PROMOCIJAS DARBS
zinātnes doktora grāda
zinātnes doktore (Ph.D.) lauksaimniecības,
meža un veterinārās zinātnēs iegūšanai

OGLEKĻA UZKRĀJUMS VECĀS MEŽAUDZĒS HEMIBOREĀLAJOS MEŽOS AR SAUSĀM MINERĀLAUGSNĒM

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CARBON STOCK IN OLD-GROWTH STANDS ON MINERAL SOILS IN HEMIBOREAL FORESTS

DOCTORAL THESIS
for the doctoral degree
Doctor of Science (Ph.D.)
in Agriculture, Forestry and Veterinary Sciences

LATVIJAS VALSTS MEŽZINĀTNES INSTITŪTS “SILAVA”
LATVIAN STATE FOREST RESEARCH INSTITUTE “SILAVA”

LATVIJAS BIOZINĀTŅU UN TEHNOLOĢIJU UNIVERSITĀTE
LATVIA UNIVERSITY OF LIFE SCIENCES AND TECHNOLOGIES

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Promocijas darbs izstrādāts Latvijas Valsts mežzinātnes institūtā “Silava”. Doktorantūras studiju laiks Latvijas Biozinātņu un tehnoloģiju universitātes Meža fakultātē no 2017. līdz 2020. gadam. Darbs izstrādāts pētījuma “Lēmumu pieņemšanas atbalsta rīka izstrāde, integrējot informāciju no vecām daļēji dabiskām mežaudzēm precīzākai oglekļa bilances novērtēšanai” (ERAF, Nr. 1.1.1.1/19/A/130) ietvaros, dati iegūti arī pētījumā “Siltumnīcefekta gāzu emisiju un CO_2 piesaistes novērtējums vecās mežaudzēs”.

The PhD thesis was prepared in Latvia State Forest Research Institute “Silava”. The PhD studies were carried out in Latvia University of Life Sciences and Technologies, Forestry Faculty in the period from 2017 to 2020. Preparation of the thesis was carried out in the project “Development of a decision support tool integrating information from old-growth semi-natural forest for more comprehensive estimates of carbon balance” (ERDF, No 1.1.1.1/19/A/130)”. Data gathered also in research “Assessment of greenhouse gas emission and CO_2 *sequestration in old forest stands”.*

Oficiālie recenzenti / *Official reviewers:*
1. Dr.silv. Andis LAZDIŅŠ, Latvijas Valsts mežzinātnes institūts “Silava” / *Latvian State Forest Research Institute “Silava”;*
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ANOTĀCIJA

Lielā daļā Eiropas, arī Latvijā, ir novērojama mežaudžu novecošanās, kā rezultātā ir izveidojies nozīmīgs biomasas un līdz ar to oglekļa uzkrājums, kas tuvojas piesātinājuma līmenim (Vilén et al. 2012; Nabuurs et al. 2013; Senf et al. 2021). Vecās audzes ir nozīmīgas bioloģiskās daudzveidības nodrošināšanā meža ainavā. Empīriskais datu materiāls, kas raksturotu oglekļa uzkrājumu šādās audzēs un to lomu klimata pārmaiņu mazināšanā, ir neliels un fragmentēts. Īpaši svarīga ir informācija par Eiropas boreālo un hemiboreālo mežu zonā augošajām vecajām mežaudzēm – šiem mežiem ir fundamentāla un pieaugoša loma gan bioekonomikā, gan klimata neitralitātes mērķu sasniegšanā. Promocijas darba mērķis ir novērtēt oglekļa uzkrājumu vecās, saimnieciskās darbības ilgstoši neietekmētās priežu, egļu, bērzu un apšu mežaudzēs sausieņos.

