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Plant Debris and Its Contribution to Ecosystem Carbon Storage in Successional *Larix gmelinii* Forests in Northeastern China

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Abstract: Plant debris, including woody debris and litter, is an essential but frequently overlooked component of carbon (C) storage in forest ecosystems. Here, we examined the C storage of plant debris and its contribution to total ecosystem C storage in an age sequence of six larch (*Larix gmelinii*) forest stands (15, 36, 45, 54, 65, and 138 years old) in northeastern China. The plant debris C storage increased from 6.0 ± 0.5 Mg·C·ha^{-1} in the 15-year-old stand to a maximum of 9.3 ± 1.8 Mg·C·ha^{-1} in the 138-year-old stand. The C storage of woody debris increased during stand development in a sigmoidal pattern, increasing from 0.7 ± 0.2 Mg·C·ha^{-1} in the 15-year-old stand to 4.7 ± 1.3 Mg·C·ha^{-1} in the 138-year-old stand. However, the C storage of litter (4.6−5.4 Mg·C·ha^{-1}) did not vary with stand age in this larch chronosequence. In addition, the ratio of woody debris to live tree biomass C storage was relatively stable across stands (approximately 3.3%). These results highlight the importance of considering successional development and stand characteristics in assessing changes of plant debris and total ecosystem C storage in the larch forest ecosystem.

Keywords: fine woody debris (FWD); coarse woody debris (CWD); litter; ecosystem carbon storage; *Larix gmelinii*; age sequence

1. Introduction

Plant debris, defined as woody debris and litter, plays an important role in the carbon (C) cycling of forest ecosystems [1–3]. Forest litter is the largest source of organic matter in the organic layer and mineral soils, and woody debris provides energy, nutrient, and habitat for microbes during decomposition [4–7]. These components of forest ecosystems represent important C storage that is as long-lasting in the woody debris C pool as that of live biomass [8,9] and with a large C flux between the ecosystem and the atmosphere [10,11].

Numerous factors influence the dynamics of forest plant debris. Forest productivity, decomposition rate, canopy cover, stand history and forest age can influence accumulation in or losses of plant debris C from an ecosystem. Forest age directly determines storage accumulation of plant debris [2,12,13]. Thus, insight into the dynamics of plant debris will help forest managers understand the impact of current management regimes on material cycles and energy flow of forest ecosystems. At an ecosystem scale, several studies of coarse woody debris (CWD) described a general "U-shaped curve" in the age sequence of different forest stands, where young and old stands have the highest CWD amount [13–15]. The establishment of the curve requires the assumption that the beginning of succession is due to a catastrophic disturbance, e.g., residual fallen logs and standing snags after a catastrophic fire [4,14,16]. However, this curve is clearly not applicable to a planted forest after excessive harvesting [17,18].

Since the late 1970s, the Chinese government has afforested millions of hectares of deforested land, farmland and wasteland. At present, China has the largest plantation area in the world (47.1 Mha in 2013), accounting for nearly 30% of the national forest area (164.6 Mha in 2013) [19]. These planted forests have commonly been considered as C sinks, with large amounts of C sequestrated in live tree biomass over the past few decades [20,21]. In general, live tree biomass C storage of planted stand increases over time in a sigmoidal manner [22–24]. The temporal dynamics of woody debris and litter during forest development is also important for forest management and assessment [25]. However, few studies have examined the C dynamics of plant debris in these forests [26]. The objective of this study was to quantify the C storage of plant debris and its contribution to total ecosystem C storage in an age sequence from planted larch (*Larix gmelinii*) stands to secondary and primary stands in northeastern China.

2. Materials and Methods

2.1. Study Sites

This study was conducted at six larch stands (48°02′−48°06′ N, 129°04′−129°16′ E, 279−370 m above sea level) located in the middle of the southern slope of the Xiaoxing'anling region in northeastern China (Table 1). The study area belongs to temperate forests characterized by a continental monsoon climate. The mean annual temperature is −0.5 °C; the temperature of the coldest month (January) is −24.2 °C, and the temperature of the warmest month (July) is 20.3 °C. The mean annual precipitation is 650 mm, of which 65–80% falls in summer [27]. These forest stands include three plantations (15, 36 and 45 years old), two secondary forests (54 and 65 years old), and one primary forest (138 years old) (Table 1).

