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Biotic and Abiotic Determinants of Soil Organic Matter Stock and Fine Root Biomass in Mountain Area Temperate Forests—Examples from Cambisols under European Beech, Norway Spruce, and Silver Fir (Carpathians, Central Europe)

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Abstract: Forest ecosystems significantly contribute to the global organic carbon (OC) pool, exhibiting high spatial heterogeneity in this respect. Some of the components of the OC pool in a forest (woody aboveground biomass (wAGB), coarse root biomass (CRB)) can be relatively easily estimated using readily available data from land observation and forest inventories, while some of the components of the OC pool are very difficult to determine (fine root biomass (FRB) and soil organic matter (SOM) stock). The main objectives of our study were to: (1) estimate the SOM stock; (2) estimate FRB; and (3) assess the relationship between both biotic (wAGB, forest age, foliage, stand density) and abiotic factors (climatic conditions, relief, soil properties) and SOM stocks and FRB in temperate forests in the Western Carpathians consisting of European beech, Norway spruce, and silver fir (32 forest inventory plots in total). We uncovered the highest wAGB in beech forests and highest SOM stocks under beech forest. FRB was the highest under fir forest. We noted a considerable impact of stand density on SOM stocks, particularly in beech and spruce forests. FRB content was mostly impacted by stand density only in beech forests without any discernible effects on other forest characteristics. We discovered significant impacts of relief-dependent factors and SOM stocks at all the studied sites. Our biomass and carbon models informed by more detailed environmental data led to reduce the uncertainty in over- and underestimation in Cambisols under beech, spruce, and fir forests for mountain temperate forest carbon pools.

Keywords: forest characteristics; fine roots biomass; soil organic matter; Cambisols; mountain temperate forests; Carpathians

1. Introduction

Forest ecosystems significantly contribute to global organic carbon (OC) sequestration [1,2], storing 80% of the aboveground OC pool and 40% of the soil organic carbon (SOC) pool [3,4]. In the case of forests, a very high heterogeneity of the OC stock was noted, which was explained via both abiotic factors—such as topographic effects [5–9], morphogenetic processes [10], and soil properties [11–14]—and biotic factors—such as the tree species composition [15–20], silviculture treatment [10,12] and stand age [21,22]. The quantification of the OC pool in forests that cover large areas of land is important not only from a research point of view but more importantly in the context of expected changes due to climate change and deforestation observed all over the world [23–26].
The total OC pool in a forest is partitioned between OC accumulated in aboveground biomass (AGB), belowground biomass (BGB) and the soil organic matter (SOM) stock [9]. The estimation of AGB for a forest is relatively easy. Effective models for calculating AGB for forests based on stand characteristics (i.e., tree species, age, diameter at breast height) have already been introduced [27]. Similarly, remote sensing data provide global information on AGB for forests with high accuracy [28–31]. In contrast, the estimation of BGB and the SOM stock is more difficult and expensive in terms of time and money [5,32,33]. Therefore, a model that allows for a reliable estimation of both BGB and SOC stocks based on readily available data remains to be developed [22].

In the case of BGB, the quantity of coarse root biomass (CRB) can be estimated quite reliably using the already developed allometric models noted above [27], while in the case of fine root biomass (FRB), there is no proven, reliable method. Fine roots are difficult to study, as they have a short lifespan (less than one to nine years) [34], significant seasonal variability [18,35], and a high rate of decomposition [36]. In addition, the estimation of SOC stocks based on biotic and abiotic factors is difficult, because it is necessary to take into account events occurring both in the present day and in the past, since the amount of SOC depends on the balance between the accumulation and decomposition of organic matter at present, but also on the initial quantity [10]. However, it should be emphasized that the field measurements of both SOC stocks as well as biomass accumulated in litter are accurate [5,10,32,33,37], while measurements of FRB involve a considerable degree of uncertainty [38,39].

The estimation of both the BGB and SOM stock is also challenging due to their functional and not fully understood linkages, including the seasonal effects of living roots on organic matter turnover [40–42]. Generally, due to slow OC and nutrient turnover, the coarse root distribution represented by CRB may be more important for long-term ecosystem productivity [43,44]; however, fine roots also indirectly determine the size of the OC pool in forest ecosystems [45–48]. Fine roots may be considered a vital element of the physical connection between trees and soil [48], and by releasing various substances into the surrounding soil, they control the decomposition of dead organic matter, which then leads to the allocation of OC [49]. Additionally, special attention should be paid to FRB due to its important role in the biogeochemical cycle, which is an important part of the ecophysiology of trees [50].

As noted earlier, tree species directly affect AGB and CRB, but may also indirectly affect FRB and SOC stocks by altering the dynamics of soil organic matter decomposition [51,52]. Tree species are thought to influence microbiological decomposition mainly by varying the content of lignin, nitrogen, and alkaline and acid cations [15,53,54]. Conifers have a higher lignin content in their needles (25 to 33% dry weight) than broadleaf trees do in leaves (20 to 25% dry weight) [55], resulting in different litter quality, which later affects decomposition rates. As a result, there are different SOC stocks under different tree species. For example, in temperate mountain forests, a higher SOC stock in organic soil horizons (i.e., litter consisting of different fresh, non-decomposed or slightly decomposed organic material) was observed in comparison with that in the mineral part of soil under coniferous species [5], while in soil found under broadleaved species, more SOC is stored in the mineral part of the soil [56]. From all the above-mentioned studies, it may be concluded that in the case of forests, taking into account the tree species is very important in relation to the estimation of both FRB and SOM.

As previous studies have shown, remote sensing data provide global information on AGB found in forests with a rather high degree of accuracy [28–31], while allometric models based on detailed data from forest inventories [27] provide information on AGB and FRB in forests with a very high degree of accuracy. Thus, if we knew the relationship between AGB and both the BGB and SOM stocks, the elucidation of these relationships would improve future global OC pool models for forests. Such knowledge would significantly contribute to better use of the capabilities of global Earth observation missions (e.g., GEDI, BIOMASS) to determine global and regional OC pools in forests. The authors of [28] highlighted the
urgent need to link soil organic carbon stock data with aboveground biomass data on the basis of Earth observation missions yielding forest inventory data.

The determination of a relationship between AGB and the less accurately identified SOC stock and FRB requires the field and laboratory research on study plots for which very detailed forest inventory data are available [57]. A potentially broad set of abiotic and biotic factors should be taken into account in these investigations [10,22,56].

We hypothesized that it may be possible to estimate both the SOC stock and FRB using easily available data obtained from national forest inventories (NFI) characterizing stands—notably, woody aboveground biomass (wAGB) in mountain temperate forests in the Polish Carpathians. In this regard, we aimed to both determine and evaluate the relationship between selected forest stand characteristics, i.e., wAGB, forest age, stand density, foliage, (coming from NFI) and both FRB and SOM stocks in mountain area temperate forests in the Western Carpathians consisting primarily of the most common stand species: i.e., European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst), and silver fir (*Abies alba* Mill.). We decided to take into account available abiotic factors (i.e., elevation, hillslope exposure, hillslope gradient, mean annual air temperature (MAT), mean annual precipitation (MAP), soil properties), as they all affect the species-specific patterns of aboveground biomass accumulation in mountain area temperate forests [58]. Considering above- and belowground OC pools, the main objectives of our study were: (1) to estimate SOM stocks, (2) estimate FRB, and (3) assess the relationship between both abiotic and biotic factors and the SOM stock and FRB in the studied soils.

