

Article

Availability and Structure of Coarse Woody Debris in Hemiboreal Mature to Old-Growth Aspen Stands and Its Implications for Forest Carbon Pool

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Abstract: European aspen deadwood is extensively studied as a habitat for saproxylic species, while less is known of its dynamics and role in carbon sequestration. We studied unmanaged mature (41–60 years), moderately overmature (61–80 years), overmature (81–100 years), and old-growth (101–140 years) and managed mature and moderately overmature aspen stands on fertile mineral soils. In unmanaged stands, marginal mean CWD volume was from $67.3 \pm 12.1 \text{ m}^3 \text{ ha}^{-1}$ in moderately overmature to $92.4 \pm 5.1 \text{ m}^3 \text{ ha}^{-1}$ in old-growth stands, with corresponding marginal mean CWD carbon pool $8.2 \pm 1.6 \text{ t ha}^{-1}$ and $12.5 \pm 0.7 \text{ t ha}^{-1}$ (all $p > 0.05$), respectively. High CWD volume was present in most stands, by at least two-thirds of plots comprising more than $20 \text{ m}^3 \text{ ha}^{-1}$, and about half of CWD was larger than 30 cm in diameter. Changes in CWD species composition toward a higher proportion of deciduous deadwood in old-growth stands, together with a high volume of recently dead trees, suggest early senescence of the dominant aspen cohort.

Keywords: aspen senescence; carbon pool; deadwood; decline; overmature; *Populus tremula*



Citation: Šēnhofa, S.; Šņepsts, G.; Bičkovskis, K.; Jaunslaviete, I.; Liepa, L.; Straupe, I.; Jansons, Ā. Availability and Structure of Coarse Woody Debris in Hemiboreal Mature to Old-Growth Aspen Stands and Its Implications for Forest Carbon Pool. *Forests* **2021**, *12*, 901. <https://doi.org/10.3390/f12070901>

Received: 8 June 2021

Accepted: 9 July 2021

Published: 11 July 2021

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1. Introduction

European aspen (*Populus tremula* L.) is an early-succession species in boreal and hemiboreal forests [1], with scattered occurrence [2–4] but high ecological importance. Aspen is commonly regarded as ‘keystone species’ in the boreal and hemiboreal forests because both living and dead aspen trees host more specialist and endangered species than other tree species in the region [4–7]. Information of aspen deadwood volume and characteristics, however, is limited, with only some insights from studies in boreal [6,8–11] and hemiboreal [12] forests.

Besides the maintenance of biodiversity [13,14], deadwood has an important role in carbon dynamics [15], estimated to comprise 8% of the total carbon pool in forests globally [16]. The deadwood persistence and turnover are affected by a number of factors, including disturbance dynamics, forest zone, site type and soil moisture regime, dominant species, stand age, and productivity [17–19]. Large knowledge gaps on the effect of the abovementioned factors on carbon pools remain and are substituted by internationally accepted standards. Latest studies show that even seemingly small improvement by empirical-based variables has a substantial effect on estimated global carbon stock [20]. Currently, the majority of knowledge on forest carbon pools is derived from studies performed in managed forests. The vast deadwood diversity in unmanaged, old-growth forests, however, hampers accurate estimations of carbon storage within it and has derived contrasting results on whether old-growth forests are a carbon sink or source [21–28]. While few studies have addressed the carbon budget in hemiboreal deciduous forests [29–32],

including one in the old-growth forests [33], none have been performed in aspen-dominated stands. However, studies of stands older than the longevity of the pioneer cohort are emphasized as critical to improve the understanding of old forests in the global carbon cycle [34]. Knowledge of carbon balance in stands dominated by relatively short-lived species and how this balance changes with stand age is necessary in order to improve the accuracy of greenhouse gas emission and carbon sequestration models.

We aimed to quantify the availability of coarse woody debris (CWD) and its carbon pool and to characterize CWD structure in hemiboreal aspen stands. We intended to represent CWD and its carbon pool regarding species composition, pose, diameter, and decay classes with regard to its variation along with stand age from maturity to old-growth state.

2. Materials and Methods

This study was conducted in European aspen (*Populus tremula* L.) stands in hemiboreal forests (based on European Forest Types [35]) in Latvia. According to Latvian National Forest Inventory (NFI, 2014–2018), forests cover 52% of the land. Aspen is the fourth most common tree species, following Scots pine (*Pinus sylvestris* L.), silver and downy birch (pooled *Betula pendula* Roth and *Betula pubescens* Ehrh.), and Norway spruce (*Picea abies* (L.) Karst.), and constitutes 8% and 9% of the total forest land and volume, respectively. Data consist of two sets: our measured stands at the age of 101 to 140 years, and NFI (2014–2018) measured stands at the age of 41 to 100 years (Figure 1).

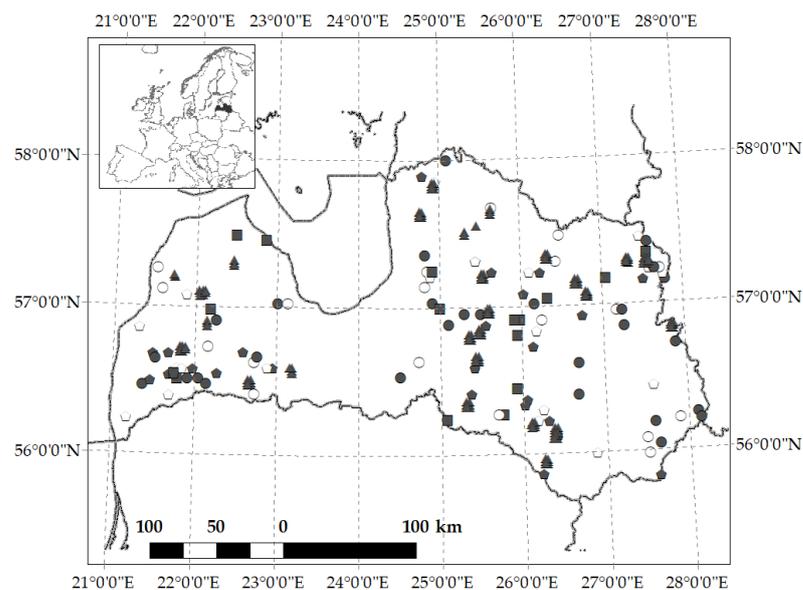


Figure 1. Distribution of sample plots in mature (●, 41–60 years) moderately overmature (◆, 61–80 years), overmature (■, 81–100 years), and old-growth (▲, 101–140 years) European aspen (*Populus tremula* L.) stands, with dark symbols indicating unmanaged stands in all age groups, and clear circles (○) and pentagons (◓) indicating managed mature and moderately overmature stands.