The plantation stands were originally occupied by secondary broadleaved and Korean pine (*Pinus koraiensis*) mixed forests [28]. Over the recent decades, large areas of these forests have been turned into *Larix* plantations. The original mixed forests were harvested after clear cut, and two-year-old *Larix gmelinii* seedlings were then replanted with an initial stand density of 3333 trees/ha. Three plantations were pure *L. gmelinii* stands. The two secondary stands were dominated by *L. gmelinii* (>85% tree basal area at breast height (TBA), with a total basal area at breast height of 1.3 m) accompanied by *Abies nephrolepis*. The primary stand was also dominated by *L. gmelinii* (>70% TBA) accompanied by *Tilia amurensis* and *A. nephrolepis*. Three 20 m × 20 m plots were located randomly within each forest stand. The soil in all plots is normal dark brown forest soil (Bori-Udic Cambosols Mottlic according to China Soil Taxonomy) developed from the same parental materials. The basic information for each stand is given in Table 1.

Table 1. Stand characteristics of the six *Larix gmelinii* stands.

Stand (years)	15	36	45	54	65	138
Location	48.03° N 129.26° E	48.08° N 129.26° E	48.10° N 129.24° E	48.05° N 129.17° E	48.06° N 129.09° E	48.08° N 129.07° E
Altitude (m)	370	368	288	329	279	345
Slope (°, aspect)	9.6 N	13.8 SW	1.2 NW	1.1 SE	1.6 S	1.9 NW
Mean DBH (cm)	7.9	19.6	21.9	14.6	15.7	15.7
DBH_{Max} (cm)	10.5	28.3	30.9	47.2	53.7	55.7
Mean Height (m)	8.0	12.7	13.4	10.7	10.3	12.6
$Height_{Max}$ (m)	9.3	15.4	16.1	20.6	25.0	29.6
TBA (m^2/ha)	14.6	31.7	44.5	48.1	48.6	63.1
Stand Density (stems/ha)	2192	1075	1058	900	758	900
Forest Origin	Plantation	Plantation	Plantation	Secondary	Secondary	Primary

Abbreviations: DBH, diameter at breast height of 1.3 m; DBH_{Max} and $Height_{Max}$, the maximum DBH and tree height, respectively; TBA, tree basal area at breast height.

2.2. Field Investigation

We sampled plant debris, trees and soil from a total of 18 plots (20 m × 20 m each) within six forest stands. For this study, we divided plant debris into three categories: fine woody debris (FWD), CWD, and litter. The CWD was further divided into standing snags (including standing dead tree and stump) and fallen logs and was defined as wood ≥10 cm in diameter at the large end. The FWD was defined as wood between 2 cm and 10 cm in diameter. Litter was defined as fresh and semi-decomposed leaf litter, reproductive organs, fallen bark, small dead wood <2 cm in diameter and other dead plant materials in the surface litter layer. These plant debris components were collected and weighed directly in three replicated plots from each forest stand in June and July 2014.

Within each selected plot, we marked all the woody debris (including snags and logs) and then cut down all snags. We harvested and weighed all snags and logs in each plot. For further analysis, we selected three parts of each CWD (middle and both ends) to sample three 10- to 20-cm long discs with a chain saw from each CWD. The three discs were weighed in the field (fresh weight) and in the lab (after oven-drying at 85 °C for 72 h) to determine the ratio between the fresh weight and the oven-dried weight.

In addition, five subplots of 2 m × 2 m size in each plot were set up for a litter survey. Litter, including fresh and semi-decomposed leaf litter, reproductive structures, fallen bark, small dead wood <2 cm diameter (at the large end) and other dead plant material in the surface litter layer, was collected and weighed after oven drying at 65 °C for 48 h. The oven-dried CWD and litter samples (CWD discs and litter from all subplots) were ground (1 mm sieve) for C analysis.