### 2. Materials and Methods

#### 2.1. Study Area and Study Plot Selection

The study area is located in the Western Carpathians (Central Europe). The climate in the study area is moderately cold with average monthly summertime temperatures varying from 16 °C in the foothills to 8 °C atop the highest peaks. The average monthly winter temperature stays below 0 °C, reaching −8 °C at the highest elevations. The average annual air temperature reaches 7 °C [59]. Our study sites differed slightly in terms of climate characteristics (Table 1) and differed strongly in terms of tree species type—the selected sites were covered with beech, spruce, fir, and mixed stands. The present-day forest structure in the Polish part of the Western Carpathians is mainly the product of centuries of forest use—with significant forest gains occurring since around 1850. However, over time, primeval beech and fir–beech forests were replaced by spruce plantations at most of the study sites [60–62]. Beech and fir-beech forests occupy a much smaller area today.

Table 1. Characteristics of the investigated study sites.

| Study Site | Coordinates       | Elevation Range Min–Max (m a.s.l.) | Hillslope Gradient Range Min–Max (°) | Hillslope Exposure Range Min–Max (°) | Mean Annual Air Temperature (°C) | Mean Annual Precipitation (mm) |
|------------|-------------------|-----------------------------------|-------------------------------------|-------------------------------------|---------------------------------|---------------------------------|
| 1          | 49°26′54″ N 19°03′05″ E | 701–808                           | 13–24                               | 4–165                               | 5.1                             | 1127                            |
| 2          | 49°11′30″ N 22°28′12″ E | 940–1067                           | 11–21                               | 276–316                             | 4.6                             | 1068                            |
| 3          | 49°38′01″ N 18°58′36″ E | 768–887                           | 15–25                               | 218–319                             | 5.2                             | 1103                            |
| 4          | 49°34′28″ N 19°41′09″ E | 706–753                           | 2–22                                | 44–540                              | 5.5                             | 978                             |
| 5          | 49°29′27″ N 20°36′35″ E | 575–658                           | 21–26                               | 59–79                               | 6.3                             | 1021                            |
| 6          | 49°37′44″ N 19°28′30″ E | 836–937                           | 16–20                               | 32–358                              | 4.8                             | 1134                            |
| 7          | 49°25′10″ N 22°01′56″ E | 602–624                           | 8–16                                | 100–266                             | 6.1                             | 870                             |

Our study was carried out on selected NFI plots, which are regular grids of study sites located 4 km from each other featuring L-shaped trails—plots part of the ICP Forest system (https://icp-forests.net/ (accessed on 15 May 2020)). The above study plots were established for the purpose of the assessment of forest damage across the European Union. A total of 32 plots out of 2450 plots located in the Western Carpathians were selected for study purposes (Figure 1), all of which had to meet the following conditions: (1) the studied
plots had to represent very similar soils: i.e., loamy texture, medium depth Cambisols developed from cover-beds originating in flysch rocks [63,64] and (2) all the plots had to be situated in a similar relief position (i.e., linear hillslope); thus, the areal drainage conditions could be expected to be quite similar (digital elevation model produced as part of Poland’s national GIS project). The selected study plots were located at seven study sites (Table 1) and composed of five circular plots each ($r = 12$ m). The study plots were located 200 m away from each other in a regular pattern. Together, all the study sites formed an L-shaped trail (Figure 1). We excluded three study plots due to the presence of young forest, resulting in a lack of accurate tree stand measurements, decreasing the accuracy of the biomass assessment [21].

![Figure 1](image.png)

**Figure 1.** Study area on a map of Europe (A), distribution of study sites (B) (numbers), and distribution of study plots (numbers with letters, e.g., 6A, 6B) at each study site (C).

2.2. Field Survey

Field sampling was conducted in 2017 (June to November). For each study plot, a soil profile was described according to [65] and then sampled (total of 32 soil profiles). One soil pit at each study site (plot labeled ‘C’ according to the A to E lettering at Figure 1) was excavated to the lithic contact (seven reference soils), while in the other study plots, soil pits were excavated to approximately 50 cm (25 soil profiles). Rock fragment (coarse particles, diameter > 2 mm) content in each soil horizon was estimated using standard charts (templates) commonly used in soil surveys [65]. Soil profiles were not established in close proximity of tree stems (up to 5 m, as this distance represented averaged conditions in the investigated study plots).

A core sampler (100 cm$^3$, in stony soils: 63.5 cm$^3$) was used to collect undisturbed soil samples (which also incorporated fine roots) using 10 cm intervals (0 to 10 cm, 10 to 20 cm, 20 to 30 cm, 30 to 40 cm) at each of the 32 study sites. Each sample was collected in triplicate. In addition, bulk soil samples (disturbed samples; ca. 1 kg) from selected genetic soil horizons were collected. Bulk samples from litter—defined as the surface layer of the forest floor for the purpose of the current paper, consisting of different fresh, non-decomposed or slightly decomposed organic material, with recognizable tissues—were collected using a metal frame: 10 cm x 10 cm, taking into account the representativeness of the sampling point. Every soil sample was then placed in a sterile polyethylene bag.
(Whirl-Pak®) and stored at ~4 °C before laboratory analysis. The investigated soils were classified according to the WRB [66].

2.3. Sample Pretreatment, Laboratory Analysis and Soil Organic Matter Stock Estimation

Litter samples were air-dried, crushed and homogenized for further analysis. From undisturbed soil samples (taken using the core sampler) fine roots were hand-picked and dried to constant mass at 70 °C and weighed with an accuracy of 0.1 g. Prior to drying, live and dead fine roots were distinguished by their color, elasticity and degree of bark cohesion [38,39]. Based on an analysis of 30% of randomly selected samples, a share of 10% (in mass) of dead fine roots was determined. Therefore, for the purpose of further analysis, it was assumed that 90% of the mass of fine roots in a given sample are live roots, and these values were selected for subsequent models. This approach is consistent with findings by [18,67,68], all of whom demonstrated that in the middle and at the end of the growing season, the amount of live fine roots is very large in total FRB. Dead fine roots were classified as non-humic substances in soil organic matter. We used the volume of the core sampler as a sample volume for calculations (Equation (1)). Soil material from undisturbed soil samples (without live fine roots) was dried at 105 °C and weighed. Then, the bulk density (BD) was calculated according to [32]. The calculation procedure according to [32] excludes coarse particles (Ø > 2 mm), as they are not a component of soil bulk density (Equation (1)).

\[
BD = \frac{\text{mass}_{\text{sample}} - \text{mass}_{\text{particles} > 2 \text{ mm}}}{\text{volume}_{\text{sample}} - \frac{\text{mass}_{\text{particles} > 2 \text{ mm}}}{\text{density}_{\text{particles} > 2 \text{ mm}}}}
\]  

(1)

Disturbed bulk soil samples (taken separately, in parallel) were air-dried, gently crushed, and sieved through a 2 mm mesh steel sieve. Rock fragments (Ø > 2 mm) were determined by weighing. Based on this measurement, the content of rock fragments determined during fieldwork (see above) was calibrated. Soil properties for fine soil (Ø < 2 mm) and litter subsamples were determined. The soil and litter pH were measured potentiometrically in distilled water (1:2.5) [69] using a pH meter (Elmetron CPI-505) with a glass electrode (Elmetron ERH-11). The concentration of total carbon (TC) and nitrogen (N) was determined in triplicate (and then averaged) using dry combustion gas chromatograph with a CHN analyzer (Elementar vario MICRO cube elemental analyzer). Due to the absence of carbonates in the studied soils, it was assumed that TC corresponds to SOC [70]. The SOC stock was herein calculated according to [32]. The soil texture was determined using the combined sieving and hydrometer method [71].

