



Article

Soil Organic Carbon Accumulation in Post-Agricultural Soils under the Influence Birch Stands

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Received: 7 July 2019; Accepted: 4 August 2019; Published: 8 August 2019



Abstract: The aim of this study was to demonstrate the effects birch renewal on the soil organic carbon accumulation and on dehydrogenase activity. We selected 12 research plots with birch stands of different ages (1–4 years, 5–8 years, 9–12 years, and 13–17 years) to determine soil texture, pH, total carbon and nitrogen levels, and base cation content. The total organic carbon stock was calculated for the soil profiles. Additionally, dehydrogenase activity was determined. Naturally regenerated birch stands on post-agricultural land facilitated carbon accumulation. Based on our results, dehydrogenase activity is useful in assessing the condition of post-agricultural soils, and its determination allowed for us to assess the processes occurring in post-agricultural soils that are associated with the formation and carbon distribution.

Keywords: afforestation; birch stands; carbon stock; dehydrogenase activity

1. Introduction

Poland has one of the largest forest areas in Europe; forests occupy 29% of the country's territory and cover an area of 9.1 million hectares [1]. Forest stands on arable lands occupy nearly 25% of the forest area. The soil and soil processes are crucial in maintaining the productivity of forest ecosystems [2]. Soil is an important reservoir of carbon, and it is estimated that the global soil carbon stocks amount to more than 1500 Pg C, which are significantly higher than those of the atmosphere (750 Pg C) or the biomass of terrestrial ecosystems (650 Pg C) [3]. Recently, the mechanisms that are responsible for carbon stabilisation in soils have received considerable interest due to their relevance in our understanding of the global carbon cycle [3]. The fertility and productivity of soils depend on soil organic matter (SOM), which serves as a nutrient reservoir and it therefore plays an important role in nutrient cycling [4]. Changes in soil management are the main factor that affects SOM dynamics [5]. For example, transforming natural ecosystems into arable fields generally depletes soil organic carbon (SOC) reserves by as much as 75% (mostly between 30 and 50%), depending on the climate zone and the ecosystem type [6]. However, such losses can be limited by converting arable land into grassland and forest [7]. Afforestation positively affects various soil properties, and the soil organic carbon values of afforested sites are generally higher than those of bare sites [8]. Afforestation also positively influences the physical soil characteristics, which are important for maintaining soil stability and productivity [9–11].

In recent years, the interest in soil quality has been stimulated by the growing awareness of the fact that the soil is an important component of the biosphere. It functions not only to produce food, timber, and other forest resources, but it also plays a role in maintaining the local, regional, and global

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quality of the environment. Karlen et al. [12] and Gil-Sotres et al. [13] state that soil quality enables the healthy functioning of an ecosystem and it maintains its biological production. One of the most important factors in determining soil fertility are the soil biological properties in relation to the activity of microorganisms and higher organisms (plants and animals), including enzymes that are secreted by them [14]. Dehydrogenase activity, as an integral part of an intact cell and soil microflora activity, can provide information regarding the biologically active population of microorganisms in a given soil [15]. Soil microbial and enzymatic activity responds relatively quickly to slight changes in soil conditions and can reflect the changes in soil quality before they can be detected by other soil analyses [16]. Dehydrogenase plays a significant role in the biological oxidation of soil organic matter by transferring hydrogen from organic substrates to inorganic acceptors [17]. In this sense, the determination of dehydrogenase activity can be used to reflect the changes in soil biology [18,19], including assessing soil quality, the influence of soil management on soil quality, and the degree of regeneration of degraded soil [13,20]. Afforestation induces a rapid increase in microbial biomass, with changes apparent within one year of tree planting [21]. In a previous study, afforestation increased bacterial PLFAs by 20-120%, whereas it had a stronger impact on the development of fungal communities (increases by 50-200%) [22].

In this context, the main aim of this research was to determine the effects of changes in soil management from agriculture to forestry on the soil organic carbon accumulation and on enzymatic activity. Dehydrogenase activity, which plays a key role in the carbon cycle, was determined, and we tested the following hypotheses: (1) natural birch regeneration has a positive effect on the soil organic carbon accumulation and (2) dehydrogenase activity reflects the changes that occurred in the soil of the studied chronosequence.

