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Parent Material Effect on Soil Organic Carbon Concentration under Primeval European Beech Forests at a Regional Scale

Viliam Pichler ^{1,*}, Erika Gömöryová ¹ , Christoph Leuschner ², Marián Homolák ¹, Ioan Vasile Abrudan ³ , Magdaléna Pichlerová ⁴ , Katarína Štrelcová ¹, Alfredo Di Filippo ⁵  and Roman Sitko ¹

- ¹ Faculty of Forestry, Technical University in Zvolen, T. G. Masaryka 24, 960 01 Zvolen, Slovakia; erika.gomoryova@tuzvo.sk (E.G.); marian.homolak@tuzvo.sk (M.H.); katarina.strelcova@tuzvo.sk (K.S.); sitko@tuzvo.sk (R.S.)
- ² Plant Ecology and Ecosystems Research, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany; cleusch@gwdg.de
- ³ Faculty of Silviculture and Forest Engineering, Transilvania University Brasov, 500036 Brasov, Romania; abrudan@unitbv.ro
- ⁴ Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, T. G. Masaryka 24, 960 01 Zvolen, Slovakia; magdalena.pichlerova@tuzvo.sk
- ⁵ Department of Agriculture and Forest Sciences, University of Tuscia, Via San Camillo de Lellis, 01100 Viterbo, Italy; difilippo@unitus.it
- * Correspondence: pichler@tuzvo.sk



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Abstract: The research presented herein explores soil organic carbon concentration (SOCC) under monodominant primeval forests of European beech trees and their association with parent material on a regional scale. Soil sampling to a maximum depth of 0.8 m was conducted in six localities in the West, East, and South Carpathians, Eastern Albanides, and Central Apennines, situated on different parent materials. Samples were analysed for SOCC by the dry combustion method. The average SOCC values representing individual localities ranged from 12.5 g kg⁻¹ to 154.8 g kg⁻¹ with a 99.7% coefficient of variation. SOCC association with climatic variables and forest stand volume data available from the literature were assessed by a Pearson correlation coefficient. Differences in SOCC among localities caused by site conditions were treated as a fixed factor in Welch's ANOVA and found to be significant ($p < 0.05$) in the majority of cases. The associations between SOCC and climatic variables or stand volume were nonsignificant or perturbed. Since they validly explained less than 10% of the overall SOCC variance, the results of multiple comparison tests were assessed and interpreted in view of distinct parent materials.

Keywords: *Fagus sylvatica* L.; old-growth forests; soil organic carbon concentration; soil parent material; regional variability; Welch's ANOVA

1. Introduction

Soil organic carbon (SOC) plays an important role in the formation and conservation of soil structure, available water-holding capacity, soil nutrient cycling, and soil biodiversity [1–3]. Also, carbon sequestration enhances the resilience of soils in response to global change [4]. In recent years, numerous studies have dealt with the dynamics and climate change mitigation potential of soil organic carbon sequestration and its vulnerability [5–8]. For instance, harvesting may cause soil C stock depletion in the forest floor, upper mineral soil and in subsoil [9–15]. In this context, SOC concentration (SOCC) and stock are used as indicators in numerous sustainable forest and soil management schemes and framework agreements [16–18]. Although SOC concentration and stock are separate SOC characteristics, they are closely linked and SOCC may explain up to 90% of SOC stock variability [19]. However, there is a persistent lack of baseline SOC content values needed to develop and apply forest and soil conservation or management plans, even in forest areas of paramount importance for humanity, such as Natural World Heritage forest sites [20]. Under certain

