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White Spruce Plantations on Abandoned Agricultural Land: Are They More Effective as C Sinks than Natural Succession?

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Abstract: The objective of this study was to compare organic carbon (C) accumulation in plantations (PL) and natural succession (NS) established on fallow lands along a 50-year chronosequence in the eastern mixed forest subzone of Quebec (Canada). Above- and below-ground woody biomass were estimated from vegetation measurement surveys, and litter and soil (0–50 cm depth) C from samplings. At the year of abandonment, total C content of both PL and NS sites averaged 100 ± 13 Mg C ha⁻¹. Over 50 years, total C content doubled on NS sites and tripled on PL sites (217.9 ± 28.7 vs. 285.7 ± 31.0 Mg ha⁻¹) with respect to fallow land. On NS sites, the new C stocks accumulated entirely in the vegetation. On PL sites, C accumulated mostly in the vegetation and to a lesser extent in the litter, whereas it decreased by a third in the soil. As a result, the net C accumulation rate was 1.7 ± 0.7 Mg ha⁻¹ yr⁻¹ greater on PL sites than on NS sites over 50 years. By the 23rd year, PL sites became greater net C sinks than NS sites in the fallow lands of the study area, even with the loss of soil C.

Keywords: forest carbon sequestration; afforestation; white spruce; plantations; natural succession; abandoned agricultural land

1. Introduction

A global warming of +1.8 °C to more than 5 °C is projected by 2100 in northern North America, very likely due to increased concentrations of anthropogenic greenhouse gases [1], of which carbon

dioxide (CO₂) is the most important. Fighting global warming involves reducing CO₂ sources, but also increasing CO₂ sinks. Converting treeless, previously non-forested areas into plantations (afforestation) is recognized by the Kyoto Protocol as a method to increase CO₂ sinks [2], because trees can sequester CO₂ from the atmosphere and store it in living and dead organic matter through plant photosynthesis [3]. But do plantations established on abandoned agricultural soils sequester more CO₂ than would natural succession on the same sites? This fundamental question has rarely been answered in earlier studies of forest restoration after agricultural land abandonment, most of which addressed only either plantation or natural succession. Few have compared the two approaches regarding their potential for C sequestration, especially in northern regions like Canada.

In recent years, extensive areas of agricultural land have been abandoned in eastern North America, Europe, East Asia and South America [4], mainly due to “agricultural industrialization” or “agricultural restructuring” [5]. In eastern Canada (Ontario to Newfoundland), 35% of farm grasslands were abandoned between 1951 and 1991 [6]. The abandoned agricultural lands were usually the least productive. In the province of Quebec, 100,000 ha of abandoned agricultural lands were surveyed between 1997 and 2007; 45% of these were located in the Bas-Saint-Laurent region, which has a low agriculture potential [7].

Worldwide, more area of abandoned agricultural land is now being restored by tree plantations than by natural succession [8]. The most appropriate choice for forest restoration depends on the objectives pursued, land conditions and resource availability [9]. Objectives generally include recovery of composition, structure, natural habitat, ecosystem processes and services [10], especially carbon storage, regulation of climate and water flow, supply of clean water and maintenance of soil fertility.

If herbaceous vegetation persists for a long time before woody vegetation is established on abandoned agricultural lands, Cuesta *et al.* [11] recommend restoration by plantation in order to reduce soil erosion, increase biological diversity, and create carbon sinks. In other cases, natural regrowth can have many advantages over typical forest plantations for storing C: (1) it is much less expensive and does not require the intensive effort of planting; (2) it involves tree species which are naturally adapted to the site and should be more resilient to disturbances; and (3) it has the additional benefit of ultimately restoring mature vegetation which approximates the original vegetation, thus restoring ecosystems and biodiversity in fragmented landscapes [12]. Total annual C accumulation in natural succession forests on abandoned farmland can also be significant. For example, in Ontario, it represents approximately 5% of the annual anthropic CO₂-C emissions [13]. That being said, tree plantation can complement natural succession by nursing the establishment of late-succession tree species and stopping site degradation [9].

The effectiveness of C plantations around the world to slow down atmospheric CO₂ accumulation was quantified by van Minnen *et al.* [14], who compared the net ecosystem productivity (NEP) of plantations and natural succession that would otherwise grow in the same areas. The more the NEP of plantations surpassed that of natural succession, the more effectively plantations sequestered C. On the basis of ecological and environmental constraints alone, tropical plantations were the most effective C sinks. Those in high latitudes were the least effective because of low growth rates. In various parts of Canada and Russia, NEP can remain lower in plantations than under natural succession for as long as 50 years [14]. Betts [15] and Schaeffer *et al.* [16] also question C plantations at high latitudes, arguing that the use of conifer seedlings can decrease the land albedo and increase

temperature; the resulting biophysical feedback on climate could cancel out the low net C sequestration. Given this, van Minnen *et al.* [14] only recommend the establishment of C plantations at high latitudes if C sequestration is combined with other objectives, such as water protection and soil erosion control.

