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Tree biomass – a fragile carbon storage in old-growth birch and aspen stands in hemiboreal Latvia

LAURA ĶĒNIŅA [1]*, DIDZIS ELFERTS [2, 1], IEVA JAUNSLAVIETE [1], ENDIJS BĀDERS [1], GUNTARS ŠŅEPSTS [1] AND ĀRIS JANSONS [1]

[1] *Latvian State Forest Research Institute "Silava", Riga St. 111, Salaspils LV-2169, Latvia*
[2] *University of Latvia, Faculty of Biology, Jelgava St. 1, Riga LV-1004, Latvia*

* *Corresponding author: laura.kenina@silava.lv*

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Abstract

Birch (*Betula pendula* Roth, *Betula pubescens* Ehrh.) and European aspen (*Populus tremula* L.) stands dominate the deciduous forests of Northern Europe. Due to increasing forest protections, more deciduous stands will reach the old-growth stage. Thus, data on the carbon storage potential in such areas are essential. We aimed to establish a benchmark for carbon stocks of the main carbon pools in old-growth deciduous hemiboreal stands. Carbon pools were calculated from measurements in forty old-growth (104–148 years-old) deciduous stands in forests on fertile mineral soil. The carbon stock in these stands is distributed across tree biomass (~ 60%), mineral soil (~ 30%), the forest floor (~ 5%), and deadwood (~ 4%). Living tree biomass and deadwood carbon pools were closely associated with stand parameters: dominant tree species, standing volume and stand density. As the stand ages and tree dieback occurs, the significance of individual large trees to maintain high density and standing volume, thus also the carbon stock of the stand, rises. Reliance on a small number of large trees makes the carbon storage in old-growth stands fragile and easily affected by natural disturbances. It happens at an earlier age for species with a relatively short life span, like birch and aspen. Our data from stands with the limited recent influence of such disturbances provide a benchmark for carbon storage potential in old deciduous stands.

Keywords: carbon pools, tree biomass, deadwood, forest floor, soil, birch, European aspen

Introduction

Forests account for a great part of the carbon storage and fluxes in different biomass pools and they differ greatly due to the huge heterogeneity at stand level (Seedre et al. 2015, Kulha et al. 2020). There is also significant variability in the carbon distribution across the main carbon pools in different forests (Pan et al. 2011). This emphasizes the importance of regional (case) studies to obtain reliable carbon stock data. In forests across Europe, numerous studies have shown that younger trees can sequester carbon at a faster rate compared to mature trees (Taylor et al. 2014, Badalamenti et al. 2019, Nord-Larsen et al 2019, Uri et al. 2019, Uri et al. 2022). However, older stands may ensure higher carbon storage in living tree biomass and soil (Pregitzer and Euskirchen 2004, Badalamenti et al. 2019, Kun et al. 2020). The carbon stocks of old-growth stands are largely defined by multiple of factors such as vegetation type, soil properties, tree species, forest floor production, management and deadwood formation (Kumpu et al. 2018, Jandl et al. 2019, Mayer et al. 2020, Clarke et al. 2021), which have different influences on the carbon storage of old-growth, compared to younger, stands (Pregitzer and Euskirchen 2004, Ruel and Gardiner 2019, Molina-Valero et al. 2020). Old-growth forest is defined as an ecosystem with overgrown old trees, large amounts of over-sized deadwood, multiple canopy layers which contain rich species composition, and with broad variation in tree size and spacing (Buchwald 2005). Stand age is typically determined as the age of the dominant cohort of trees. However, what "old" means varies across tree species and regions, and sometimes, even within a region (O'Brien et al. 2021). Old-growth forests are essential providers of a broad range of ecosystem services including carbon storage (Brockerhoff et al. 2017). However, actual studies of carbon pools at old-growth stages, where huge heterogeneity between stands has been observed, are sparse (Seedre et al. 2015, Yuan et al. 2016).

There are four major forest carbon pools – living tree biomass, soil, deadwood and the forest floor – each store a certain amount of the total forest carbon (Seedre et al. 2015, Triviño et al. 2015). Tree biomass is a large and dynamic forest carbon pool (Finér et al. 2003, Uri et al. 2012, Badalamenti et al. 2019), which is strongly impacted by management as well as by the type, frequency and severity of natural disturbances and/or aging at the old-growth stage (Gregow et al. 2017). Soil also stores a large amount of carbon and in boreal forests it is a more stable carbon pool than in temperate forests (Deluca and Boisvenue 2012, Bradshaw and Warkentin 2015, Mayer et al. 2020). However, there is still insufficient information on soil carbon storage and sequestration rates at the old-growth stage (Pregitzer and Euskirchen 2004, Jandl et al. 2007, Nord-Larsen et al. 2019).

Birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) and European aspen (*Populus tremula* L.) are the most abundant tree species in the European hemiboreal region (Caudullo and Rigo 2016, Dubois et al. 2020). Both tree species are ecologically valuable, fast-growing, early-succession species (Dubois et al. 2020, Hardenbol et al. 2020, Šēnhofa et al. 2020). Compared to coniferous, birch and aspen stands have a shorter life span. Therefore, they reach the old growth stage faster (at 120–140 years) and the dominance of the older deciduous trees is more fragile (Nilsson et al. 2002, Robalte et al. 2012, Gregow et al. 2017, Hardenbol et al. 2020). The dominance of the older deciduous trees also lasts for shorter periods of time compared to coniferous stands, as demonstrated by the higher deadwood amounts in these stands (Köster et al. 2015, Stakėnas et al. 2020, Šēnhofa et al. 2020). Only a few studies on biomass and soil carbon in young and mature hemiboreal birch stands are available (Uri et al. 2012). But the old-growth stage of birch and European aspen has not been characterized in this respect before.

Therefore, we aim to establish a benchmark for carbon pools, including living tree biomass, deadwood, soil (0–80 cm) and the forest floor, in old-growth birch and aspen stands on mesotrophic mineral soils in hemiboreal Latvia. We hypothesize that, in the absence of stand replacing disturbances, a decline in stand density due to tree dieback is a significant factor affecting the carbon pools of old-growth deciduous stands.

Material and methods

Study area and sample plot selection

Latvia is located in the European hemiboreal forests: a transitional zone between the coniferous boreal forest and the deciduous temperate-north forests (Ahti et al. 1968). According to National Forest Inventory (NFI) data (NFI 2022), aspen and birch trees cover 34% (1.023 M ha) of the total forest area in Latvia. The share of these tree species is similar to those in other Baltic States (Sepp and Kaasik 2002). These tree species make up 36% of the forest area (29% birch and 7% aspen) and 34% of the standing volume (26% birch and 8% aspen) in Estonia (Valgepea et al. 2020). Forest types *Hylocomniosa* and *Oxalidosa* (Bušs 1997) are the most common in Latvia, occupying 40% of the total forest area. Both forest types have fresh mesotrophic mineral soil, suitable for most of the common tree species. Due to slight differences in soil fertility, *Hylocomniosa* has a higher share of Scots pine dominated stands and *Oxalidosa* – a higher share of grey alder (*Alnus incana* (L.) Moench) and European aspen dominated stands, but both have similar shares of Norway spruce and birch dominated stands. In these forest types, the ground vegetation layer is mainly occupied by common wood sorrel (*Oxalis acetosella* L.) and European blueberries (*Vaccinium myrtillus* L.), but the moss layer by glittering woodmoss (*Hylocomium splendens* Hedw.) and wind-blown mosses (*Dicranum* spp.) (Bušs 1997). *Hylocomiosa* has medium fertile sandy loam, loamy and clay soil, whereas *Oxalidosa* has typical podzolic or soddy podzolic, loamy soil, sandy loam, less clay or fine sand (Bušs 1997). The climate at the sampled sites can be characterized as temperate moist continental, yet with the explicit coastal features of the Baltic Sea (Avotniece et al. 2017). According to the Latvian Environment Geology and Meteorology Centre, the mean annual temperature is +7°C (the coldest –3°C in February and warmest +18°C in July) and the mean annual precipitation is 686 mm, with 334 mm falling during the growing season (May to September).

Stands older than 100 years (aspen) or 120 years (birch) were pre-selected and checked on site for the occurrence of the chosen forest types (*Hylocomniosa*, *Oxalidosa*), stand age, dominance of main tree species (> 50% from the volume), no human intervention (no signs of former logging), in remote location (> 5 km from villages and > 1 km from roads) on state-owned forest property. Only stands which met all the eligibility criteria were used for the collection of field data.

Field data collection

The measurements in the birch and aspen stands were performed between 2018 and 2019. In total, 40 old-growth deciduous stands were assessed, including 15 birch (123 to 148-year-old) and 25 aspen stands (104 to 135-year-old). Altogether, 213 sampling plots (6 to 8 sample plots in each stand) of 500 m^2 (of 12.62 m radius) were established in these stands (Figure 1; Table 1; Supplementary Table 1s).

In the sampling plot, tree species, stand's tree layer (the first or second one) and the diameter at breast height (DBH) for all the living trees (DBH ≥ 6.1 cm) were recorded. The first layer included the tallest trees in the stand, the height of which do not differ more than 20% from the mean height of the trees in this layer. The second layer included shorter threes with the height at least 25% of the mean of the first layer. The height of five living birch or aspen trees in the first layer and three living trees from each tree species in the first and second layers were measured. The tree height and DBH of all the standing dead trees (≥ 6.1 cm) were measured. Standing dead trees were categorized as