Our measured stands were randomly pre-selected from protected forests across Latvia, based on species composition (at least 50% of the overstory growing stock comprised by aspen), age limit (≥ 101 years), and site type. We included stands located on *Hylocomiosa* and *Oxalidosa* (local classification by Bušs [36] site types on fertile mesic mineral soils, as these are two the most common site types (17% and 44% of the area, respectively) for the aspen-dominated stands in Latvia. The selected forests have various types of protection determined by legislation and voluntary by state forests, mostly microreserves for protected species and habitats. These forests have received no silvicultural measures for at least four decades, although no documentation of prior management was available. Sites that showed signs of former logging were excluded. Only sites that met all aforementioned

criteria were measured. Overall, our study included 150 sample plots (mean 5.8 plots per stand) from 26 aspen-dominated stands at the age of 104 to 134 years (Table 1). Throughout this paper, this group is referred to as ‘old-growth stands’ (101–140 years), with the degree of naturalness based on the Buchwald [37] classification ‘n6—Old-growth forest’.

Table 1. Characteristics (marginal mean \pm standard error) of old-growth European aspen (*Populus tremula* L.) stands.

No.	N	Overstory					Understory			CWD Volume, m ³ ha ⁻¹
		Species		A	DBH, cm	Height, m	Growing Stock, m ³ ha ⁻¹	Species	Growing Stock, m ³ ha ⁻¹	
		Aspen	Other							
1	6	10	–	109	49.0 \pm 1.6	39.4 \pm 0.1	687 \pm 99	5S5L	118.3 \pm 28.6	123.5 \pm 9.7
2	6	9	1S	114	57.1 \pm 3.2	38.2 \pm 0.3	555 \pm 40	5S5L	116.3 \pm 20.7	142.2 \pm 20.5
3	6	9	1S	118	48.0 \pm 1.7	38.1 \pm 0.2	602 \pm 42	10S	168.8 \pm 14.9	28.1 \pm 10.1
4	6	9	1B	118	44.0 \pm 2.2	38.9 \pm 0.5	620 \pm 83	10S	78.0 \pm 14.4	111.2 \pm 10.5
5	6	10	–	108	46.0 \pm 1.9	39.5 \pm 0.2	812 \pm 55	10S	111.8 \pm 16.6	79.6 \pm 15.4
6	8	7	1B1P1S	109	41.0 \pm 2.7	32.1 \pm 0.6	623 \pm 73	9S1Ba	126.8 \pm 12.8	75.2 \pm 15.2
7	8	8	2B	106	47.0 \pm 2.7	32.3 \pm 0.5	471 \pm 31	8S1O1B	81.3 \pm 13.2	50.3 \pm 13.0
8	3	9	1B	134	53.5 \pm 0.8	35.2 \pm 0.1	579 \pm 90	9S1A	224.4 \pm 21.0	61.0 \pm 27.8
9	6	8	1S1B	114	44.9 \pm 2.0	36.7 \pm 0.2	628 \pm 50	10S	109.4 \pm 11.4	113.4 \pm 10.4
10	6	9	1S	104	55.6 \pm 2.8	39.2 \pm 0.7	783 \pm 66	10S	193.7 \pm 17.8	137.8 \pm 29.0
11	6	8	1B1S	113	56.1 \pm 2.9	38.7 \pm 0.2	753 \pm 35	10S	138.9 \pm 13.9	74.9 \pm 13.7
12	6	9	1S	109	47.3 \pm 1.7	38.4 \pm 0.1	770 \pm 51	6S3L1A	67.8 \pm 11.5	59.7 \pm 11.0
13	6	8	2S	104	46.3 \pm 2.2	37.2 \pm 0.7	601 \pm 52	7S3L	105.8 \pm 19.0	60.2 \pm 9.1
14	6	9	1S	104	49.3 \pm 2.0	39.3 \pm 0.2	712 \pm 71	9S1L	95.4 \pm 12.1	174.1 \pm 22.9
15	6	8	2S	117	47.7 \pm 2.1	33.0 \pm 0.5	598 \pm 52	10S	122.5 \pm 20.3	104.5 \pm 21.8
16	6	8	1S	117	54.2 \pm 1.2	36.2 \pm 0.1	761 \pm 69	5S4L1B	46.2 \pm 3.1	70.0 \pm 15.4
17	6	9	1B	116	52.0 \pm 2.4	39.1 \pm 0.2	721 \pm 64	7S2L1M	85.4 \pm 9.5	26.6 \pm 10.7
18	6	9	1S	111	50.1 \pm 3.6	39.9 \pm 0.3	950 \pm 77	10S	90.3 \pm 8.6	94.6 \pm 14.9
19	6	10	–	118	45.2 \pm 1.1	37.1 \pm 0.2	764 \pm 48	9S1L	185.3 \pm 27.5	147.4 \pm 27.6
20	6	7	2S1B	107	52.0 \pm 2.9	37.4 \pm 0.4	622 \pm 60	10S	99.9 \pm 9.6	132.5 \pm 35.4
21	6	7	2S1B	113	51.6 \pm 2.2	36.4 \pm 0.3	709 \pm 71	10S	106.6 \pm 14.9	112.3 \pm 18.7
22	4	9	1S	107	50.4 \pm 2.9	33.8 \pm 0.2	381 \pm 37	5Ga3As1Bc1S	14.1 \pm 3.3	71.0 \pm 34.9
23	2	5	4P1O	117	37.8 \pm 10.1	27.6 \pm 3.2	446 \pm 31	9L1S	5.3 \pm 0.0	10.7 \pm 3.8
24	3	9	1B	104	41.4 \pm 1.5	29.4 \pm 0.3	617 \pm 61	9S1B	77.0 \pm 14.0	56.8 \pm 42.2
25	8	8	1S1B	118	46.7 \pm 2.0	37.7 \pm 0.2	599 \pm 47	9S1M	131.9 \pm 14.5	106.5 \pm 24.6
26	6	9	1S	108	55.6 \pm 2.1	38.1 \pm 0.1	689 \pm 50	8S2M	102.5 \pm 7.2	99.3 \pm 20.6