For all live trees with a diameter at breast height (DBH) ≥3 cm in each plot, the tree height (m) and DBH (cm) were measured. The biomass of each tree was calculated using allometric equations in relation to biomass components (leaf, bark, branch, stem, and root) according to the DBH (cm) and height (m) by species [29]. The ages of the three planted stands were calculated from the record of afforestation history. For each secondary and primary stand, the ages of the 10 trees with the largest DBH were determined by performing a tree-ring analysis [30]. The age of the fifth largest tree (DBH) in each natural larch stand was used as the representative of the stand age [31].

We also sampled 54 replicated soil profiles from the six stands (three soil profiles from each plot) to estimate the soil C storage. Soils were separately sampled at depths of 0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm. The soil bulk density at each depth was estimated using a standard container (100 cm^3, 50.5 mm in diameter and 50 mm in height). The soil gravimetric moisture was measured after oven drying for 48 h at 105 °C. The soil subsamples were air dried for two weeks at room temperature (approximately 25 °C) after the removal of debris and plant material and were then ground and sieved (0.15 mm) for C analysis. The C concentrations of the plant debris and soil were determined using an elemental analyzer (2400 II CHN Elemental Analyzer; Perkin-Elmer, Boston, Massachusetts, USA), and a factor of 0.5 was used to convert the live biomass to C content.

2.3. Statistical Analyses

The differences in C storage of different forest stands were analyzed with a one-way analysis of variance (ANOVA). We plotted the C storage ($Mg \cdot C \cdot ha^{-1}$) of the plant debris (D) and live tree biomass (T) against the stand age (years) using a nonlinear logistic function (Equation (1)):

$$C_{DT} = \frac{W}{1 + \alpha e^{-\lambda \mathrm{age}}} \tag{1}$$

where C_{DT} is the C storage of each component of plant debris and tree biomass and age is the forest stand age. W, α and λ are the coefficients of the function. Due to different trends, we plotted the C storage of the soil and total ecosystem against the stand age using a simple linear model (Equation (2)) and a revised sigmoidal model (Equation (3)), respectively:

$$C_{Soil} = a + b\mathrm{age} \tag{2}$$

$$C_{Eco} = \frac{W}{1 + \alpha e^{-\lambda \mathrm{age}}} + \varepsilon \tag{3}$$

where C_{Soil} and C_{Eco} are the C storage in soil and total ecosystem, respectively; *a* and *b* are regression coefficients; ε represents the initial soil organic C storage of the stand development.

3. Results

3.1. Carbon Storage in Plant Debris

The investigated C storage of plant debris increased steadily and significantly with increasing stand age, from 6.0 ± 0.5 Mg·C·ha^{-1} in the 15-year-old stand to 9.3 ± 1.8 Mg·C·ha^{-1} in the 138-year-old stand (F = 7.3, p = 0.001; Figure 1a). The increase was mainly attributed to the increase in woody debris, especially in CWD, because the C storage of the litter represented an age-independent pattern with 4.6−5.4 Mg·C·ha^{-1} in the six larch stands (F = 0.4, p = 0.821; Figure 1a). The CWD C accounted for 91−97% of the C storage of woody debris. Specifically, the C storage of woody debris significantly increased from 0.7 ± 0.2 Mg·C·ha^{-1} in the 15-year-old stand to 2.3 ± 1.0, 2.7 ± 0.4, 2.4 ± 1.3, 3.8 ± 2.6 and 4.7 ± 1.3 Mg·C·ha^{-1} in the 36-, 45-, 54-, 65-, and 138-year-old stands, respectively (F = 8.7, p < 0.001).

Because the C storage of woody debris increased but the litter remained stable with increasing stand age, the relative contribution of the two major components of plant debris changed with stand development (Figure 1b). The proportion of litter reached 89% of the total plant debris C storage in the 15-year-old stand and then fell to 49% in the primary larch stand (138-year-old stand), which was almost equal to the proportion of woody debris (51%). The relative contribution of fallen logs and standing snags to CWD C storage indicated a certain variation with stand age (Figure 1b). The relative proportion of logs to CWD increased with increasing stand age, from 42% in the 15-year-old stand to 68% in the 138-year-old stand.

