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Morphological Variation in Absorptive Roots in Downy Birch (*Betula pubescens*) and Norway Spruce (*Picea abies*) Forests Growing on Drained Peat Soils

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Abstract: Peatland drainage based on ditch systems is a widely used forestry management practice in the boreal and hemiboreal forests to improve tree growth. This study investigated the morphological variation in absorptive roots (first- and second-order roots) across the distance gradient from the ditch with four sampling plots (5, 15, 40, and 80 m) in six drained peatland forests dominated by Downy birch and Norway spruce. The dominating tree species had a significant effect on the variation in absorptive root morphological traits. The absorptive roots of birch were thinner with a higher specific root area and length (SRA and SRL), higher branching intensity (BI), and lower root tissue density (RTD) than spruce. The distance from the ditch affected the absorptive root morphological traits (especially SRA and RTD), but this effect was not dependent on tree species and was directionally consistent between birch and spruce. With increased distance from the ditch (from plot 5 to plot 80), the mean SRA increased by about 10% in birch and 5% in spruce; by contrast, the mean RTD decreased by about 10% in both tree species, indicating a potential shift in nutrient foraging. However, soil physical and chemical properties were not dependent on the distance from the ditch. We found a species-specific response in absorptive root morphological traits to soil properties such as peat depth, pH, and temperature. Our results should be considered when evaluating the importance of morphological changes in absorptive roots when trees acclimate to a changing climate.

Keywords: absorptive roots; morphological variation; drained peatland forests; distance to ditch; Downy birch; Norway spruce



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1. Introduction

Peatland drainage has been an essential component of forestry management practices in boreal and hemiboreal zones [1,2]. In Estonia, approximately 20% of the forests grow on peatlands, from which 14% are drained [3]. The artificial drainage in peatlands based on ditch networks was carried out to lower the water table level and promote aeration of the root zone [1]. Improved tree growth was observed as a result of peatland drainage in many boreal coniferous forests [4,5]. Much research has reported the stimulating role of distance from the ditch on tree growth; sites located near to the ditch result in a higher tree growth [6,7]. This is due to the enhanced aeration of the substrate and more rapid decomposition rate of organic matter, caused by lowered water table levels at distances near ditches [6,8]. Truu et al. [9] showed that the distance from drainage ditches affected soil microbial communities; however, such an effect was dependent on the dominant tree species and the specific site conditions. Fine roots (diameter < 2 mm) are key peat-forming

elements in peatland ecosystems [10] but are understudied in most trait-related research in peatland forest ecosystems. Most of the available research is concerned with studying fine root production, fine root growth, and phenology in forested peatlands [11,12], while very little is known about the morphology of fine roots, especially the absorptive roots (defined as first- and second-order roots) [13,14] of trees growing in peat soils. These studies are also scarce in the drained peatland forests.

Absorptive roots with primary development and their ectomycorrhizal (ECM) fungal associates are the most physiologically active parts of the fine root system and are responsible for resource acquisition [15,16]. Absorptive roots with their small diameters and short lifespan are the most responsive component of the fine root system to changes in environmental factors [14,17]. Recent studies have shown that absorptive root morphological traits can vary widely across plant species [18] and soil nutrient patches, such as pH [19,20], carbon-to-nitrogen ratio (C/N), as well as available phosphorous (P) [21], and water resources [22,23]. Growing evidence suggests that trees optimize their resource uptake by modifying absorptive root morphological traits [18,24]. Several root morphological traits have been commonly used as potential indicators of the resource acquisition efficiency of trees [25]. For example, specific root area (SRA) and specific root length (SRL) are used to evaluate the relationship between root resource acquisition and root construction costs [26,27]. A reduction in absorptive root diameter leads to increases in SRA and SRL, and finally to enhanced resource uptake and intensive growth [28,29]. Root tissue density (RTD) is associated with root lifespan and survival [28,30]. Branching intensity (BI), which is also referred to as branching pattern [31], root tip frequency [18], or specific root tip density [32], determines the plastic responses of the absorptive roots to nutrient patches, influencing water and nutrient uptake rates and function [33]. Overall, knowledge of the absorptive root morphological responses of trees growing at drained histosols is insufficient. Understanding the root response characteristics of trees at drained peatlands not only contributes to the elucidation of the resilience of different tree species, and drained peatland forest's functioning, but also helps in the better management of practices in peatland forest ecosystems.

Downy birch (*Betula pubescens* Ehrh.) is a deciduous early-successional pioneer tree species [34], and Norway spruce (*Picea abies* (L.) H.Karst.) is a late-successional conifer in boreal forests [35]. Recently, it has been shown that forests dominated by birch and spruce growing at initially similar drained histosols caused tree-species-specific changes in the soil chemical properties, including pH, nitrogen content (N), and C/N ratio, and affected the soil bacterial communities [9]. This study investigated the effect of distance from the ditch on the morphological variation in absorptive roots at drained histosols of forests dominated by Downy birch and Norway spruce. The relationship of the absorptive root morphological variation in trees with forest stand and soil properties was assessed in this study. We proposed the following hypotheses: (1) the effect of distance from the ditch on absorptive root morphological variation is similar between birch and spruce; (2) the mean SRA and SRL increase, while the mean RTD decreases, with distance from the ditch.

2. Materials and Methods

2.1. Characteristics of the Stands

Six drained peatland forests in the Järvselja experimental forest area in the eastern part of Estonia were selected as study sites. Three stands dominated by Downy birch (*Betula pubescens*), and three stands dominated by Norway spruce (*Picea abies*), were under investigation in 2018. The abbreviations B1–B3 and S1–S3 were used for birch and spruce stands, respectively (Table 1). In each stand, a gradient with four sampling plots at distances of 5, 15, 40, and 80 m from the ditch was selected. In one of the spruce stands (S3), the most distant plot from the ditch was at 40 m, and plots at 5 m and 15 m were duplicated toward the next ditch at the same stand. A detailed description of the study sites and soil properties (Table 1) is available in a previously published paper by our team [9]. Briefly, all stands were classified as a drained *Oxalis* forest site type [36] and soils were classified as

histosols [37]. All studied stands were drained in the 1970s using open-ditch networks [38]. At each sampling plot, the stand density (trees ha⁻¹), stand basal area (BA, m² ha⁻¹), and diameter at breast height (DBH, cm) of all trees with DBH > 5 cm were measured on a 5 × 20 m rectangular area (short side parallel to the distance gradient) (Table 2).