N—number of sample plots; species composition is based on the proportion of the species growing stock in the respective stand layer: 10 = 90% . . . 100%, 9 = 80%...89%, 8 = 70%...79%, etc. A—aspen; S—spruce (*Picea abies* (L.) Karst.); B—birch (pooled *Betula pendula* Roth and *Betula pubescens* Ehrh.); P—pine (*Pinus sylvestris* L.); L—lime (*Tilia cordata* Mill.); Ba—black alder (*Alnus glutinosa* (L.) Gaertn.); O—oak (*Quercus robur* L.); As—ash (*Fraxinus excelsior* L.); M—maple (*Acer platanoides* L.); Ga—gray alder (*Alnus incana* (L.) Moench); Bc—bird cherry (*Padus avium* Mill.).

All measurements were performed in 2019. In each sample plot, for living trees, a diameter at breast height (DBH) of ≥ 6.1 cm was measured using a caliper (accuracy ± 0.1 cm), and data on species and stand layer were noted. Height was measured using Vertex clinometer (accuracy 0.1 m) for five overstory and three understory trees of the dominant species; stand height was estimated by corresponding height to the quadratic mean diameter of overstory aspen. The same overstory trees were sampled by increment cores to measure age. For each standing dead tree (stems and snags), we measured DBH ≥ 6.1 cm and height and noted species (aspen, other deciduous, or coniferous) and decay class. For lying CWD, we measured length (≥ 1.0 m) using a ruler (accuracy 0.1 m) and the diameter at both ends (diameter at thicker end ≥ 6.1 cm), and noted species (aspen, other deciduous, or coniferous) and decay class at the thickest end. The decay class was observed visually and using the ‘knife method’. All CWD was divided into five decay classes (applied from Mäkinen et al. [38], Table 2).

Table 2. Description of decay classes, density (dry weight per raw volume), and carbon concentration [38]. Basic density and carbon concentration are applied from Köster et al. [39].

Decay Class		Description	Basic Density, kg m ³	Carbon Concentration, %
1	Recently dead	Wood hard, knife blade penetrates a few millimeters. Bark attached to the stem.	391.3	47.2
2	Weakly decayed	The outer layer of wood starts to soften, knife blade penetrates 1–2 cm. Loose bark, branches present.	330.6	47.4
3	Moderately decayed	The wood of outer layers of stem soft, the core still hard, knife blade penetrates <5 cm. Loose, fragmented bark.	230.6	47.4
4	Very decayed	Wood soft through the log, knife blade penetrates the wood in its entirety. No branches, most of the surface covered with mosses.	161.1	46.6
5	Almost completely decomposed	Lost consistency of wood, breaks up easily. Surface covered with lichens, mosses, and dwarf shrubs.	60.7	46.3

National Forest Inventory (NFI, 2014–2018) data with the corresponding parameters were used (Table 3). We selected 111 sample plots with an overstory dominated by aspen (at least 40% of the growing stock) at the age of 41 to 100 years, growing on *Hylocomiosa* and *Oxalidososa* site types. The selected plots were divided into ‘managed’ and ‘unmanaged’ based on the presence of fresh stumps found during the previous 15 years (since the first NFI measurement), while no information on tree removal before that time was available. The NFI data were first used to characterize the mean quantity of CWD and CWD carbon pool in managed and unmanaged stands, followed by further assessment of unmanaged stands only. The selected NFI plots were divided into age groups of ‘mature stands’ at the age of 41 to 60 years, ‘moderately overmature’ at the age of 61 to 80 years, and ‘overmature’ at the age of 81 to 100 years, and are referred respectively throughout this paper.

Table 3. Characteristics (marginal mean \pm standard error) of mature (41–60 years), moderately overmature (61–80 years), overmature (81–100 years), and old-growth (101–140 years) European aspen (*Populus tremula* L.) stands according to management type.

Characteristics	Stand Type and Age					
	Managed		Unmanaged			
	41–60	61–80	41–60	61–80	81–100	101–140
Stand age, years	50.1 \pm 1.3	67.9 \pm 1.1	53.1 \pm 1.0	70.1 \pm 1.2	86.9 \pm 1.1	111.8 \pm 0.5
Site index, m	28.0 \pm 1.0	27.2 \pm 1.0	28.8 \pm 0.4	27.3 \pm 0.7	25.7 \pm 0.8	25.4 \pm 0.2
DBH, cm	36.2 \pm 2.2	42.8 \pm 2.7	37.1 \pm 1.5	39.5 \pm 1.3	50.4 \pm 2.2	49.0 \pm 0.6
Height, m	28.0 \pm 1.1	31.9 \pm 1.1	29.7 \pm 0.4	32.4 \pm 0.7	33.8 \pm 0.9	36.8 \pm 0.2
Total basal area, m ² ha ⁻¹	29.2 \pm 2.5	34.2 \pm 3.0	32.2 \pm 1.4	39.5 \pm 2.3	41.8 \pm 1.9	50.3 \pm 0.9
Total growing stock, m ³ ha ⁻¹	330 \pm 30	447 \pm 48	377 \pm 21	526 \pm 36	577 \pm 37	774 \pm 16
Total number of trees, ha ⁻¹	1388 \pm 245	1049 \pm 241	1421 \pm 173	1087 \pm 143	942 \pm 108	1134 \pm 67
Overstory basal area, m ² ha ⁻¹	21.8 \pm 1.7	26.1 \pm 2.6	24.3 \pm 1.5	29.9 \pm 2.3	30.4 \pm 1.7	38.9 \pm 0.8
Overstory growing stock, m ³ ha ⁻¹	278 \pm 26	383 \pm 45	320 \pm 21	443 \pm 36	470 \pm 34	664 \pm 14
Overstory number of trees, ha ⁻¹	308 \pm 34	262 \pm 29	366 \pm 34	345 \pm 33	229 \pm 25	246 \pm 7
Aspen basal area, m ² ha ⁻¹	14.0 \pm 2.0	17.6 \pm 2.4	14.6 \pm 1.2	20.3 \pm 2.3	21.9 \pm 2.1	32.1 \pm 0.8
Aspen growing stock, m ³ ha ⁻¹	187 \pm 25	276 \pm 42	205 \pm 18	316 \pm 38	355 \pm 39	566 \pm 15
Aspen number of trees, ha ⁻¹	363 \pm 139	162 \pm 35	296 \pm 71	273 \pm 68	126 \pm 18	202 \pm 18
Objects	19	19	30	26	17	26
Sample plots	19	19	30	26	17	150

Latvian National Forest Inventory data are used for mature, moderately overmature, and overmature stands, and our measured data are used for old-growth stands.