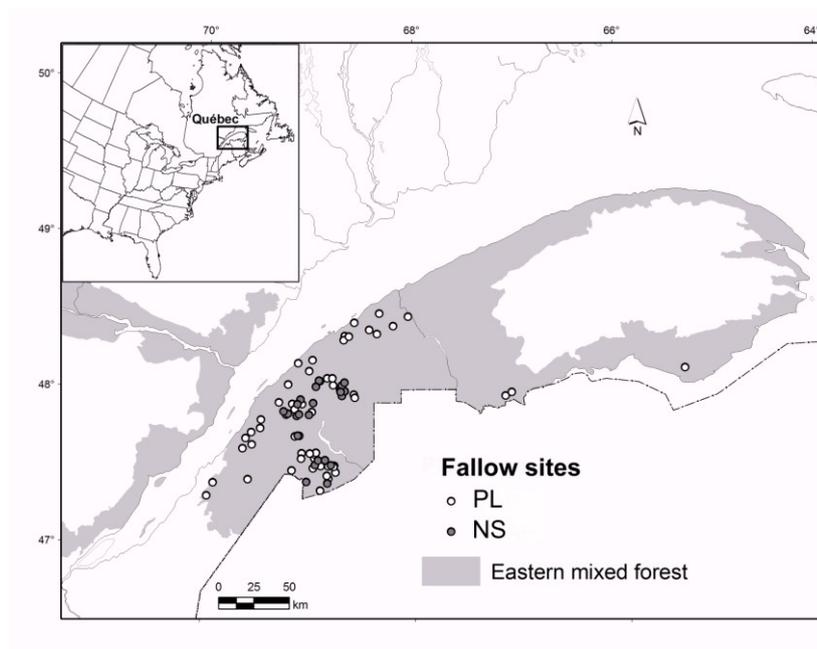
Considering that (1) 67% of the afforestation on private lands in Canada occurred in Quebec between 1990 and 2002 [17], (2) almost half of the abandoned agricultural land in Quebec was located in the Bas-Saint-Laurent region between 1997 and 2007 [7], and (3) we had already estimated CO₂ sequestration in plantations established on abandoned agricultural lands of southern Quebec [18,19], we compared organic C sequestration in plantations (PL) and natural succession (NS) established on fallow lands along a 50-year chronosequence in the Bas-Saint-Laurent region, to verify whether the increase of C sinks justified the effort of planting in this region.

2. Experimental Section

2.1. Study Area

The study area is located in southeastern Quebec, between latitude 47° and 48.5° N, in the Eastern balsam fir (*Abies balsamea* [L.] Mill.)–yellow birch (*Betula alleghaniensis* Britton) bioclimatic subdomain [20] (Figure 1). The mean annual temperature ranges from 1 to 4 °C [21]. The growing season lasts 150–160 days [22]. Growth conditions are: 1250–1450 degree-days above 5 °C, 250–300 mm precipitations during the growing season, and a cumulative vapour pressure deficit of 1050–1350 mbar (1 mbar = 0.1 kPa) during the growing season [21]. The parent soil material originates from the Appalachian Mountains and is composed of sedimentary rocks, shales, sandstone, conglomerates and volcanites. Soils are generally deep, well-drained loam to sandy loam, and classified as orthic humo-ferric Podzols [23].

Figure 1. Location of plantation (PL) and natural succession (NS) established on fallow lands and sampled in the Bas-Saint-Laurent region in eastern Quebec, Canada.



2.2. The Chronosequence Approach

To facilitate comparisons, PL and NS sites established on fallow lands were selected to be as similar as possible, except in age. Selection criteria were: size (>1 ha of fallow land), soil order (Podzol), water regime (mesic), and soil texture (sand to sandy loam). Previous land use (cropland, grassland or pasture) remained unknown in most cases, and year of abandonment could often only be roughly estimated (± 5 years) by consulting the current land owner. The chronosequence was composed of 54 PL sites (0 to 55 years old) and 27 NS sites (0 to 45 years old). The mean area of NS sites was 26 ha, except two sites of 200 ha. Since no significant effect of site preparation on C sequestration had been detected for PL sites in a previous study [18], this factor was not considered in the present study. Plantation sites had been planted with 4-year-old bareroot seedlings. Density of plantations was 2500 tree seedlings ha⁻¹ for those aged 25 years or less, and ranged from 2217 to 2917 tree seedlings ha⁻¹ for older ones. Plantations had never been thinned. The planted species was indigenous white spruce (*Picea glauca* [Moench] Voss), alone or mixed with up to 25% of (exotic) Norway spruce (*Picea abies* [L.] Karst), (indigenous) black spruce (*Picea mariana* [Mill.] BSP), (indigenous) white pine (*Pinus strobus* L.), (indigenous) red pine (*Pinus resinosa* Ait.), or (indigenous) tamarack (*Larix laricina* [Du Roi] K. Koch). Plantation sites were measured during the summer of 2004, and NS sites, during the summer of 2005.

2.3. Tree and Shrub Measurements

A single 400-m² (0.04-ha) plot was established on each site at a location chosen as representative of the site. The plot was circular ($R = 11.28$ m) when tree density was low, and square (20 m \times 20 m) or rectangular (10 m \times 40 m) when tree density was high. A 10-m buffer zone surrounded it. Because of differences in spatial distribution of vegetation, the measurement protocol differed between PL and NS sites and along the chronosequence.