2. Materials and Methods

The soil samples were collected from 12 research plots at four locations in the Mazowieckie province of Poland (Table 1, Figure 1). The study area is characterized by the following climatic conditions: average annual rainfall of 629 mm, average annual temperature of $8.4\,^{\circ}$ C, and a growing season of 210 days. The area in which the sample plots were located was dominated by fluvioglacial and glacial sand and loam with Gleysols, Cambisols, Podzols, and Arenosols [23]. The study plots were used as cropland in the past.

The study plots were divided into four groups based on the age of the self-seeded birch trees: I—1–4 years, II—5–8 years, III—9–12 years, and IV—13–17 years. In each plot, we took three soil samples from the 0–5, 5–15, and 15–50 cm layers. The samples were air-dried, sieved through a 2-mm-mesh, and the following physicochemical properties were determined [24]: pH (potentiometrically, in 1 M KCl and $\rm H_2O$ solution), texture (using laser diffraction in an Analysette 22: Fritsch, Idar-Oberstein, Germany), nitrogen, and organic carbon contents (with a LECO CNS True Mac Analyser: Leco, St. Joseph, MI, USA), C/N ratio, basic cations content (in 1 M ammonium acetate, using a Thermo Scientific iCAP 6000 ICP OES analyser, Thermo Fisher Scientific, Cambridge, UK). The data presented is the mean of the three soil replicates.

The results were used to calculate the carbon stock in the soils of the chronosequences, based on bulk density (BD), which were determined using Kopecky's cylinders. The carbon stock was calculated according to the following formula:

$$SOCstock = C \times BD \times T/100 \tag{1}$$

where SOCstock is the carbon stock in the soil (kg·m⁻²), C is the carbon content in the soil layers (g·kg⁻¹), BD is bulk density [g·cm⁻³], and T is the thickness of the soil layers (cm).

Fresh samples, with natural moisture content, were taken to determine dehydrogenase (DH) activity (DH) via the Lenhard method, according to the Casida procedure. The DH activity was expressed as μ mol TPF kg⁻¹ h⁻¹ [25].

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The biomass [kg·ha⁻¹] of the aboveground and belowground parts of the stands in groups I–IV was determined, using the trunks, branches, assimilation apparatus, bark, and roots. For this, 10 trees were randomly selected at each location and were separated into trunk, branches, assimilation apparatus, bark, and roots. All the parts of the tree were weighed in the field while using portable scales with an accuracy of 0.01 g. Samples from each of the components from each tree model were collected to determine the relationship between fresh and dry biomass. Briefly, the samples were oven-dried at 105 °C and then weighed. On the basis of appropriate fresh-to-dry mass ratios, we calculated the dry biomass of the components for each tree.

Basic statistical data were calculated (i.e., the arithmetic mean and measures to determine the degree of differentiation among the results—standard deviation). The obtained data did not show normality, the Shapiro–Wilk test was used to check the normal distribution. Tukey's HSD multiple comparisons of means were used in post hoc analysis to assess the effect of the age of regenerated birch trees and soil depth on the studied soil properties. Principal components analysis (PCA) was used to interpret the relationships among the studied variables, while the Pearson's correlation was applied to determine the relationships between dehydrogenase activity and soil properties. By applying Ward's method, the samples were grouped according to DH activity and carbon content. Average and standard deviation (SD) were presented in tables. Differences with p < 0.05 were considered to be statistically significant. Statistical analyses were performed in the Statistica 10 software (StatSoft Inc., Tulsa, OK, USA).

Study Site	GPS	Soil Type
Mińsk Maz.	52°10′ N, 21°40′ E	Brunic arenosol
Kozienice	51°24′ N, 21°26′ E	Brunic arenosol
Dobieszyn 1	51°35′ N, 21°10′ E	Brunic arenosol
Dobieszyn 2	51°33′ N, 21°09′ E	Brunic arenosol

Table 1. Location of research plots and soil type.