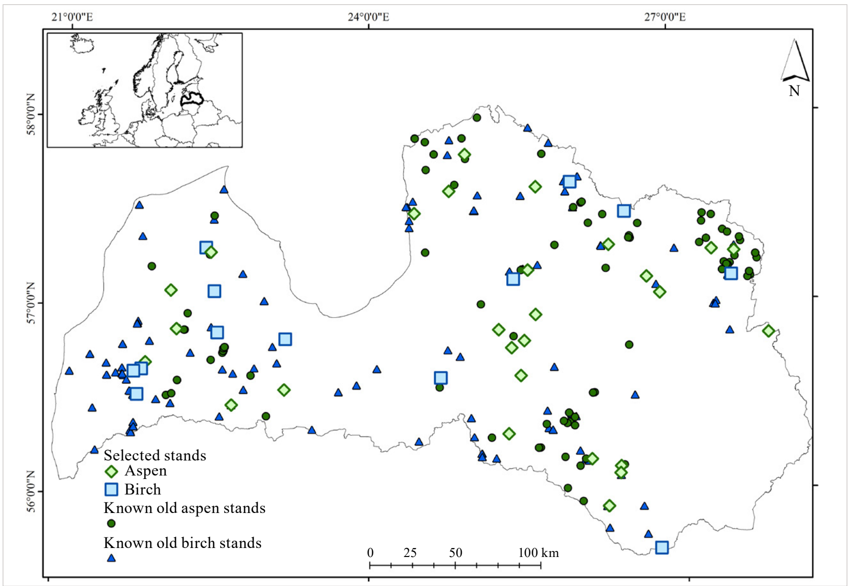

Figure 1. Distribution of known old-growth birch and aspen stands in Latvia

Assessed old-growth stands indicated by rhombuses for aspen; and by squares for birch. Green circles represent known old-growth aspen stands in Latvia in accordance with the set criteria; blue triangle indicate known old-growth birch stands

Table 1. Stand characteristics by dominant tree species. Mean standing volume, stand density, and basal area of the first layer trees. The table includes mean values ± confidence interval 95%

Characteristics	Birch stands	Aspen stands
Mean tree diameter at breast height, cm	38 ± 1.5	49 ± 1.1
Mean quadratic tree height, m	30 ± 0.7	37 ± 0.4
Mean standing volume, m^3 ha^{-1}		
First layer	417 ± 30	669 ± 29
Second layer	73 ± 15	105 ± 19
Stand density, trees ha^{-1}		
First layer	296 ± 21	243 ± 13
Second layer	364 ± 110	328 ± 60
Basal area, m^2 ha^{-1}		
First layer	30 ± 3	39 ± 2
Second layer	8 ± 2	10 ± 2
Mean stand age, years	130 ± 2	112 ± 1
Number of sampling plots	67	146

ones with tops and with broken tops (snags). For lying deadwood, the diameter of both ends (≥ 14.1 cm at the ticker end) and the length were measured within the sampling plot, and for standing deadwood, diameter, height, and the category of decay stage. In the centres of the sampling plots, we inscribed smaller, quarter circle subplots (with an area of 25 m^2), in which living trees and deadwood of smaller diameters were recorded (2.1 to 6.0 cm for standing trees and 6.1 to 14.0 cm diameter of lying deadwood). Three living birches and aspens of the first layer trees in each sample plot were cored using a Pressler increment borer to detect stand age. In aspen stands at such age soft stem rot was very common. In cases where all trees had rot, the ones with the smallest rot-affected area were selected and the number of missing years were estimated based on distance to the pith and the average width of the 10 closest measurable annual rings. For deadwood, the decay stage was estimated in five classes, from fresh to almost completely decayed according to Sandström et al. (2007), and the tree species were recorded (if possible).

The analysis of the forest floor and mineral soil carbon pools included data from 10 birch and 23 aspen stands. At three systematically located points at the edge of the sampling plot (0°, 90°, and 180°), soil and forest floor sampling were performed. At each point, a single soil sample was taken at fixed depths (0–10 cm; 10–20 cm; 20–40 cm; 40–80 cm) using 100 cm^3 metal cylinder. 10 by 10 cm forest floor samples (organic layer (O horizon) made of undecomposed, fresh and wholly decayed plant or animal debris without mineral material (IPCC 2000)) were taken.

Data analysis

Tree height for living and dead standing trees was expressed as function of tree DBH, using Näslund's model (as referenced in Mehtätalo et al. 2015). The volume of living and dead standing trees was calculated based on tree DBH and tree species in accordance with the local equation, based on Liepa (1996). The volume of the dead standing trees with broken tops and lying deadwood was calculated using Huber's formula (as referenced in Šēnhofa et al. 2020). The individual living tree biomass was calculated as a sum of above- and below-ground biomass using local biomass models for the main tree species in Latvia (Scots pine, Norway spruce, birch and European aspen) according to Liepiņš et al. (2017). For cases, where the biomass models have not been developed, the birch model was used. Biomass was calculated for all measured living trees and shrubs (from 2.1 cm DBH). A carbon content of 50% for converting tree biomass into carbon was used for living tree biomass carbon stock estimation (IPCC 2006). The necromass of deadwood and the carbon stock both for standing and lying logs were estimated from the volume and decay class-specific density and carbon content from the parameters of the main tree species in Estonia developed by Köster et al. (2015) and tested for Latvia (Ķēniņa et al. 2019b).