On 0- to 5-year-old PL sites, all planted trees in the plot were measured for diameter at stump height (DSH) and height (H), whereas unplanted trees and shrubs were measured in a 127-m² subplot ($R = 6.36$ m) for diameter at breast height (DBH) or DSH, if DBH was not measurable. On 10- to 55-year-old PL sites, all planted trees in the plot were measured for DBH, and a subsample of 15 randomly chosen trees was measured for H; unplanted vegetation was measured in a 40-m² subplot (2 m \times 20 m) for DBH or DSH.

On NS sites younger than 30 years, all trees and shrubs with DBH ≥ 1 cm in the plot were measured for either DBH and H, or DSH. On NS sites aged 30 years or more, all trees in the plot with a DBH ≥ 9 cm were measured for DBH and H, whereas trees and shrubs with DBH < 9 cm were measured within a 50-m² subplot (7.07 m \times 7.07 m) for DBH or DSH.

Both live and dead trees were measured. DSH (mm) was measured with an electronic vernier scale, and DBH (cm), with a diameter tape. H was measured with a ruler (cm; trees or shrubs less than 3 m in height) or a vertex hypsometer (m; trees or shrubs more than 3 m in height).

2.4. Sampling of Litter and of Vegetation Shorter than 1.3 m

On PL sites, litter was sampled at four random locations in the 400-m² plot, using a 177-cm² punch. On NS sites, litter was sampled in four 1-m² locations established in the center of each quarter of the 400-m² plot. Litter included forest floor (L and F layers and dead herbaceous plants) as well as live herbaceous plants and mosses, because they were all entangled. On NS sites, woody debris (diameter > 0.5 cm) were also sampled with litter. Finally, on NS sites aged 30 years or more, aboveground biomass of saplings and shrubs shorter than 1.3 m was sampled separately from the litter in each 1-m² location. All samples were placed in paper bags and kept in cool conditions until they were transferred to a freezer (−15 °C) at the laboratory.

2.5. Soil Sampling

Two pits, randomly placed along a diagonal of the 400-m² plot, were dug in PL and NS sites. In each pit, soil was sampled at 10-cm depth intervals down to 50 cm in PL sites, and at depths of 0–10 cm, 10–20 cm, 20–40 cm and 40–60 cm in NS sites. For each layer, two volumetric samples (200 cm³ each) and one bulk sample were taken. The H layer of the forest floor was included in the 0–10 cm sample. Also, in NS sites, soil was sampled down to 60 cm (0–10 cm, 10–20 cm, 20–40 cm and 40–60 cm) with a bucket auger at five locations, after removal of the L and F fractions of the organic layer. All samples were stored in cool conditions until they were transferred to a freezer (−15 °C) at the laboratory.

2.6. Laboratory Analyses

Once defrosted, saplings and shrubs, woody debris, herbaceous plants and mosses, and forest floor samples were oven-dried (65 °C, 48–72 h), weighed and ground (250 µm mesh). All soil samples were air-dried (48–72 h) and sieved through 2 mm mesh; subsamples were ground again through 250 µm mesh. Volumetric soil samples were weighed before and after sieving through 2 mm mesh, in order to calculate bulk density as described by Federer *et al.* [24]. Total C content was determined on the basis of oven-dried mass (105 °C) for all ground subsamples, following dry combustion with a LECO CR-412 carbon analyser. Total C content was presumed to equal organic C content, since the sampled soils were acid Podzols containing no calcareous minerals.

2.7. Total C Content Estimation

Organic C content was estimated for woody vegetation, litter and soil at each site. Biomass (anhydrous) of woody vegetation was computed using allometric equations reported in the Appendix A of Tremblay *et al.* [18] for aboveground biomass, and those from Li *et al.* [25] for coarse root biomass. Aboveground biomass of saplings and shrubs shorter than 1.3 m on NS sites aged 30 years or more, estimated from samples, was also included in the aboveground vegetation pool. A conversion factor of 0.50 g C per g of anhydrous biomass was used for deciduous trees; the value was 0.49 for conifers [26]. Litter included the L and F layers, live or dead herbaceous plants and mosses, and woody debris (for NS sites); soil included the 0–50 cm and H layers. For NS sites, samples from the 40–60 cm soil depth were used to estimate soil C content in the 40–50 cm layer. Biomass of fine roots

(diameter < 2 mm) was not assessed as such in this study, since it was not possible to separate them all from the sampled soil; therefore, the soil C stocks may include some fine roots. Calculation of C stocks in soil and litter is described in Tremblay *et al.* [27].

2.8. Statistical Analyses

Stem abundance was analyzed by a quasi-general linear model (GLM) to correct for over dispersion, with vegetation type, species type (commercial, non-commercial) and number of years since abandonment as dependent variables. Vegetation composition was analyzed using the non-parametric multivariate analysis of variance procedure “adonis” of the “vegan” R package [28] with the default settings. Organic C concentrations in soils and C stocks in ecosystem compartments were fitted using a linear mixed-effects model, first by maximizing the log-likelihood (ML) with vegetation type (NS and PL), soil depth (ordered categorical variable), and age (continuous variable) as fixed effects; this model was used to allow for the homogenization of variance error that best fitted the data, based on comparisons of the Akaike (AIC) scores and residual plots. Individual sites were considered as random effects in the model. When the residual plots showed a non-linear pattern with age, the variable (age)² was added to the model. The final models were refitted by maximizing the restricted log-likelihood (REML). Specific contrasts were built to compare vegetation types at 0 and 50 years. The analyses were performed with the “nlme” R package [29] and the R software v. 2.15.2 [30].

