measures (transferred influence) on SOC content.

Based on our results, it is possible to state that age of stand has an influence on SOC content. In spruce stands in the study area an increasing trend of SOC was proven in the O horizon (a similar result was found by Côté *et al.*, 2000), and a decreasing trend of SOC was proven in the A horizon (Fig. 2a). Cao *et al.* (2019) also found a decreasing trend of SOC with stand age in horizons below the upper horizon, but in the upper horizon they found the opposite trend. An increasing SOC content in the O horizon with increasing stand age can be explained by decomposition. In general, the decomposition process is slower in coniferous stands due to their litter chemistry (Reich *et al.*, 2005; Hobbie *et al.*, 2006), where biological diversity and activity in the soil is lower (Augusto *et al.*, 2015). Spruce litter is more acidic and richer in lignin than *e.g.* beech litter, hampering litter decomposition (Kern *et al.*, 2016). Therefore, the litter accumulates on the soil surface and in the O horizon with increasing age of stand, and little is transported to the A horizon (Mareschal *et al.*, 2010; Lorenz & Sören, 2019). Subsequently the SOC content in the A horizon gradually decreases with stand age. In deciduous stands an increasing trend of SOC was proven only in the O horizon, similar results were found in the study by Chen & Shrestha (2012). However, the SOC content in this horizon in all age groups is considerably lower than in spruce stands (Fig. 2b). This again relates to decomposition. Deciduous stands create better conditions for decomposition, primarily in terms of soil pH, quality and character of litterfall, biological activity, bioturbation and rhizo-decompositon (Jandl *et al.*, 2007; De Schrijver *et al.*, 2012). In the A horizon, the trend of SOC was not statistically proven, this could relate to a considerable variance in SOC content in individual age groups. For this reason, we decided to use preferably median values of SOC for comment on the results, but the mean values of SOC are also displayed in Fig. 2b. The mean values of SOC in individual age groups would indicate an increasing trend of SOC, but in our research this could be an inaccurate statement. For a more categorical result, it would be necessary to take more samples and give a more balanced representation of samples. However, the variance (interquartile ranges) showed overall higher SOC content in age groups in deciduous rather than in spruce stands (Figs. 2a and 2b). The SOC content in the A horizon fluctuated slightly in age groups of stands, but it is possible to state that SOC content throughout the life of stands was more balanced in comparison with spruce stands. A fluctuating level of SOC storage with age of stands was also demonstrated in oak stands in Austria (Bruckmann *et al.*, 2011).

In this research, the dynamics of SOC content throughout the life of production stands is demonstrated. Attention is paid to age of stand, age groups respectively, which were determined according to the development stages of stands and forest management practices carried out in production stands. Based on this research, it can be indirectly deduced, through age of stand, that management measures conducted within the care of stands and stand tending in the 10-60 and 61-80-year age groups did not show a negative effect, which would manifest in SOC content, in either of the stand groups. On the contrary, SOC content in the A horizon in these age groups is the highest in spruce stands and high in deciduous stands (Figs. 2a and 2b). Based on detected SOC content in age groups which correspond to individual growth developmental stages, and management measures conducted within them, it is possible to indirectly deduce that management intensity was at an optimal level in the study area, because some studies confirm that over-intense management measures (*e.g.* thinning) can lead to reduced SOC (Bravo-Oviedo *et al.*, 2015; Ruiz-Peinado *et al.*, 2017; Zhang *et al.*, 2018).

In relation to the problem of spruce stands dying off at lower elevations, it will be necessary to perform sanitation measures (primarily felling) over large areas. Therefore, it would be useful to know the optimal age of felling in relation to carbon sequestration. Our results show that it would be potentially appropriate to conduct felling in spruce stands as early as 81-120 years of age. This is due to the acceptable ratio between SOC content in the O and the A horizon - SOC content in the A horizon is comparable with older stands, and in the O horizon it is not too high. In terms of carbon sequestration, it would probably not be effective to fell older stands (141 years and more), because there is a high SOC content in the O horizon and SOC content in the A horizon is decreased (Fig. 2a). Moreover, the O horizon is very often disrupted by felling (Holuša *et al.*, 2018; Mayer *et al.*, 2020; Çömez *et al.*, 2021) and carbon can be released back into the atmosphere. In the context of the impact of climate change, it is also possible to assume that spruce stands will not be able to survive to the age of 141 years and more in the required health and wood quality at lower elevations (Dušek, 2015; Šrámek *et al.*, 2015; Holuša *et al.*, 2018). The issue of optimal felling age with regard to carbon sequestration was also studied by Van Kooten *et al.* (1995). On the other hand, in deciduous stands, there is a possible increasing trend of SOC with stand age, which would better indicate that felling could rather be conducted in older stands (141 years and more) in terms of carbon sequestration (Fig. 2b). This closely relates to felling maturity, felling age and also to physical age of deciduous trees, especially beech and oak (Pulkrab *et al.*, 2014), parameters which take longer than for spruce.