Soil temperature (Ts, °C) was measured at a 10 cm depth using a temperature logger (Comet Systems Ltd., Rožnov pod Radhoštěm, Czech Republic). Soil volumetric water content (VWC, m³ m⁻³) was recorded monthly at a 5–10 cm depth by a ProCheck reader equipped with a GS3 sensor (Decagon Devices Inc., Pullman, WA, USA) at four sampling plots of all stands during April–October 2015 (Figure S1A–F). In addition, soil VWC was measured with water content reflectometers (model CS615, Campbell Scientific Inc., Logan, UT, USA) collected in 1 min intervals and stored as 10 min averages on a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA) at two sampling plots (5 and 40), of two stands (B2 and S1), in 2015 (Figure S1B,D) and 2018. In 2018, the mean annual air temperature during April–October was 13 °C, and the sum of monthly precipitations during August–October was 145 mm in Järvselja (Figure S2). To compare the precipitation dynamics in 2015 and 2018, the sum of monthly precipitation (mm) was averaged over ten weather stations in South Estonia (ilmateenistus.ee, accessed on 1 December 2021) for 2015 and measured at SMEAR station (smear.emu.ee, accessed on 1 December 2021) for 2018 (Figure S2). Soil physical-chemical parameters, including pH_{H2O}, total C (TC), total N (TN), total P (TP), dissolved organic carbon (DOC), potassium (K), sulfur (S), water-soluble ammonium and nitrate nitrogen (NH₄-N and NO₃-N, respectively), and phosphate phosphorus (PO₄-P) and calcium ion (Ca²⁺) concentrations, were measured with the standard methods [39] in the lab of the Estonian Environmental Research Centre. In addition, the concentrations of dissolved organic carbon (DOC) were measured from soil using a Vario TOC equipped with a TNb detector (Elementar GmbH, Langensfeld, Germany). All the chemical parameter values were presented based on dry soil.

Table 1. Geographical coordinates, and means ± standard errors of fine root biomass and soil characteristics of the four sampling plots per stand (B1–B3, birch stands; S1–S3, spruce stands) and of the three replicate stands per birch and spruce [9].

Replicate Stands	Geographical Coordinates	Fine Root Biomass (g m ⁻²)	Peat Depth (cm)	pH _{H2O}	Soil Temperature -10 cm (°C)	Soil Water Content -10 cm (m ³ m ⁻³)
B1	N 58°18′24.8 E 27°15′23.1	222 ± 33	43 ± 2	4.38 ± 0.05	11.76 ± 0.04	0.21 ± 0.02
B2	N 58°17′21.4 E 27°19′3.2	206 ± 50	87 ± 1	5.68 ± 0.05	12.00 ± 0.21	0.23 ± 0.03
B3	N 58°18′37.0 E 27°21′11.8	251 ± 25	77 ± 3	4.85 ± 0.03	11.86 ± 0.08	0.30 ± 0.06
Means for birch		226 ± 20	69 ± 6	4.97 ± 0.16	11.87 ± 0.07	0.25 ± 0.03
S1	N 58°18′6.3 E 27°16′54.0	242 ± 40	49 ± 2	5.08 ± 0.13	11.68 ± 0.18	0.32 ± 0.03
S2	N 58°17′49.3 E 27°14′53.4	289 ± 71	36 ± 5	4.93 ± 0.30	10.76 ± 0.10	0.24 ± 0.03
S3	N 58°15′14.5 E 27°17′44.2	140 ± 42	65 ± 6	4.04 ± 0.05	11.23 ± 0.07	0.19 ± 0.02
Means for spruce		217 ± 33	51 ± 4	4.63 ± 0.16	11.23 ± 0.12	0.25 ± 0.02

2.2. Collection of Root Samples and Preparation

Root sampling from three birch and three spruce stands in the Järvselja forest area were carried out in September–October 2018. We collected five root samples per sampling plot at distances of 5, 15, 40, and 80 m from the ditch with a spade from the 20 cm deep topsoil layers at random locations. A total of 125 root samples were collected from all six stands, packed in plastic bags, transported to the lab, and stored at 4 °C until further processing in the lab. In the lab, five to six approximately 10 cm long fine root segments

of birch and spruce were removed from each root sample. Tree fine roots were separated from the fine roots of understory vegetation visually according to their morphology and color. Fine root segments of each sample were washed free of soil particles, kept with water in plastic containers, and stored in the freezer ($-18\text{ }^{\circ}\text{C}$) until further absorptive root morphological analysis.

Table 2. Means \pm standard errors of the stand characteristics of four sampling plots per stand (B1–B3, birch stands; S1–S3, spruce stands) and of the three replicate stands per sampling plot at the distances of 5, 15, 40, and 80 m from the ditch. BA—basal area; DBH—diameter at breast height. Small letters show a statistically significant difference (one-way ANOVA, followed by Tukey’s HSD; $p < 0.05$) of the mean stand characteristics among three birch and three spruce stands, and also among four distances from the ditch.