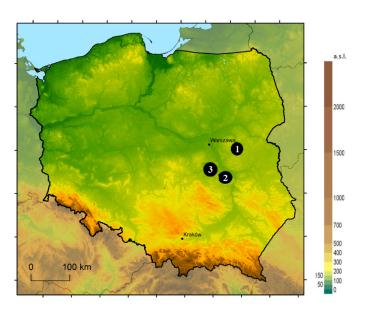


Figure 1. Localization of study plots (1—Mińsk Maz., 2—Kozienice, 3—Dobieszyn 1, and Dobieszyn 2).

3. Results

The soils differed in terms of pH values. The highest average pH was recorded in soils from the youngest birch stands (groups I and II); in the surface soil layer of these stands, the pH in H_2O was 4.52 and 4.62, respectively. The lowest pH was recorded in soils of the oldest stands (group IV) (Table 2).

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All of the sites were similar in terms of silt, and clay contents; there were no statistically significant differences of the studied chronosequences. Slight differences were noted in the sand content (Table 2). We also found no statistically significant differences in the C contents of the subsequent soil layers. There were no significant differences in the rate of organic matter decomposition, being expressed as the C/N ratio. The highest C/N ratio was recorded for the soil of the youngest birch stands (group I, average 22.3) and the lowest for the soil of the oldest birch stands (group IV, average 16.6). There were statistically significant differences in the Ca content (Table 2).

The total carbon stock did not significantly differ among the groups (Table 3). A slightly lower than average carbon stock was found in soils of the younger stands (groups I and II), while the values were above the average in the soils of the older stands (groups III and IV). However, these differences were not statistically significant. The average carbon stock depended on the age of the forest stand and it ranged from 4.34 to 6.16 kg·m⁻². The carbon stock in the different soil layers changed with the age of the tree stands (Table 3). In the soils of the younger stands (groups I and II), a greater amount of accumulated carbon was found in the upper layer (0–5 cm) as compared to the same layer in the older stands (groups III and IV). In the soils of groups I and II, the proportion of the total carbon, which was determined to a depth of 50 cm, in the surface layer accounted for about 28%, while it accounted for 13.6% in the soils of the oldest stands. The highest amount of C in the deeper layers was recorded in soils of the oldest stands; the carbon in the 15–50-cm soil layer of group IV accounted for nearly 60% of the total carbon stock, while it did not exceed 40% in the soils of group I.

Dehydrogenase activity was used as a proxy for the biological activity of the studied soils and it varied among the sites. The highest mean value of dehydrogenase activity was recorded for group I soils and the lowest for group II–IV soils (Figure 2), which indicated a decrease in dehydrogenase activity with stand age. A strong relationship between dehydrogenase activity and the basic cation content was determined while using Pearson's correlation coefficient (Table 4). The correlation coefficients between dehydrogenase activity and K, Ca, and Mg contents were 0.81, 0.64, and 0.60, respectively.

Table 5 presents the components of the aboveground and belowground biomass of the examined stands. The biomass components significantly increased with stand age. In the youngest stand (group I), the average aboveground biomass was 2521.5 kg·ha⁻¹ and the root biomass was 1058.7 kg·ha⁻¹. In the oldest stand (group IV), the aboveground biomass was 30 times higher than that in the youngest stand, whereas the root biomass was more than 12 times higher in the older group IV than in the younger (group I) stand.

The first two axes of the PCA explained 46.2% of the variance of the analyzed soil properties (Figure 3). The first axis explained 31.74% of the variability and it was mainly related to the basic cation content, while the second axis explained 14.47% of the variability and it was associated with the C and N contents and with the pH. The results of the PCA analysis confirmed the dependence of dehydrogenase activity on the amounts of basic cations that are available. The C and N levels were higher in the soils of the older stands. To discriminate the distinction of the studied chronosequence of birch stands, we performed a cluster analysis, which enabled us to identify the two main groups differing in dehydrogenase activity and carbon content. The youngest stands (groups I and II) clearly differed from the oldest stands (groups III and IV) (Figure 4).

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Table 2. Soil properties of the studied chronosequence of birch stands, with statistic test results.