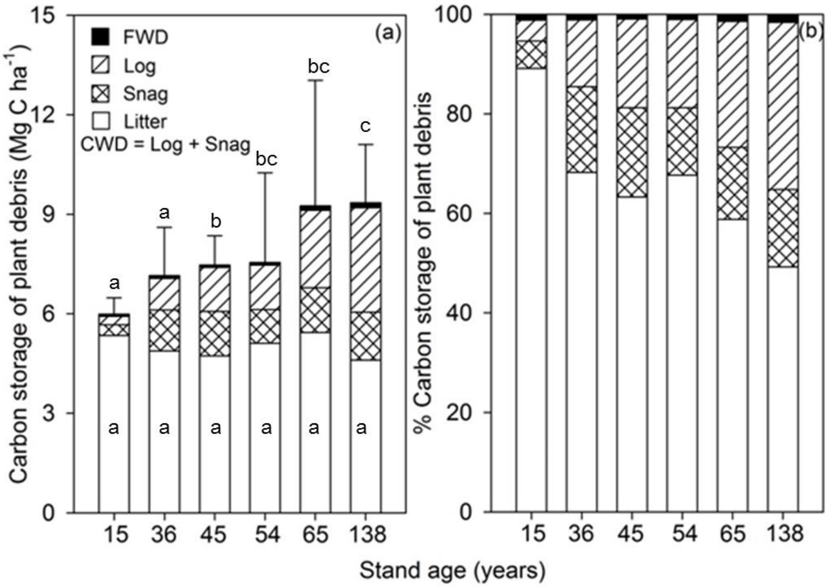

Figure 1. Absolute (**a**) and relative (**b**) distribution within plant debris carbon components for the six *Larix gmelinii* stands. FWD, fine woody debris; CWD, coarse woody debris.

3.2. Carbon Storage in Ecosystem

The total ecosystem C storage increased significantly from 92.3 ± 22.3 Mg·C·ha^{-1} in the 15-year-old stand to 121.5 ± 25.5, 159.2 ± 26.2, 217.0 ± 59.9, 211.7 ± 47.5, and 295.1 ± 55.3 Mg·C·ha^{-1} in the 36-, 45-, 54-, 65-, and 138-year-old stands, respectively (F = 18.0, p < 0.001; Figure 2a). The C storage in the tree biomass was 15.7 ± 3.3, 57.3 ± 2.6, 78.4 ± 16.7, 98.6 ± 16.0, 104.3 ± 20.9, and 145.3 ± 32.8 Mg·C·ha^{-1} in these stands, respectively. The tree C storage represented only 17% of the total ecosystem C storage in the 15-year-old stand, whereas it was nearly half of that in the other stands (ranging from 45 to 49%; Figure 2b). Compared with the tree biomass, soil organic C storage exhibited a non-steady but positive trend with increasing stand age, from 70.9 ± 18.5 Mg·C·ha^{-1} (77% of the total) in the 15-year-old stand to 140.5 ± 20.7 Mg·C·ha^{-1} (47% of the total) in the 138-year-old stand (Figure 2). Compared to the amount of C stored in trees (17−49%) and soil (46−77%), plant debris only accounted for 3−7% of the total ecosystem C storage across the stands. The highest proportion of plant debris to the total ecosystem C storage was found in the 15-year-old stand (6.5%), and the lowest proportion was in the 138-year-old stand (3.2%). The contribution of woody debris C storage to the total ecosystem C storage increased from 0.7% in the 15-year-old stand to 1.1−1.9% in the older stands. On the contrary, the relative contribution of litter C storage to the total ecosystem C storage decreased from 5.8% in the 15-year-old stand to 4.0%, 3.0%, 2.4%, 2.6%, and 1.6% in the 36-, 45-, 54-, 65-, and 138-year-old stands, respectively.

