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Understory Species Identity Rather than Species Richness Influences Fine Root Decomposition in a Temperate Plantation

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Abstract: Different silvicultural treatments that are applied at plantation establishment may drive different vegetation succession pathways. These divergent vegetation types subsequently feed back to influence soil carbon and nitrogen cycles. One potential mechanism of feedback is through litter decomposition, and in particular fine root decomposition (FRD; <2 mm roots). In the present study we investigated how blade scarification, fertilization, and vegetation control influenced over- and understory vegetation 27 years after plantation, and whether these different vegetation communities affected FRD. In a design using factorial combinations of the three treatments at the Petawawa Research Forest (Laurentian Hills, ON, Canada), we conducted an in situ FRD experiment, with fine roots from the entire vegetation community (both over- and understory) of each plot. The different silvicultural treatments affected overstory basal area, understory species richness and FRD. No correlation was noted between understory species richness and FRD. Instead, we found that understory vegetation (especially fern and herb) cover best explained FRD. We conclude that silvicultural treatments affect FRD through subsequent vegetation succession and that this effect is more likely due to species-specific effects inducing a favorable soil environment than to a higher species richness *per se*.

Keywords: fine root decomposition; silvicultural treatments; species richness; understory vegetation; soil organic carbon

1. Introduction

Plant–soil interactions are complex and involve a myriad of abiotic and biotic factors. The interactions in natural forests contribute to effectively absorb atmospheric CO₂, however these processes can be easily disrupted by disturbances such as plantation management practices. Given that the land area devoted to tree plantations is expected to increase in coming years [1], whether for primarily protective functions for the provision of services or for intensive timber production [2] and in the context where global temperatures are expected to rise by 1–3 °C during the next century [3], it is critical to more rigorously evaluate the mechanisms of soil carbon (C) dynamics associated with different management practices in plantations.

Whether in temperate or boreal regions, the present forest overstory [4] and understory [5] composition is often a result of past forest management decisions. Although the mechanisms involved are not yet clear, the combined influence of silvicultural practices and subsequent forest vegetation succession can strongly affect soil organic carbon (SOC) cycling directly through soil disturbance as well as changes in microclimate, or indirectly through multiple factors such as changes in vegetation

composition, decomposer community, litter input and subsequent litter decomposition rate. Regarding the effect of vegetation composition on SOC, both plant species identity and diversity could play an important role. For example, it has been suggested that different tree species planted within the same sites may influence SOC differently through differences in litterfall C inputs [4]. The differences in litterfall C inputs are especially marked when basal area and canopy cover differ widely among species [6,7]. For example, low C stocks have been observed in forest soils in which litterfall C inputs and basal area were also low [6]. Differences related to C inputs have also been reported between deciduous and conifer trees (i.e., a higher root biomass has been associated with deciduous trees compared to conifers) [8]. A higher C input to soils (i.e., with an increased root productivity and turnover) was also reported in more diverse forest stands [9,10]. However, it is still not clear whether plant species identity or plant species diversity has the most influence on soil C stocks.

When studying C inputs, particular attention should be given to roots, since root litter contribution to soil C may equal or be greater than that of foliar litterfall [4,11]. Several factors such as climate and environmental variables, soil biota and root chemistry are known to influence root decomposition [12–14]. For example, roots characterized by high lignin concentrations or high C: N and lignin: N ratios are associated with low rates of decomposition [12,15,16] whereas roots with high N concentrations decompose faster [17,18]. Therefore, any factor that may influence root chemistry such as land use (e.g., N addition) and plant species composition [14] should be taken into account when studying root decomposition. However, uncertainties remain regarding the effect of plant species on root decomposition. The presence of multiple pathways via which plant diversity may affect root decomposition (e.g., root litter quality, soil biota, and soil abiotic conditions). As well, different measures of plant diversity (e.g., plant species richness, and the presence/absence of individual functional groups) may vary in their effects on decomposition [19,20]. Both these could explain the lack of consistency among studies. Recent investigations have provided evidence that plant diversity is more likely to affect root decomposition via changes in root chemical traits and soil biota, rather than via changes in root morphological traits or soil abiotic conditions [21]. Among root chemical traits, root lignin, N, K and Mg concentrations have been reported as important mediators of the plant diversity-root decomposition relationships [21]. In a rare study of tree root litter mixtures on a diversity gradient [22], the authors observed that root tissue chemical traits, rather than plant species richness (SR), explained more of the variation in root decomposition rate. Similarly, Prieto et al. [23] found that plant species identity effect (i.e., low tissue quality of *Carex humilis* in mixtures) was more important than additive diversity effects to control root decomposition of prairie plant mixtures. Given the uncertainties surrounding the role of plant species diversity *per se* vs. plant species identity on root decomposition and soil C stocks in forests, more studies simultaneously investigating these factors are needed.