Chronosequence	Depth	pH in H ₂ O	pH in KCl	С	N	. C/N	Na	K	Ca	Mg	Sand	Silt	Clay
	- o _F	1 2 -	F	%			cmol (+)·kg ^{−1}			%			
	0–5	4.52 ± 0.14 a	3.88 ± 0.12^{a}	1.57 ± 0.33 a	0.07 ± 0.02 a	22.3 ± 6.5 a	0.17 ± 0.05 a	$0.95 \pm 0.30^{\text{ a}}$	1.62 ± 0.21 ab	1.57 ± 0.57 a	83 ± 4 ^a	14 ± 3 ^a	2 ± 1 ^a
I	5–15	4.73 ± 0.30 ab	3.97 ± 0.19 a	1.17 ± 0.71 ^a	0.07 ± 0.03 a	14.1 ± 4.9 a	0.21 ± 0.07 a	1.05 ± 0.47 a	1.60 ± 0.57 ab	1.60 ± 0.70 a	84 ± 4 ab	13 ± 3 ^a	2 ± 1 ^a
	15-50	5.03 ± 0.48 a	4.23 ± 0.16 a	0.49 ± 0.49 a	0.03 ± 0.02^{b}	19.0 ± 16.2 a	0.25 ± 0.07 a	$1.50 \pm 0.40^{\text{ a}}$	1.69 ± 0.56 a	2.60 ± 0.85 a	79 ± 11 ^a	18 ± 7 ^a	3 ± 2 ^a
	0–5	4.62 ± 0.31 a	3.98 ± 0.07 a	1.30 ± 0.31 a	0.09 ± 0.07 a	15.2 ± 6.5 a	0.22 ± 0.10 a	1.98 ± 0.30 a	2.13 ± 0.71 a	2.23 ± 1.39 a	76 ± 2^{b}	19 ± 2 a	4 ± 1 a
II	5–15	4.87 ± 0.23 a	4.13 ± 0.26 a	1.10 ± 0.47 a	0.32 ± 0.35 a	11.1 ± 2.7 a	0.21 ± 0.10 a	1.39 ± 1.34 a	2.37 ± 1.11 ^a	2.30 ± 1.48 a	$78 \pm 5^{\text{ b}}$	18 ± 4 ^a	4 ± 2 ^a
	15-50	5.29 ± 0.38 a	4.35 ± 0.39 a	0.16 ± 0.10 a	0.04 ± 0.03 ab	8.4 ± 5.3 a	0.22 ± 0.07 a	1.96 ± 0.34 a	2.25 ± 1.01 ^a	3.55 ± 0.31 a	80 ± 5 a	17 ± 4 ^a	3 ± 1 ^a
	0–5	4.58 ± 0.15 a	3.79 ± 0.12^{a}	1.38 ± 0.58 a	0.11 ± 0.06 a	15.8 ± 7.2^{a}	0.20 ± 0.10 a	0.80 ± 0.25 a	1.38 ± 0.14 b	1.44 ± 0.32 a	83 ± 7 ^{ab}	14 ± 5 ^a	2 ± 2 ^a
III	5–15	4.60 ± 0.20 ab	3.94 ± 0.15 a	1.19 ± 0.63 a	0.06 ± 0.04 a	19.7 ± 4.9 a	0.19 ± 0.06 a	0.81 ± 0.27 a	1.41 ± 0.18 ^a	1.51 ± 0.37 a	86 ± 4 ab	12 ± 3 ^a	2 ± 1 ^a
	15-50	4.91 ± 0.36 a	4.27 ± 0.05 a	0.68 ± 0.53 a	0.05 ± 0.05 ab	18.2 ± 15.1 a	0.21 ± 0.05 a	1.07 ± 0.55 a	1.35 ± 0.24 ab	1.92 ± 0.52 a	87 ± 3 ^a	12 ± 2 ^a	2 ± 1 ^a
IV	0–5	4.38 ± 0.13 ^a	3.85 ± 0.25 a	1.39 ± 0.50 a	0.09 ± 0.06 a	16.6 ± 6.2^{a}	0.21 ± 0.03 a	1.11 ± 0.18 a	1.66 ± 0.31 ab	1.97 ± 0.27 a	85 ± 7 ab	13 ± 5 ^a	2 ± 1 ^a
	5–15	$4.35 \pm 0.30^{\text{ b}}$	3.93 ± 0.09 a	1.33 ± 0.55 a	0.15 ± 0.06 a	11.5 ± 2.7 a	0.23 ± 0.03 a	1.10 ± 0.26 a	1.41 ± 0.19 b	1.81 ± 0.38 a	88 ± 1 ^a	11 ± 1 ^a	1 ± 1 ^a
	15–50	4.65 ± 0.59 a	4.13 ± 0.29^{a}	$1.11 \pm 0.90^{\text{ a}}$	0.19 ± 0.02^{a}	12.2 ± 8.9 a	0.22 ± 0.08 a	1.19 ± 0.33^{a}	1.54 ± 0.09 a	2.22 ± 0.58 a	88 ± 2^{a}	11 ± 2^{a}	2 ± 1 ^a