The obtained soil and forest floor samples were prepared and analyzed in the LVS EN ISO/IEC accredited Laboratory of forest environment of the Latvian State Forest Research Institute "Silava" according to the LVS ISO 10694:2005 standard. The physicochemical parameters, such as soil bulk density, coarse fragments, total carbon concentration, and inorganic carbon concentration, in the soil samples were determined according to the corresponding ISO standard. Organic carbon concentration in the soil was expressed as the difference between the concentration of total carbon and inorganic carbon.

The total ecosystem carbon stock was calculated as a sum of all measured carbon pools: biomass (for all species, independently of stem layer or species, if not specified differently), in deadwood, forest floor and soil.

Linear mixed effects models (LMER) were used to evaluate the effect of species, stand density, standing volume, proportion (from standing volume) of species in stand composition (hereafter called as species unit), and all two-way interactions between species (independent variables) on the dependent variable: the carbon stocks of living tree biomass (also separate model for above- and below-ground biomass). Linear regression was used to test the effect of species, forest type, stand density, standing volume, and species unit in soil and forest floor carbon stocks. To reduce the heterogeneity of dependent variables, carbon stocks of deadwood, soil and forest floor were log transformed before introducing in the models. After removing non-significant interaction terms or main variables (at the significance level 0.05), the final models were chosen using the Akaike information criterion (AIC). In all models, stand ID was used as a random factor, as there were multiple plots per stand. If there was a significant effect or interaction with more than two levels, a PostHoc test comparing the estimated marginal means was used.

Data analysis was performed using R 4.1.0. software environment (R Core Team 2021). R libraries "lme4" (Bates et al. 2015) and "lmerTest" (Kuznetsova et al. 2017) were used to perform linear mixed-effects models, and library "emmeans" (Lenth 2021) to calculate estimated marginal means.

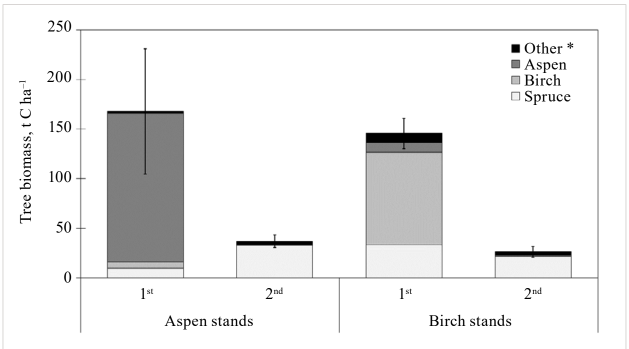

Figure 2. Mean tree biomass carbon stock of the first (1st) and second (2nd) layers by species in old-growth aspen and birch stands (error bars show ± 95% confidence intervals)

Other species includes, for example *Pinus sylvestris* L., *Tilia cordata* Mill., *Alnus glutinosa* (L.) Gaertn., *Alnus incana* (L.) Moench.

Table 2. Carbon stocks (mean, t C ha^{-1}) in the five major forest carbon pools for birch and aspen old-growth stands on mineral soils in hemiboreal Latvia. Confidence interval, ± 95%, along with the sampling size (*n*) provided in brackets if it differed from sampling size in Table 1

Carbon pools, t C ha^{-1}	Birch	Aspen
Living tree biomass	172 ± 18	205 ± 13
Above-ground biomass	133 ± 14	166 ± 11
Below-ground biomass	39 ± 4	39 ± 3
Deadwood	10 ± 3.2	13 ± 2.4
Lying deadwood	6 ± 2.4	8 ± 1.8
Dead standing trees	2 ± 1.5	3 ± 1.1
Dead standing trees with broken tops	1 ± 0.6	2 ± 0.4
Mineral soil	113 ± 41 (30)	105 ± 18 (69)
Forest floor	9 ± 4 (36)	17 ± 5 (69)
Total ecosystem carbon stock*	**316 ± 46 (10)**	**342 ± 29 (21)**

Note: * Total ecosystem carbon stock, i.e. the sum of all assessed carbon pools includes living tree biomass, deadwood, forest floor, and mineral soil

Results

The standing volume of the first layer ranged broadly across sample plots in the birch and aspen stands: from 158.7 to 652.5 m^3 ha^{-1}, and from 285.3 to 1199.7 m^3 ha^{-1}, respectively, characterizing within and between stand heterogeneity. The stand density in the first layer was between 80 and 500 trees ha^{-1} in sample plots in aspen stands and between 120 and 540 trees ha^{-1} in the birch stands.

The carbon storage in living tree biomass ranged from 88 to 271 t C ha^{-1} in the birch and from 70 to 318 t C ha^{-1} in the aspen sampling plots (Figure 2). The mean carbon stock in the living tree biomass for the birch and aspen old-growth stands was 172±17.5 t C ha^{-1} and 205±12.5 t C ha^{-1}, respectively, and there were no significant differences between these two tree species. The largest share of the mean living tree biomass carbon stock was stored in the above-ground biomass: 77% of living tree biomass carbon stock in the birch and 81% of living tree biomass carbon stock in the aspen stands (Table 2). In the birch stands, birch and spruce formed the major share of the first layer, with 68% and 22% of the carbon stock, respectively. In the aspen stands, minimal shares of tree biomass carbon were stored by spruce (11%) and birch (7%). In the second layer, most of the living tree biomass carbon in the aspen and birch old-growth stands was stored by spruce (76 to 85% of the second layer living tree carbon stock, respectively).