The present study is part of a long-term experiment at the Petawawa Research Forest in Ontario, Canada. This experiment was established in 1986 to evaluate the ecophysiological response of white pine and white spruce to three intensive silvicultural treatments: blade scarification (a complete removal of organic layer), fertilization, and vegetation control (with herbicide) [24]. After 25 years on the present study site, Poirier et al. [5] reported that silvicultural treatments (i.e., soil scarification and vegetation control) led to distinct overstory and understory vegetation communities, characterized by contrasting structure and functional composition which strongly impacted C and N cycling, partly through an effect on soil pH in the mineral soil. More specifically, Poirier et al. [5] reported that while the vegetation control treatment was characterized by a Hardwood shrub-rich forest, soil scarification and the combination of soil scarification and vegetation control treatments led to a Hardwood herb-rich and a Softwood monoculture dominated forest respectively. The authors stated that the greater herb cover in the Hardwood herb-rich community could be associated with increased litter decomposition rates given its high-quality, nutrient-rich litter added to forest floor [25] which represents an important source of food for soil biota. However, neither litter decomposition rates nor understory vegetation species richness have yet been measured on this site.

In the present study, 27 years after plantation establishment, we investigated the influence of blade scarification, fertilization, and vegetation control on over- and understory vegetation composition and attributes, and whether this subsequent vegetation succession affected fine root decomposition (<2 mm). We also investigated the relationships among fine root decomposition (FRD), fine root chemistry, plant species diversity (SR), plant species identity and soil properties, in an attempt to better understand the mechanisms controlling fine root decomposition and the potential link with SOC and N concentrations in surface mineral soil. We hypothesized that:

- (i) A faster fine root decomposition is associated with higher plant species diversity (SR);
- (ii) A faster fine root decomposition will be associated with higher SOC and N in the mineral soil;
- (iii) Plant species identity is a more important driver of fine root decomposition compared to plant SR *per se*.

2. Materials and Methods

2.1. Site Description

The plantation is located within the Petawawa National Research Forest in the Great Lakes St-Lawrence Forest Region, on the north shore of Cartier Lake (45°57'50" N, 77°34'45" W) at an elevation of 170 m above sea level. The climate of the region is characterized by mean annual temperature of 4.3 °C and an average rainfall of 853 mm [26]. The soils consist of deep, well-drained loam to sandy loam developed from acidic glaciofluvial till [24] and are classified as an Orthic Humo-Ferric Podzol [27] or Haplorthod [28].

2.2. Experimental Design

The site at Cartier Lake was clearcut in the summer of 1985 and the experimental plantation was established in 1986. Before clear-cutting, the forest on the experimental site was composed of aspen (*Populus tremuloides* Michaux), white birch (*Betula papyrifera* Marshall) and white spruce (*Picea glauca* (Moench) Voss), with lesser components of yellow birch (*Betula alleghaniensis* Britton), basswood (*Tilia americana* L.), white pine (*Pinus strobus* L.) and balsam fir (*Abies balsamea* (L.) Miller) [24]. The experimental site was on a flat lake plain beside Cartier Lake; soil drainage was constant throughout and texture was relatively homogeneous within the four blocks. The experimental design consisted of eight treatments (plots) replicated in four randomized complete blocks (8 × 4 = 32 plots in total). Whole plots (20 by 40 m plots with 5 m buffers) were 2³ factorial: two levels of three treatments, assigned randomly in the blocks. The control plots were first clearcut and planted without subsequent silvicultural treatment. The main treatments were blade scarification (S: levels 0 and 1), fertilization (F: levels 0 and 1) and vegetation control treatment (V: levels 0 and 1). Level 0 represented undisturbed condition following harvest and Level 1 the application of the treatment. Blade scarification represented complete removal of the organic forest floor, in the spring before planting. Fertilization consisted of an annual application of the slow-release fertilizer Osmocote (17:6:10 N-P-K plus micronutrients; N as 9.1% NH₄⁺ and 7.9% NO₃⁻). In the first growing season, 30 g of Osmocote were spread on the soil surface around each tree and this amount was increased each year to 40, 60, 80, 135 and 200 g in the second, third, fourth, fifth and sixth growing seasons, respectively. The vegetation control treatment represented an annual midsummer application of glyphosate isopropylamine salt (trade name Roundup®) at a rate of 2.0 kg·ha⁻¹ of active ingredient for each of the four years following plantation establishment. In April 1986, each 20 by 40 m whole plot was divided in two 20 by 20 m subplots and planted with 100 trees (3 year-old bareroot stock) each, of local provenances of white spruce and white pine. Since our design is factorial and to simplify the study, only the subplots with white pine were studied.