conditions, baseline indicator values can be derived from unmanaged, undisturbed forests for reasons of comparing changes due to disturbance or time [21]. Therefore, our study focused on SOCC in some of the remaining primeval European beech forests (*Fagus sylvatica* L.) that have not seen intense exploitation or large-scale fire disturbance during several centuries [22]. These forest remnants are scattered throughout East-Central, South-Eastern, and Southern European mountains satisfying the habitat characteristics of European beech [23–27] and their SOC content might be approaching its long-term maxima for this type of forest. While climate and vegetation are important factors affecting SOC [28], there is growing evidence that parent material strongly affects organic carbon (OC) inputs to soils and its subsequent stabilization through various types of bonding with the mineral matrix of soils [19,29–32]. In particular, silt- and clay-protected C and microaggregate-protected C pools [33] strongly depend on soil clay-size fraction that can contain six main types of minerals: phyllosilicates, i.e., clay minerals (*sensu stricto*), metallic oxides and hydroxides, primary minerals, e.g., mica, and—in some soils—carbonates or short-range order aluminosilicate minerals, such as allophane [34].

In contrast, the association between SOC content and forest productivity is generally loose [35,36]. The role of individual factors affecting OC content in forest soils also varies among different scales, such as those of soil particle, pedon, plot, landscape, region, and beyond [37]. The research objective of this study was to evaluate the effect of parent material under remnants of European beech primeval forests at the regional scale, including against the backdrop of possible SOCC association with climate and forest productivity data available from the literature. Another related objective was to provide a baseline of target SOCC values and range of variability for nature conservation and close-to-nature forestry in comparable beech ecosystems of the concerned region. Such data are scarce because the majority of available OC inventories in forest soils only include topsoil [38]. Monodominant beech forests were selected as the species stands out in terms of ecological plasticity, expansion, and importance for forest management and nature conservation [22,39,40]. In view of the proposed relative similarity of site conditions in the concerned localities [23,27], our working hypothesis was that the regional scale variability of SOCC in undisturbed European beech forests is mainly determined by different soil parent materials, known to produce mineral fractions featuring distinct SOC-binding and -stabilising capacity.

2. Materials and Methods

Soil sampling was conducted in six strict primeval beech forest preserves in the East-Central, Southeastern and Southern areas of Europe (Figure 1). The concerned area encompassed ca $3.72 \cdot 10^5$ km², spanning parts of several neighbouring biogeographical provinces according to Udvardy [41]: Central European Highlands, Middle European Forest, and Balkan Highlands. Five of the localities (Havešová, Uholka, Rajcě, Izvoarele Nerei, Val Cervera) are included on the World Heritage List [22]. Their biomass has neither been removed nor have they been subject to massive forest fires in the known past. The sampled locations were framed by moderate variability of annual heat:moisture index (AHM) and forest stand volume (FSV) representing large parts of the temperate zone of Europe, with a coefficient of variation of $CV_{AHM} = 22.53\%$ and $CV_{FSV} = 16.63\%$ (Tables 1 and 2).



Figure 1. Position of primeval beech forests (marked by black concentric circles) in East-Central, South-Eastern, and Southern Europe.

Table 1. Geographical location and climatic characteristics of the research localities. Climate characteristics were collected from [23,24,42–45]. They were adjusted based on the gradient of +50 mm in precipitation, and $-0.5\text{ }^{\circ}\text{C}$ per 100 m gain in altitude in cases where only data from a nearby meteorological station were available. Abbreviations: MAT—mean annual temperature, MAP—mean annual precipitation, AHM—annual heat:moisture index.

Locality	Country	Orographic Unit	Geographical Coordinates	Elevation (m a.s.l.)	Aspect	Slope ($^{\circ}$)	MAT ($^{\circ}\text{C}$)	MAP (mm)	AHM
Vtáčnik	Slovakia	West Carpathians	48°37'351' N, 18°38'700' E	1150	S	19	4	1050	13.3
Havešová	Slovakia	East Carpathians	49°00'645' N, 22°19'538' E	650	SE	20	6	900	17.8
Uholka	Ukraine	East Carpathians	48°16'080' N, 23°37'341' E	800	SE	22	5.5	1300	11.9
Izvoarele Nerei	Romania	South Carpathians	45°07.364' N, 22°04.596' E	1250	SW	21	4	1150	12.2
Rajcë	Albania	Northern Albanides	41°09.971' N, 20°31.847' E	1350	E	20	6	1800	8.9
Val Cervara	Italy	Central Apennines	41° 49.641' N, 13° 43.933' E	1800	NNW	23	7.2	1211	14.2

Table 2. Geological, soil, and vegetation characteristics of the research localities. Data were collected from [46–52]. Soils are presented according to [53].