3. Results

3.1. Vegetation Composition and Density

For the first 20 years after land abandonment, natural succession began with grass; shrubs and small trees (DBH ≤ 9 cm) then appeared between 20 and 30 years, followed by shrubs and taller trees (DBH > 9 cm) after 30 years. As a result, species composition was very different for NS and PL sites (Figure 2). The non-parametric multivariate analysis showed that 29.1% ($P = 0.001$) of the difference in plant species composition could be explained by the two vegetation types. On the one hand, more commercial and non-commercial species were generally found on NS sites than on PL sites. Commercial species were trees, planted or not, with an economical value, whereas non-commercial species included non-planted trees, shrubs or herbs with no economical value. *Picea glauca*, the main planted indigenous species on PL sites, was also present in NS sites, but other *Picea* (including the non-indigenous *Picea abies*), *Pinus* and *Quercus* species were only found on PL sites. On the other hand, many small and tall brush species recorded on NS sites were absent from PL sites. Note that the N-fixing *Alnus rugosa* [DuRoi] Sprengel was more often observed on NS than on PL sites.

Tree planting strongly influenced the abundance of plant species which colonized the sites over time. Vegetation of PL sites was mainly composed of commercial species maintaining the same stem density over time (2340 stems ha⁻¹ on average; Figure 3); non-commercial species were present during the first years (average: 790 stems ha⁻¹) but then almost completely disappeared. By contrast, on NS sites, density of both commercial (average: 390 stems ha⁻¹) and non-commercial species (average: 3350 stems ha⁻¹) increased over time, the latter reaching a much higher level ($P_{\text{vegetation type} \times \text{years}} = 0.024$).

Figure 2. Relative frequency of commercial and non-commercial plant species for plantation (PL) and natural succession (NS) established on fallow lands.

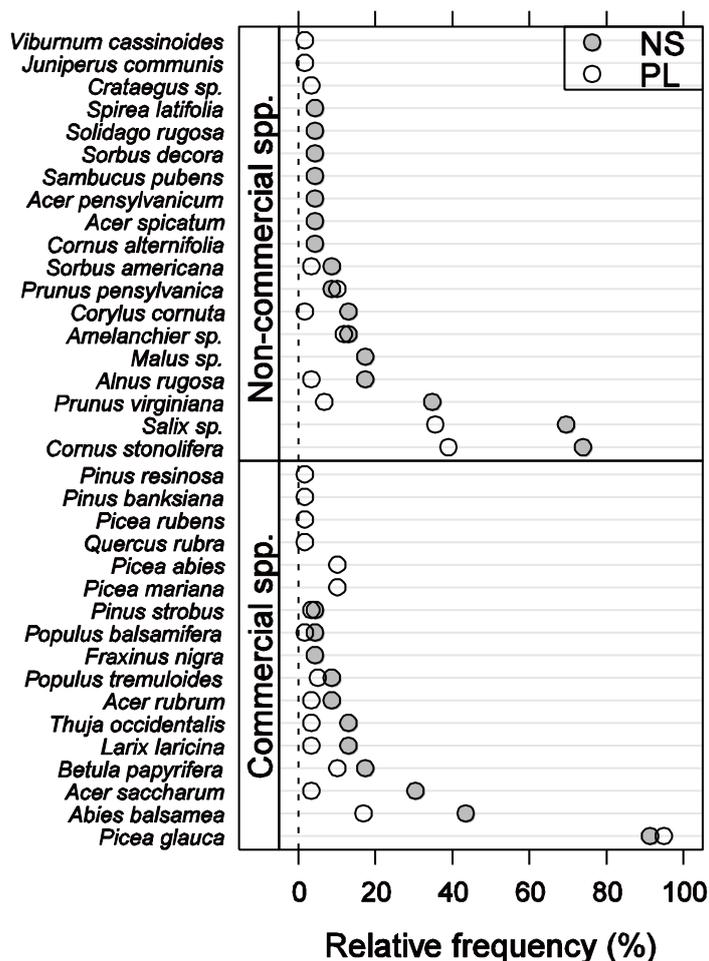
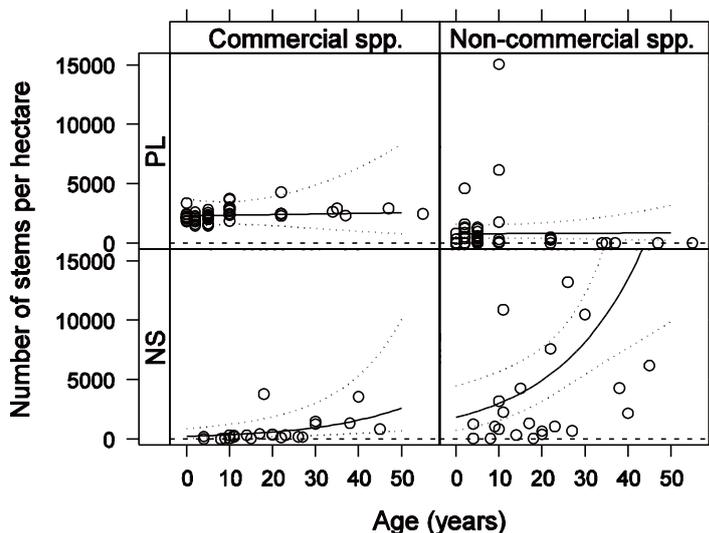