2.3. Vegetation

Evaluation of understory vegetation species richness (the number of species present in the community) was made in June 2013, using three 50 by 50 cm quadrats randomly distributed on each plot (3 quadrats \times 32 plots = 96 samples in total). Basal area (in $\text{m}^2 \text{ha}^{-1}$) was determined in summer 2014, for each of the 32 plots, using a two-factor metric prism (2 m^2/ha basal area factor). All trees that were validated by the prism were counted. The basal area was then estimated by multiplying the number of counted trees by the basal area factor. This information was used to estimate deciduous versus conifer basal area for each of the plots.

2.4. Soil Sampling, Fine Root Decomposition and Root Chemistry

The surface mineral soil (0–15 cm depth, after removing the organic layer when necessary) was sampled by taking three randomly located cores per plot ($n = 96$) with an 8-cm-diameter metal soil corer, at the end of July 2013. Soils were sieved through a 2 mm stainless steel sieve and kept frozen until analysis. Given the difficulties associated with the differentiation of roots according to plant species, the roots from the cores were not differentiated and represented the entire vegetation community of each plot. These fine roots were removed, washed and dried in a forced-air oven at 65 °C to constant weight, then separated into two parts; one part was used for the decomposition experiment, while the second was used for chemical analyses. For the decomposition experiment, 0.35 ± 0.02 g of root dry mass of each of the 96 samples were placed in mesh bags (5 \times 10 cm each) with a pore size of 50 microns (ANKOM Technology, Macedon, NY, USA). On 4 October 2013, the mesh bags were buried (inserted vertically in the soil) between 5 and 10 cm soil depth in the respective plot where originally sampled and collected on 21 May 2014. After collection, roots were carefully removed from mesh bags. Visible fungal hyphae were removed after drying roots at 65 °C to constant weight. These roots were then reweighed, and fine root decomposition was calculated as mass loss percentage. The remaining roots (the roots that were not used for decomposition experiment) were used for root chemistry; the root samples were weighed and finely ground using a ball-mill mixer MM 200 (Retsch©, Haan, Germany). C concentration was determined by dry combustion (Trumac CNS-1000, LECO Corp., St. Joseph, MI, USA) and the concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were determined by digestion (Parkinson and Allen, 1975) followed by atomic absorption spectroscopy.

2.5. Soil Analyses

Soil texture was assessed by decantation [29] and soil pH was measured in a prepared 0.01 M CaCl_2 solution that was added to soil in a 1:2 soil to liquid mixture. Cation exchange capacity (CEC) and base cations (Ca, Mg, K and Na) were assessed using an unbuffered $\text{NH}_4\text{Cl}-\text{BaCl}_2$ 0.1 M solution [30] and measured by inductively coupled plasma emission (Optima 4300 DV ICP-OES, Perkin-Elmer Inc., Waltham, MA, USA).

Soil organic carbon was determined by the Walkley-Black method and soil N was determined using the Kjeldhal method, to be consistent with previous studies on the same site [24]. The analyses were performed on air-dried soil samples, finely ground ($<150 \mu\text{m}$) with a ball-mill mixer MM 200 (Retsch©, Haan, Germany).

2.6. Statistical Analyses

All statistical analyses were performed with R software version 4.0.2. Available online: <https://www.r-project.org/> (accessed on 13/10/2020).