Stand Characteristics	Species	Replicate Stands	Stand Values (Per Stand)	Distances from the Ditch (m)	Stand Values (Per Sampling Plot)
Stand density (trees ha ⁻¹)	Birch	B1	2000 \pm 294	5	1400 \pm 0
		B2	2100 \pm 268	15	1633 \pm 260
		B3	1325 \pm 229	40	1867 \pm 546
				80	2333 \pm 233
	Spruce	S1	1075 \pm 138 ^b	5	1200 \pm 178
		S2	1900 \pm 183 ^a	15	1600 \pm 289
		S3	1340 \pm 169 ^{ab}	40	1433 \pm 376
				80	1550 \pm 150
BA (m ² ha ⁻¹)	Birch	B1	25 \pm 4	5	24 \pm 1
		B2	20 \pm 3	15	23 \pm 5
		B3	18 \pm 3	40	21 \pm 6
				80	16 \pm 1
	Spruce	S1	32 \pm 6	5	30 \pm 7
		S2	28 \pm 4	15	29 \pm 3
		S3	22 \pm 1	40	20 \pm 2
				80	25 \pm 4
DBH (cm)	Birch	B1	15 \pm 2	5	15 \pm 0 ^a
		B2	14 \pm 1	15	16 \pm 2 ^a
		B3	14 \pm 1	40	16 \pm 1 ^a
				80	11 \pm 0 ^b
	Spruce	S1	20 \pm 1	5	19 \pm 1
		S2	17 \pm 1	15	17 \pm 2
		S3	16 \pm 2	40	16 \pm 2
				80	17 \pm 0

2.3. Absorptive Root Morphology

First- and second-order roots, defined as absorptive roots [13,14], were assessed in this study. Four random subsamples were created from fine root segments of a sample. Absorptive roots of each subsample (about 20–40 tips) were randomly taken from fine root segments and counted under the microscope. Subsequently, absorptive roots were cleaned with a small soft brush to remove all soil and organic debris. The total number of absorptive roots sampled and analyzed per stand ranged from 2026 to 2335 and from 2054 to 2546 in birch and spruce stands, respectively. Absorptive roots of each subsample were placed in a transparent water-filled tray with minimum overlap and scanned. The length (L , cm), surface area (SA , cm²), and volume (V , cm³) of a sample and the mean absorptive root diameter (D , mm) were directly measured by the WinRHIZO™ Pro 2003b image analysis system (Regent Instruments Inc., Chemin Sainte-Foy, QC, Canada). The absorptive roots of each subsample were oven-dried at $65\text{ }^{\circ}\text{C}$ for 4 h to constant weight and weighed to 0.05 mg accuracy. All root morphological parameters were calculated on the subsample level. The mean absorptive root length (L , mm) and dry weight (W , mg) were

calculated by dividing the length and dry weight of the absorptive roots by the number of absorptive roots in a subsample, respectively. Specific root area (SRA, $\text{m}^2 \text{kg}^{-1}$) was calculated as the surface area divided by the dry weight of absorptive roots. Specific root length (SRL, m g^{-1}) was calculated as the absorptive root length divided by the dry weight of absorptive roots. Root tissue density (RTD, kg m^{-3}) was calculated as the dry weight divided by the calculated volume of the absorptive roots [15]. Branching intensity was expressed as the number of absorptive roots per unit of length (BI_L , cm^{-1}) and per unit of dry weight (BI_w , mg^{-1}) [33,40].

2.4. Data Analyses

Statistical analyses were carried out using the STATISTICA 7.1 software (StatSoft Inc., Tulsa, OK, USA). In all cases, a level of statistical significance of $p < 0.05$ was accepted. The normality of the variable distribution was verified using the Shapiro–Wilk and Kolmogorov–Smirnov tests. A one-way analysis of variance (ANOVA), followed by Tukey’s HSD, was performed to test the differences of absorptive root morphological traits, stand and soil characteristics between sampling plots, replicate stands, and tree species. The multiple stepwise regression analysis was applied to determine which soil and root-related properties significantly influenced absorptive root morphology in birch and spruce. For this aim, three groups of soil factors were examined: (1) soil temperature, soil water content, peat depth, and soil $\text{pH}_{\text{H}_2\text{O}}$; (2) soil chemical factors (C/N ratio, DOC, N, K, P, Ca, and S); and (3) tree-related factors (FRB, FRB per stand BA (kg m^{-2}), fine root turnover (yr^{-1}), and ratio of tree/understory root biomass). A linear regression analysis was further used to determine the relationship between absorptive root morphological traits and the significant factors of the stand and soil characteristics within birch and spruce. A correlation matrix (Pearson’s r ; $p < 0.05$) was constructed to observe the correlations between the stand and soil characteristics, as well as between absorptive root morphological traits and stand and soil properties. A type III general linear model (GLM) was used to assess the impacts of the forest stand and distance from the ditch (m) on absorptive root morphological traits in birch and spruce. Redundancy analysis (RDA) (CANOCO program; ter Braak and Smilauer, 2002) was used to describe the relationships between absorptive root morphological traits, tree species, forest stands, sampling plots, stands, and soil characteristics.

3. Results

3.1. Stand and Soil Characteristics

The average stand density and BA were similar between birch and spruce stands (Table 2). The mean DBH was significantly smaller in birch than spruce stands ($p < 0.01$, Table 2). The seasonal variation in mean soil VWC was comparable between birch and spruce stands (Figure S3A,B). Among the spruce stands, the stand density in S2 was significantly higher than that in S1 ($p < 0.01$, Table 2), while the stand density in S3 was similar to those in S1 and S2 (Table 2).

Among the studied sampling plots, the mean DBH in birch stands at plot 80 was significantly lower than those in the rest of the sampling plots ($p < 0.05$, Table 2). Spruce fine root biomass per stand basal area (FRB/BA) tended to be lower in plots close to the ditch and increased significantly between plot 15 and plot 40 (49 ± 5 and $119 \pm 8 \text{ kg m}^{-2}$, respectively, $p < 0.05$, Figure 1B). FRB in spruce was positively related to BA ($r = 0.60$; $p < 0.05$, Figure S4). Soil VWC was similar along with distances from the ditch in all stands in 2015 (Figure S1A–F). The exception was S1, where the mean soil VWC was significantly lower at plot 40 than plot 5 ($p < 0.001$, Figure S1D). However, in B2, the mean soil VWC was significantly greater at plot 40 than plot 5 measured in 2018 (0.41 ± 0.09 and $0.19 \pm 0.04 \text{ m}^3 \text{ m}^{-3}$, respectively, $p < 0.05$). The seasonal variation in mean soil VWC in the studied stands in 2015 and 2018 was similar, especially during September–October (Figure S2). There was no significant relationship between the precipitation and soil VWC in 2015 and 2018 (Figure S2). The mean soil temperature was also similar between sampling

plots of the stands during April–October 2018, ranging from 8.9 ± 2.0 to 16.6 ± 1.8 °C between S1 at plot 5 and B2 at plot 5, respectively.