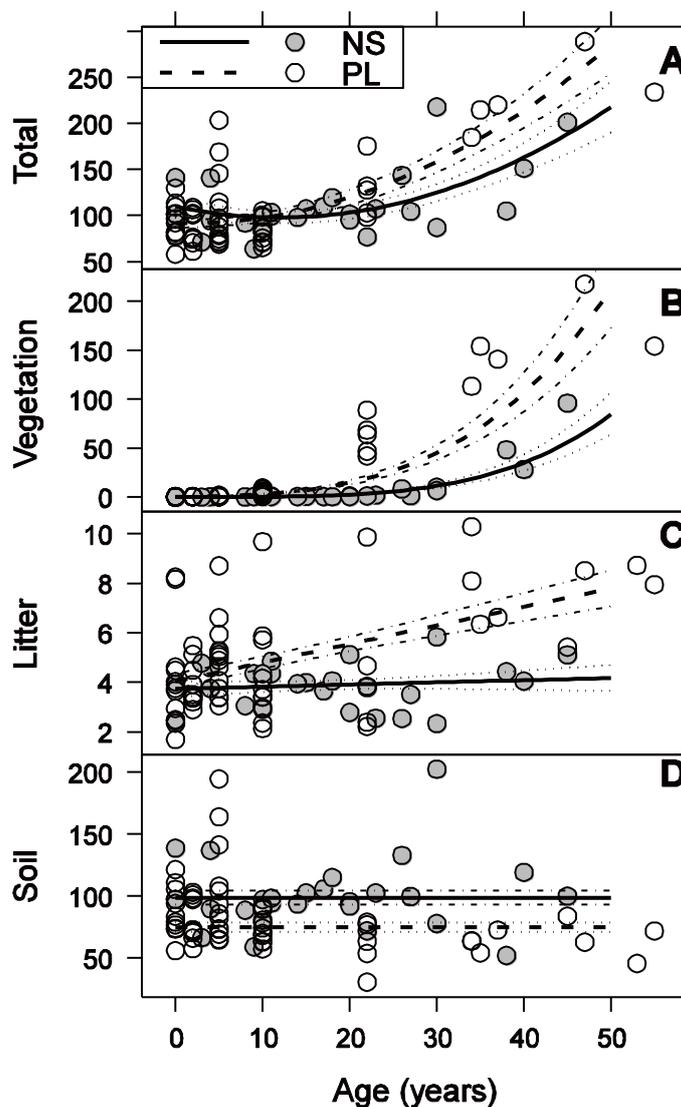
Figure 3. Stem abundance of commercial and non-commercial plant species for plantation (PL) and natural succession (NS) established on fallow lands. Dashed lines represent limits of the 95% confidence interval.



3.2. Vegetation C Stock

Plants (aboveground woody biomass and coarse roots) accumulated organic C following a non linear relationship with age over the 50 years ($P_{age2} < 0.001$), and at a rate that was $2.6 \pm 0.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (mean \pm SE) greater on PL sites than on NS sites ($P_{vegetation\ type \times\ age} < 0.001$; Figure 4B). As a result, after 50 years, the vegetation C stock was 1.5 times greater on PL sites than on NS sites (214 vs. 84 Mg C ha^{-1} , respectively; $P < 0.001$: Table 1).

Figure 4. Carbon (C) stocks (Mg ha^{-1}) accumulated (A) in the whole ecosystem, and in the three compartments: (B) vegetation (aboveground woody biomass + coarse roots), (C) litter (litter + live or dead herbaceous plants and mosses + coarse woody debris), and (D) soil: 0 to 50 cm, for the chronosequence of plantations (PL) and natural succession (NS) established on fallow lands. The lines show the model-predicted means and associated SE. The dots show C stocks at each site.



For both vegetation types, the sequestered C was mainly in vegetation, of which 92% was in the aboveground part on PL sites and 81% on NS sites (Table 1). The sequestered C in coarse roots was in the same range on PL and NS sites, but represented 8% and 19% of sequestered C in vegetation, respectively.

Table 1. Adjusted means of soil bulk density (g cm^{-3} , 0–50 cm depth) and C stocks (Mg ha^{-1} , standard error in brackets) in the ecosystem compartments predicted at age 0 and 50 years according to fallow site type (NS: natural succession; PL: plantation). Soil: 0 to 50 cm; litter: litter + herbaceous plants and mosses, live or dead, + coarse woody debris; vegetation: aboveground woody biomass and coarse roots. The probabilities of statistical difference between site types were assessed with a two-sided *t* test.