Jansons and Līcīte [40] describe inventory plot sampling design in detail. All measurements were performed in circular sample plots (500 m²). If the sample plot crossed two distinctly different stands, it was divided into sectors. Only plots with a sector area of ≥ 400 m² were used in this study. For all overstory trees, DBH was measured, and the stand basal area was calculated. Tree height was measured for 8 to 19 trees of each overstory species, depending on the number of species in the plot, and stand height was calculated. Increment cores of three overstory trees were used to determine stand age. Measurements of CWD were conducted using a concentric design: within a 12.62 m radius, standing CWD with a diameter at breast height and lying CWD with a diameter of the thicker end ≥ 14.1 cm was measured; and within a 5.64 m radius, CWD with a respective diameter ≥ 6.1 cm was measured. Height of all standing trees and length (≥ 1.0 m) of lying trees was measured, and decay class and species (aspen, other deciduous, or coniferous) were noted. CWD was divided into three groups, according to decay class: ‘recently dead’ with wood hard, bark intact, ‘moderately decayed’ with all succeeding phases of decomposition starting from loose bark to the cover of epiphytic mosses on $<10\%$ of the visible stem surface, and ‘very decayed’ with a cover of epiphytic mosses on $\geq 10\%$ of the visible stem surface. Our measured decay classes were integrated according to NFI descriptions to compare the volume of CWD among decay classes at different stand ages. The adjusted decay classes were (1) ‘recently dead’, (2) ‘weakly decayed’, and (3 + 4 + 5) ‘moderately to almost completely decomposed’ (Table 2).

For both data sets, the volume of whole trees was calculated using equations developed by Liepa [41], and the volume of stumps and snags was calculated using Huber’s formula (Equation (1)). For CWD carbon pool calculation, volume was converted to mass using decay class-specific density and carbon content for aspen (Table 2), both applied from a study by Köster et al. [39].

Huber’s formula:

$$V = \frac{L \pi d_m^2}{4} \quad (1)$$

V = Stump/snag volume,

L = Length of the log or height of the stump, and

d_m = Mid-diameter of the log or the stump.

We used linear mixed models, incorporating ‘stand’ as a random effect (several plots were measured in the same stand) to assess how quantities of CWD and CWD carbon pool differed among groups based on stand parameters (age, site index, basal area), stand management, CWD pose, species composition, and decay class. The same models were used to calculate marginal mean values of stand and CWD parameters and their standard errors. Data were analyzed using SPSS 14.0 for Windows; all tests were performed at $\alpha = 0.05$.

3. Results

We did not find a significant (both $p > 0.05$) difference between managed and unmanaged stands within both mature and moderately overmature stands (Table 4). as well as no significant difference (all $p > 0.05$) appeared among the age groups.

Lying CWD was 62% to 85% of the total volume among the age groups and management types, however, we did not find significant differences ($p > 0.05$) for quantities of standing and lying CWD among the stand age groups of each management type, with the exception of significantly lower standing CWD volume in unmanaged mature stands compared to that in old-growth stands ($p < 0.05$). The CWD carbon pool size also had no significant differences ($p > 0.05$) among stand age groups for each CWD type and in total, with the exception of significantly higher standing CWD carbon pool in old-growth stands compared to that in unmanaged mature and moderately overmature stands (both $p < 0.05$).

Table 4. Coarse woody debris (CWD) volume and CWD carbon pool size in mature (41–60 years), moderately overmature (61–80 years), overmature (81–100 years), and old-growth (101–140 years) European aspen (*Populus tremula* L.) stands by CWD pose and stand type.

CWD Pose	Stand Type	Stand Age, Years	Number of Sample Plots	CWD Volume, m ³ ·ha ⁻¹		CWD Carbon Pool, t·ha ⁻¹	
				Marginal Mean	SE	Marginal Mean	SE
Standing	Managed	41–60	19	7.6	6.0	1.0	0.9
		61–80	19	5.3	6.0	0.7	0.9
	Unmanaged	41–60	30	16.6	4.8	2.2	0.7
		61–80	26	13.8	5.2	1.9	0.7
		81–100	17	26.1	6.4	3.5	0.9
101–140	150	31.9	2.2	4.6	0.3		
Lying	Managed	41–60	19	12.5	12.0	1.4	1.5
		61–80	19	31.0	12.0	4.1	1.5
	Unmanaged	41–60	30	53.3	9.6	6.6	1.2
		61–80	26	53.5	10.3	6.4	1.3
		81–100	17	47.5	12.9	5.3	1.6
101–140	150	60.5	4.3	8.0	0.5		
Total	Managed	41–60	19	20.1	14.2	2.4	1.8
		61–80	19	36.3	14.2	4.8	1.8
	Unmanaged	41–60	30	69.9	11.3	8.7	1.5
		61–80	26	67.3	12.1	8.2	1.6
		81–100	17	73.5	15.3	8.8	2.0
101–140	150	92.4	5.1	12.5	0.7		

Latvian National Forest Inventory data are used for mature, moderately overmature, and overmature stands, and our measured data are used for old-growth stands. SE—standard error.

We further analyzed deadwood characteristics within unmanaged stands. Stand age and site index were significant factors for CWD volume and CWD carbon pool (all $p < 0.001$), contrary to stand basal area (both $p > 0.05$). However, this was described by only weak positive correlations between both stand age and site index and CWD volume (for both $p < 0.05$, $r = 0.15$) and CWD carbon pool size ($p < 0.01$, $r = 0.19$ and $p < 0.05$, $r = 0.14$, respectively).