In terms of density of stocking and canopy of stands, which change with management interventions, the predicted effects on SOC content were not statistically proven in any of the groups of stands (similar results in Nilsen & Strand, 2008; Mayer *et al.*, 2020), except for the effect of canopy on SOC in the O horizon in deciduous stands. However, in spruce stands, it is noticeable that stands with less than full density of stocking had a higher SOC content in the A horizon (Fig. 3a). A study by Hernandez *et al.* (2016) conducted in Pinus taeda forests, also confirms a higher SOC in stands with lower stand density. In the study area, it probably indicates that sparse stands, stands with lower levels of density of stocking, are able to sequester more SOC. Similarly, also in deciduous stands, it is evident that a higher SOC content in the A horizon was detected in stands with lower values of density of stocking (Fig. 3b). Moreover, interquartile ranges of SOC in deciduous stands indicate a decreasing trend of SOC with density of stocking, but the median and mean values are too different for clear interpretation. More samples for individual levels of density of stocking would be needed. The increasing trend of SOC with canopy of stands in the O horizon, which was found in deciduous stands (Fig. 4b), can be explained by the decomposition rate (Prescott *et al.*, 2002). It is known that a higher and denser canopy of stands slows down decomposition and litter accumulates, whereas an open canopy or removal of canopy causes soil C loss due to higher insolation and warmer, more favourable soil microclimatic conditions, which stimulate faster decomposition and soil respiration (Kulmala *et al.*, 2014; Mayer *et al.*, 2017).

The impact of selected stand characteristics on SOC content was studied in stands distinguished as either spruce or deciduous on the basis of predominant main tree species. Mixed stands and the effect of species mixing on SOC were not considered for analysis, although species mixing can have an influence on soil properties (Horváth *et al.*, 2021). The reason for this was that an adequate number of samples would not be represented in individual age groups, and categories of density of stocking and canopy, when divided into spruce, deciduous and mixed stands. Although the chosen division into spruce and deciduous stands, as two broad groups, may seem imprecise, this division was made to compare them primarily in relation to spruce monocultures dying-off in the context of climate change, and to assess the ability of deciduous stands to replace dying spruce stands with a comparable carbon sequestration function (in comparable climate conditions).

Based on comparison of spruce and deciduous stands, it is possible to summarize that deciduous stands had a higher SOC content in the A horizon (this is also confirmed by Dawud *et al.*, 2016; Kern *et al.*, 2016). This is important, because it is known that deeper soil horizons (mineral horizons) are more suitable for long-term and stable carbon sequestration. On the other hand, a higher SOC content in the O horizon was detected in spruce stands (Fig. 6). Similar results were found in a study by Kern *et al.* (2016). It is relatively well documented that conifers tend to store a relatively higher amount of SOC in a labile form in the organic layer (Wiesmeier *et al.*, 2013).

In terms of suitability of deciduous stands as a replacement for dying spruce stands in the context of carbon sequestration, it was found that deciduous stands sequester more SOC in the A horizon primarily at lower elevations (2^{nd}-4^{th} FVZs). Unfortunately, only one sample (stand) was represented in the 1^{st} FVZ, therefore it could not be used to compare and comment on the results (Fig. 5a). It is lower elevations that are most affected by the die-off of spruce stands. In addition, broadleaved trees show a more stable increase in SOC stock after afforestation than other tree species (Hou *et al.*, 2019). Therefore, deciduous stands are considered appropriate in terms of carbon sequestration with a potential to replace dying spruce stands, especially within this elevation range. Moreover, deciduous and mixed stands are considered to be more resistant to drought, as one of the serious impacts of climate change (Pretzsch *et al.*, 2018; 2020; Pardos *et al.*, 2021) and form natural tree species composition of forest at these lower elevations, which is in the context of modern forestry practice based on rich composition of tree species. At the middle elevation (5^{th} FVZ), where spruce begin to occur naturally, the SOC content was higher in spruce stands than in deciduous stands (Fig. 5a and 5b).

A higher SOC content can also be assumed in the 6th FVZ, but only one sample (stand) was represented, therefore this is only an estimation, which would have to be confirmed by further analysis.

Acknowledgements

The authors wish to thank the anonymous reviewers for their valuable and insightful comments for improvement of the manuscript. The team of authors, and Palacký University, thank the Forest Management Institute for providing data, and J&I Leckie for linguistic proofreading of the text.

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