Compartment	Age = 0 years				Age = 50 years			
	NS	PL	Difference	<i>P</i>	NS	PL	Difference	<i>P</i>
Bulk density	0.975 (0.031)	0.888 (0.021)	0.086 (0.031)	0.005	0.854 (0.042)	0.767 (0.043)	0.086	0.005
Soil (0–50 cm)	96.6 (9.6)	82.0 (4.7)	−14.5 (10.7)	0.173	97.9 (15.6)	53.9 (10.6)	−44.1 (18.9)	0.020
Litter	3.7 (0.3)	4.0 (0.3)	0.3 (0.4)	0.490	4.2 (0.5)	7.8 (0.7)	3.6 (0.9)	<0.001
C stocks								
Aboveground vegetation	0.5 (0.3)	0.0 (0.1)	0.5 (0.3)	0.067	67.9 (21.1)	196.6 (42.5)	128.7 (21.3)	<0.001
Coarse roots	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.434	16.3 (2.7)	16.9 (2.7)	0.6 (0.2)	0.014
Total	109.6 (11.8)	91.8 (5.5)	−17.8 (11.8)	0.135	217.9 (28.7)	285.7 (31.0)	67.8 (28.1)	0.018

3.3. Litter C Stock

The litter C stock increased more rapidly with time on PL sites than on NS sites ($P_{\text{vegetation type} \times \text{years}} = 0.006$), resulting in an 86% difference after 50 years (Figure 4C; Table 1). However, even after 50 years, the ecosystem's litter compartment remained small compared to the vegetation biomass and soil compartments.

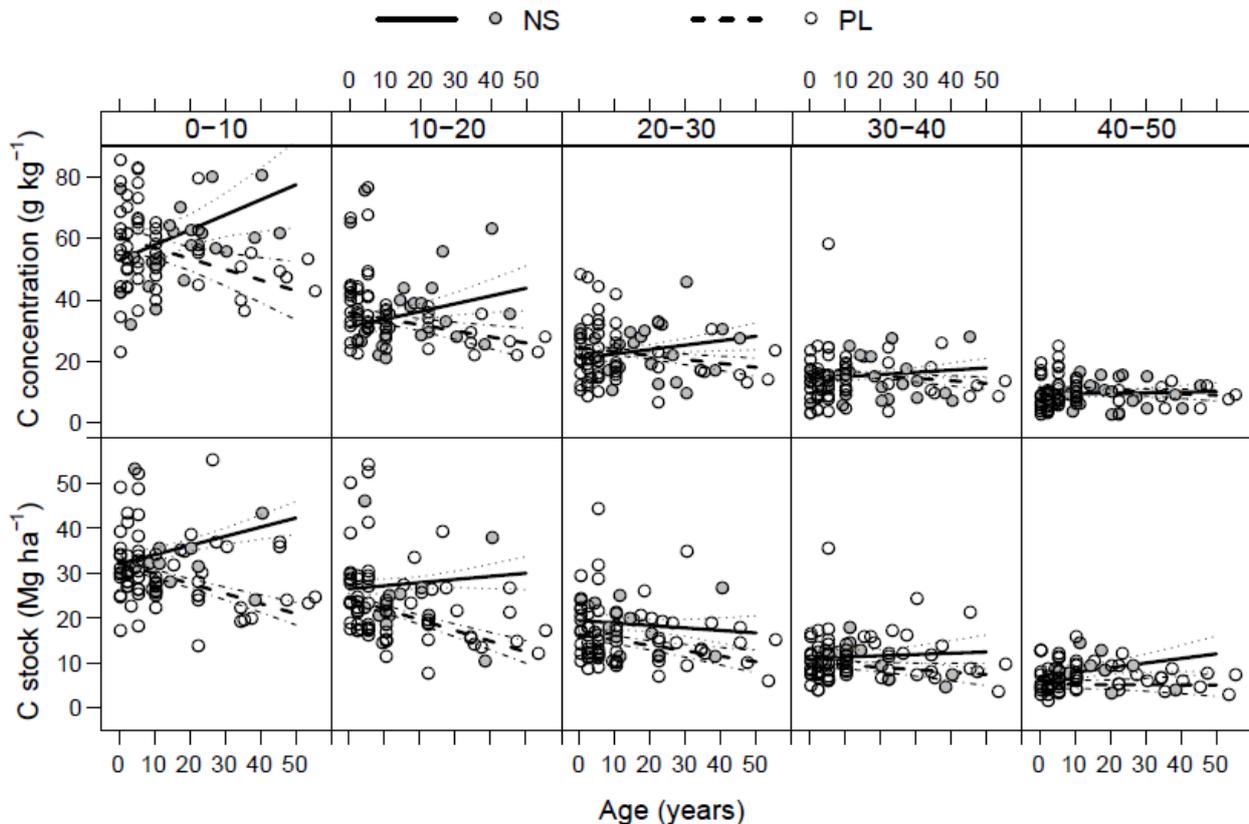
3.4. Soil C Stock

No clear trend over time was present for soil C stock in the first 50 cm of soil tested as a whole ($P_{\text{vegetation type} \times \text{years}} = 0.258$). On average, PL sites contain $24.0 \pm 6.7 \text{ Mg ha}^{-1}$ less C than NS sites ($P < 0.001$; Figure 4D). However, the contrast analysis reveals that after 50 years, soil C stocks on PL sites are $44.1 \pm 18.9 \text{ Mg ha}^{-1}$ lower than on NS sites, and that this difference is statistically significant ($P = 0.020$; Table 1). Compared to sites at age zero, this represents a 34% average loss of soil C.