A large CWD volume was frequently present in assessed stands (Figure 2). The volume of at least 20 m³ ha⁻¹ was found in 77% to 89% of sample plots depending on stand age. This proportion gradually decreased for larger CWD quantities, yet, at least 50 m³ ha⁻¹ was present in 43% to 75% of sample plots.

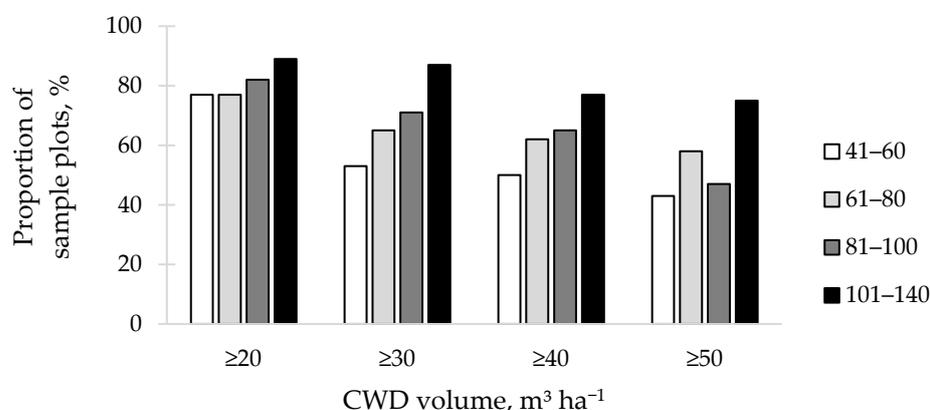


Figure 2. Occurrence of a particular coarse woody debris (CWD) volume according to stand age in unmanaged European aspen (*Populus tremula* L.) stands.

Most of the CWD consisted of deciduous deadwood (Figure 3). Aspen and other deciduous species (mostly *Betula pendula* Roth, *B. pubescens* Ehrh., *Alnus incana* (L.) Moench, *Corylus avellana* L., and *Salix caprea* L.) together accounted for 55% to 85% of CWD among the stand age groups. The proportion of aspen CWD was similar (all $p > 0.05$) in all age groups. The proportion of coniferous CWD was similar among mature, moderately overmature, and overmature stands (all $p > 0.05$), and in all these age groups, coniferous deadwood constituted a significantly higher ($p < 0.05$) portion of CWD than that in old-growth stands. For deciduous deadwood, significant ($p < 0.05$) differences were only found between mature and old-growth stands.

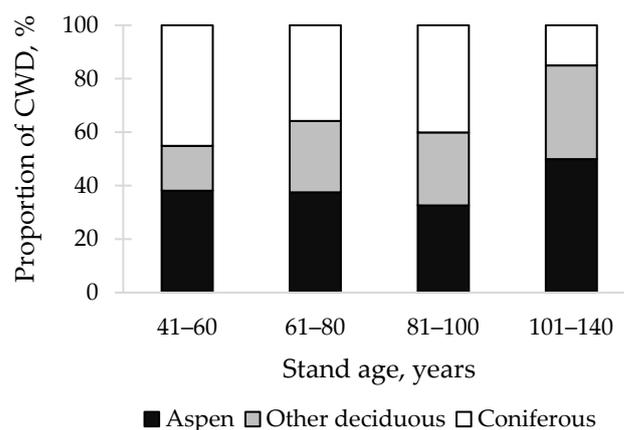


Figure 3. The proportion of coarse woody debris (CWD) by groups of species (aspen, other deciduous, and coniferous) in mature (41–60 years), moderately overmature (61–80 years), overmature (81–100 years), and old-growth (101–140 years) unmanaged European aspen (*Populus tremula* L.) stands.

Mean CWD diameter was 15.6 ± 1.4 cm (\pm standard error) in mature stands, 20.9 ± 1.4 cm in moderately overmature, 20.4 ± 1.8 cm in overmature, and 20.6 ± 0.6 cm in old-growth stands. Mature stands had a significantly thinner mean diameter of debris than old-growth stands ($p < 0.05$), but similar to that in both groups of overmature stands (both $p > 0.05$).

The volume of large CWD tended to increase with stand age, yet no significant differences (all $p > 0.05$) were found within each diameter group (Figure 4). About half of the CWD volume consisted of debris larger than 30 cm in diameter: from 48% (33.5 ± 9.3 m³ ha⁻¹) in mature stands to 64% (47.3 ± 12.3 m³ ha⁻¹) in overmature stands. Moreover, debris with a diameter greater than 40 cm formed from 19% (13.2 ± 7.0 m³ ha⁻¹) in mature stands to 44% (32.3 ± 9.2 m³ ha⁻¹) in overmature stands.

We used adjusted decay classes to assess differences in CWD volume among stand age groups (Figure 5). The most distinct differences were found for recently dead wood, with the highest volume of such CWD in old-growth and mature stands: 12% and 17%, respectively. However, old-growth stands had significantly higher recently dead CWD volume than both overmature stand groups (both $p < 0.05$), while mature stands had no significant differences from others (all $p > 0.05$). The proportion of weakly decayed debris was similar in all age groups, ranging from 31% of total CWD in moderately overmature to 40% in mature stands.