Due to the need to carry out an analysis for comparable values for further analysis, the studied SOC was converted into SOM using the conversion factor 1.724 [72], as precise data (obtained via experimental research) allowing the conversion of wAGB, CRB, and FRB into the OC pool remain unavailable.

2.4. Stand Characteristics and Coarse Root Biomass Estimation

We obtained data on tree species and DBH (diameter at breast height) for all trees with DBH > 7 cm. This approach omits small trees and shrubs; however, their biomass yields only a small contribution to total biomass, as biomass increases exponentially with DBH [21]. These data had been previously collected as part of NFI by the Polish Forest Research Institute and were verified in the course of our fieldwork in 2017 (June to October). The wAGB was calculated using biomass equations based on meta-analysis (Equation (2)) for European tree species [27] basing on DBH (cm):

\[
\ln (\text{AGB}) = \ln (\beta_0) + \beta_1 \ln (d) + \epsilon
\]  

(2)

where: AGB—woody aboveground biomass (kg), β0, β1—model parameters (coefficients): beech—β0 = −1.6594; β1 = 2.3589, spruce—β0 = −1.8865; β1 = 2.3034, fir—β0 = −2.3958; β1 = 2.4497, other coniferous trees—β0 = −1.6173; β1 = 2.3177, other deciduous trees—
\[ \beta_0 = -1.1972; \beta_1 = 2.3417, \varepsilon \text{—an error that is assumed to be normally distributed with a mean of 0 and standard deviation, } d \text{—DBH (cm) (for more details, see [27]).} \]

Additionally, we calculated the stand density (ind. ha\textsuperscript{-1}). The biomass of foliage was calculated using models provided by [73] for beech and spruce forests (Equation (3)):

\[
M = a \times X^b
\]

where: \( M \)—foliage biomass (Mg ha\textsuperscript{-1}), \( a, b \)—model parameters, spruce—\( a = 4.4073, b = 0.3544 \), beech—\( a = 0.8813, b = 0.4151 \), \( X \)—stand basal area (m\textsuperscript{2} ha\textsuperscript{-1}). Model parameters for fir forest were obtained from [74]: \( a = -3.07447, b = 2.81850 \).

The biomass of coarse roots (CRB; diameter of root > 2 mm) was calculated for beech, spruce, and fir separately using general equations (Equation (4)) [27].

\[
\ln(CRB) = \ln(\beta_0) + \beta_1 \ln(\varepsilon) + \varepsilon
\]

where: CRB—coarse root biomass (kg), \( \beta_0, \beta_1 \)—model parameters, spruce—\( \beta_0 = -3.7387; \beta_1 = 2.4323 \), beech—\( \beta_0 = -3.3713; \beta_1 = 2.3424 \), fir—\( \beta_0 = -4.0287; \beta_1 = 2.9457 \), other species—\( \beta_0 = -3.1677; \beta_1 = 2.2796 \), \( \varepsilon \)—an error that is assumed to be normally distributed with a mean of 0 and standard deviation, \( d \text{—DBH (cm) (for more details, see [27]).} \)

2.5. Data Analysis

We employed machine learning techniques to determine the effects of selected biotic forest stand characteristics and abiotic factors on FRB and SOM stocks (Table 2). Owing to a large number of predictions and interactions among them, machine learning and explanatory tools [75] enable the generation of a clear description of the meaning of each given prediction and its partial dependence. From different machine learning algorithms, we selected a random forest algorithm—a technique based on multiple decisions or tree classifications, which increases model stability and accuracy [76]. The random forest model has been successfully used for vegetation modeling [77]. We used R software [78] (version 4.0.2. “Taking Off Again”; R Core Team, 2019) for data analysis. All models were developed using the caret package [79] for model development and the DALEX package for the visual explanation and exploration of predictive models [75]. To understand how the said models work, we used variable importance and partial dependence plots. We quantified the variable importance using the drop-out loss function, i.e., loss-decrease root mean square error (RMSE). This function informs us how much the model RMSE increases when a particular variable is shuffled within a given dataset. Literally, it shows how much model quality we lose when we replace a particular variable with its random permutations [75]. The higher drop in losses in the RMSE indicates the higher importance of the variable for proper prediction. The partial dependence plots show the change in the model output along with an increasing value of a particular predictor, assuming all other variables at the constant (mean) level [75]. Literally, this is the prediction of the model using all variables at the constant level and manipulating only the variable of interest. Such an approach simulates the experimental rule ceteris paribus, which means ‘all equal, without the single manipulated’ and allows to see how FRB and SOM stocks vary along each of the predictors, without changing other variables. These marginal predictions allow one to make conclusions about the explicit impact of a particular variable.
To assess the FRB and SOM, we developed separate regression models for each examined dominant tree species stand and training models to decrease RMSE using the caret package [79]. To demonstrate the model’s quality, we provided RMSE and $r^2$—coefficient of determination indicating the proportions of variability explained by the model.

3. Results

3.1. Predictor Variances Among Beech-, Spruce- and Fir-Dominated Forests

The analyzed forest stand characteristics varied between study plots and between tree species (Tables 3–5). Similar findings were also obtained for climatic and morphologic predictors as well as the herein analyzed soil property predictors (Table A1). Both the morphology and properties of the investigated soils were very similar (Table A1). The texture was loamy throughout the studied soil profiles (silt loam, sandy loam, and loam) (Table S1 from Supplementary Materials). The soil structure was subangular or angular blocky, transitioning into massive in the bottom part of the soil. In addition, the soil consistence changed gradually with the depth of the soil profile from soft in the uppermost horizons to very hard in the lowermost part of the soil (Table 6). The gradual decrease in SOC content with soil depth occurred in all the study plots (Figure 2). According to tree species groups, the studied plots’ soil texture varied slightly—the highest silt and clay content was observed under fir-dominated forests, while the lowest silt content was under beech forest and clay content under spruce forest (Table A1).
Table 3. Woody aboveground biomass stock and litter biomass stock.