To test the effect of silvicultural treatments on all studied variables (vegetation diversity, basal area of the overstory, mass loss for root decomposition and soil properties), we applied a linear mixed-effect model, developed using the *lme* function in the *nlme* package [31], with the three silvicultural treatments as fixed factors and blocks and plot identity as random factors. In all linear mixed-effect models,

the normality of residuals and homogeneity of variance were tested, and transformations were performed when necessary. Statistical significance was set at the 0.10 level given the inherent high variability in forest soil properties. When there were significant treatment interactions, the averages of treatment-level combinations were compared with the combination of interaction treatment Level 0 with the α level adjusted for the number of comparisons using Bonferonni's adjustment.

Canonical correspondence analysis (CCA) was carried out to relate silvicultural treatments to over- and understory vegetation characteristics (plant species richness, total basal area, functional composition; that is whether trees are deciduous or conifers, using respective basal area) using the *rda* function of the *vegan* package [32]. Variance partitioning was used to determine the unique, shared, and total explained variation contributed by each set of explanatory variables using the *varpart* function of the *vegan* package and represented schematically by Venn diagrams. The significance of each partition was determined by permutation testing using partial redundancy analysis (*rda* function available in the *vegan* package) and ANOVA. We used the *rcorr* function (Pearson correlation coefficient) of the *Hmisc* package [33] to quantify the association among all measured soil and root variables.

3. Results

3.1. Effects of Silvicultural Treatments on Overstory and Understory Vegetation

Twenty-seven years after plantation establishment, vegetation control led to distinct plant community composition and attributes (Figure 1 and Table 1. Also see Supplementary material Tables S1 and S2). We observed a higher overstory volume (total basal area) and a dominance of conifers when vegetation control was applied, while a higher understory vegetation diversity (species richness) and a dominance of deciduous trees was observed in the absence of vegetation control.

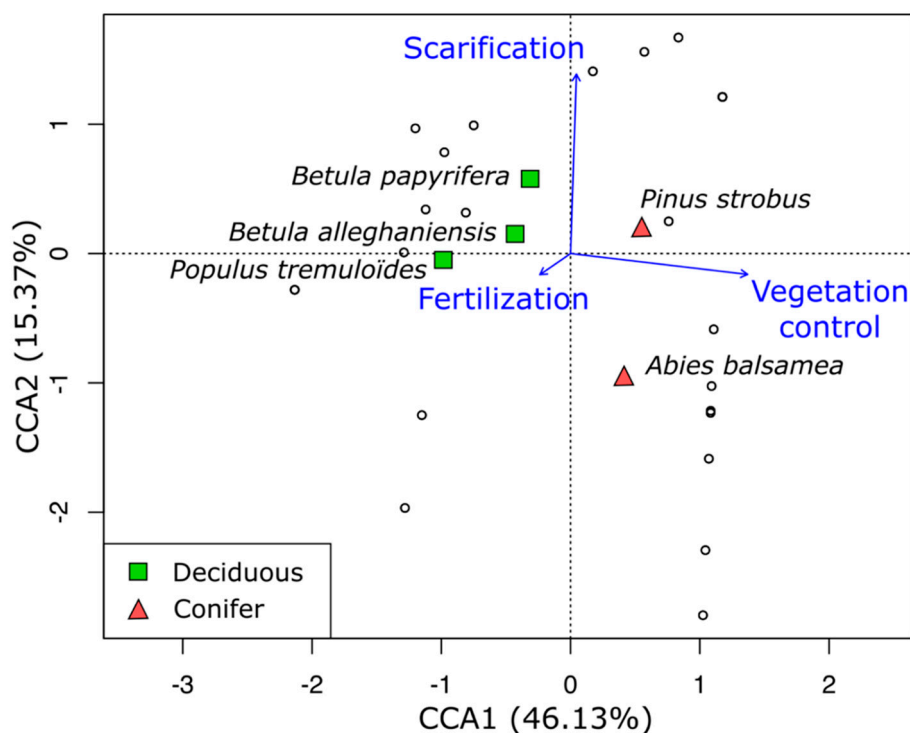


Figure 1. Canonical correspondence analysis of overstory vegetation composition using silvicultural treatments 27 years after establishment of a white pine plantation. Silvicultural treatments significantly explained overstory vegetation composition variation at $p < 0.001$ (R^2 adj = 0.49).