Locality	Parent Material	Soil	Humus Form	Plant Community	Forest Stand Volume ($\text{m}^3\text{ ha}^{-1}$)
Vtáčnik	Andesite	Cambic Andosol	Moder	<i>Dentario bulbiferae-Fagetum</i>	645
Havešová	Sandstones, claystone (flysch)	Dystric Cambisol	Moder	<i>Dentario glandulosae-Fagetum</i>	701
Uholka	Sandstones, marlstones (flysch)	Dystric Cambisol	Moder	<i>Fagetum dentariosum Fagetum asperulosum</i>	770
Izvoarele Nerei	Crystalline schists (mica-schists)	Dystric Cambisol	Moder	<i>Hieracio rotundati-Fagetum</i>	620
Rajcë	Serpentinite, gabbro, dolomite	Eutric Cambisol	Moder	<i>Fagetum asperuletosum</i>	807
Val Cervara	Limestones	Rendzic Leptosol	Moder	<i>Polysticho-Fagetum</i>	497

2.1. Soil Sampling and Analyses

Soil samples were taken from soil profiles aligned along a 60 m long transect placed in segments featuring optimum stage of development, identified according to [54]. There

was one 60 m transect in each locality, with five soil profiles excavated to 0.8 m depth or bedrock boundary (Figure 2).

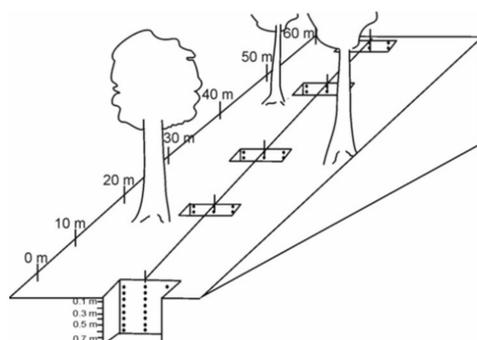


Figure 2. Soil sampling scheme along a 60-m long transect.

Three 100 g soil samples were taken from the left, central, and right sections in every 0.1 m layer of each profile, i.e., 24 soil samples were collected from each soil of the five soil profiles, 1.0 m × 0.8 m in size. Thus, there were 120 soil samples taken from each locality transect for individual analysis. Soil samples were air-dried, ground, and passed through a 2-mm mesh sieve. Soil pH was determined in water and 1 M KCl suspension of air-dried soil (1:2.5 ratio) using a calibrated electrode after 24 h. The C and N contents in the fine earth (<2 mm) were determined by Vario MACRO Elemental Analyzer (CNS Version, Elementar GmbH, Hanau, Germany), which employs the dry combustion method. Because elemental analyzer provides total carbon contents, inorganic C content was measured separately for each sample by a volumetric device and subtracted from the total carbon in order to obtain SOC mass concentration (g kg^{-1}). C:N ratio was calculated and assessed with regard to the presence of particulate organic matter (>10) as opposed to minerally associated organic matter (<13) [55]. Ammonium oxalate, citrate bicarbonate dithionite, and sodium pyrophosphate solutes were used for the determination of extractable iron oxides. The concentration of Fe oxides was measured by atomic absorption spectrophotometer (Thermo ICE 3000). The concentration of amorphous inorganic Fe (g kg^{-1}) represents the difference between ammonium oxalate- and sodium pyrophosphate extractable Fe, while the concentration of crystalline Fe (g kg^{-1}) represents the difference between citrate bicarbonate dithionite- and ammonium oxalate-extractable Fe. The presence of allophane in Dystric Andosol was determined by the Fieldes and Perrott test [56]. Soil bulk density (SBD) was determined from undisturbed soil samples (200 cm^3) collected from the soil profile by metal cylinders. Stoniness was established as the sum of the coarse fraction (>20 mm) volume, derived from its relative area on the soil profile wall [57], determined by image analysis, and the volume of gravel (2–20 mm) measured in the undisturbed soil samples. Root growth limiting soil bulk density was calculated based on soil textural compositions using [58].