| Study Plot | Woody Aboveground Biomass Stock (wAGB) | Plot Type * | Litter C/N Litter Ratio | Time of Fieldwork |
|------------|----------------------------------------|-------------|-------------------------|-------------------|
|             | Beech | Spruce | Fir | Other Species | Total |                     |                     |
| 1A          | 38.48 | 245.59 | -   | -             | 284.07 | spruce | 33.20 | 35  | 22 September 2017 |
| 1B          | 1.30  | 211.54 | -   | -             | 212.84 | spruce | 16.05 | 17  | 22 September 2017 |
| 1C          | -     | 185.62 | -   | 2.25          | 187.87 | spruce | 22.00 | 21  | 22 September 2017 |
| 1D          | -     | 95.50  | -   | -             | 95.50  | spruce | 24.18 | 25  | 22 June 2017 |
| 1E          | -     | 118.75 | -   | 33.75         | 152.50 | spruce | 25.46 | 26  | 22 June 2017 |
| 2A          | 334.45| -      | -   | -             | 334.45 | beech  | 12.73 | 34  | 7 July 2017 |
| 2B          | 197.05| -      | -   | -             | 197.05 | beech  | 10.86 | 32  | 7 July 2017 |
| 2C          | 36.81 | -      | -   | -             | 36.81  | beech  | 31.51 | 25  | 7 July 2017 |
| 2D          | 437.26| -      | -   | -             | 437.26 | beech  | 13.03 | 31  | 7 July 2017 |
| 2E          | 441.70| -      | -   | -             | 441.70 | beech  | 8.54  | 27  | 7 July 2017 |
| 3A          | -     | 15.14  | 0.39| -             | 15.53  | spruce | 19.50 | 21  | 20 June 2017 |
| 3B          | -     | 25.55  | -   | -             | 25.55  | spruce | 4.02  | 29  | 20 June 2017 |
| 3C          | 31.01 | 67.70  | 3.49| -             | 102.15 | spruce | 15.51 | 31  | 20 June 2017 |
| 3D          | 12.82 | 90.49  | -   | -             | 103.31 | spruce | 17.90 | 22  | 20 June 2017 |
| 3E          | 9.85  | 28.62  | 0.25| -             | 38.71  | spruce | 18.13 | 25  | 20 June 2017 |
| 4A          | -     | 104.93 | 40.29| -             | 145.23 | spruce | 8.04  | 22  | 28 August 2017 |
| 4B          | -     | 15.49  | 60.22| 9.02          | 84.74  | fir    | 10.46 | 36  | 28 August 2017 |
| 4C          | -     | 8.45   | 226.53| -            | 234.98 | fir    | 10.58 | 20  | 28 August 2017 |
| 4E          | -     | 31.79  | 10.85| 128.52        | 171.15 | other  | 9.37  | 32  | 28 August 2017 |
| 5A          | -     | 2.29   | 130.77| -            | 133.06 | fir    | 8.09  | 20  | 5 November 2017 |
| 5B          | 2.88  | -      | 18.95| -             | 21.82  | fir    | 9.67  | 25  | 5 November 2017 |
| 5C          | -     | 98.47  | -   | -             | 98.47  | fir    | 17.25 | 29  | 5 November 2017 |
| 6A          | 21.09 | 2.54   | 25.53| 8.90          | 58.06  | fir    | 10.88 | 41  | 9 September 2017 |
| 6B          | -     | 15.79  | -   | -             | 15.79  | spruce | 13.53 | 23  | 9 September 2017 |
| 6C          | 128.49| -      | -   | -             | 128.49 | beech  | 9.14  | 23  | 9 September 2017 |
| 6D          | 109.81| -      | 26.43| -             | 136.23 | beech  | 11.04 | 22  | 9 September 2017 |
| 6E          | 36.55 | 9.65   | 4.55| -             | 50.76  | beech  | 5.71  | 18  | 9 September 2017 |
| 7A          | -     | 24.74  | 2.48| 82.40         | 109.62 | other  | 9.92  | 32  | 29 August 2017 |
| 7B          | 13.53 | -      | 202.98| -            | 216.50 | fir    | 7.27  | 38  | 29 August 2017 |
| 7C          | 9.67  | -      | 10.49| 28.41         | 48.57  | other  | 9.37  | 32  | 29 August 2017 |
| 7D          | -     | 48.69  | 51.86| 100.55        | 200.15 | other  | 7.10  | 35  | 29 August 2017 |
| 7E          | 7.76  | -      | 281.96| 13.69        | 303.42 | fir    | 10.45 | 25  | 29 August 2017 |

* classified based on dominating AGB (>75% of total AGB).
Table 4. Forest stand characteristics at study plots.

| Study Plot | Beech | Spruce | Fir | Others | Stand Density (ind ha\(^{-1}\)) | Foliage (Mg ha\(^{-1}\)) | Age of Dominant Species (Years) | Forest Cover or Species Composition Changes ** |
|------------|-------|--------|-----|--------|---------------------------------|--------------------------|------------------------------|-----------------------------------------------|
| 1A         | 29.7  | 70.3   | -   | -      | 15,958.3                        | 12.9                     | 99                           | NO (1933)                                    |
| 1B         | 3.7   | 92.6   | 3.7 | -      | 22,580.6                        | 11.7                     | 119                          | NO (1933)                                    |
| 1C         |       | 100    | -   | -      | 7605.3                          | 11.2                     | 114                          | NO (1933)                                    |
| 1D         | 2.5   | 95.0   | -   | 2.5    | 16495.2                         | 9.0                      | 99                           | NO (1933)                                    |
| 1E         | 21.1  | 73.7   | -   | 5.3    | 7835.2                          | 10.3                     | 99                           | NO (1933)                                    |
| 2A         | 100   | -      | -   | -      | 10,309.5                        | 2.9                      | 85                           | NO (1937)                                    |
| 2B         | 100   | -      | -   | -      | 5291.2                          | 2.4                      | 60                           | NO (1937)                                    |
| 2C         |       | -      | 100 | -      | 7605.3                          | 11.2                     | 114                          | NO (1933)                                    |
| 2D         |       | -      | -   | -      | 2718.0                          | 9.0                      | 99                           | NO (1933)                                    |
| 2E         | 100   | -      | -   | -      | 13,135.7                        | 7.0                      | 43                           | NO (1933)                                    |
| 3A         |       | 92.3   | 7.7 | -      | 6664.9                          | 6.4                      | 18                           | NO (1933)                                    |
| 3B         | 35.3  | 61.8   | 2.9 | -      | 7622.9                          | 9.5                      | 43                           | NO (1933)                                    |
| 3C         | 12.1  | 87.9   | -   | -      | 6984.4                          | 9.6                      | 43                           | NO (1933)                                    |
| 3D         |       | 26.1   | 73.9| -      | 9920.0                          | 10.5                     | 105                          | NO (1933)                                    |
| 4A         |       | 22.7   | 45.5| 31.8   | 4399.0                          | 7.8                      | 60                           | NO (1937)                                    |
| 4B         |       | 8.0    | 92.0| -      | 9988.2                          | 12.0                     | 75                           | NO (1933)                                    |
| 4C         |       | 30.0   | 10.0| -      | 11,985.9                        | 6.7                      | 85                           | NO (1933)                                    |
| 4D         |       | 9.5    | 90.5| -      | 9035.4                          | 9.8                      | 85                           | NO (1935)                                    |
| 4E         | 58.3  | 41.7   | -   | -      | 2589.5                          | 4.2                      | 33                           | YES (1935)                                   |
| 5A         |       | 100    | -   | -      | 11,191.4                        | 9.8                      | 45                           | NO (1935)                                    |
| 5B         |       | 32.8   | 67.2| 0.0    | 3368.4                          | 3.7                      | 60                           | NO (1933)                                    |
| 5C         |       | 12.5   | 37.5| 18.8   | 5435.1                          | 5.2                      | 14                           | NO (1933)                                    |
| 5D         |       | 100    | -   | -      | 6689.6                          | 2.1                      | 55                           | YES (1933)                                   |
| 5E         | 54.2  | 45.8   | -   | -      | 10,159.1                        | 2.3                      | 55                           | YES (1933)                                   |
| 6A         | 73.3  | 24.4   | 2.2 | -      | 9408.5                          | 1.6                      | 30                           | YES (1933)                                   |
| 6B         |       | 33.3   | 5.6 | 60.1   | 3662.6                          | 5.7                      | 45                           | NO (1937–1938)                               |
| 6C         | 77.7  | 92.3   | -   | -      | 5221.5                          | 10.4                     | 115                          | NO (1937–1938)                               |
| 7A         |       | 31.3   | 37.5| 18.8   | 3215.4                          | 5.6                      | 45                           | NO (1937–1938)                               |
| 7B         | 18.8  | 31.3   | 50.1| -      | 4421.1                          | 5.6                      | 45                           | NO (1937–1938)                               |
| 7C         | 21.7  | 69.6   | 8.6 | -      | 9484.8                          | 13.9                     | 91                           | NO (1937–1938)                               |