The carbon storage in deadwood between the sampling plots ranged from 0.3 to 53.8 t C ha^{-1} in the aspen stands and 0.7 to 40.3 t C ha^{-1} in the birch stands. Deadwood carbon pool size was similar between the birch and aspen stands (Table 2). Lying deadwood accounted for the majority (64% and 63%) of the total deadwood carbon pool in comparison to the other deadwood types in the birch and aspen stands. In the birch and aspen stands, carbon stocks of dead standing trees, and dead standing trees with broken tops were small and similar. Most of the stored carbon was in deadwood with decay stages 1 (recently dead) to 3 (moderately decayed) both in the old-growth birch and aspen stands. Completely decomposed wood accounted for only 2–3% of the total deadwood carbon stock.

According to the linear mixed effects models, above- and below-ground biomass carbon stock are determined by the standing volume of the first layer trees ($p < 0.001$) (Figures 3 and 4). Dominant tree species interaction with stand density and stand volume was significant for above-ground tree biomass carbon (both $p < 0.001$). The carbon storage of below-ground biomass is determined by the dominant tree species of the stand ($p < 0.001$) (Figure 4). Moreover, the dominant tree species of the stand ($p < 0.001$) and the interactions between the dominant tree species of the stand and the proportion of dominant tree species in the stand composition (both $p < 0.001$) had a significant influence on the carbon storage of below-ground biomass. The results of the models indicated that the carbon stock of the above-ground and also living tree biomass in the old-growth birch and aspen stands increased with rising stand density ($p < 0.001$) (Table 3; Figures 3 and 5). This effect was tree species dependent and notably more pronounced for the birch than for aspen stands (Table 3; Figures 3B and 5B). Only below-ground biomass carbon was determined by dominant tree species and its interaction with the proportion of the dominant tree species in the stand composition (Figure 4). According to the linear mixed-effects model, the deadwood carbon stock increased as the standing volume increased, and the stand density decreased (Table 3; Figure 6).

The forest floor carbon stock was not affected by the dominant species or other factors included in the linear regression (e.g. forest type, stand density, standing volume, species unit) (Table 2). Based on a similar analysis, mean carbon stocks in the entire sampled soil profile (0–80 cm) were similar between the old-growth birch and

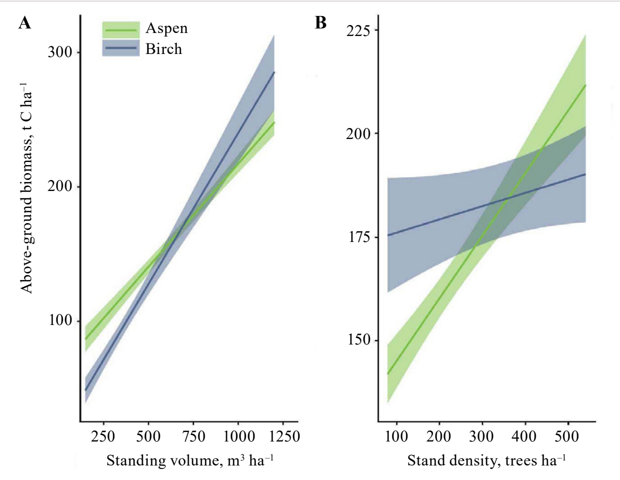

Figure 3. Model predicted change of the above-ground biomass carbon stock in response to (A) standing volume (M, m^3 ha^{-1}); (B) stand density (trees ha^{-1}) in old-growth birch and aspen stands. Mean (t C ha^{-1}) values ± 95% confidence interval

Table 3. The main effects of the explanatory variables and their interactions on the carbon stocks of the living tree biomass and deadwood (Satterthwaite generalized linear mixed-effect model)

Explanatory variable	*Sum Sq*	*Num DF*	*Den DF*	F value (*p*-value)
Living tree biomass				
Species	130	1	204.1	0.7
Stand density	5652	1	200.3	30.9 ***
Standing volume	78738	1	197.4	430.6 ***
Stand density by species	3370	1	200.3	18.4 ***
Standing volume by species	4027	1	197.4	22.0 ***
Deadwood biomass				
Species	1.9	1	184.8	4.2 *
Stand density	3.2	1	204.3	7.0 **
Standing volume	2.5	1	199.2	5.6 *
Standing volume by species	2.0	1	205.2	4.5 *

Notes: Species – birch, aspen; species unit – dominant tree species proportion of volume. *Sum Sq* stands for sum of squares, *Num DF* stands for numerator degrees of freedom, *Den DF* stands for denominator degrees of freedom. *p*-value shown as (*): $p < 0.05$; (**): $p < 0.01$; (***): $p < 0.001$.