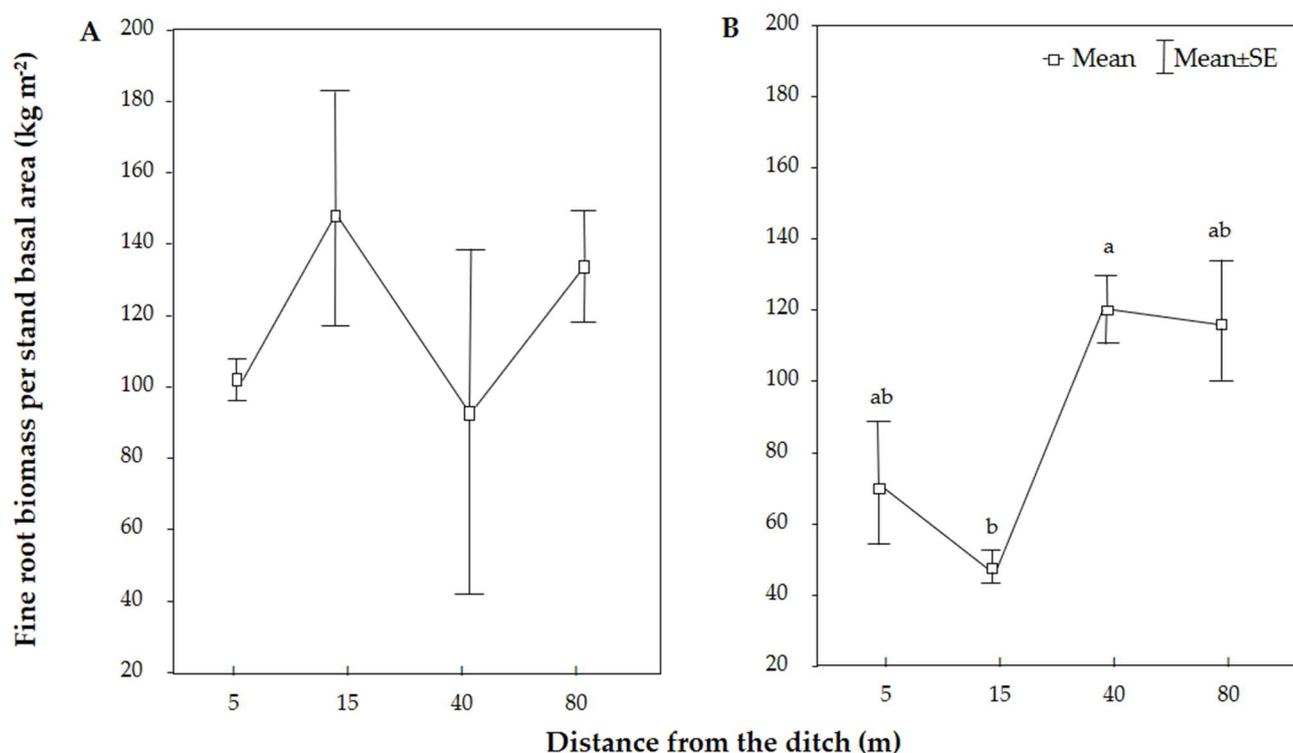


Figure 1. Means of the fine root biomass per stand basal area (FRB/BA, kg m^{-2}) with the standard error bars of three replicate stands per sampling plot at the distances of 5, 15, 40, and 80 m from the ditch in Downy birch (A) and Norway spruce (B). Small letters indicate a statistically significant difference (one-way ANOVA, followed by Tukey's HSD; $p < 0.05$) of the mean spruce FRB/BA between four sampling plots.

3.2. Variation in Absorptive Root Morphology across Tree Species and Distance from the Ditch

Absorptive root morphology was significantly different between birch and spruce (Table 3). The absorptive roots of birch tended to be thinner (0.227 ± 0.002 vs. 0.274 ± 0.003 mm), shorter (1.14 ± 0.05 vs. 1.84 ± 0.02 mm), and have a lower RTD (258 ± 5 vs. 293 ± 6 kg m^{-3}) than spruce. The mean absorptive root W was 2.6 times lower in birch than spruce (Table 3). The mean absorptive root SRA and SRL were higher for birch than spruce (Tables 3 and S1). Similarly, BI_L and BI_W were higher in birch than spruce (Tables 3 and S1).

Along the distance gradient from the ditch, the mean SRA increased significantly toward plot 80 in birch and spruce (Table 3). The mean SRL of birch increased significantly from plot 15 to 80, while the mean SRL of spruce was higher at plot 15 than 5 (Table 3). The mean RTD decreased significantly with distance from the ditch (from plot 5 to plot 80) in birch and spruce stands (from 262 ± 11 to 242 ± 10 kg m^{-3} and from 295 ± 6 to 276 ± 1 kg m^{-3} , respectively, Table 3). The mean absorptive root D of birch was similar between four sampling plots, while it varied between plot 15 and plot 80 in spruce stands (Table 3). A significant decrease in the mean L and W of the absorptive root of birch was found from plot 15 to plot 40. The mean absorptive root L of spruce was comparable between four sampling plots, while the mean W varied significantly between plot 5 and plot 15 (Table 3).