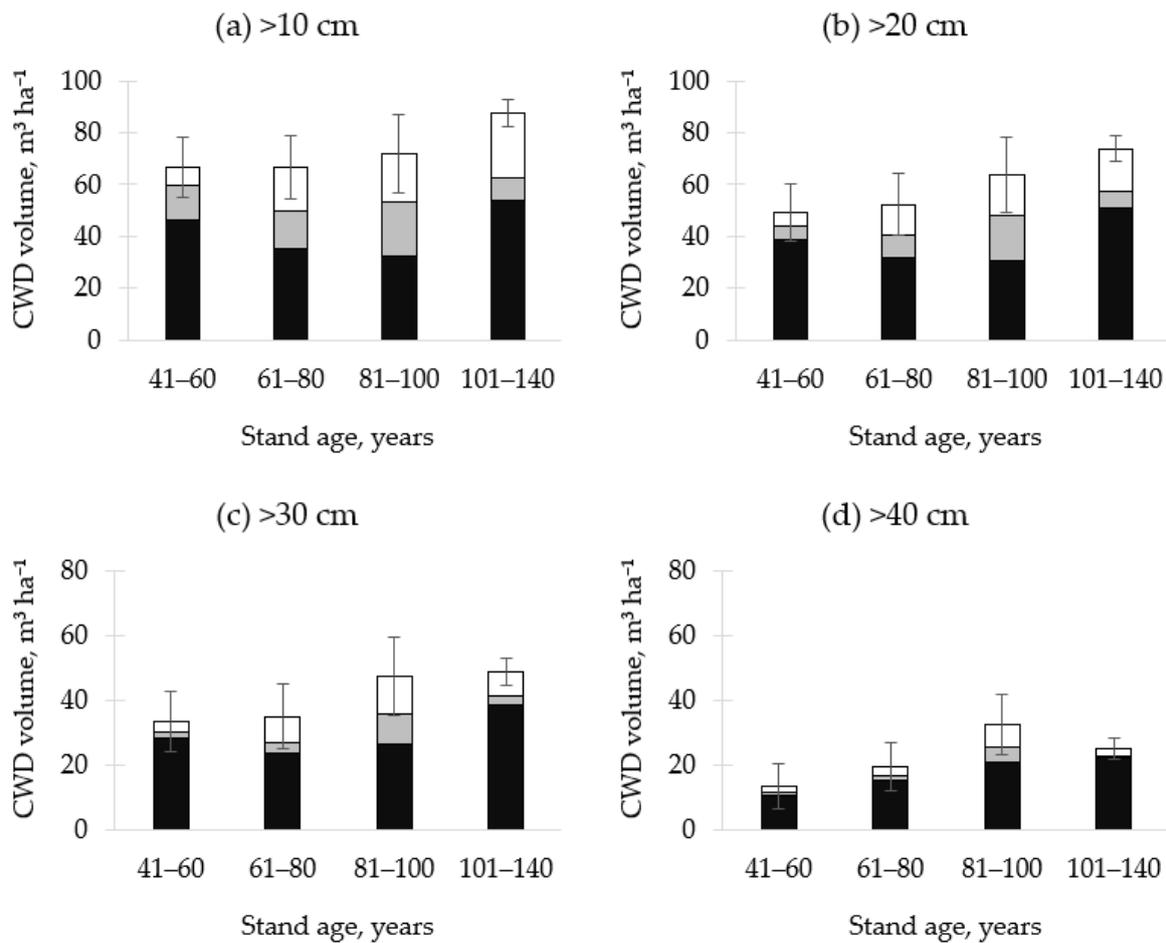


Figure 4. The marginal mean volume (\pm standard error of total volume) of aspen (black stacked bars), other deciduous (gray stacked bars) and coniferous (clear stacked bars) coarse woody debris (CWD) in mature (41–60 years; $n = 30$), moderately overmature (61–80 years; $n = 26$), overmature (81–100 years; $n = 17$), and old-growth (101–140 years; $n = 150$) unmanaged European aspen (*Populus tremula* L.) stands by groups of CWD diameter: (a) >10 cm, (b) >20 cm, (c) >30 cm, and (d) >40 cm.

In all stand age groups, moderately to almost completely decomposed wood formed from 44% ($40.4 \pm 3.5 \text{ m}^3 \text{ ha}^{-1}$) in old-growth stands to 68% ($45.6 \pm 8.9 \text{ m}^3 \text{ ha}^{-1}$) in moderately overmature stands. In old-growth stands, CWD distribution was categorized into five decay classes. The first two were the same as for adjusted decay classes (Figure 5), moderately decayed CWD accounted for 21% ($19.8 \pm 1.8 \text{ m}^3 \text{ ha}^{-1}$), and very decayed and almost completely decomposed CWD accounted for 14% ($12.6 \pm 1.5 \text{ m}^3 \text{ ha}^{-1}$) and 9% ($7.9 \pm 1.1 \text{ m}^3 \text{ ha}^{-1}$) of total CWD in old-growth stands, respectively.