2.2. Statistical Analyses

Owing to heteroscedasticity of the SOCC data, revealed by the Levene test ($p = 0.002$), Welch's one-way analysis of variance and the Games–Howell post-hoc multiple comparisons test [59,60] were used to assess SOCC differences caused by lithology, climate, and forest site productivity, defined as the potential of a particular forest stand to produce aboveground wood volume [61], that were treated together as a single fixed effect determining SOCC in the respective localities. The proportion of SOCC variability explained by locality was assessed as $1 - \text{SSW} / \text{SST}$ in analogy to classic one-way ANOVA [62], where SSW and SST are the within-group and total sums of squares, respectively. However, this estimate had to be taken with caution due to the violation of data homoscedasticity. The input for the Welch's ANOVA consisted of 30 average SOCC values, each representing one whole soil profile, five for each locality. SOCC average for each profile was calculated from

values in 0.1 m soil layers, from 0.10 to 0.80 m depth, determined from three soil samples in each individual layer (Figure 2). Data representing certain points from which soil samples could not be obtained due to the presence of boulders or solid bedrock outcrops were imputed by means of the Expectation-Maximization (EM) algorithm [62].

The normality of SOCC distribution was verified by the two-sample Kolmogorov–Smirnov test. Association between SOCC on the one hand and the annual heat:moisture index $AHM = (MAT+10)/(MAP/1000)$, and forest stand volume (FSV) as a proxy value in lieu of forest productivity, on the other hand, were assessed by multivariate stepwise regression and Pearson’s coefficient of correlation. Soil bulk density (SBD) was not regarded as an independent variable in relation to SOCC because the two properties mutually affect each other, e.g., SBD tends to decrease with rising SOM concentration [17,63]. MAT and MAP were compiled from literature sources quoting mean values from local stations or their interpolations (Table 1). Results were considered statistically significant if $p < 0.05$. Excel software and the Real Statistics Resource Pack software (Release 4.3) were used to run the analyses [62].

3. Results

3.1. Soil Physical and Chemical Properties

The results of soil physical and chemical analyses for all localities are provided in Table 3. The prevailing soil textural class was loam. Val Cervara was the only locality with a strongly skeletal subsoil. The coefficient of variation for SBD was 27.71% and 22.55% in topsoil and subsoil, respectively. The growth of tree roots was likely unrestricted by either stony soil content (except for Val Cervara) or the calculated growth-limiting SBD ($1400\text{--}1600\text{ kg m}^{-3}$). Soil reaction was strongly acid or acid in four cases; only the subsoil at Val Cervara and Rajcë had a neutral pH. The amount of crystalline Fe was highest in the Rajcë soil derived from ophiolite substrate. The subsoil in Havešová bore signs of mottling due to episodic waterlogging and capillary fringe formation on a poorly pervious clay-bearing substrate.

Table 3. Soil physical and chemical properties. Abbreviations: BD—bulk density, SF—stony fraction, Alp—allophane, Mot—mottling, P—presence, A—absence, Sn—sand, Sl—silt, Cl—clay, Cr—crystalline Fe oxides, Am—amorphous Fe oxides.