Table 3. Means \pm standard errors of absorptive root morphological traits of the three replicate stands per sampling plot at the distances of 5, 15, 40, and 80 m from the ditch and of the four sampling plots per birch and spruce. D—diameter (mm), L—length (mm), W—dry weight (mg), BI_L —branching intensity per length (cm^{-1}), BI_w —branching intensity per mass (mg^{-1}), SRA—specific root area ($m^2 kg^{-1}$), SRL—specific root length ($m g^{-1}$), and RTD—root tissue density ($kg m^{-3}$). Small letters indicate a statistically significant difference (one-way ANOVA, followed by Tukey’s HSD; $p < 0.05$) of the mean absorptive root morphological traits between four sampling plots within birch and spruce. Capital letters denote a statistically significant difference (one-way ANOVA, followed by Tukey’s HSD; $p < 0.05$) of the mean absorptive root morphological traits of four sampling plots between birch and spruce.

		Distances from the Ditch (m)				Means of Four Sampling Plots
Root Traits	Stands	5	15	40	80	
D (mm)	Birch	0.227 \pm 0.013	0.231 \pm 0.012	0.221 \pm 0.003	0.229 \pm 0.011	0.227 \pm 0.002 ^B
	Spruce	0.278 \pm 0.007 ^{ab}	0.265 \pm 0.004 ^c	0.272 \pm 0.005 ^{abc}	0.281 \pm 0.009 ^{ab}	0.274 \pm 0.003 ^A
L (mm)	Birch	1.12 \pm 0.14 ^{abc}	1.27 \pm 0.09 ^a	1.01 \pm 0.19 ^c	1.16 \pm 0.13 ^{abc}	1.14 \pm 0.05 ^B
	Spruce	1.90 \pm 0.06	1.82 \pm 0.07	1.86 \pm 0.07	1.78 \pm 0.02	1.84 \pm 0.02 ^A
W (mg)	Birch	0.0124 \pm 0.0035 ^{abc}	0.0141 \pm 0.0026 ^a	0.0105 \pm 0.0025 ^c	0.0123 \pm 0.0027 ^{abc}	0.0124 \pm 0.0007 ^B
	Spruce	0.0339 \pm 0.0021 ^a	0.0301 \pm 0.0012 ^c	0.0324 \pm 0.0020 ^{abc}	0.0305 \pm 0.0016 ^{abc}	0.0317 \pm 0.0009 ^A
BI_L (cm^{-1})	Birch	9.58 \pm 1.10 ^{bc}	8.45 \pm 0.67 ^{bc}	11.26 \pm 1.90 ^a	9.40 \pm 1.15 ^{bc}	9.67 \pm 0.58 ^A
	Spruce	5.44 \pm 0.12	5.60 \pm 0.23	5.53 \pm 0.23	5.73 \pm 0.03	5.58 \pm 0.06 ^B
BI_w (mg^{-1})	Birch	99.0 \pm 22.9 ^{abc}	82.2 \pm 15.4 ^c	121.4 \pm 24.6 ^{ab}	106.3 \pm 26.8 ^{ab}	102.2 \pm 8.1 ^A
	Spruce	31.1 \pm 1.6 ^c	34.3 \pm 1.4 ^a	32.5 \pm 2.3 ^{abc}	34.6 \pm 1.6 ^{abc}	33.1 \pm 0.8 ^B
SRA ($m^2 kg^{-1}$)	Birch	69 \pm 6 ^{abc}	68 \pm 4 ^c	71 \pm 4 ^{abc}	75 \pm 6 ^a	71 \pm 2 ^A
	Spruce	50 \pm 1 ^{bc}	51 \pm 1 ^{abc}	50 \pm 1 ^{bc}	53 \pm 2 ^a	51 \pm 1 ^B
SRL ($m g^{-1}$)	Birch	100 \pm 14 ^{abc}	95 \pm 11 ^c	105 \pm 4 ^{abc}	108 \pm 14 ^a	103 \pm 3 ^A
	Spruce	57 \pm 2 ^c	62 \pm 1 ^a	59 \pm 2 ^{abc}	60 \pm 3 ^{abc}	59 \pm 1 ^B
RTD ($kg m^{-3}$)	Birch	262 \pm 11 ^{ab}	262 \pm 4 ^{ab}	264 \pm 17 ^{ab}	242 \pm 10 ^c	258 \pm 5 ^B
	Spruce	295 \pm 6 ^{ab}	300 \pm 7 ^{ab}	300 \pm 4 ^{ab}	276 \pm 1 ^c	293 \pm 6 ^A

3.3. Relationships between Absorptive Root Morphology and the Characteristics of Soil and Stands

Multiple stepwise regression analysis revealed that the mean RTD had a significant negative relationship with peat depth among birch stands; the mean RTD was higher at the stand with a thinner peat layer (Figure 2A). In spruce, the mean absorptive root D had a positive relationship with soil pH, while RTD was negatively related to soil pH (Figure 2B,C). The mean absorptive root D also showed a positive relationship with FRB ($R^2 = 0.43$, $p < 0.05$), while RTD was negatively related to FRB ($R^2 = 0.38$, $p < 0.05$). Among the studied soil chemical factors, RTD in spruce was related to soil C/N, P, and Ca ($R^2 = 0.89$, $p < 0.05$). The mean absorptive root BI_w in spruce showed a significant relationship with soil temperature, with fewer branched absorptive roots toward warmer soils (Figure 2D).

According to Pearson’s correlation analyses, the peat depth in birch stands had a positive correlation with soil pH ($r = 0.87$; $p < 0.001$) and Ca concentration ($r = 0.87$; $p < 0.001$) (Table S2). Soil pH in spruce stands was negatively correlated with peat depth ($r = -0.70$; $p < 0.01$) and C/N ratio ($r = -0.077$; $p < 0.01$), while it was positively correlated with soil Ca concentration ($r = 0.69$; $p < 0.01$) (Table S2).