* calculated on the basis of the occurrence of each individual tree species; ** data prepared based on Polish Tactical Military Map (published by Wojskowy Instytut Geograficzny, WIG) compiled and published in the 1930s, scale 1:100,000.

Table 5. Coarse root biomass (CRB).

| Study Plot | Beech (Mg ha\(^{-1}\)) | Spruce (Mg ha\(^{-1}\)) | Fir (Mg ha\(^{-1}\)) | Others (Mg ha\(^{-1}\)) | Total (Mg ha\(^{-1}\)) |
|------------|-------------------------|--------------------------|----------------------|--------------------------|------------------------|
| 1A         | 6.53                    | 61.89                    | -                    | -                        | 68.42                  |
| 1B         | 0.22                    | 54.41                    | -                    | -                        | 54.63                  |
| 1C         | -                       | 47.57                    | -                    | 0.64                     | 48.21                  |
| 1D         | -                       | 24.02                    | -                    | -                        | 24.02                  |
| 1E         | -                       | 27.79                    | -                    | -                        | 35.26                  |
| 2A         | 56.87                   | -                        | -                    | -                        | 56.87                  |
| 2B         | 33.58                   | -                        | -                    | -                        | 33.58                  |
| 2C         | 6.31                    | -                        | -                    | -                        | 6.31                   |
| 2D         | 74.04                   | -                        | -                    | -                        | 74.04                  |
| 2E         | 74.47                   | -                        | -                    | -                        | 74.47                  |
| 3A         | -                       | 3.37                     | -                    | 0.09                     | 3.45                   |
| 3B         | -                       | 5.48                     | -                    | -                        | 5.48                   |
| 3C         | 5.35                    | 15.81                    | -                    | 0.79                     | 21.94                  |
| 3D         | 2.21                    | 21.39                    | -                    | -                        | 23.61                  |
### Table 5. Cont.

| Study Plot | Beech | Spruce | Fir | Others | Total (Mg ha⁻¹) |
|------------|-------|--------|-----|--------|----------------|
| 3E         | 1.71  | 6.47   | 0.05| -      | 8.23           |
| 4A         | -     | 27.39  | 9.06| -      | 36.45          |
| 4B         | -     | 3.57   | 13.71| 2.25  | 19.53          |
| 4C         | -     | 2.04   | 52.38| -      | 54.42          |
| 4E         | -     | 7.86   | 2.44| 36.27  | 46.57          |
| 5A         | -     | 0.52   | 30.22| -      | 30.74          |
| 5B         | 0.50  | -      | 4.32| -      | 4.82           |
| 5C         | -     | -      | 22.06| -      | 22.06          |
| 6A         | 3.61  | 0.58   | 5.81| 2.15   | 12.15          |
| 6B         | -     | 3.30   | -   | -      | 3.30           |
| 6C         | 22.04 | -      | -   | -      | 22.04          |
| 6D         | 18.83 | 2.10   | 5.91| -      | 24.74          |
| 7A         | 26.43 | -      | 6.09| 0.55   | 33.07          |
| 7B         | 2.31  | -      | 47.83| -      | 50.14          |
| 7C         | 1.71  | -      | 2.34| 9.26   | 13.31          |
| 7D         | -     | -      | 10.88| 16.87  | 27.74          |
| 7E         | 1.38  | -      | 65.98| 3.16  | 70.33          |

### Table 6. Morphology and basic properties of the referenced soils.

| Study Plot | Consistency | Sand (%) | Silt (%) | Clay (%) | Texture | C/N | pH (H₂O) |
|------------|-------------|----------|----------|----------|---------|-----|----------|
| 3C         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.48|
| 3D         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.29|
| 3E         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3F         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3G         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3H         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3I         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3J         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3K         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3L         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3M         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3N         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3O         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3P         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3Q         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3R         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3S         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3T         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3U         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3V         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3W         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3X         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3Y         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|
| 3Z         | n.a.        | n.a.     | n.a.     | n.a.     | n.a.    | 2.88|

1 Structure: SB—subangular blocky, AB—angular blocky, GR—granular, MA—massive. 2 Consistence: SO—soft, SHA—slightly hard, HA—hard, VHA—very hard. 3 Texture according to USDA: L—loam, Silt-loam, SL—sandy loam. n.a.—not analyzed.
Figure 2. Relationship between soil organic matter concentration and elevation for the studied soil depths ((A) 0 to 10 cm, (B) 10 to 20 cm, (C) 20 to 30 cm, (D) 30 to 40 cm), assessed using linear models. X-axis and Y-axis present standardized values.
The FRB and SOM stock varied between the analyzed tree species forest types, but with no significant differences at the 0 to 40 cm depth examined in the study (Table 7). However, some differences in FRB content were identified for individual soil layers. For example, in beech stands, the FRB content was relatively low in the uppermost part of the soil (mean 1.4 Mg ha\(^{-1}\) ± SD 1.2 Mg ha\(^{-1}\) in the 0 to 10 cm layer) and decreased with depth (mean 0.6 Mg ha\(^{-1}\) ± SD 0.8 Mg ha\(^{-1}\) in the 30 to 40 cm layer) (Figure 3). The FRB in soils under spruce forest was much higher than that under beech, especially in the 0 to 10 cm soil layer (Figure 3). It also strongly decreased with the soil layer from 1.7 Mg ha\(^{-1}\) in the 0 to 10 cm layer (mean) to 0.4 Mg ha\(^{-1}\) in the 30 to 40 cm layer (mean). In fir forest, the amount of FRB was rather close to values determined under spruce forest. The highest FRB values noted across all the sampled soil layers of 0 to 40 cm (Table 7) were detected under fir forest (mean 6.5 Mg ha\(^{-1}\) ± SD 4.9 Mg ha\(^{-1}\)). Slightly lower values were typical for other types of forest (beech and spruce forest). The proportion of FRB in the total biomass stock (wAGB, BGB, SOM) equaled a maximum of 3.6%, and 1.7% and 8.9% in spruce, beech and fir forest, respectively. The highest OC content in fine roots was noted in beech forests, and the lowest in spruce forests (Table 8).