Locality	Depth (m)	BD (kg m^{-3})	SF (m m^{-3})	Texture (%)			pH		Fe (g kg^{-1})		CaCO ₃	Alp	Mot
				Sn	Sl	Cl	H ₂ O	KCl	Cr	Am			
Vtáčnik	0.1	870	0.11	21.6	50.9	27.5	5.05	4.55	8.82	0.24	A	P	A
	0.5	1010	0.25	29.1	51.3	19.6	5.25	4.85	10.33	0.02	A	P	A
Havešová	0.1	970	0.13	10.1	71.6	18.3	4.77	3.34	9.97	0.88	A	A	A
	0.5	1140	0.24	15.4	62.9	21.7	5	3.43	13	0.58	A	A	P
Uholka	0.1	830	0.2	5.8	59.4	34.8	4.68	3.45	15.57	1.65	A	A	A
	0.5	1300	0.26	9.4	58.5	32.1	4.75	3.6	15.92	2.56	A	A	A
IzvoareleNerei	0.1	580	0.07	49.6	32.9	17.5	4.05	3.51	9.79	0.57	A	A	A
	0.5	890	0.36	54	27.8	18.3	4.59	4.15	10.84	0.45	A	A	A
Rajcë	0.1	1000	0.1	13.6	62.3	24.1	5.56	4.48	95.64	0.52	A	A	A
	0.5	1210	0.14	5.4	40.9	53.7	6.29	5.19	161.11	3.76	A	A	A
Val Cervara	0.1	593	0.12	4.1	68.3	27.6	5.84	4.78	19.66	0.56	P	A	A
	0.5	522	0.66	4.8	66.5	28.7	6.96	6.21	20.03	1.52	P	A	A

3.2. Soil Organic Carbon Variability

Soil organic carbon concentration varied considerably among localities (Figure 3, Table 4), with an average of 59.77 g kg^{-1} , but its distribution did not significantly deviate from normality assumption. The coefficient of variation (CV) among sites (99.72%) was several times higher than that for individual sites (6.77–27.35%), MAT (23.03%), MAP (25.02%), AHM (22.53%), and FSV (16.63%). Also, CV among sites in the subsoil was nominally higher (117.59%) than in the topsoil (74.88%). Separate correlation between SOCC and AHM ($R = 0.07$, $R^2 = 0.01$, $p = 0.72$) was negligible, while that between SOCC and FSV ($R = -0.53$, $R^2 = 0.29$, $p = 0.00$) was modest and clearly spurious since it implied SOCC decrease with increasing aboveground biomass. Results of separate analyses were

paralleled by multivariate stepwise regression, whereby it did not identify explanatory climatic or FSV variables. The C:N ratio > 10 indicated the presence of particulate organic matter (POM) in the majority of localities (except for Havešová and Uholka).