The general linear model (GLM) showed that forest stands had a significant effect on the variation in absorptive root morphological traits such as L, BI_L , and RTD only in birch. Distance from the ditch also influenced the mean RTD in birch (Table S3).

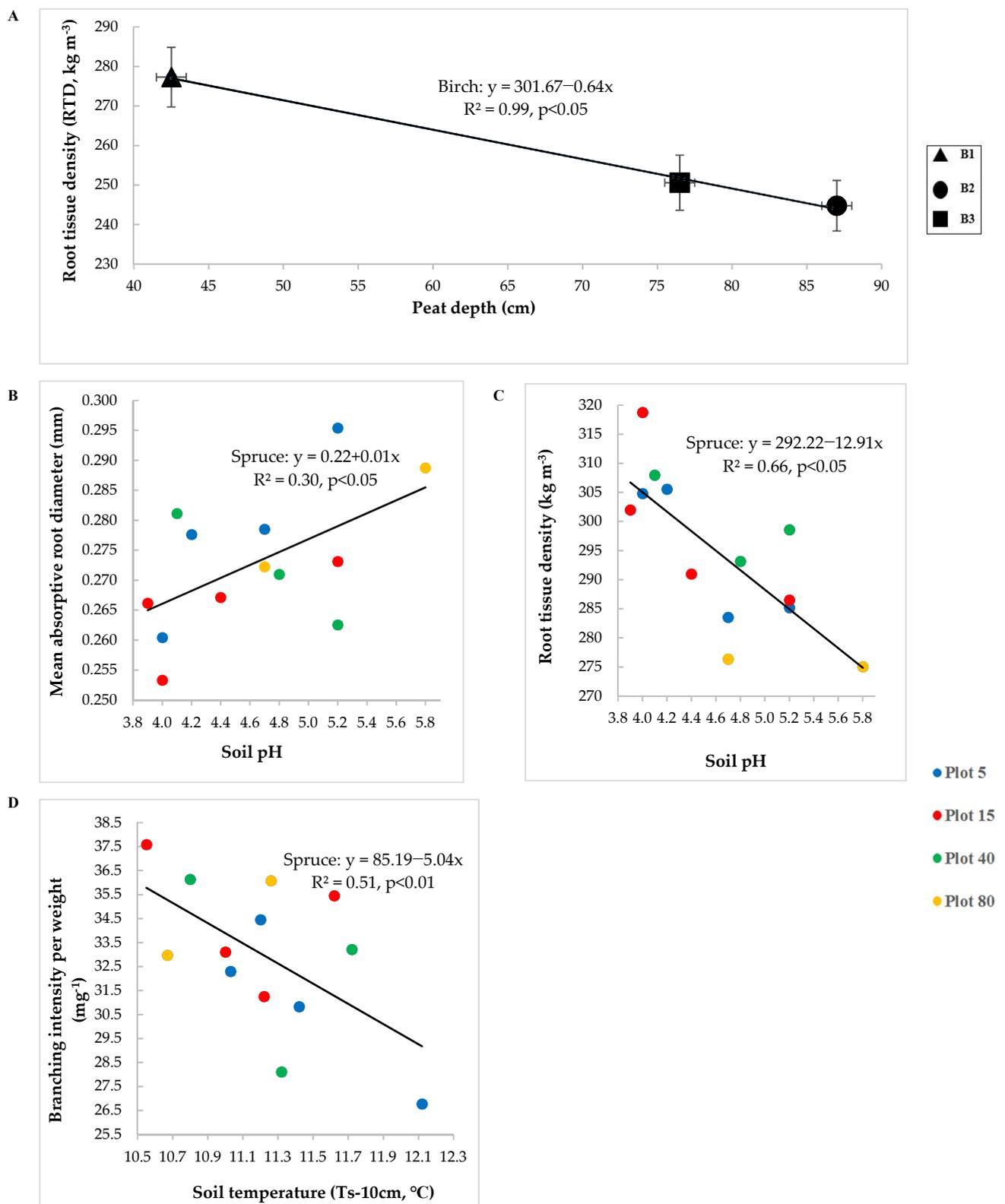


Figure 2. Relationships between absorptive root morphological traits of studied stands in birch (A) and all sampling plots (5, 15, 40, and 80) in spruce with the soil characteristics (B–D). The soil temperature was measured from a depth of 10 cm.

Based on RDA forward selection analysis, a total of 65.4% of the variation in absorptive root morphological traits was explained by tree species, B1 and S2 stands, sampling plots lo-

cated 15 m and 80 m from the ditch, and stand density, BA, FRB, soil N and P concentration, and soil water content ($p < 0.05$, Figure 3A). The first axis described 63.2% of the root trait variation, which was strongly related to the variations in BI_w , SRA, W, and L of absorptive roots depending on the tree species (Figure 3A). RTD was weakly related to the second axis of the biplot that explained only about 1.5% of the root trait variation and indicated a lower value of RTD toward a 80 m distance from the ditch (Figure 3A). However, when analyzed separately by species, the BI_w and root tip mass were most strongly related to the first axis and explained significantly by soil C/N ratio and Ca concentration in birch (Figure 3B) and soil temperature in spruce (Figure 3C). A significant relationship between turnover rates and absorptive root diameter was depicted in both tree species; thicker roots revealed higher turnover rates (Figure 3B,C).