Table 1. Impact of silvicultural treatments on overstory volume (Basal area), understory vegetation diversity (Species richness), fine root decomposition (FRD) and fine root C and macronutrients, 27 years after establishment of a white pine plantation ($n = 96$). S = scarification, F = fertilization, V = vegetation control, 0 = no treatment, 1 = application of treatment. Values are mean and standard errors are presented in brackets.

	Species Richness	Basal Area (m ² ha ⁻¹)	FRD (%)	C (g kg ⁻¹)	N (g kg ⁻¹)	Root C:N	P (g kg ⁻¹)	K (g kg ⁻¹)	Ca (g kg ⁻¹)	Mg (g kg ⁻¹)
S0F0V0	4.2 (±0.3)	28.0 (±1.9)	20.6 (±0.01)	411.7 (±11.8)	7.4 (±0.5)	58.6 (±4.2)	1.27 (±0.15)	3.35 (±0.35)	11.1 (±0.96)	0.93 (±0.12)
S1F0V0	5.7 (±0.6)	23.0 (±1.8)	19.0 (±0.01)	392.6 (±15.2)	7.9 (±0.5)	51.0 (±3.4)	1.23 (±0.16)	4.55 (±0.71)	9.17 (±0.79)	0.86 (±0.10)
S0F1V0	3.8 (±0.5)	31.5 (±2.1)	18.1 (±0.01)	414.5 (±13.8)	6.7 (±0.5)	65.3 (±4.5)	1.27 (±0.12)	4.2 (±0.58)	12.67 (±0.7)	0.85 (±0.05)
S1F1V0	5.6 (±0.3)	26.0 (±1.5)	26.1 (±0.01)	425.6 (±7.8)	9.0 (±0.7)	49.7 (±3.5)	1.6 (±0.19)	4.55 (±0.58)	8.75 (±0.83)	1.05 (±0.20)
S0F0V1	1.7 (±0.5)	46.5 (±3.1)	13.6 (±0.00)	429.4 (±10.2)	7.5 (±0.6)	61.4 (±4.9)	1.23 (±0.12)	2.47 (±0.17)	4.96 (±0.36)	0.76 (±0.07)
S1F0V1	2.2 (±0.5)	41.5 (±1.7)	18.2 (±0.01)	436.1 (±8.9)	7.2 (±0.4)	62.9 (±3.9)	1.31 (±0.11)	2.78 (±0.22)	4.94 (±0.81)	0.63 (±0.03)
S0F1V1	4.0 (±0.8)	27.0 (±1.1)	16.0 (±0.01)	431.4 (±11.0)	7.4 (±0.4)	60.2 (±3.5)	1.27 (±0.09)	3.31 (±0.2)	8.28 (±1.01)	0.83 (±0.06)
S1F1V1	2.8 (±0.7)	37.0 (±2.4)	18.5 (±0.01)	417.4 (±12.6)	7.9 (±0.5)	55.0 (±3.5)	1.35 (±0.14)	3.54 (±0.44)	5.7 (±0.86)	0.75 (±0.04)
	V *	V ***	V ** S × F × V **	V **	S **	S **	NS	V *** F **	V *** S *** F **	V **

*. **. *** the symbols indicate the significance at 0.1, 0.05 and 0.01 probability levels, respectively; NS indicates not significant.

3.2. Effects of Silvicultural Treatments on Fine Root Decomposition and Chemistry

We observed a significant effect of the silvicultural treatments on fine root decomposition. The fastest FRD occurred when scarification and fertilization treatments were combined without vegetation control and the slowest was recorded when vegetation control was applied alone (Table 1). Fine root C, fine root C: N and macronutrients also responded to silvicultural treatments (Table 1). Vegetation control resulted in higher root C and lower root Mg. Blade scarification was associated with higher root N concentration. Root K increased with fertilization and decreased with vegetation control. Scarification and vegetation control contributed to lower root Ca concentration, while fertilization was associated with an increase in root Ca. The root C: N decreased with scarification alone while root P concentration was not affected by the silvicultural treatments.