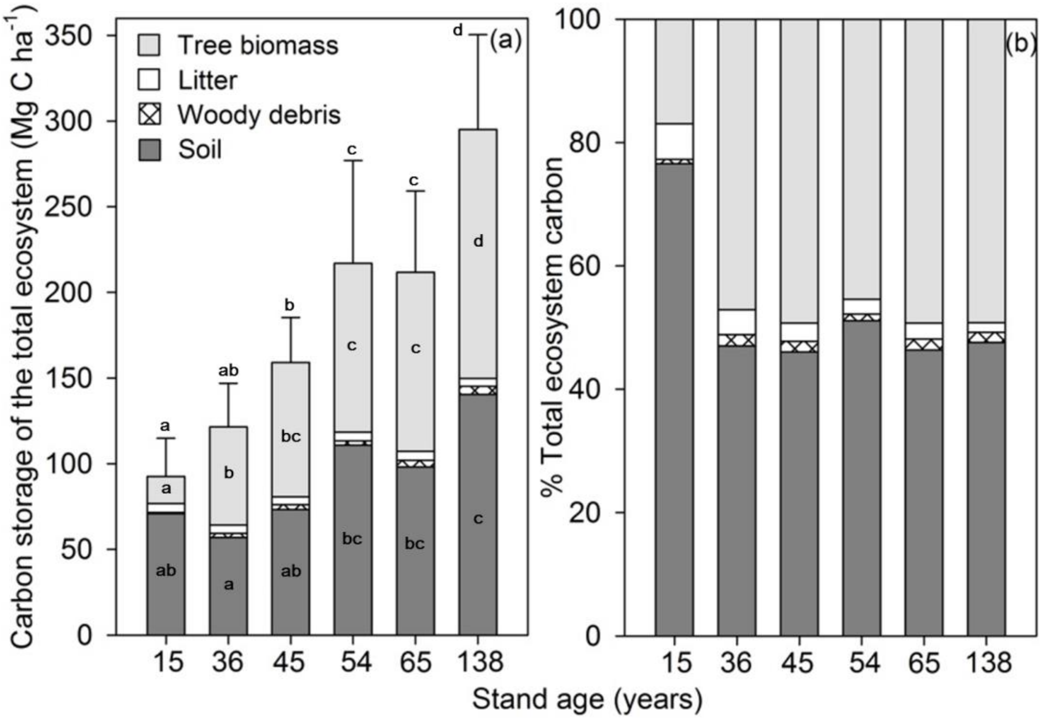

Figure 2. Absolute (**a**) and relative (**b**) distribution within ecosystem carbon components for the six *Larix gmelinii* stands.

3.3. Carbon Storage as a Function of Stand Age

The C storage of FWD and CWD exhibited a similar trend to tree biomass C storage in the age sequence (Figure 3). The observed relationship between the C storage of FWD and CWD and the stand age could be well described as a sigmoidal model ($R^2 > 0.78$, $p < 0.001$; Equation (1), Figure 3a). Similarly, the live biomass displayed a rapid increase rate until approximately 40 years old, then gradually decreased in productivity (based on the slope of the curve of tree biomass in Figure 3b). As a result, C storage of woody debris was significantly and positively correlated with that of live biomass (Figure 4a–e). However, the litter C storage did not vary with stand age (Figure 3a) or live biomass C storage (Figure 4f) in this larch chronosequence. Moreover, the C storage of mineral soil from 0 to 100 cm depth indicated an increasing but fluctuating trend over the stand age ($R^2 = 0.72$, $p = 0.02$; Figure 3b).