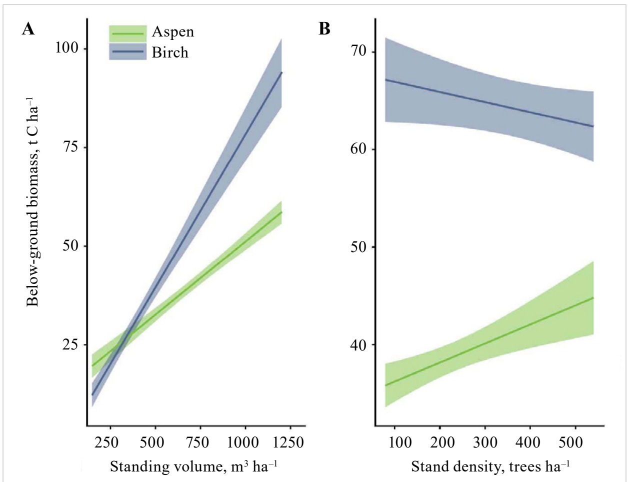

Figure 4. Model predicted change of the below-ground biomass carbon stock in response to (A) standing volume (M, m^3 ha^{-1}); (B) stand density (trees ha^{-1}) in old-growth birch and aspen stands. Mean (t C ha^{-1}) values ± 95% confidence interval

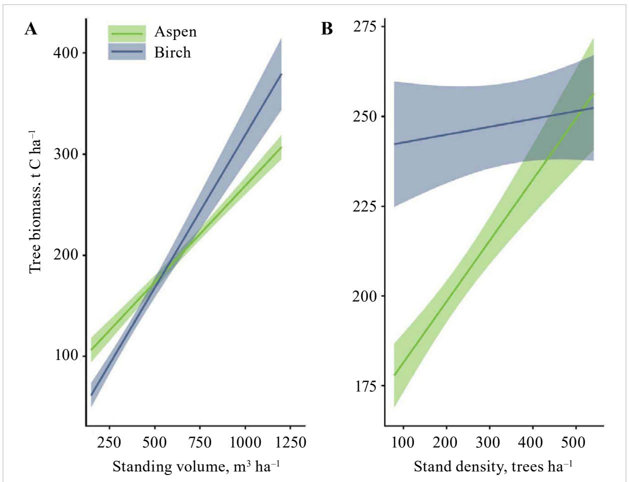

Figure 5. Model predicted change of the living tree biomass carbon stock in response to (A) standing volume (M, m^3 ha^{-1}); (B) stand density (trees ha^{-1}) in old-growth birch and aspen stands. Mean (t C ha^{-1}) values ± 95% confidence interval

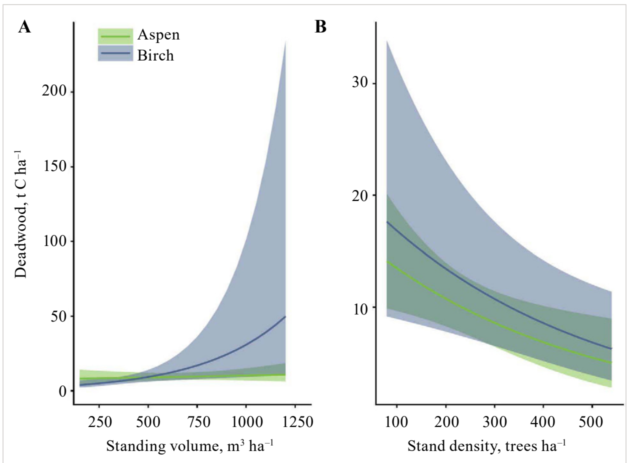

Figure 6. Predicted deadwood carbon stock in response to (A) standing volume (M, m^3 ha^{-1}) and (B) stand density (trees ha^{-1}). Mean (t C ha^{-1}) values ± 95% confidence interval

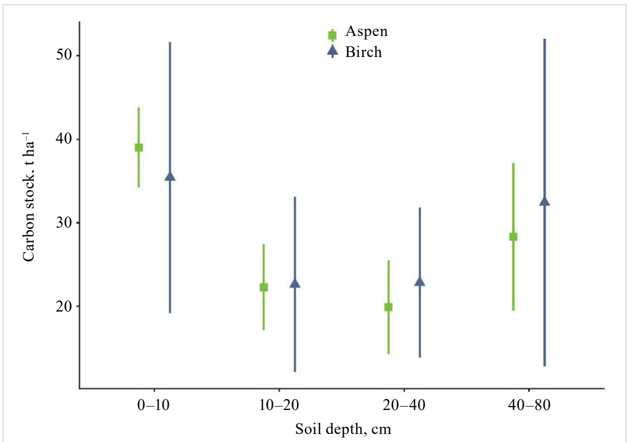

Figure 7. Differences in the mean soil carbon stock at different soil depths. Error bars show ± 95% confidence intervals

aspen stands. The carbon stocks within the sampled mineral soil layers (0–10 cm; 10–20 cm; 20–40 cm; 40–80 cm) were relatively similar but varied greatly between sampled stands (Figure 7). More than 30% of the soil organic carbon was concentrated in the upper 10-cm layer.