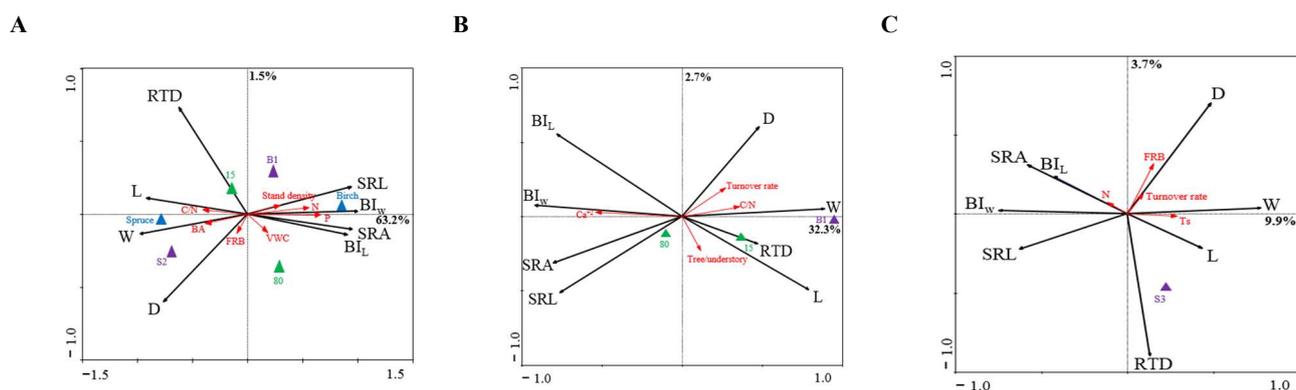


Figure 3. The ordination biplot based on redundancy analysis (RDA, manual forward selection) of absorptive root morphological traits, including D—diameter (mm), L—length (mm), W—dry weight (mg), BI_L —branching intensity per length (cm^{-1}), BI_w —branching intensity per mass (mg^{-1}), SRA—specific root area ($\text{m}^2 \text{kg}^{-1}$), SRL—specific root length (m g^{-1}), and RTD—root tissue density (kg m^{-3}) (black arrows) for both studied tree species, Downy birch and Norway spruce (A), and separately for birch (B) and spruce (C). In all figures, absorptive root morphological traits were shown in relation to the tree species (blue triangles), forest stands (purple triangles), sampling plots (green triangles), and studied stand and soil characteristics (red arrows). The relative eigenvalues of axis 1 and axis 2 were 63.2% and 1.5%, respectively, and in total, the model described 65.4% of the variation in absorptive root traits (Figure 3A, $p < 0.05$).

4. Discussion

4.1. Absorptive Root Morphological Variation in the Tree Species at Drained Peat Soils

Absorptive roots exhibit several morphological traits that determine the plant's resource uptake strategies and mediate plant feedback to ecosystem functioning [17,24]. However, the morphology of absorptive roots of different tree species in hemiboreal peatland forests with organic soils has been poorly characterized.

We observed that the considerable variation in the absorptive root morphological traits is linked to the different tree species (i.e., deciduous vs. coniferous). The absorptive roots of birch were thinner and had a lower RTD; thus, their SRA and SRL were 1.4 and 1.7 times higher than those of spruce, respectively. Our results observed from the drained peat soils are congruent with an earlier study performed at the alkaline soils, which showed that the absorptive root SRA and SRL of deciduous trees (black alder and silver birch) were 1.5–2.5 times higher than those of conifer (Scots pine) tree species [18]. Species with contrasting root morphology may exhibit different nutrient foraging strategies [41,42]. Compared to the deciduous trees, evergreen conifers typically exhibit thicker roots and lower SRL for soil resource acquisition [43]. Root branching intensity per length and mass unit was also influenced by tree species identity, being 2 and 3 times higher in birch than spruce, respectively, aligning with previous studies [33,40].

However, the mean SRA and SRL of birch at drained peat soils were lower than the same values of deciduous trees at alkaline soils, while the mean SRA and SRL of spruce were of the same order of magnitude as those reported for conifer at the alkaline soils [18]. The mean root BI_L of birch and spruce at drained peat soils was identical to those reported for deciduous broadleaved ($5.4\text{--}9.6\text{ cm}^{-1}$) but higher compared to coniferous species (3.3 cm^{-1}) under mesic mesotrophic site conditions, respectively [33]. Differences in species identity and studied soil type can also account for the conflicting results mentioned above.

4.2. Absorptive Root Morphological Variation along with the Distance from the Ditch

Even though the morphology of the absorptive roots varied substantially among tree species, the response patterns of some root traits, such as SRA and RTD, to distance gradient from the ditch were directionally consistent for tree species. This is in agreement with our first hypothesis, suggesting that the effect of distance from the ditch on morphological variations of absorptive roots is similar between birch and spruce. The mean SRL also varied with distance gradient from the ditch, but it was only evident in birch. Similar to our result, Werger et al. [44] showed that the effect of wind intensity on the fine root morphological traits, such as SRA, SRL, and RTD, was uniform in all grassland species. However, our results contradict previously reported species-specific root morphological responses to adverse soil conditions [23,45].

Absorptive roots are functionally important for the acquisition of soil resources and are highly plastic to changes in soil properties [46]. In line with our second hypothesis, we found that the mean SRA increased while RTD decreased with distance from the ditch. This finding highlights the morphological adjustment of absorptive roots to the local soil properties at different distances from the ditch and possibly a shift in nutrient foraging. However, in our study, the soil physical and chemical properties were not dependent on the distance from the ditch. This result is in contradiction with previous studies that found that at spatially higher distances from the ditch, soil properties are becoming poor [6,8]. For instance, the aeration of the substrate, decomposition of organic matter, and nutrient availability reduced, which were attributed to the higher water table level at sites located far away from the ditch [6]. In the present study, we observed a statistically similar soil water content along with distances from the ditch, but water content tended to be higher toward plots far away from the ditch, ranging from $0.22\text{ m}^3\text{ m}^{-3}$ at plot 5 to $0.27\text{ m}^3\text{ m}^{-3}$ at plot 80 in the studied stands. On the other hand, many studies reported that the soil microclimate and hydrology of peat soils can be noticeably influenced by other factors than ditch distance, for example, topography, vegetation characteristics, tree stands, climatic conditions, as well as peat and subsoil hydraulic properties [47–49]. It will therefore be important to explore those effects to better determine soil moisture at peatland forests.