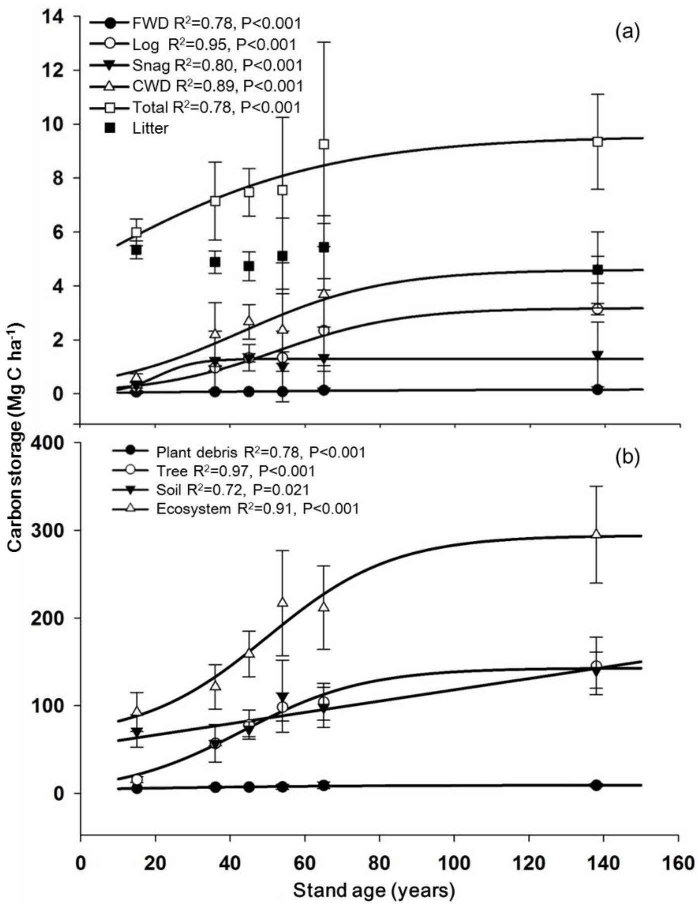

Figure 3. Carbon storage as a function of stand age for (**a**) plant debris and (**b**) ecosystem components.

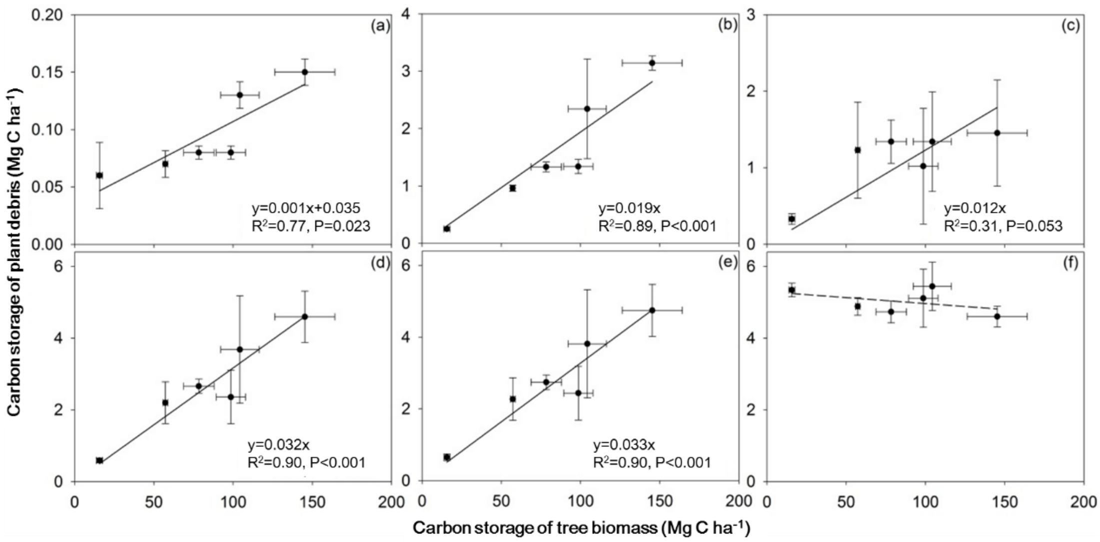

Figure 4. Relationships between carbon storage in plant debris and in live tree biomass. (**a**) Fine woody debris; (**b**) fallen logs; (**c**) standing snags; (**d**) coarse woody debris; (**e**) woody debris; and (**f**) litter.

4. Discussion

The observed C storage in woody debris, including FWD, fallen logs and standing snags, increased with stand age. This increasing trend could be well described as a sigmoidal model, which is commonly used in live vegetation growth studies [23,32,33]. However, litter C storage did not increase with stand age, but remained relatively stable (4.6−5.4 Mg·C·ha^{-1}) in this larch chronosequence (Figure 1a). Generally, stand productivity and debris decomposition together determine the storage of woody debris and litter during stand development. We demonstrated that tree biomass C storage exhibited an S-shape growth trend (Figure 3b), which is consistent with other studies on the relationship between live biomass and stand age [24,34,35]. Mature forest stand had relatively higher production of plant debris than younger plantations [15,36]. In addition, because the C storage of woody debris was persistent and slow to break down [8,9,37], its decomposition rate should be lower than that of litter. Thus, we could assume that the C storage of woody debris was more affected by the stand productivity and that the C storage in litter could quickly reach a balance between inputs (production) and outputs (decomposition) in these larch stands.