The mean total ecosystem carbon stock was only calculated for those stands that had data for all four carbon pools. It was similar in the old-growth birch and aspen stands (Table 2). Tree biomass formed the greatest percentage of the total ecosystem carbon stock, followed by mineral soil (0–80 cm), the forest floor, and deadwood (Table 2).

Discussion and conclusions

We found that the old-growth birch and aspen stands stored more total ecosystem carbon than the old-growth pine and spruce stands analysed in earlier studies in Latvia (Ķēniņa et al. 2018, Ķēniņa et al. 2019a). Although especially old aspen trees are susceptible to wood-rotting fungi (Latva-Karjanmaa et al. 2007, Arhipova et al. 2011), the effect of the presence of rot was not evaluated in our study, potentially leading to an overestimation of the carbon stock. Tree biomass formed the greatest percentage of the mean total ecosystem carbon stocks in the birch and aspen stands (57% and 60%), followed by mineral soil carbon pool (37% and 31%), forest floor (3% and 5%), and deadwood (3% and 4%) (Table 2). Above-ground biomass in turn, formed the major part of the total living tree biomass carbon pool. Other studies have likewise illustrated that living tree biomass is the dominant carbon pool (Finér et al. 2003, Seedre et al. 2015, Ķēniņa et al. 2019a). The high variability of the deadwood carbon pool size between the sampling plots reflects the heterogeneity of natural mortality within and between the old-growth stands. Previous studies of hemiboreal birch stands show that the mean deadwood carbon pool in old-growth stands is larger compared to younger mature stands (5.4 t C ha^{-1}; Table 2; Šēnhofa et al. 2020). A relatively small amount of carbon in deadwood in our studied stands indicates the absence of recent severe disturbances: thus, stands have reached their maximum biomass storing capacity. Most of the deadwood carbon stock in both deciduous old-growth stand types was in a decay stage between 1 (recently dead) and 3 (moderately decayed). Abiotic factors such as air temperature and humidity, and biotic factors such as fungi, insects, and wood properties (tree species and dimensions and dead tree position in stand; downed, standing tree) were the main aspects affecting decomposition of the dead trees in the stand (Yatskov et al. 2003, Ruel and Gardiner 2019). Since the deadwood amount and composition vary depending on the intensity and the time since the last disturbance (Martin et al. 2021), the limited amount of it as well as the decomposition stage in old-growth stands, demonstrate the minimal effect of disturbances. Consequently, the carbon storage in these stands can be used as the benchmark for storage capacity in hemiboreal aspen and birch stands.

Below-ground biomass carbon stock and its changes with increasing stand density were affected by dominant tree species (Figure 4B; Table 3), presumably reflecting the species differences in root system formation and adaptation parameters (root to shoot ratio, root length and mass) as well as inter-species differences in root system reaction to competition (Possen et al. 2011). Stand density significantly affected the carbon storage in living tree biomass, especially for birch. However, this could also be a reflection of the differences in species biology: aspen is better able to compensate the lost biomass of some trees due to natural mortality through the increased increment of the remaining trees (Table 3; Figures 3B and 5B). This is consistent with the previously described characteristics of birch (Hynynen et al. 2009), where vitality of this tree species decreased before the age of 100 years.

The mean carbon stocks of soil (0–80 cm) in our study were similar within the old-growth birch and aspen stands (Table 2). More than 30% of the soil carbon was found in the first sampled depth (0–10 cm), which is more strongly affected by different natural processes such as high microbial activity and soil respiration (Hansson et al. 2011). Our estimations support the previously gained knowledge from younger (60-year-old) silver birch (*Betula pendula* Roth) stands growing on fertile (*Oxalis*) sites in Estonia, where the upper 30 cm accumulated 38% of the total forest carbon pool (Uri et al. 2012). This also corresponds with the results from boreal, temperate, and tropical forests – where mean soil organic carbon stock decreased with increasing depth (Figure 7) (Hansson et al. 2011, Jones et al. 2019, Nord-Larsen et al. 2019). Our results for the mineral soil carbon pool size are consistent with the data from semi-natural temperate nemoral beech (*Fagus sylvatica* L.) dominated stands where the mean soil carbon pool (0–75 cm) was 114 t C ha^{-1} (Nord-Larsen et al. 2019). The substantial variation of soil carbon storage among the deciduous stands was not linked to their age, and supports the findings of other studies (mainly in a chronosequence of younger stands), in which, at some point (stand age), soil carbon saturation is reached and further increases in stand age do not lead to an ever-increasing soil carbon pool that was demonstrated in silver birch (Uri et al. 2012), grey alder (Uri et al. 2014), and Scots pine (Uri et al. 2022). Thus, soil carbon stocks in old-growth stands on mineral soils may not increase continuously, and thus do not contribute to climate change mitigation (Jandl et al. 2007, Hansson et al. 2011, Uri et al. 2012, Lutter et al. 2018).