Mean \pm SD; small letters in the upper index of the mean values mean significant differences of soils properties between chronosequence and dept.

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Table 3. Total and percentage carbon storage (kg·m $^{-2}$ —SOCstock) in soil layers of the studied chronosequence of birch stands.

Chronosequence	Depth	SOCstock (kg·m ⁻²)	Total SOCstock in All Layers	% Participation SOCstock
	0–5	0.94		27.5
Ι	5–15	1.43	4.57	32.2
	15–50	2.20		40.2
П	0–5	0.78		24.1
	5–15	1.37	4.34	38.4
	15–50	2.19		37.5
	0–5	0.82		18.0
III	5–15	1.49	5.41	29.1
	15–50	3.10		52.8
IV	0–5	0.69		13.6
	5–15	1.54	6.16	27.7
	15–50	3.93		58.6

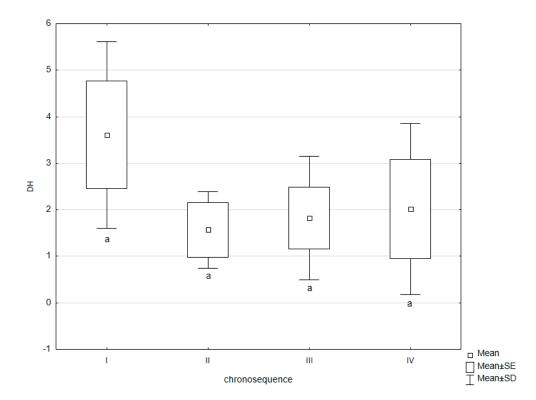


Figure 2. Dehydrogenase activity (DH) (μ mol TPF·kg $^{-1}$ ·h $^{-1}$) in first soil layers of the studied chronosequences of birch stands.

Table 4. Correlations between dehydrogenase activity (DH) and basic soil properties.

	pH_{H2O}	pH_{KCl}	Na	K	Ca	Mg	С	N	Sand	Silt	Clay
DH	-0.04	-0.13	0.43	0.81 *	0.64 *	0.60 *	0.09	0.10	-0.20	0.20	0.11

^{*} p < 0.05.

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Chronosequence	Stem	Branches	Foliage	Bark	Roots	
I	867.6 ^b	548.0 ^b	863.5 ^b	242.4 ^b	1058.7 ^b	
II	7947.7 ^{ab}	1924.9 ^b	1745.9 ab	1931.4 ab	2866.8 b	
III	23907.2 ab	5147.2 ^{ab}	2299.7 ab	4581.3 ab	6485.4 ^{ab}	
IV	54307.9 a	11357.8 ^a	3242.6 ^a	9173.7 ^a	13492.7 a	

Small letters in the upper index of the mean values mean significant differences.