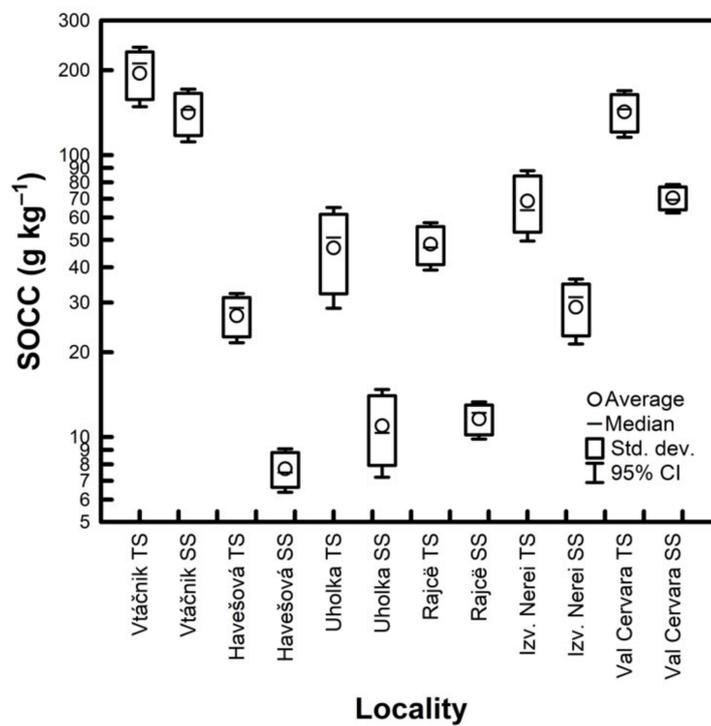


Figure 3. Average and median soil organic carbon concentration (SOCC) in both topsoil (TS: 0.00–0.20 m) and subsoil (SS: 0.20–0.80 m) for each locality. The vertical axis is in a logarithmic scale.

Table 4. Average soil organic carbon concentration (SOCC) for each locality and plot, calculated from 24 values in each soil profile. The coefficient of variation (CV) was calculated from plot averages in each locality. Abbreviations: Avg.—average.

Locality	SOCC (g kg ⁻¹)					Avg.	CV (%)	C:N Ratio	
	Profile No							TS	SS
	1	2	3	4	5				
Vtáčnik	112.18	154.99	171.96	179.26	155.41	154.76	16.82	14.8	16.6
Havešová	14.34	10.43	12.94	11.21	13.74	12.53	13.27	8.5	5
Uholka	22.08	25.75	20.5	10.98	20.51	19.96	27.35	9.3	6.4
Izvoarele Nerei	47.46	43.01	34.09	29.9	39.76	38.85	17.98	14.1	14.4
Rajčě	21.17	20.11	18.76	21.37	22.48	20.78	6.77	16.8	10.7
Val Cervara	78.88	96	89.02	94.98	83.52	88.48	8.3	13.7	13.1

3.3. Differences among Localities

Welch's ANOVA indicated the presence of significant SOCC differences among localities ($F_{5, 10.51} = 112.67, p < 0.0001$), and the proportion of SOCC variability explained by the locality factor was estimated at ca 90%. In the absence of a strong or moderate SOCC relationship with climate, the significant pair-wise differences identified by the Games–Howell test (Table 5) were associated with distinct fine earth fractions (<2 mm), derived from diverse parent material in the respective localities. When ordered according to SOCC in the individual localities as the expression of their SOC-binding and -stabilising capacity, flysch-

derived phyllosilicates (Havešová, Uholka) and crystalline Fe oxides from an iron-bearing ophiolitic substrate (Rajčė) ranked lowest, followed by mica-schists-derived sand fraction partaking in the origin of macroaggregates (Izvoarele Nerei), and calcium/carbonates from limestone (Val cervara). The highest SOCC was associated with short-range order alumino-silicate minerals represented by andesite-supplied allophane (Vtáčnik).

Table 5. Games–Howell post-hoc multiple comparison test of soil organic carbon concentration (SOCC) differences between localities, characterized by main SOC-binding agents and mechanisms: ALP—allophane, PHS—phyllosilicates, MS—micaceous sand, FOX—iron oxides, CAC—Ca²⁺ and carbonates. PHS+ represents the higher proportion of phyllosilicates in Uholka compared to Havešová (PHS).