3.3. Effects of Subsequent Vegetation on Fine Root Decomposition

The variation partitioning analysis revealed that understory vegetation abundance alone explained 41.8% of the FRD (Figure 2A). Within understory vegetation, the same variation partitioning analysis identified a stronger contribution of fern cover (25.5%) compared to herb and shrub covers, in controlling FRD (Figure 2B). We also found that the abundance of 8 of the 32 referenced species (see Supplementary material Table S1 for details) best explained fine root decomposition (Table 2).

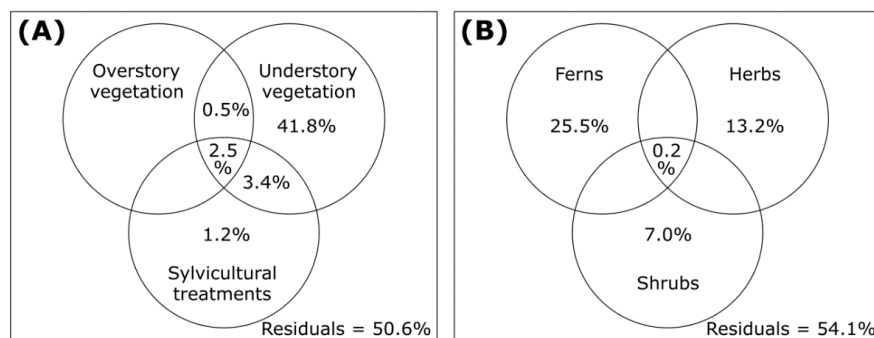


Figure 2. Venn diagram displaying the results of unique, shared, and total variation of the fine root decomposition explained by (A) the three silvicultural treatments and over- and understory vegetation percent cover, (B) understory vegetation composition.

Table 2. Understory vegetation species (abundances) that best explained fine root decomposition (FRD), according to a forward selection of explanatory variables. The (+) sign represents a positive relationship between the abundance of the species and FRD.

	Correlation with FRD	Adj R ²	Adj R ² Cum	F	p-Values
<i>Onoclea sensibilis</i>	(+)	0.104	0.104	12.034	0.010
<i>Trientalis borealis</i>	(+)	0.106	0.210	13.553	0.006
<i>Polytrichum sp</i>	(+)	0.123	0.332	18.077	0.002
<i>Rubus idaeus</i>	(+)	0.052	0.385	8.841	0.015
<i>Maianthemum canadense</i>	(+)	0.031	0.415	5.771	0.016
<i>Lycopodium obscurum</i>	(+)	0.025	0.440	4.954	0.050
<i>Diervilla lonicera</i>	(+)	0.020	0.460	4.329	0.039
<i>Fern sp</i>	(+)	0.021	0.481	4.623	0.037

3.4. Effects of Silvicultural Treatments on Surface Mineral Soil Properties

Silvicultural treatments had different effects on mineral soil chemical properties (Table 3). Blade scarification treatment resulted in lower soil pH and exchangeable Ca, while vegetation control contributed to lower exchangeable Mg and K. Exchangeable K decreased in response to the combined effect of scarification and vegetation control. The mineral SOC was significantly lower following scarification but silvicultural treatments did not affect mineral N concentration. Consequently, the soil C: N was also significantly lower with blade scarification.

Table 3. Impact of silvicultural treatments on surface mineral soil (0–15 cm) properties, 27 years after establishment of a white pine plantation ($n = 96$). S = scarification, F = fertilization, V = vegetation control, 0 = no treatment, 1 = application of treatment. Values are the mean, and standard errors are presented in brackets.