The forest floor carbon pool, although small in numerical values, is considered an important transfer point between the surface and the soil carbon pools (Jandl et al. 2007). Forest floor carbon stocks were almost twice as large in the old-growth aspen stands compared to the old-growth birch stands (Table 2). Our estimated forest floor carbon stock in the birch stands was close to the forest floor carbon stock in the temperate semi-natural beech forest (6.9 t C ha^{-1}) (Nord-Larsen et al. 2019). Since the forest floor carbon stock tends to reach its maximum value after about 70 years of stand development (Pregitzer and Euskirchen 2004), the great range in forest floor carbon between the studied deciduous stands might be explained by variation in standing volume and thus litter influx. Though, previous studies have highlighted the effect of dominant tree species as well as ground vegetation and fauna, speed of mineralization of different litter on the forest floor carbon (Hansson et al. 2011, Vesterdal et al. 2013, Lutter et al. 2018).

These carbon pool data illustrate that the largest and most varied carbon pool in the old-growth birch and aspen dominated stands is the living tree biomass, which was significantly affected by the stand density and standing volume of the stand first tree layer. Individual dieback of the large first layer trees due to natural disturbance and/or aging may significantly reduce the carbon storage in old-growth forests. The resulting fragility is also affected by the notably shorter (in comparison to native conifers) life span of these tree species. We have further managed to quantify the mineral soil carbon pool, which was the second largest carbon pool, thus expanding the current knowledge of soil carbon in hemiboreal old-growth deciduous stands. However, further studies are needed to investigate soil carbon dynamics and emissions in old-growth stands.

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Supplementary Table 1s. Characteristics of old-growth European aspen and birch stands

Species	Age	First layer				Second layer			
		DBH, cm	H, m	Volume, $m^3\ ha^{-1}$	Density, trees ha^{-1}	Species	DBH, cm	H, m	Volume, $m^3\ ha^{-1}$
10A	110	48	39	687	207	5L5S	24	21	109
9A1S	115	57	38	565	167	5S5L	15	15	100
9A1S	119	47	38	602	223	10S	20	21	165
9A1B	119	44	39	620	243	10S	20	19	70
10A+B	109	46	39	812	266	10S	19	18	108
7A1B1P1S	110	41	32	623	385	9S1Ba	20	19	122
8A2B	107	47	33	473	200	8S1O1B	19	16	71
9A1B	135	53	35	579	180	9S1A	22	19	211
8A1S1B	114	44	37	628	283	10S	20	20	104
9A1S	104	55	39	783	210	10S	24	22	188
8A1B1S	114	55	39	753	233	10S	23	22	133
9A1S	109	47	38	770	277	7S3L	23	20	58
8A2S	104	46	37	601	250	7S3L	24	22	99
9A1S	104	50	39	712	237	9S1L	19	19	91
8A2S	118	48	33	598	230	10S	22	19	110
8A1S	118	53	36	761	250	6S3L1B	23	19	42
9A1B	116	51	39	721	250	8S2L	20	17	78
9A1S	111	48	40	950	303	10S	19	19	88
10A	118	45	37	764	280	9S1L	23	21	180
7A2S1B	107	52	38	622	203	10S	23	22	96
7A2S1B	113	51	36	709	287	10S	23	22	102
9A1S	108	50	34	383	125	7Ga3As	18	16	13
9A1B	105	41	29	617	340	9S1B	19	17	77
9A1B	119	45	38	599	240	10S	20	20	125
9A1S	104	55	38	689	190	9S1L	20	18	90
8B2S	129	42	29	372	233	6S4L	18	17	115
7B3S	148	31	27	242	270	10S	14	13	61
7B2S1P	126	33	28	336	307	9S1B	18	17	69
7B2S1A	126	38	31	479	310	8S1B1O	18	16	52
8B2S	131	40	30	464	273	9S1B	19	17	65
5B2A1P1S1O	123	41	30	514	280	5S3Ba2O	15	14	59
5B2A1P1S1O	127	41	30	514	280	5S3Ba2O	15	14	59
7B3S	140	42	31	356	236	6S2M1L1Ga	16	17	91
4B4S2Ba	140	30	25	299	367	10S	19	16	38
6B2A1S1Ba	125	43	33	450	230	8S1Ba1L	19	18	52
5B3S2P	124	39	30	531	324	10S	21	19	126
5B2S2A1P	124	36	27	400	345	8S2Ga	18	15	48
5B2S1A1Ba	136	35	27	316	365	8S1Ba1B	14	15	103
5B3A2S	124	32	32	445	367	10S	18	17	47
5B3S1P1A	138	39	34	531	305	10S	20	21	70

Notes: Species composition is based on the proportion of the species volume in the respective stand layer: 10 = 90%…100%, 9 = 80%...89%, 8 = 70%...79%, etc. A – European aspen (*Populus tremula* L.); S – Norway spruce (*Picea abies* (L.) Karst.); B – birch (pooled *Betula pendula* Roth and *Betula pubescens* Ehrh.); P – Scots pine (*Pinus sylvestris* L.); L – lime (*Tilia cordata* Mill.); Ba – black alder (*Alnus glutinosa* (L.) Gaertn.); O – Common oak (*Quercus robur* L.); As – ash (*Fraxinus excelsior* L.); M – Norway maple (*Acer platanoides* L.); Ga – gray alder (*Alnus incana* (L.) Moench).