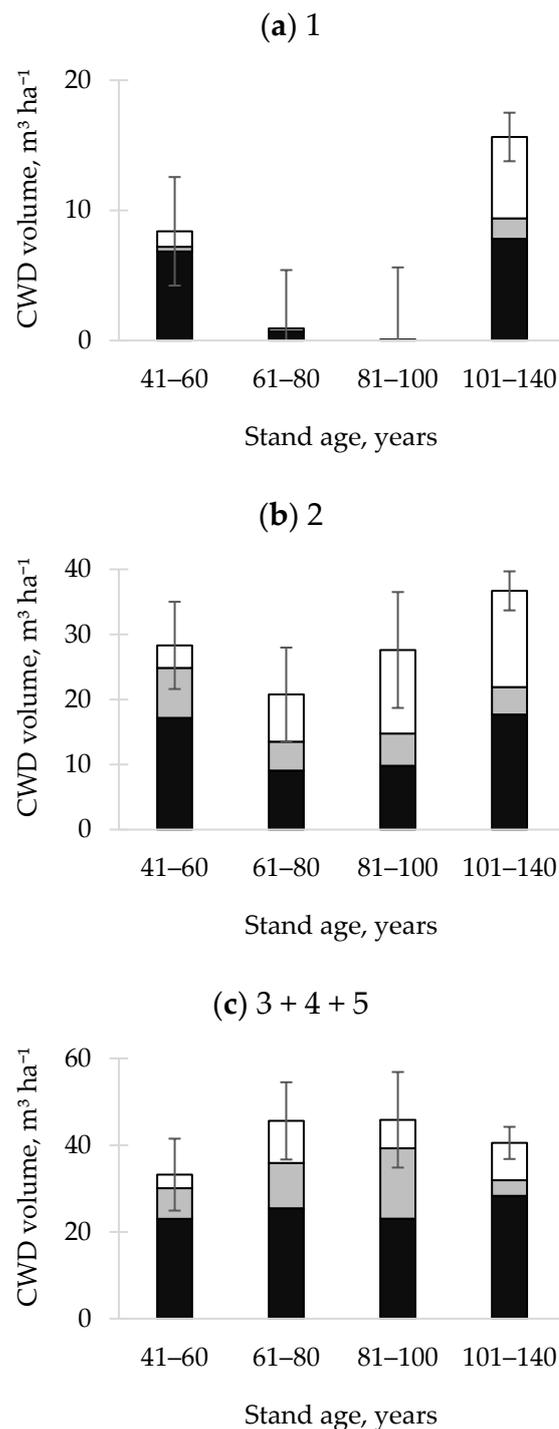


Figure 5. The marginal mean volume (\pm standard error) of coarse woody debris (CWD) in mature (41–60 years; $n = 30$), moderately overmature (61–80 years; $n = 26$), overmature (81–100 years; $n = 17$), and old-growth (101–140 years; $n = 150$) unmanaged European aspen (*Populus tremula* L.) stands by adjusted decay classes: (1) recently dead, (2) weakly decayed, and (3 + 4 + 5) moderately to almost completely decomposed.

4. Discussion

This study characterizes CWD volume, composition, and structure in aspen stands from mature to old-growth age. The information on the histories of the studied old-growth stands is not available; however, we assume that the age of the overstory corresponds well with time since stand origin after disturbance. The present stand composition with aspen

as the dominant species in the overstory could almost exclusively form only if regeneration of the species is abundant enough, i.e., after a large-scale disturbance, such as forest fire or clear-cutting. This is supported by the species-specific regeneration requirements, as aspen is essentially a pioneer species [9], with limited regeneration capacity under lack of sufficiently large canopy gaps [42–44], and as a shade-intolerant species [45], it has difficulties to reach canopy-layer if regenerated in gaps.

We did not find a significant differences between managed and unmanaged stands, that could indicate an effect of the continuous removal of lower-dimension and vitality trees (i.e., potential deadwood) from the conventionally managed stands [46,47]. The CWD volume in the studied managed stands, however, considerably exceeded deadwood volume that is reported in other countries in Northern Europe: 5.9 m³ ha⁻¹ for managed stands in Finland [48], 7.6 m³ ha⁻¹ for managed stands in Sweden [47], and 13.7 m³ ha⁻¹ across forests in Estonia [49]. Our results are also somewhat higher than the mean CWD volume across forests in Latvia for managed and unmanaged stands together: according to NFI, 19.8 m³ ha⁻¹. The studied unmanaged stands comprised about 70 to 90 m³ ha⁻¹, which is in between average deadwood volume of 40 to 170 m³ ha⁻¹ in boreal unmanaged forests [11,50–52].

As expected, age was a significant factor affecting CWD volume in the unmanaged stands since deadwood tends to accumulate under the absence of tree removal [53–55]. Such tendency has been often reported in coniferous-dominated forests [8,17,47,54,56], whereas for birch, stand age was not a significant factor affecting CWD volume at the range of 71 to 150 years [33]. For trembling aspen (*Populus tremuloides* Michx.), the volume of CWD significantly increased for older stands and was comparable with our estimates: 63.1 m³ ha⁻¹ in young stands, 76.8 m³ ha⁻¹ in mature, and 101.4 m³ ha⁻¹ in old stands [57].

Site index showed a significant but very weak positive effect on CWD volume and was in accordance with results of other studies in younger stands [58–60]. However, another indicator of stand productivity, stand basal area, had a non-significant effect on CWD volume, presumably due to a wide range of the studied stand age.

In stands undergoing increased tree death from senescence and natural disturbance, a negative relationship between deadwood volume and stand basal area occur, i.e., disturbance decreases the basal area of living trees and simultaneously increases deadwood volume [8]. Our study only included stands where old aspen still formed the dominant cohort. The old aspen trees with large diameters were still alive and did not contributed to CWD, thus, lacking a relation between CWD volume and basal area. Likewise, the relation between basal area and CWD volume was absent in old-growth hemiboreal birch stands [33]. Both aspen and birch are pioneer species, typically undergoing canopy transition from early- to late-successional species after reaching their life span [61]. For aspen, lifespan commonly reaches 90 years [62], although species longevity might reach up to 200 years [9,63]. The studied old-growth stands were somewhere in between these ages, thus might represent stands in early senescence (see below), although aspen might persist in old-growth conditions for a prolonged time [44].

In European boreal forests, the majority of deadwood-dependent species need from 20 to 30 m³ ha⁻¹ deadwood for their presence [64]. Yet, deadwood volume per se is an insufficient measure [65–67], and additional characteristics are important for saproxylic species diversity. This includes deadwood species diversity, especially the abundance of temperate deciduous deadwood [47], and deadwood spatial and temporal continuity [68]. Our studied aspen stands had a high proportion of deciduous debris (pooled aspen and other deciduous species), accounting for 55% of total CWD in mature stands to 85% in old-growth stands (Figure 3). The higher portion of coniferous deadwood in mature stands likely originated from understory spruce, which typically forms small fractions of debris due to self-thinning [11]. As stand ages, death from the senescence of aspen and other pioneer species (*B. pendula*, *B. pubescens*, and *A. incana* were most common) increases, forming canopy gaps. These might provide access to more resources for understory trees,

decreasing their mortality, hence, probably explaining the thrice lower volume of coniferous CWD in old-growth stands than that in mature stands.

Various deadwood species supply substrates of different chemical compositions, as well as provide a more diverse layout of debris poses, as a share of standing trees and snags and lying deadwood is species-specific [54]. We found about 60% to 85% of CWD lying, similarly to findings of aspen deadwood in old-growth coniferous-dominated forests: 60% to 75% [8,9]. Aspen typically tends to snap, forming both broken snags and lying deadwood [54,69]. Stems of low density are more fragile to breakage [70,71], and aspen stems are characteristic of crumbling into pieces when a tree falls, possibly leading to underestimation of aspen CWD if the broken pieces are shorter than the minimum measured length of a particular study. Additionally, smaller (shorter) debris has a larger proportion of surface area exposed to decomposer colonization and a higher degree of soil contact that increases moisture of the deadwood [70]. Both of these factors contribute to an increased deadwood turnover rate for smaller debris. Besides the size, deadwood pose largely affects substrate conditions, with dry snags and leaning logs being a less suitable substrate for wood-decaying fungi compared to moist deadwood [18,72], thus prolonging deadwood's life span [10,73].