	pH	Exch.Ca (mmol (+) kg ⁻¹ soil)	Exch.Mg (mmol (+) kg ⁻¹ soil)	Exch.K (mmol (+) kg ⁻¹ soil)	C Concentration (g kg ⁻¹)	N Concentration (g kg ⁻¹)	Soil C: N
S0F0V0	4.3 (±0.1)	2.36 (±0.63)	0.23 (±0.05)	0.26 (±0.03)	18.25 (±3.12)	1.32 (±0.14)	13.20 (±1.1)
S1F0V0	4.2 (±0.1)	1.62 (±0.25)	0.21 (±0.04)	0.23 (±0.02)	15.59 (±1.84)	1.32 (±0.07)	11.50 (±1.0)
S0F1V0	4.6 (±0.1)	3.88 (±0.97)	0.34 (±0.08)	0.31 (±0.03)	19.23 (±3.83)	1.35 (±0.16)	13.30 (±1.1)
S1F1V0	4.1 (±0.1)	1.22 (±0.21)	0.17 (±0.03)	0.21 (±0.02)	14.25 (±0.87)	1.24 (±0.06)	11.70 (±0.8)
S0F0V1	4.2 (±0.2)	2.21 (±0.38)	0.13 (±0.02)	0.17 (±0.01)	16.06 (±1.40)	1.19 (±0.07)	13.30 (±0.5)
S1F0V1	4.1 (±0.1)	1.07 (±0.22)	0.13 (±0.02)	0.18 (±0.01)	12.99 (±1.22)	1.20 (±0.05)	10.70 (±0.7)
S0F1V1	4.3 (±0.1)	2.56 (±0.48)	0.21 (±0.04)	0.20 (±0.02)	19.33 (±2.20)	1.32 (±0.08)	14.30 (±1.0)
S1F1V1	4.3 (±0.0)	1.73 (±0.24)	0.22 (±0.04)	0.20 (±0.03)	14.78 (±1.70)	1.11 (±0.08)	13.60 (±1.4)
	S *	S ***	V **	V ***	S *	NS	S *

*, **, *** the symbols indicate the significance at 0.1, 0.05 and 0.01 probability levels, respectively; NS indicates not significant.

3.5. The Relationship between Fine Root Decomposition and Surface Mineral Soil Properties

Correlation analyses among all measured variables showed no correlations between FRD and soil properties (see Supplementary material, Table S3).

4. Discussion

The aim of our study was to investigate how the influence of three silvicultural treatments (blade scarification, fertilization, and vegetation control) on over- and understory vegetation, 27 years after plantation establishment, affected fine root decomposition. We hypothesized that a faster FRD will be associated with higher SR and higher SOC and N in the mineral soil, and also that plant species identity could be a more important driver of community fine root decomposition than plant SR *per se*. We started from the statistically validated observation that the three silvicultural treatments had an effect on both forest total overstory volume (basal area) and understory vegetation diversity (species richness), 27 years after plantation establishment (Figure 1, Table 1). Neither of our two hypotheses that faster fine root decomposition will be associated with a higher plant species diversity, and that a faster FRD will result in higher SOC and N in the mineral soil were validated. However, we did find that species identity is important for FRD.

4.1. Silvicultural Treatment Effects on Overstory and Understory Vegetation

Vegetation control had a negative effect on understory species richness while it increased total overstory volume (Figure 1, Table 1). These opposing effects underline the trade-off between maintaining biodiversity and maximizing target tree productivity (for wood products). A complementary study on the same study site [5] analyzed vegetation community composition and showed that blade scarification led to the development of a hardwood (mainly aspen) herb-rich community, suggesting that both vegetation control and scarification treatments affected overstory and understory vegetation.

The fastest FRD was observed when blade scarification and fertilization were combined without vegetation control. Conversely, the slowest FRD was observed on plots where vegetation control was applied alone (Table 1). Vegetation control by herbicide seems to have other negative effects on fine roots, since Shan et al. [34] reported a significant decrease in fine root production and mortality in response to this treatment, which resulted in lower soil C storage. Given the generally positive relationship between biodiversity and ecosystem functioning [35], we expected to observe a faster FRD associated with a higher understory species richness, however, this was not the case. The lack of plant species richness effect on FRD in our study was observed elsewhere [22]. In this latter study, tree root decomposition in tropical plantations was mediated by root quality (structural, anatomical, and chemical characteristics) and soil environment rather than by tree species richness. Similarly, in a leaf litter mixing study on the latter experimental site, only species-specific effects on decomposition rate were observed [36]. In our study, we did not find correlations between FRD and fine root chemistry (please see Table S3 of the Supplementary material showing only significant correlations among all vegetation, root and soil measured variables). Instead, variance partitioning identified that understory vegetation cover, especially fern and herb cover, was the stronger driver of FRD compared to overstory vegetation, silvicultural treatments and soil properties (Figure 2). In a boreal forest in northern Sweden, De Long et al. [37] also noted a stronger effect of understory plant functional group removal on leaf litter decomposition rate, compared to either successional stage or increased soil temperature.