The result of no age- or biomass-related patterns for litter C storage in this study contrasts with that reported by Pregitzer and Euskirchen [38], who observed that the amount of C storage in the litter layer increased with stand age in temperate coniferous forests. Peichl and Arain [39] measured ecosystem C pools in an early successional sequence (2- to 65-year-old stands) of temperate *Pinus strobus* plantations in southeastern Canada. They found that C storage in the litter layer increased considerably from a 2-year-old stand to a 15-year-old stand, but there was no further age-related increase beyond a stand age of 15 years. Our study did not include stands less than 15 years of age, so we did not determine when the litter C storage achieved a balance between inputs and outputs. Nevertheless, it could be argued that the C accumulation in litter peaked at a stand age younger than 15 years. However, C storage of woody debris was similar to that of live trees in the larch stands of the current study (older than 80 years, Figure 3).

The relative contribution of plant debris C storage to the total ecosystem C storage averaged 4.7% (3.2–6.5%) across stand ages, which is comparable to that of temperate forests in Maoer Mountain (3.3%) [40], Dongling Mountain (2–6%) [41], temperate forests in Changbai Mountain (2–9%) [42], and temperate *Larix* forests in the Daxing'anling region (4.4%) [43] of northeastern China. However, this proportion is substantially lower than that of temperate forests in other regions of the world (8–47%) [44–47]. Numerous factors, e.g., forest structure, stand age, site productivity, decomposition rate and disturbance regime, may influence the accumulation of plant debris [5,15,48]. The large discrepancy of plant debris C storage and the relative contribution to ecosystems from these forests in northeastern China and those of similar forest types in other regions of the world may be derived not only from the variability in ecosystem development but also from the difference in stand history and disturbance regime. Excessive harvesting that occurred before reforestation programs in China has lowered stand productivity and created a shorter time for accumulation of woody debris in the stands of the current study. Furthermore, many plant debris studies in other regions have tended to intentionally sample older, undisturbed forests with large amounts of fallen logs and standing snags [5] or forests that were recently affected by catastrophic disturbances [49,50], which resulted in higher estimates of the C storage of plant debris compared to this study.

Although we estimated the C stocks of the whole forest sector in an age sequence of six larch forest stands in northeastern China, some uncertainties should be noted. First, a coefficient of 0.5 was used to convert live biomass to C, which could induce an uncertainty in our results. The C concentration of larch among different tissues (including foliage, twig, stem, bark and root) varies from 0.45 to 0.54 in this region [51–53]. Second, although we calculated C storage in tree biomass, other components of live biomass were omitted, including the understory and herb layer. These items of omission may lead to an underestimate (approximately 2%) [40,41] of C storage in live biomass.

5. Conclusions

We investigated the successional development of C storage in woody debris and litter across an age sequence (15-, 36-, 45-, 54-, 65-, and 138-year-old stands) of six larch forest stands in northeastern China. We found that the C storage in woody debris represented an "S-shape" that increased with increasing stand age, but C storage in litter did not exhibit any age dependence in these forest stands.

With the development of the larch forest, the C storage of litter and woody debris exhibited two different outcomes. The litter C storage (ranging 4.6–5.4 Mg·C·ha^{-1}) and the ratios of woody debris to tree biomass C storage (dead:live ratio, ranging from 2.5 to 4.1%) exhibited a relatively stable trend with increasing stand age. The relative contribution of woody debris to the total ecosystem C storage increased (from 0.7 to 1.6%) but that of litter decreased (from 5.8 to 1.6%) with increasing stand age. Taken together, our findings demonstrated that plant debris dynamics were closely correlated with the stand characteristics of larch forests in northeastern China. Forest managers could more effectively develop a management policy for plant debris by referring to the dynamics of live vegetation biomass.

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Conflicts of Interest: The authors declare no conflict of interest.

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