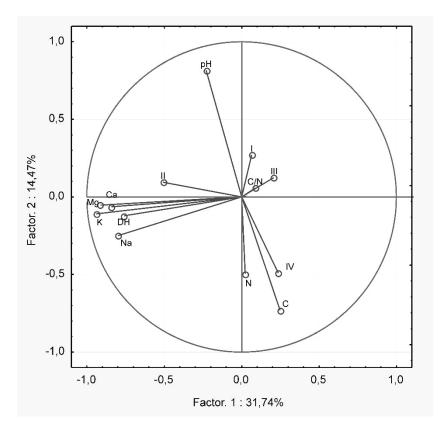


Figure 3. Projection of soil properties of birch stands chronosequence of on a plane of the first and second factors in the PCA (I—from 1 to 4 years, II—from 5 to 8 years, III—from 9 to 12 years, and IV—from 13 to 17 years; DH—dehydrogenase activity; C—carbon content; N—nitrogen content).

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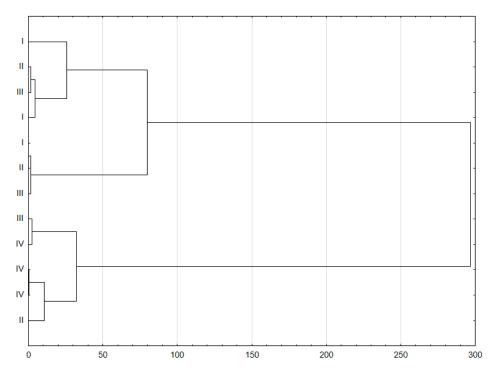


Figure 4. Dendrogram with group identified in the cluster analysis. The dehydrogenase activity and carbon content in surface layers were used for diagram preparation. I–IV—studied chronosequences of birch stands.

4. Discussion

Our results support the hypothesis that natural birch regeneration has a positive effect on the soil organic carbon accumulation. The tendency to increase carbon stocks was observed in the studied chronosequence of the birch tree stands. Several studies have shown that the decomposition of soil organic matter exceeded the input of organic matter from the trees in the initial following afforestation [26,27]. In the younger stands, the soil organic carbon accumulation was the greatest in the surface layer. In the 5-cm layer, accumulation accounted for about 30% of the total accumulation in the 50-cm deep soil column. Conversely, carbon accumulation was considerably lower than in the deeper soil layers in the 5-cm layer of the soils from the older stands. In the group I soils, accumulation in the deeper layers constituted 40% of the total stock of carbon, while it accounted for 60% in group IV. This increase in C accumulation in the deeper layers of the soils is associated not only with the processes of transporting dissolved organic compounds downwards, but also with an effect of supplying organic debris from the root systems. This is confirmed by the increase in root biomass in particular groups of stands. Subsoil soil organic carbon (SOC) storage may be promoted by the translocation of OM into deeper soil layers as DOC with the percolating water and due to bioturbation by soil animals [28]. Kotroczó et al. [29] found that plants cause greater changes in soil properties through their roots and secretions than via litter. In this sense, aboveground OM only probably has limited effects on SOM levels when compared to belowground OM [28]. Roots are a key component of the belowground part of the forest ecosystem, constituting the basic source of SOM that significantly affects soil microbiological activity [30,31]. Over time, soil organic matter input increases with the productivity of the forest stands, and the soils switch from being a C source to a C sink [32]. According to Laganiere et al. [33], the positive impact of afforestation on soil organic carbon stock is more pronounced in the cropland soils than in pastures or natural grasslands. Afforestation usually results in the establishment of higher plant biomass, and trees modify the quality and quantity of litter inputs and microclimatic conditions, such as moisture and temperature. Deng and Shangguang [34] highlight the importance of previous land use, tree species, soil depth, and forest age in determining soil C and N changes in a range of environments

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and land use transitions. In our study, birch stands, through aboveground and belowground biomass accumulation, had a positive effect on the quality of SOM, as expressed by the C/N ratio, which is an indicator of the extent of plant nitrogen being made available to plant residues. Li et al. [35] state that land use changes from agricultural areas to forest alter the ratios between soil C, N, and P. Springob and Krichmann [36] found that a soil C/N ratio of >20 could limit SOM mineralisation. According to Cools et al. [37], tree species are the main factor in explaining the variability of the C/N ratio. The content of better decomposed soil organic matter increases with stand age. At the same time, soil acidity and nutrient uptake increase with tree growth. Riqueiro-Rodríguez [38] note that the Pinus radiate more drastically decreases the soil pH than *Betula alba*. In another study, the acidifying affect of afforestation on mineral soil has been confirmed by a significant decrease in soil pH in the 0–5-cm layer and by a slightly weaker decrease in the 5–15-cm layer [39].