An increase in SRA and a decrease in RTD toward higher distances from the ditch observed in this study can support the more efficient acquisition of soil resources. Indeed, strategies that increase the absorptive surface area per unit mass are thought to be more effective at increasing the potential of a root system to uptake resources [28]. Moreover, we found that at drained spruce peatland forests, FRB per stand BA tended to be lower at sites close to the ditch, and this could probably reflect more advanced root foraging near the ditch than farther distances, as fewer roots in the belowground supported the same basal area unit in the aboveground at sites close to the ditch.

The soil microbial communities are essential drivers in the mineralization of organic matter and mediate soil nutrient cycling [50]. Previous studies showed shifts in the soil bacterial and fungal communities with distance gradient from the ditch [9,51]. For example, Qiu et al. [52] revealed that fungal diversity was higher at a plot 5 m from the ditch related to the well-drained soil condition and the improvements in nutrient availability compared to the plot at a 75 m distance with poor drainage condition. Therefore, changes in fungal community structures in peat soil might serve as a sensitive indicator for changes in soil properties. Given also the complementarity between absorptive roots and associated mycorrhizal fungi in nutrient foraging, further investigation should pay attention to both

root and root-associated-fungi traits to better identify tree growth responses and peatland forest functioning.

4.3. Absorptive Root Morphological Variation with the Stand and Soil Properties

Here, the absorptive root morphology was substantially influenced by the soil physical and chemical properties, including peat depth, pH, and temperature. However, all of these soil factors were similar along with distances from the ditch. The two examined tree species growing at similar drained histosols showed different responses in their absorptive root morphological traits to the local soil properties. Correspondingly, several studies revealed that the response of the absorptive root morphological traits to the soil conditions varies across plant species [18,23]. Similarly, we found that absorptive root morphology varied between stands of the same forest type, but such variations differed between birch and spruce. For example, forest stands affected the variations in absorptive root morphological traits such as L , BI_L , and RTD only in birch. The mean RTD in the three birch stands was negatively related to the peat depth, which varied from 43 to 57 cm between B1 and B2, respectively. Among all studied spruce stands, soil pH was the main soil factor affecting absorptive root morphological variation. Mean absorptive root D was lowest, while RTD was highest in the most acidic spruce forest soils ($pH = 3.8\text{--}4.0$). Similar to our findings, the significant negative relationships between RTD and soil pH were shown previously [53,54]. In addition, in this study, soil pH was negatively correlated with peat depth in spruce stands. This suggests that at more acidic soils with thicker peat depths, the decomposition rate and available nutrients were probably lower. Therefore, producing thinner roots with low RTD at acidic soils in spruce stands could support the more resource acquisition strategy. Doi et al. [20] also showed the production of thinner second-order roots at more acidic soils, attributed to the higher nutrient absorption efficiency.

Soil temperature ranged from 10.6 to 12.1 °C at spruce forests. Root branching intensity (per mass unit) exhibited a high sensitivity following the soil temperature range at drained peat soils of spruce stands. Decreased soil temperature significantly increased the root branching intensity of spruce, consistent with previous research in spruce stands [55]. In a recent analysis of root traits, Liese et al. [33] showed that the root BI is a key trait determining the root plastic responses to a changing environment. Low soil temperature influenced nutrient availability by low mineralization rates [56]. The high branching intensity of the absorptive roots at the less warm soils was probably due to the rapid and extensive proliferation into peat soils to enhance resource uptake.

5. Conclusions

Here, we detected tendencies in absorptive root morphological traits, such as SRA , SRL , BI , and RTD , in both examined tree species, Downy birch and Norway spruce, along with distance gradient from the ditch. Irrespective of tree species, SRA increased while RTD decreased toward higher distances from the ditch, indicating an acclimation in absorptive roots of trees to soil differences along with distances from the ditch. However, in this study, we could not show the variability in soil properties caused by distance from the ditch. There may exist other factors that influenced the soil local hydrology and microclimate rather than ditch distance, and these should be taken into consideration by future studies in drained peatland forests. We also pointed out the influence of soil physical and chemical factors, such as peat depth, pH, and temperature, on the species-specific responses of absorptive root morphology in birch and spruce growing at similar drained histosols.

Nevertheless, we showed that evaluating absorptive root morphology alone is not a good indicator for describing changes in root foraging along with distances from the ditch. These absorptive root morphological traits should be further used in much wider analyses, such as root nutrient uptake capacity and with the associated ECM fungal communities, to better predict patterns in the root acclimation of trees and forest functioning at drained stands.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13010112/s1>, Figure S1A–F: Soil volumetric water content (VWC, $\text{m}^3 \text{m}^{-3}$) measured with a ProCheck reader equipped with a GS3 sensor (Decagon Devices Inc.) at sampling plots of 5, 15, 40, and 80 (m) distances from the ditch of replicate stands for birch (B1–B3) and spruce (S1–S3) and with reflectometers (model CS615, Campbell Scientific Inc., Logan, UT, USA) at sampling plots 5 and 40, of replicate stands B2 and S1, during April–October 2015, Figure S2: The sum of monthly precipitation (mm) for 2015 and 2018 and the means \pm standard errors of the soil VWC from CR1000 logger data of plots 5 and 40, and replicate stands B2 and S1, from April to October 2015 and 2018, Figure S3A,B: The means of soil VWC for birch and spruce at sampling plots (5, 15, 40, and 80) averaged over relevant replicate stands during April–October 2015, Figure S4: Relationship between fine root biomass and stand basal area in all sampling plots in Norway spruce, Table S1: The means \pm standard errors of absorptive root morphological traits of sampling plots (5, 15, 40, and 80) in replicate stands for birch (B1–B3) and spruce (S1–S3), and of all sampling plots per birch and spruce replicate stand studied in 2018, Table S2: Pearson’s correlation analyses between soil parameters of the forest stands for birch and spruce, Table S3: The effects of forest stands and distance from the ditch (m) on absorptive root morphological traits in birch and spruce performed by general linear model (GLM).

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