Handa et al. [38] observed that plant functional type controlled leaf litter decomposition across a range of biomes; reducing litter functional types decreased decomposition rate of litter mixtures. In the present study, principally percent cover of ferns (*Onoclea sensibilis*), herbs (*Trientalis borealis*), and moss (*Polytrichum sp.*) contributed to best explain FRD (Table 2). Given the absence of a root chemistry effect, we suggest that the increased FRD associated with these species could be due to indirect effects. Two factors may contribute to a favorable decomposition environment; one is increased soil moisture, the other by locally increasing soil pH [37,39], since microbes are sensitive to soil pH [40]. In the

present study, we did not measure soil moisture nor the microbial community, and no correlation was found between FRD and soil pH. A species-specific response related to litter quality, such as proximate carbon chemistry: lignin, lignin/N, solubles and fibres (not measured in the present study), could also represent a mechanism influencing root decomposition. In an earlier study on the same site, Poirier et al. [5] observed a preponderant role of herb cover rather than overstory functional composition (whether trees are deciduous or conifers) on mineral and subsurface soil properties, particularly mineral N availability.

4.2. Silvicultural Treatment and Fine Root Decomposition Effects on Soil Properties

We observed differences in soil properties under plots where blade scarification (which represents a complete removal of organic layer) and vegetation control were applied (Table 3). Notably, blade scarification contributed to lower soil pH, and SOC concentration, while no effects of the three silvicultural treatments were observed on N concentration in surface mineral soil, suggesting that the C and N cycles are decoupled in this situation. The lower exchangeable bases and lower soil pH under scarification and vegetation control treatments may be related to greater leaching of bases under these conditions, accompanying greater nitrification with higher soil temperatures (observed earlier on this site by Munson et al. [24] and elsewhere by Vitousek and Matson [41]). Given the frequently observed role of vegetation cover on soil properties [4,42–47], we suggest that the effects of silvicultural treatments could be due, at least partially, to subsequent differences in vegetation cover among treatments, as also observed by Poirier et al. on the same site [5].

We expected the increase of FRD to have a positive effect on SOC and N concentrations [48]. However, contrary to our hypothesis, we observed no correlations between FRD and soil properties, suggesting that in the present study the observed effects of silvicultural treatments on SOC and N did not occur through FRD.

Twenty-seven years after conifer plantation establishment in a temperate forest, C concentrations in the surface mineral soil (0–15 cm) following blade scarification have not recovered to the levels of control plots, which underlines the need to be prudent when choosing silvicultural treatments in a context of C mitigation by plantation establishment (for example for carbon credits) and by soil carbon stabilization. Our study also demonstrates that silvicultural and vegetation succession impacts on soil C and N cycles are important to consider over long periods, in order to understand vegetation feedback, both aboveground and belowground inputs, on these processes with succession.

5. Conclusions

Our experiment continues a series of studies conducted at the Cartier Lake experimental intensive silviculture plantation since its establishment in 1986. Twenty-seven years after plantation establishment, silvicultural treatments represent disturbances that clearly induced changes in both plant species diversity and composition as well as soil properties. These vegetation changes rather than soil properties influenced fine root decomposition to a greater degree. We observed that understory vegetation identity (especially fern and herbs), rather than understory species richness, overstory basal area, root chemistry or soil properties, explained to a greater degree the fine root mass loss during decomposition. This is a rare study to identify to the species level the understory species influencing FRD. However, we are not able to identify the precise mechanism of control. A study measuring variables such as soil temperature and moisture, fine root turnover, soil microbial community structure and activity, would be useful to describe the directed dependencies among these variables, thus moving from a correlative to a causal approach.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/11/10/1091/s1>, Table S1: Description of understory vegetation cover in the subplots of the plantation measured during the 2013 growing season, Table S2: Total basal area of the various overstory functional composition (whether trees are deciduous or conifers) and individual contributions by species, Table S3: Significant correlations among all vegetation, root and soil measured variables.

Author Contributions: R.K. designed the experiment, performed the experiment, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper. D.A.A. discussed underlying concepts, provided editorial advice and reviewed drafts of the paper. A.D.M. conceived and designed the experiment, contributed materials/analysis tools, wrote the paper, reviewed drafts of the paper. All authors have read and agreed to the published version of the manuscript.

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