**Table 7.** FRB and SOM stocks (0 to 40cm) at each plot type.

| Plot Type | Mean (Mg ha\(^{-1}\)) | Max | Min | Q1 | Q3 |
|-----------|------------------------|-----|-----|----|----|
| beech     | FRB 3.2                | 5.5 | 1.2 | 1.2 | 4.1 |
|           | SOM 162.9              | 213.3 | 128.5 | 147.6 | 170.1 |
| spruce    | FRB 3.4                | 10.2 | 0.0 | 1.5 | 3.9 |
|           | SOM 142.3              | 224.5 | 56.6 | 124.2 | 162.6 |
| fir       | FRB 6.5                | 13.8 | 1.2 | 2.3 | 11.0 |
|           | SOM 95.5               | 143.3 | 78.6 | 79.3 | 97.6 |

Q1, Q3—first quartile, third quartile.

**Figure 3.** Distribution of fine roots biomass stock at the studied soil depths for the analyzed tree stands, expressed using boxplots. The box range denotes the interquartile range, line within the box—the median; whiskers indicate the minimum and maximum within range of three times interquartile ranges. Points indicate outliers. The different letters above the bars indicate statistically significant differences.

**Table 8.** C content (%) and C/N ratio range of FR at each plot type.

| Plot Type | Mean C (%) | Max C (%) | Min C (%) | Q1 C (%) | Q3 C (%) |
|-----------|------------|------------|------------|----------|----------|
| beech     | 47.0       | 56.8       | 37.4       | 40.5     | 51.9     |
|           | C/N 46     | 63         | 29         | 39       | 55       |
| spruce    | 34.2       | 47.8       | 28.1       | 30.9     | 34.2     |
|           | C/N 40     | 52         | 28         | 31       | 47       |
| fir       | 40.7       | 50.3       | 26.5       | 32.2     | 49.5     |
|           | C/N 40     | 51         | 23         | 32       | 50       |

Q1, Q3—first quartile, third quartile.
The SOM stock also varied with stand species. The highest values were noted for spruce stands. In these stands, the SOM stock was highest in the uppermost part of the soil (mean 63.4 Mg ha$^{-1} \pm$ 29.1 Mg ha$^{-1}$) and decreased substantially in the below-lying layer (mean 30.0 Mg ha$^{-1} \pm$ 16.6 Mg ha$^{-1}$ in the 10 to 20 cm soil layer), and subsequently in the two deepest layers (Figure 4). In beech forest, the SOM stock reached similar values (mean 61.2 ha$^{-1} \pm$ 19.4 Mg ha$^{-1}$ in the 0 to 10 cm soil layer) and then decreased proportionately with decreasing depth (mean 32.6 Mg ha$^{-1} \pm$ 5.6 Mg ha$^{-1}$ in the 30 to 40 cm soil layer) (Figure 4). In fir forest, the SOM stock was smaller than that under spruce and beech forest. The SOM stock decreased from 43.5 Mg ha$^{-1}$ (mean) in the 0 to 10 cm layer to 13.1 Mg ha$^{-1}$ (mean) in the 30 to 40 cm soil layer (Figure 4). The highest SOM stock in the entire sampled 0 to 40 cm soil layer was detected in soils under beech forest (mean 162.9 Mg ha$^{-1} \pm$ 27.4 Mg ha$^{-1}$) (Table 7). Slightly lower SOM stocks were detected under spruce in comparison with beech forest (mean 142.3 Mg ha$^{-1}$), while much lower SOM stocks were noted in fir forest (mean 95.5 Mg ha$^{-1}$).

3.2. Determinants of Soil Organic Matter Stock and Fine Root Biomass in Beech-, Spruce- and Fir-Dominated Forests

Models explaining the SOM stock showed the lowest RMSE for spruce and fir forests (23.49 Mg ha$^{-1}$, $r^2 = 0.75$) and the highest for all the analyzed plots (RMSE = 37.57 Mg ha$^{-1}$, $r^2 = 0.22$), indicating the high importance of dominant tree species. The RMSE for the model of SOM for beech forest was 29.51 Mg ha$^{-1}$ ($r^2 = 0.74$) (Table 9). The most important predictors of the SOM stock were different under the investigated tree species (Figure 5A–D). In beech forest, slope and in spruce forests, stand density were the most important predictors determining the SOM stock. In beech forest, other predictors (stand density, elevation, soil pH) were of lower variable importance than the stand density (Figure 5A). However, these variables had higher values for spruce forest (Figure 5B). In fir forest, the most important predictors were FRB, clay content, and elevation (Figure 5C). The SOM stock under all the studied tree species was fairly constant relative to the analyzed soil properties, which means that the difference between the determinants is more pronounced than that between the dominants (Figure 6).
Figure 5. Importance of variables in SOM stock models for beech (A), spruce (B), fir (C) forest and all plots (D). This importance is expressed by loss-drop in RMSE when a given variable is perturbed. Abbreviations—see explanation in Table 2.
Figure 6. Partial dependence plots (pdp) showing average predictions of the SOM stock. Lines show average predictions for continuous predictors, assuming mean values of all remaining predictors. Abbreviations—see explanation in Table 2. Explanation of interpretation of pdp included in Section 2.5.
For all the analyzed tree species, the SOM stock increased with higher wAGB stock, dominant age, C/N soil ratio, and FRB (only in beech and fir forests). A similar tendency was observed for stand density, but with a slightly decreasing tendency under beech forest, and for litter mass with a slight decrease under fir forest (Figure 6). In addition, the SOM stock under beech forest responded positively to higher elevations, while the SOM stock under spruce forest responded negatively over 800 m a.s.l., and over 600 m a.s.l. under fir forest. Hillslope exposure determined the SOM stock under spruce forest, with an abrupt decrease in SOM stock with western hillslope exposure and a slight increase under beech forest with the same hillslope exposure (Figure 6).

For all the species-dominated forests studied, we found the highest importance of C/N ratio for soil, clay content and hillslope exposure (Figure 7A–C). The clay content and hillslope exposure were also the first and fourth most important variables for spruce FRB (Figure 7B), while the hillslope gradient and elevation were the second and third, respectively. For beech FRB, the most important predictor was the clay content, with a lower importance of stand density and pH litter, as well as the silt content (Figure 7A). The C/N ratio for soil was the most important predictor of fir FRB, followed by the clay and silt content, MAT, and SOM (Figure 7C). FRB was highest with northern hillslope exposure and increased with MAT, elevation, and hillslope gradient; on the other hand, relief-dependent predictors did not affect spruce and beech FRB significantly (Figure 8). FRB responded negatively to soil and litter variables (litter C/N ratio, clay content, soil pH). In contrast, FRB increased with increasing soil C/N ratio, especially in fir forests (Figure 8). FRB decreased with increasing wAGB and, in the case of spruce stands, with stand density.