Our estimated CWD volume in the old-growth stands was affected by gradual decay. This should most certainly apply to aspen, as it is among the species with a relatively fast turnover rate, with 85% of the initial mass lost in 27 years for logs 5–25 cm, 43 years for logs 25–60 cm, and 106 years for bark [74]. Another study has suggested a much longer aspen decomposition time, 110 to 120 years [10]. Still, aspen has the strongest loss of wood density during decomposition also if compared with other short-lived species, i.e., birch [10,39] and black alder [39].

Softwood CWD has a longer turnover time than hardwoods [10]. Although no distinction between the softwood species was made, it should predominantly consist of spruce, as pine rarely occurred in the studied stands. For spruce in unmanaged boreal forests, deadwood half-lives varied from 12 to 27 years for standing snags and from 20 to 40 years for lying debris [52]. Relatively rapid decomposition for spruce was also reported in the boreal old-growth forest where spruce at the last decay stage was estimated to be dead for 34 years [75]. A longer half-life duration was found for softwood snags in forests across Switzerland, about 45 to 48 years [76].

Considering the decomposition times, the old-growth stands could comprise some legacy deadwood in the last decay classes that have originated from the previous (pre-disturbance) generation. Alternatively, deadwood from the previous generation could be omitted in our measurements. That could be if the legacy deadwood appears in the form of buried CWD [77], as only visible debris was measured, including that overgrown by mosses but still forming distinctive appearance from the ground layer. This might lead to underestimation of total deadwood stocks, as well as total carbon stocks, if the buried CWD is not accounted into forest floor carbon estimates..

The overmature stands had low or absent recently dead and weakly decomposed CWD. A similar pattern of CWD availability regarding stand age has been described for *P. tremuloides* [19]. The wood of more decomposed classes was similar for all stand age groups, indicating that overmature stands are at a state of stand development when mortality due to self-thinning has diminished while mortality due to senescence has not become apparent yet. This might be a concern for saproxylic species, as they show a preference for deadwood of a particular decomposition level [78–80].

The spatial availability showed rather regular CWD distribution for all stand age groups, with at least two-thirds of the plots comprising at least 20 m³ ha⁻¹ at all age groups. Our results coincide with an extensive study across Europe by Puletti et al. [81] that showed that 72% of sample plots comprise deadwood amount up to 25 m³ ha⁻¹. Observations of much higher deadwood volume are often related to damage to living trees [55,82], however, stands with signs of notable damage to living trees were omitted in the selection of our study areas.

Deadwood is also an important carbon pool that partly acts as a carbon source to the atmosphere and partly redistributes carbon to soil [83,84]. The vast heterogeneity of deadwood (e.g., tree species, type, size, pose, level of decay) that determine the richness of saproxylic organisms [67,85] makes it complicated to assess carbon storage within it. For aspen, controversial findings of its carbon concentration throughout proceeding decomposition have been reported claiming no effect [20], reduced [39,86], or increased [87] carbon concentration along the decay stages. Precise calculations are also hampered by species-specific features related to characteristic decay from inside of living trees that complicate both live and dead aspen wood estimations.

Aspen is susceptible to heart rot infection caused by *Phellinus tremulae* (Bond.) Bond. and Borisov [88,89]. Infected aspen trees are found through all stand development stages, including these younger than 40 years. Trees severely infected while alive have a faster transition through decay classes after death [90]. This, on the one hand, hinders the assessment of total deadwood volume due to part of already-dead wood still enclosed or attached to living trees. On the other hand, mature aspen stems are commonly hollowed by heart rot [9,50], leading to overestimated deadwood volume if the hollow of the dead stem is not excluded from deadwood estimates.

Forest restructuring by senescence among dominant trees or disturbances alters stand carbon balance with reduced photosynthesis and increased heterotrophic respiration. There are various mutually non-exclusive hypotheses for stand biomass dynamics with respect to carbon pathways along stand succession [91]. Whether old-growth forests continue to accumulate, decline, or stabilize carbon balance, largely depends on stand development after early succession [34]. Small-scale disturbances could have a minor effect on ecosystem production, as forests shifting from early- to late-successional species remained stable ecosystem production regardless of increased heterotrophic respiration from enlarged deadwood volume [92]. However, debris, as discussed above, persists as a CO₂ source over several decades, affecting the net carbon balance of the stand [26], especially for aspen with a relatively fast decomposition rate [10,74]. Thus, alternatively, even with relatively small patches of increased deadwood volume (increased net emissions), gradual changes in species composition could switch forests from a carbon sink to a source of CO₂ to the atmosphere [26]. A study that focused on multiple succession pathways in old boreal forests found a decline in total ecosystem carbon pool from transition to late-succession stages irrespective of tree species combinations [34]. All these relations, however, might be interrupted by unpreventable stand-replacing disturbances that cause old, carbon-saturated forests to release large amounts of carbon into the atmosphere [93,94]. This might also affect forest landscapes as the disturbance regimes are changing with climate change [95].

5. Conclusions

There was a large CWD volume in both managed and unmanaged stands. The CWD profile was diverse in species composition and layout of debris poses. Substantial CWD volume was comprised of large diameter units and was frequently found in the studied stands. Our estimated CWD volume and CWD carbon pool represent rather maximum mean quantities regarding the high probability of decayed heartwood or hollowed trees (assessment not included in this paper) in aspen stands that have reached maturity. Considering stand age, changes in CWD species composition together with the high volume of recently dead debris suggests early senescence of dominant aspen cohort in old-growth stands. Further monitoring studies would render the understanding of stand development pathway through dominant pioneer species substitution, regarding CWD carbon pool and CWD dynamics for a relatively short-lived tree species.

Author Contributions: Conceptualization, Ā.J., I.J., and G.Š.; methodology, G.Š. and S.Š.; formal analysis, G.Š., K.B., and I.J.; data curation, I.S. and I.J.; writing—original draft preparation, S.Š. and I.J.; writing—review and editing, G.Š., Ā.J., and L.L.; project administration, Ā.J. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the LVM project “Carbon cycle in forest ecosystem”.

Data Availability Statement: Not applicable.

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

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