The examination of soil C concentrations and stocks according to depth revealed more details about these differences. Firstly, both variables tend to increase on NS sites but decrease on PL sites, though only in the first 30 cm of soil ($P \leq 0.097$; Figure 5). Secondly, the differences in soil C between PL and

NS sites tend to decrease with soil depth. Finally, both organic C concentrations and C stocks decrease with soil depth ($P \leq 0.001$, Figure 5).

Figure 5. Soil C concentrations and stocks according to site age, fallow site type (plantation [PL] and natural succession [NS]), and soil depth (10-cm layers from 0–10 to 40–50 cm). Lines show model predictions and their SE; dots show site means.



3.5. Total C Stock

The relationship between total organic C stocks in the whole system and age was quadratic during the 50 years ($P_{age^2} = 0.001$), with slightly different rates for the two vegetation types ($P_{vegetation\ type \times\ years} = 0.019$; Figure 4A). At 50 years, on average, PL sites stored 31% more C in the ecosystem than NS sites ($P = 0.018$; Table 1). The calculated rate of C accumulation was $1.7 \pm 0.7\text{ Mg ha}^{-1}\text{ yr}^{-1}$ greater on PL sites than on NS sites ($P = 0.018$; Table 1). According to the regression analysis, the ecosystem C stock in PL sites became statistically higher than in NS sites after 23 years ($\Delta C_{total} (PL-NS)$ at 23 years = $+21.6 \pm 10.9\text{ Mg C ha}^{-1}$, $P = 0.05$).

The average 0–50 cm depth soil bulk density values differed between the two vegetation types ($P = 0.007$) and among site age ($P = 0.021$; Table 1). The interaction vegetation type \times age was insignificant ($P = 0.685$).

4. Discussion

4.1. Vegetation

After 50 years, vegetation was the dominant C sink on abandoned agricultural land. The sequestered C was mainly in aboveground vegetation. Sequestered C in coarse roots seemed proportionally higher on NS sites than on PL sites, probably because of the higher root:shoot ratio of shrubs compared to trees [31]. Though vegetation C stocks reached the levels in soils (0–50 cm) on NS sites and even exceeded them on PL sites, this C pool remains more vulnerable to disturbances than the soil C pool [32].

The mean sequestration rate in biomass of PL sites was about twice that of NS sites after 50 years. This agrees with the results of Anderson *et al.* [33], who estimated from 91 studies around the world that biomass accumulated, on average, 1.2 times faster in plantations than on naturally regenerating sites, following stand-clearing disturbances like fire or agriculture. The lower sequestration rate of NS sites is probably attributable to the 20-year delay before natural succession establishment. Such delays have also been reported at higher and lower latitudes: 15–20 years in Latvia at $\sim 57^\circ$ N [34], 10–42 years in UK at $\sim 54^\circ$ N [35], and 20–55 years in the Mediterranean region at $\sim 40^\circ$ N [36,37]. The distance from the seed stand is probably not the main explanation, since wind dispersal of seeds can occur over much larger distances. For example, birch seeds can travel over 1 km in open terrain during winter [38]. Ruskule *et al.* [34] rather suggest that, on rich soils, the development of a dense herbaceous vegetation cover can hinder the establishment of tree species. This explanation is consistent with the inhibition model of succession [39], and very likely applies to our study, since the soils were generally deep and well-drained, with a sandy to sandy loam texture, and host to a dense herbaceous plant cover on sites less than 20 years old.

There were generally more tree species on NS sites than on PL sites. Fifty years after agricultural land abandonment in a subtropical humid region of China, Zhang *et al.* [40] also found that the tree layer had greater species richness in secondary deciduous forests than in pine plantations. This was also the case for the herbaceous layer, but not for the shrub layer. This result suggests not only that plant biodiversity was greater on NS sites, but also that seed scattering by surrounding trees was not a problem. Also, the fact that many small and tall brush species recorded on NS sites were absent from PL sites suggest that the vegetation structure was more heterogeneous on NS sites than on PL sites.

4.2. Litter

Fifty years after land abandonment, litter C was 86% higher on PL sites than on NS sites. On the one hand, the higher C stock of PL litter might be due in part to the composition of conifer needles, which leads to a slower litter decomposition [41]. On the other hand, NS litter could have remained stable because of its more degradable leaves and of the 20-year delay before natural succession development.