Models explaining FRB showed the lowest RMSE for beech forest (1.41 Mg ha$^{-1}$, $r^2 = 0.68$), and the highest for fir forest (RMSE = 4.39 Mg ha$^{-1}$, $r^2 = 0.83$). The RMSE for the model of FRB in the studied spruce forest was 3.60 Mg ha$^{-1}$ ($r^2 = 0.41$) and for all plots the RMSE equaled 2.92 Mg ha$^{-1}$ ($r^2 = 0.29$) (Table 9). The importance of predictors for FRB differed among the analyzed tree species (Figure 7).

### Table 9. Evaluation of model performance for tree stands' biomass based on RMSE (root mean square error), $r^2$ (coefficient of determination) and CV (coefficient of variation).

| Plot Type | RMSE | $r^2$ | CV |
|-----------|------|------|----|
| **SOM**   |      |      |    |
| All plots | 37.57| 0.22 | 0.31|
| Beech     | 29.51| 0.74 | 0.18|
| Spruce    | 23.49| 0.75 | 0.32|
| Fir       | 23.49| 0.75 | 0.24|
| **FRB**   |      |      |    |
| All plots | 2.92 | 0.29 | 0.87|
| Beech     | 1.41 | 0.68 | 0.42|
| Spruce    | 3.60 | 0.41 | 0.88|
| Fir       | 4.39 | 0.83 | 0.81|
Figure 7. Importance of variables in FRB content models for beech (A), spruce (B), fir (C) forest and all plots (D). This importance is expressed by a loss-drop in RMSE when a given variable is perturbed. Abbreviations—see explanation in Table 2.
Figure 8. Partial dependence plots (pdp) showing average predictions of FRB content. Lines show average predictions for continuous predictors, assuming mean values of all remaining predictors. Abbreviations—see explanation in Table 2. Explanation of interpretation of pdp included in Section 2.5.
4. Discussion

4.1. Relationships Between Selected Forest Characteristics and Fine Root Biomass

In our study, foliage biomass and stand density were variables with a slight impact on FRB (Figure 8). The absence of this relationship confirms the results of previous studies conducted in various conditions focused on the determination of the relationship between aboveground metrics (e.g., DBH, basal area) and FRB both at the tree- and stand-level [18,80–82]. High accuracy was achieved only for a few sites [83]. In addition, in the case of the use of stand characteristics obtained from Earth Observation missions to evaluate FRB in the boreal and cool-temperate forestlands in Canada at the stand level, a close relationship was not determined [84]. This may be explained by the fact that such models did not reflect temporal and spatial heterogeneity in FRB in various ecosystems [83]. Nevertheless, considering the significance of FRB in the productivity and biogeochemical cycles of ecosystems, efforts are still pursued to yield reliable estimates using already available predictors, even though this represents only a small proportion of belowground biomass [18,80,85].

In our study, the stand density was found to be a highly important predictor of FRB in beech forest, which confirms a physiological link between FRB that has to take up water and nutrients, the sapwood area that transports the said nutrients, and foliage mass, where water is transpired. This is indirectly consistent with the findings of [86], who found that FRB is stand age-dependent. It is noteworthy that the FRB distribution in the soil should be related to nutrient availability [87,88], soil bulk density and pH [85,89], and the thickness of organic soil horizons [90]. These findings were confirmed in our study, which underscores the importance of soil properties affecting FRB (Figure 8). The soils in our study were selected for their similarity at the study plot scale; thus, in this case, only very detailed microscale studies would allow for a better understanding of the reason for any differences.

One reason for the absence of a close relationship between the selected forest predictors (foliage biomass, stand density, wAGB) and FRB in our study may be the impact of site-specific factors (e.g., soil biological activity, present-day and historical natural disturbances) determining FRB production, which results in the inapplicability of the same models to different study sites, and especially those on a larger scale [35]. A possible explanation for the weak effect of the selected forest predictors on FRB in our study may be the fact that the turnover rate of particulate organic matter (to which fine roots belong) may be more than an order of magnitude faster than that of mineral-associated organic matter, as determined by [91] for subalpine soils in the Swiss Alps. It may, therefore, be assumed that a small share of dead fine roots transforms into SOM, but most of them are already decomposed.

The lower impact of the forest predictors on FRB discussed in our study may be the effect of the methodology of NFI data collection. In the course of forest inventory work (our database), trees with DBH < 7 cm and herbaceous plants were not taken into account. Due to their small contribution to the overall ABG pool, this drawback may be ignored; however, it is not known whether this may also be possible in the case of FRB.

At the same time, the FRB sampling methodology used according to [80,92,93] may have an effect on the results obtained. Collecting root samples in a core sampler—in triplicate—once in the period of June to November, may not take into account the spatial and temporal diversity of fine roots found across the studied plots [18]. On the other hand, the findings in [94] emphasized the advantages of soil-core methods (cylinders) for the validation of other FRB estimation methods; therefore, it may be assumed that the most accurate method was chosen for our research work. In the described shallow organic soil horizons (Table 6: 2 to 4 cm), roots were not detected during field description. In all likelihood, root biomass found in very deep organic horizons typical of soils in cold areas (i.e., Finland, Sweden, Canada) or typical of organic soils (peatlands) will be significant. Following a review of the abovementioned sources and the results discussed here, it may be concluded that special FRB determination methods should be developed.
4.2. Relationships Between Selected Forest Characteristics and Soil Organic Matter Stock

The SOC stock is usually the result of a balance between organic matter input and organic matter decomposition [13,16] and depends on the amount of organic matter previously found in the soil as a result of past soil–vegetation relationships [10]. In our study, we did not find a major impact of the wAGB stock on the SOM stock (Figure 7). However, a high importance of stand density was noted in finding relationships between stand characteristics and the SOM stock. Most likely, factors other than the present vegetation have had a decisive impact on the SOM stock in our study (Figure 6) as well as that in [22,95].

The key issue here may be organic matter persistence. Some studies have shown the presence of the effect of individual factors on SOM, which may vary between different tree species [19]. For example, a significant effect of beech forests on higher SOM stock was noted [17,96], which may be explained by the high amount of foliage and litter mass documented in our study (Table 5). The findings in [97] emphasized possible differences in foliar nutrient concentrations between beech and conifer stands, which may affect litter decomposition rates among species and affect SOC stocks as a consequence. In addition, the tissue composition of roots varies between tree species and may be a factor that determines SOC [98]. Despite a large number of studies, the identification of all mechanisms of tree species composition effects on SOM and SOC stocks remains challenging [9,99] and requires more complex studies.

Many studies [90,91,100] suggest that SOM found in soils in mountain temperate forests is dominated by organic matter formed hundreds or even thousands of years ago. In our study, we found indirect evidence of this pattern, as a higher correlation between elevation and the SOM stock in the deeper parts of the soil versus the subsurface was documented (Figure 3). The authors of [16] as well as [5] used the example of forest soils in the Sudety Mountains in Poland to show that past conversion from beech to spruce forest may have resulted in an absence of significant differences in soil properties (among other properties of the SOM stock) between these two species. Here, we hypothesize that in a time sequence of spruce forests in our study that have replaced deciduous forests, a new equilibrium had not had enough time to establish itself, as explicitly suggested in [10]. It is also quite possible that in the case of deciduous forests, the relationship between selected stand characteristics and the SOM stock is always stronger, as documented in this study as well as in several other studies [101,102].