Locality and Main Local SOC-Binding Agent		Mean Difference in SOCC (A–B) (g kg ⁻¹)	Std. Error	95% Confidence Interval for MD		p-Value
A	B			Lower Bound	Upper Bound	
Vtáčnik (ALP)	Havešová (PHS)	142.23	8.25	87.14	197.31	0.001
Vtáčnik (ALP)	Uholka (PHS+)	134.8	8.41	80.69	188.91	0.001
Vtáčnik (ALP)	Izvoarele Nerei (MS)	115.91	8.52	62.36	169.47	0.002
Vtáčnik (ALP)	Rajčė (FOX)	133.98	8.24	78.87	189.1	0.002
Vtáčnik (ALP)	Val Cervara (CAC)	66.28	8.55	12.86	119.7	0.022
Havešová (PHS)	Uholka (PHS+)	7.43	1.81	−3.73	18.59	0.189
Havešová (PHS)	Izvoarele Nerei (MS)	26.31	2.27	11.87	40.76	0.005
Havešová (PHS)	Rajčė (FOX)	8.24	0.69	4.66	11.83	0
Havešová (PHS)	Val Cervara (CAC)	75.95	2.38	60.72	91.18	0
Uholka (PHS+)	Izvoarele Nerei (MS)	18.88	2.8	4.18	33.59	0.014
Uholka (PHS+)	Rajčė (FOX)	0.81	1.78	−10.45	12.08	0.999
Uholka (PHS+)	Val Cervara (CAC)	68.52	2.9	53.23	83.8	0
Izvoarele Nerei (MS)	Rajčė (FOX)	18.07	2.25	3.53	32.6	0.023
Izvoarele Nerei (MS)	Val Cervara (CAC)	49.63	3.21	33.06	66.21	0
Rajčė (FOX)	Val Cervara (CAC)	67.7	2.37	52.38	83.02	0

4. Discussion

In all but one locality, their average SOCC values were similar or slightly to moderately higher than in other old-growth or managed European beech stands and from colline to mountain sites when compared to the same depth [64–68]. In Havešová, the average SOCC value was exceptionally low, only 12.53 g kg⁻¹, despite high FSV.

4.1. Predictive Ability of Soil Classification

In the presented study, significant SOCC differences from approx. 130 g kg⁻¹ to 25 g kg⁻¹ were determined not only among members of separate soil groups acc. to WRB [53], but also within a group (Cambisols). On the one hand, the positive effects of allophane on SOCC in Vtáčnik and carbonates in Val Cervara were expected as characteristic properties of humus-rich Andosols and Rendzic Leptosols [53,69]. On the other hand, significant differences within the Cambisol group imply that SOCC could not be explained by soil classification alone. Soil units predicted high SOCC only in cases where the presence of specific SOC-binding and -stabilising agents was characteristic of the respective soil unit properties.

4.2. Role of Parent Material

Because multiple comparison tests identified highly significant SOCC differences among investigated localities, it was possible to rank the dominant mineral fractions derived from their parent material. Overall, SOCC showed a positive skew towards relatively lower values but did not significantly deviate from the normal distribution. On the long-tailed part of the observed distribution, SOCC in Vtáčnik was significantly higher than in all remaining localities due to andesite-derived allophane, in line with its exceptional

SOC-binding and -stabilising properties [70]. Because C:N > 10 is typical of POM [55], it is very likely that the allophane effect included preferential POM accumulation. POM was also represented in Val Cervara, whose second-highest SOCC was sustained by carbonates and Ca cations from limestone. Although they both provide for substantial OC binding and stabilization through bridging, condensation, or microaggregate formation [71,72], SOCC at Val Cervara was almost 66 g kg^{-1} lower than in Vtáčnik. This result contradicts the suggested near-equivalence of allophane and calcium/carbonates [73] and supports the superiority of allophane in terms of SOC binding and stabilising capacity. We hypothesize that the proximity (in 10^2 m) of andesite and limestone bedrock in the latter study might have smoothed out the difference through lateral mixing of slope deposits.

In contrast to Vtáčnik and Val Cervara, a relatively high SOCC was determined even in the absence of strong SOC-binding and -stabilising agents, combined with the lowest proportion of clay fraction (Table 3). Under such circumstances, clay- and microaggregate-protected SOC pools play only a minor role and SOC is largely stored as POM in macroaggregates ($>250 \mu\text{m}$). Macroaggregates form in conditions featuring abundant sand fraction, litter- or root-derived POM, and the presence of microaggregates [33,74]. The evidence of substantial POM presence was provided by the relatively high C:N ratio, especially in the subsoil. The case of Izvoarele Nerei supports the emerging notion that SOC sequestration is not invariably proportional to fine fraction-associated OC [75] and that some forest soils may store more carbon in the form of POM [76]. In terms of their positive effect on SOCC, macroaggregates did not compare with short-range order alumino-silicate minerals and carbonates since the average value for Izvoarele Nerei was approx. 50 g kg^{-1} lower than in Val Cervara. Also, POM is more vulnerable to mineralisation due to its lack of association with clay fraction minerals [33]. At the same time, they outperformed phyllosilicates and crystalline Fe oxides in all the remaining Cambisols by ca $20\text{--}25 \text{ g kg}^{-1}$.