The results of the cluster analysis confirmed the distinctness in terms of C content and enzymatic activity of the soils of younger stands when compared to the soils of older stands. The soil parameters pH and soil organic carbon are important factors that shape dehydrogenase activity [15,40]. The highest pH, with the highest alkaline cation content, resulted in the highest dehydrogenase activity in soils of the younger stands (Groups I and II), reflecting the previous agricultural use of the soils and the associated intensive fertilisation and liming. According to Rousk et al. [41], pH is the main determinant of the structure of soil microbial populations. Soil pH directly determines plant growth, nutrient absorption, and the intensity of biological and chemical processes in the soil. In this work, dehydrogenase activity was positively associated with exchangeable Ca, K, and Mg contents, with a higher content of basic ions leading to an increase in pH, which results in the stimulation of soil microorganisms. Soil pH may be the major factor controlling the biomass and composition of microbial communities and their maintenance demand [42]. When assessing the properties of soils that were subjected to long-term agricultural use, several authors have considered the high plant-nutrient content as evidence of systematic fertilisation [43]. For example, Ren et al. [44] have noted that catalase, saccharase, urease, and alkaline phosphatase were significantly increased by land-use conversion from farmland to forest. According to this, significant correlations between soil enzyme activities and soil properties indicate that the soil enzyme activities are closely related to soil nutrients dynamics [18]. Dehydrogenase activity differed among the soils of the studied birch stands. The activity of this enzyme reflects that changes in the soil that are associated with the growth of the birch stands. According to previous studies, enzymatic activity is strongly stimulated by SOM [15,18], and processes that are related to organic matter transformations are carried out with the participation of soil microorganisms and their enzymes [45]. In our study, no direct relationship between dehydrogenase activity and carbon accumulation was found. Dehydrogenase activity was high in the soil of the youngest stands (first age class), and subsequently considerably decreased in class II. Our results indicate a trend to increased dehydrogenase activity in the soils of the oldest stands (IV group of stands). The highest pH, with the highest alkaline cation content, resulted in the highest dehydrogenase activity in soils of the younger stands, reflecting the previous agricultural use of the soils and the associated intensive fertilization and liming. The effects of fertilization disappear in the following years of tree stand growth. Forest stands grow and provide more litter fall to the soil, which stimulates the dehydrogenase activity. With age, greater amounts of carbon were accumulated in the surface soil layers. With increased litter input and in the absence of soil cultivation, conversion from cropland to forest could result in increased SOM stocks [46]. Similarly, Kara et al. [47] and Kang et al. [48] suggest that long-term afforestation could significantly enhance SOM contents, accumulate microbial biomass, and improve potential enzyme activities.

5. Conclusions

Our results confirm the beneficial effect of birch stand regeneration on the soil properties on post-agricultural land. We observed a clear trend of increasing carbon accumulation in the soil under the influence of birch trees. With age, greater amounts of carbon were accumulated in the surface soil

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layers. Dehydrogenase activity is a suitable indicator of the condition of post-agricultural soils with birch stands and, in combination with soil chemical properties, reflects historical soil management. In this sense, the determination of dehydrogenase activity allows for an assessment of the processes occurring in post-agricultural soils, which are associated with the soil organic carbon accumulation. A high nutrient content and high pH are characteristic of post-agricultural soils, facilitating a greater biochemical activity in the initial stages of stand formation.

Author Contributions: Conceptualization, T.G. and S.M.; Methodology, T.G. and E.B.; Project administration, T.G. and S.M.; Supervision, S.M.; Writing—original draft, T.G. and E.B.; Writing—review & editing, T.G.

Funding: This research was funded by Ministry of Science and Higher Education of Poland, Grant/Award Number: DS 3420/ZELiR/2018 and the Polish National Science Centre within grant N N305 400238, entitled "Ecological consequences of the silver birch (Betula pendula Roth.) secondary succession on abandoned farmlands in central Poland".

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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