It is not at all obvious whether differences in the SOM stock between existing coniferous and deciduous forests provide a reliable basis for predicting changes in the SOM stock following conversion, as we do not know how conversion-sensitive the previously accumulated organic components are [13,16,103]. Only some studies [22] have been able to show that SOM stock growth may be observed in forests with a 10- to 30-year succession [22]. Finally, the past is likely more important, as it includes the occurrence of natural phenomena and human impact, determining what may be observed in the soil today [104].

4.3. Effect of Abiotic Factors on Fine Root Biomass and Soil Organic Matter Stock

Many studies have shown an effect of precipitation and temperature on fine root production (fine root mortality) based on seasonal studies [18,105]. A variety of interpretations of the relationship between MAT, MAP, and FRB have been formulated depending on local conditions in study areas. In mountain temperate forests, this trend may also vary between tree species due to ecological adaptation, sensitivity (e.g., drought tolerance) [106] and elevation.
In our study, FRB decreased with soil layer depth (Figure 4), which was consistent with other research studies [85,87,106]. In addition, a significant impact of climatic conditions (especially MAT) on FRB was observed (Figure 7D). In other studies, climatic factors also served as important regulators of the rate of growth of fine roots [107,108]. Similarly to FRB, the SOM stock was more strongly affected by climatic factors in our study, as shown by the vital role of elevation (Figure 7D). Many studies emphasize the crucial role of climatic variation as a factor influencing SOM and SOC stocks [5,16,109,110], as lower air temperatures and greater air moisture may lead to less decomposition of organic matter, and thus, more biomass accumulation in the soil. The same explanation is often applied to other mountain area temperate forests [5,70,111]. This tendency was observed for all our study sites without distinguishing between tree species stands. However, in some cases, climatic differences related to tree species-specific stand composition were identified as important factors [9,112]. Studies on the rate of microbial decomposition in soils occurring in mountain areas, including the effect of elevation, are relatively rarely conducted. Such research was carried out by [111,113,114], who state that the rate of microbial decomposition of cellulose in soil found in the Carpathians depends on elevation—the higher the elevation, the slower the rate of microbial decomposition; however, this relationship is not absolute, and may be strongly modified due to changes in the arrangement of the soil-plant factor (including soil pH).

Other factors associated with relief (i.e., hillslope exposure and hillslope gradient) also had a considerable impact on FRB and SOM stocks in our study (Figures 6 and 8). A greater impact of hillslope exposure (in comparison with hillslope gradient) on FRB was observed (Figure 7D), which determines the availability of light regulating plant growth and site temperature. A similar conclusion was drawn by [115]. Additionally, [116] emphasized the effect of the hillslope gradient on FRB, which declines down the hillslope gradient and was observed to some extent in our study (Figure 8). Finally, our study demonstrates that abiotic factors such as the hillslope gradient and exposure are important in determining the size of FRB and SOM stocks. It should be noted that due to the similarity of the studied soils and predictable soil depth-related variations in their key properties (pH, soil structure, SOC content) (Table 6), the effects of different soil chemical properties [117], soil erosion [10] and drainage conditions [17,118] on the SOM stock may be ruled out.

5. Conclusions

Our study provides new data on SOM stocks and FRB for mountain temperate ecosystems and discusses their determinants. Our hypothesis was partially confirmed at the end of our study. It is possible to estimate the SOM stock in mountain temperate forests in the Western Carpathians consisting primarily of the most common stand species—European beech (Fagus sylvatica L.), Norway spruce (Picea abies L. Karst), and silver fir (Abies alba Mill.)—using forest inventory data. The estimation error is smaller if the species composition of the forest as well as the impact of abiotic factors are taken into account, which was clearly shown by the root mean square error values.

Referring to the specific objectives of our study, we found the largest wAGB and SOM stocks in beech-dominated forests. We also observed a considerable impact of stand density (as one of the analyzed variables) on SOM stocks, particularly in beech forests. We determined significant relationships between relief-dependent factors and SOM stocks for all the sites studied. Soil properties (i.e., soil texture, pH, C/N) affected FRB more strongly than the SOM stock. Thus, we have shown that the SOM stock and FRB are affected for the most part by abiotic factors (relief-dependent factors, climatic conditions) as well as soil properties. For this reason, we recommend accounting for soil, climate, relief, and forest management history in models used to estimate belowground OC stocks. However, the most important source of differences is the dominant tree species.

Accounting for all the above predictors may increase the accuracy of predictions based on select conversion factors or aboveground-to-belowground biomass ratios and may better reflect the site-specific variability of stored OC. In this study, we showed that FRB
(as a link between plant and soil) and SOM stocks can be estimated using forest inventory data supported by various other environmental variables. This approach can improve the accuracy of estimating OC fluxes in forest ecosystems and a forest’s ability to sequester OC. Our results may be used to decrease the uncertainties associated with the least studied part of the forest ecosystem—fine roots and soil.

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/10.3390/f12070823/s1, Table S1. Detailed soil properties for each of the studied plots.

**Author Contributions:** Conceptualization, A.Z., M.D. and K.O.; methodology, A.Z., M.D., L.M. and M.K.D.; formal analysis, A.Z., D.S. and G.S.; investigation, A.Z.; data curation, A.Z., L.M. and M.K.D.; writing—original draft preparation, A.Z.; writing—review and editing, M.D., L.M., M.K.D., D.S., G.S. and K.O.; visualization, A.Z. and M.D.; supervision, M.D. and K.O.; funding acquisition, A.Z. and K.O. All authors have read and agreed to the published version of the manuscript.

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**Appendix A**

**Table A1.** Descriptive statistics (mean, min. max. Q1, Q3) for studied variables including the division into forest types.

| Predictor | Spruce | Beech | Fir |
|-----------|--------|-------|-----|
| **Min**   | **Max** | **Min** | **Max** |
| Air Temp  | 4.23   | 23.10  | 11.30  |
| Precip    | 10.83  | 25.00  | 19.03  |
| Elev      | 32.70  | 40.90  | 35.70  |
| Aspect    | 19.70  | 22.70  | 20.70  |
| SOM       | 1.80   | 3.20   | 2.80   |
| FRB       | 1.07   | 2.07   | 1.87   |
| pH        | 1.50   | 3.50   | 2.50   |
| Clay      | 1.00   | 2.00   | 1.50   |
| Silt      | 1.00   | 2.00   | 1.50   |
| **Mean**  | **SD** | **Mean** | **SD** |
| Air Temp  | 14.40  | 4.60   | 14.40  |
| Precip    | 16.20  | 5.20   | 16.20  |
| Elev      | 21.70  | 4.70   | 21.70  |
| Aspect    | 20.80  | 4.80   | 20.80  |
| SOM       | 2.00   | 0.60   | 2.00   |
| FRB       | 1.00   | 0.50   | 1.00   |
| pH        | 2.50   | 0.70   | 2.50   |
| Clay      | 1.00   | 0.50   | 1.00   |
| Silt      | 1.00   | 0.50   | 1.00   |

* Abbreviations explained in Table 2.
Figure A1. Exemplary reference soil profiles. Numbers refers to study plots and study sites distribution presented at Figure 1. Soil profile depths: 1C—125 cm; 4C—130 cm; 6C—140 cm; 3C—105 cm; 7C—150 cm; 5C—105 cm.

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