4.3. Soil

Fifty years after land abandonment, mineral C stock in the first 30 cm of soil decreased on PL sites, but increased on NS sites. In accordance with our results, Zhang *et al.* [40] found a higher soil C concentration in natural succession sites compared to plantation sites, 50 years after land abandonment. In both studies, the effect of planting was confounded with that of tree species, since planted seedlings were conifers whereas natural succession forests were mainly composed of broadleaf species. According to these authors, soil C varied between the two scenarios, partly because of differences in stem growth and litter cycling between the planted conifers and the natural succession deciduous forest. However, the continually decreasing C stock in mineral soil of our PL sites, even 50 years after white spruce plantation, suggests that the planned rotation of our PL sites should be longer than 50 years to allow them to reach a net gain of C in the mineral soil.

Previous land use, which was unknown or highly unsure in our study, is also a determinant factor on subsequent soil organic C dynamics [42]. Soil C stocks generally increase on depleted ex-croplands, and remain unchanged or decrease on ex-grasslands and ex-pastures with the progressive disappearance of their abundant root litter [42–46]. For example, Guo *et al.* [47] observed, in an afforested pasture with pines, that the loss of soil C was positively correlated with the mortality volume of fine roots. However, fine root dynamic (production and mortality) was not measured in our study. Nevertheless, our study sites were probably ex-grasslands or ex-pastures, because the Bas-Saint-Laurent region has a low agricultural potential, and because the Ministry of Natural Resources of Quebec provided free tree seedlings only to owners of lands with low potential for agriculture [7]. Consequently, the hypothesis of decreased fine root litter after pasture or grassland afforestation with conifer could be plausible in our study.

For a same previous land use change, natural succession could sequester more C in soil than plantation, because of the lack of soil disturbance during the change of land use and the creation of an aboveground (and possibly underground) multi-storey structure which maximizes resource exploitation [43]. In our PL sites, no difference in soil C sequestration had been observed previously among the controls or site preparation treatments [18]. However, the abundance and diversity of non-commercial species on NS sites suggests the presence of a multi-storey structure. Among non-commercial species, shrubs can play a key role, since their higher root:shoot ratio compared to trees [31] allows a higher C input to soil by root litter [45]. Finally, the higher frequency of *Alnus rugosa* on NS sites could have facilitated soil C sequestration by providing extra nitrogen input from bio-nitrogen fixation [48]. The increase in soil N under N₂ fixers is often concomitant with an increase in soil C [49].

Finally, for both PL and NS sites, organic C stocks changed only in superficial soil layers. This result is consistent with other studies [14,40]. These layers are also the most subject to changes in bulk density, since litter decomposition and consequent humification can decrease soil bulk density over time [50]. When this happens, the final C stock is underestimated, which falsely indicates a decrease in C over time. To avoid the problem, final C stocks should be multiplied by the initial:final density ratio in order to compare C content of a same soil mass [51]. In our study, the corrected difference in soil C stocks between NS and PL sites in the 0–50 cm layer after 50 years would amount to around 49 Mg ha⁻¹ rather than 44 Mg ha⁻¹ on average. However, this correction would not change our

conclusion, namely that 50 years after agricultural land abandonment, C stocks were higher on NS sites than on PL sites.

4.4. Total

The estimated total sequestration rate was $3.9 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (or $14 \pm 2 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$) for PL sites and $2.2 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (or $8 \pm 2 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$) for NS sites. The net CO₂ sequestration rate of PL sites, compared to NS sites, was thus $1.7 \pm 0.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (or $6 \pm 2 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$). As Quebec's anthropic GES emissions of 2011 was 80 Mt CO₂ eq. [52] and as the total area of abandoned agricultural available for forest conversion in Quebec in 2006 was 120,000 ha [53], planting white spruce on these areas would be equivalent to 0.1% of Quebec's anthropic GES emissions of 2011. These calculations demonstrate that, at latitudes similar to our study, vast areas would be needed to be equivalent to annual Quebec's anthropic GES emissions, because not only of the low growth rates of the vegetation, but also of the low net CO₂ sequestration rate of PL sites, compared to NS sites.

5. Conclusions

Over 50 years, the C accumulation rate on PL sites was $1.71 \pm 0.72 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ greater than on NS sites on abandoned, low-productivity agricultural lands of eastern Quebec. As a result, 31% more total C was stored on PL sites during this period, mainly in vegetation biomass. Aboveground vegetation accounted for 92% of C sequestration in vegetation on PL sites and 81% on NS sites. The lower C sequestration rate on NS sites was probably due to the 20-year delay before the appearance of natural succession. From year 23 onwards, white spruce plantations generated net C sinks more effectively than natural broadleaf succession. However, the additional C pools on PL sites (aboveground vegetation mostly, and litter to a lesser extent) are more vulnerable than soil to disturbances like insects, fire and harvesting, especially under changing climate.

Recommendations:

- (1) To promote long-term climate change mitigation, PL sites should have planned rotations of more than 50 years for them to reach a net gain of C in the mineral soil, since soil C stocks of PL sites were still decreasing after 50 years.
- (2) Longer-term studies on spruce PL sites should be continued to determine the moment when mineral soil starts to sequester C, and down to which depth. Also, measuring fine root production and mortality would allow estimation of the importance of this soil C input.
- (3) Although NS sites sequester less C, they still represent an interesting option because of other advantages, such as a lower cost, a higher plant biodiversity, and a larger soil C sink in the 0–30 cm layer.

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Conflicts of Interest

The authors declare no conflict of interest.

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