In particular, the noticeable gap in SOCC between Izvoarele Nerei and Rajcë was striking because Fe oxides, including Fe-bearing crystalline secondary minerals, are supposed to provide an important mechanism for long-term carbon storage, especially compared to the less important role of phyllosilicates [77,78]. Other studies suggested that only weakly crystalline or amorphous Fe oxides were positively correlated with SOCC or that low SOC content observed in ophiolitic soils resulted from their weak evolution and thus a variety of bedrock-inherited compositional features [79,80]. In view of our results, we speculate that one of such compositional features in Rajcë was the high magnesium content and its prevalence over calcium because Mg^{2+} ions are less effective in aggregating soils than Ca^{2+} [81,82]. Indeed, even a very high amount of crystalline Fe, similar to that in Ferralsols, did not produce higher SOCC in the Rajcë soil when compared to other members of the Cambisol group.

In contrast, it was practically identical to that in Uholka, in which only phyllosilicates accounted for mineral SOC bonding and stabilisation. The difference between SOCC in Havešová on the one hand and Uholka or Rajcë, on the other hand, was ca 8 g kg^{-1} . Very low SOCC in Havešová indicated that the relatively weakest effect of phyllosilicates as SOC-binding agent was diminished by episodic waterlogging that left signs of mottling on the Havešová profiles. Fluctuating capillary fringes have the potential to deplete SOC content through enhanced C mineralization [83,84]. Also, the low C:N ratio in both Uholka and Havešová (<10) implies that without abundant sand fraction, flysch claystone-derived soil phyllosilicates were unable to accommodate POM.

Thus, results of the presented research conducted on regional scale support indices that the fine mineral fraction is the determining factor of SOC stabilization in a majority of soils [37]. They show that under the same type of vegetation and within the climate envelope of European beech [85], the binding and stabilisation agents derived from their respective parent materials assume different ranks according to SOCC associated with their presence. Given the centuries-long, continuous organic matter supply of the concerned soils and their current SOCC levels, being mostly only slightly higher than in comparable managed or old-growth forests, it is likely that SOCC in the concerned localities represents

asymptotic maxima for similar site conditions. Therefore, attention and efforts should primarily focus on the preservation of vulnerable SOC stocks, e.g., those associated with phyllosilicates derived from flysch rock, which are also significantly threatened by erosion.

5. Conclusions

To the best of our knowledge, the presented research was the first to study SOC concentration not only in topsoil but also in the subsoil to the depth of 0.8 m under monodominant primeval forests of European beech at a regional scale. Practically, it captured SOCC values and their variability under rare and largely undisturbed beech forests and established that, in general, they were similar or slightly higher than values reported from managed or old-growth forests in similar conditions. The presented research also produced further and partly new evidence to explain established SOCC differences with regard to the need to discern between the predictive ability of soil units and parent material for SOCC, as well as realistic baseline, target, and range of variability values for forest soil conservation and management of comparable forest ecosystems. Significant SOCC differences produced by the respective SOC-binding and -stabilising agents and mechanisms enabled their ranking according to SOCC. The ranking could be used in assessing SOC vulnerability and preventing potential SOC loss caused by disturbance, mainly in soils from parent materials primarily associated with the weakest capacity for SOC binding and stabilising under similar conditions. The protection of SOC in soils featuring low SOCC and weak stabilisation is particularly critical for maintaining soil functions and forest ecosystem resilience.

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