Pētījuma rezultāti liecina, ka oglekļa uzkrājums vecās audzēs ir būtiski atkarīgs no valdošās koku sugas. Vecās priežu un bērzu mežaudzēs oglekļa uzkrājumu ietekmē relatīvi liels egļu īpatsvars audzes pirmajā stāvā un to dominance otrajā stāvā, liecinot par dabisku paaudžu nomaiņu šajā vecumā (163–218 gadi skuju koku audzēs, 104–148 gadi lapu koku audzēs). To apliecina arī būtiski mazāks pirmā stāva biezums vecās mežaudzēs salīdzinājumā ar par 54–103 gadus jaunākām (kontroles) audzēm, norādot uz zemu oglekļa uzkrājuma stabilitāti: atsevišķu I stāva koku bojāeja dabisko traucējumu un/vai vecuma ietekmē var nozīmīgi samazināt kopējo oglekļa uzkrājumu. Lielākās oglekļa krātuves vecās mežaudzēs ir koku biomasa (55–61%, vidēji 59% no kopējā ekosistēmas uzkrājuma mežos ar minerālaugsnēm) un augsne (25–37%, vidēji 30% no kopējā ekosistēmas uzkrājuma mežos ar minerālaugsnēm), un pētījumā secināts, ka oglekļa uzkrājums vecās mežaudzēs ir vidēji par 20% lielāks nekā vidēji divas reizes jaunākajās kontroles audzēs. Savukārt oglekļa uzkrāšanās efektivitāte (oglekļa uzkrājums gadā) koku biomasā un atmirušajā koksnē pētījumā analizētajās vecās priežu, bērzu un egļu mežaudzēs ir būtiski (par 27% līdz 47%, atkarībā no koku sugas) mazāka nekā kontroles audzēs. Nelielais oglekļa uzkrājums atmirušajā koksnē liecina, ka analizētajā veco audžu kopā dabisko traucējumu ietekme ilgstoši ir bijusi nenozīmīga. Tātad iegūtie dati raksturo oglekļa uzkrājuma potenciālu (maksimumu) vecās audzēs.

Promocijas darbā iegūtās atziņas pielietojamas, raksturojot veidus, kā iespējami efektīvāk sasniegt un saglabāt klimatneitralitāti ilgtermiņā, kā arī kvantificējot ietekmi, kādu uz šo mērķu sasniegšanu radītu pastiprināti saimnieciskās darbības ierobežojumi citu politiku īstenošanai. Tātad nodrošināta iespēja pieņemt pamatotus (datos balstītus) lēmumus, līdzsvarojot dažādu politiku īstenošanu meža ainavā tādā veidā, lai radītu iespējami lielāko ieguvumu sabiedrībai.

Šis promocijas darbs sastāv no tematiski vienotām sešām zinātniskajām publikācijām.

ABSTRACT

The currently observed aging trend in large parts of Europe's forests have significantly increased the amount of woody biomass and therefore carbon stock accumulated in forests over the past decades, which come to their maximum (Vilén et al. 2012; Nabuurs et al. 2013; Senf et al. 2021). Old-growth forests contribute to biodiversity conservation function and overall species richness in the forest ecosystem. Thus, data on the carbon storage in old-growth stands in Europe is limited and fragmented to provide comprehensive data to provide a better understanding of their role in climate change mitigation. Of particular importance is data from old-growth European boreal and hemiboreal forests, which play a fundamental and growing role both in the bioeconomy and in achieving climate neutrality targets. The aim of this study was to evaluate the carbon stock in old-growth Scots pine, Norway spruce, birch, and European aspen stands, where old trees are still the dominant cohort growing on dry mineral soils.

Obtained results showed that the dominant tree species had a significant impact on carbon storage in old-growth forest stands in hemiboreal Latvia. A relatively high proportion of Norway spruce in the first floor and understory influenced the carbon stock size in old-growth Scots pine and birch dominated stands, also indicating the occuring natural succession in the studied age (163 to 218 years in coniferous stands, 104 to 148 years in deciduous stands). This is also suggested by the significantly lower stand density of the first floor in old-growth stands comparing with 54 to 103 years younger control stands. This demonstrated fragility of long-term carbon storage in tree biomass – only separate death of the large first floor trees due to natural disturbance and/or aging may significantly reduce the total carbon storage in old-growth forests. Largest carbon pools in the old-growth stands were tree biomass (55–61% depending on the dominant tree species, on average 59% of the total carbon stock in forests with mineral soils) and soil (25–37% depending on the dominant tree species, on average 30% of the total carbon stock in forests with mineral soils). Old-growth stands store on average 20% higher carbon stock than two times younger control stands. Contrary, the mean annual difference in the sum of the tree biomass and deadwood carbon was significantly lower in old-growth Scots pine, Norway spruce and birch dominated stands (by 27 to 47% depending on the tree species) than in control stands. Small share of the deadwood carbon stock in the total carbon stock indicates low intensity of natural disturbances in studied old-growth stands. Thus, analyzed old-growth stands representing potential maximum carbon storage in forests on dry mineral soils in Latvia.

The gained insight into the carbon-storing capacity of old-growth stands for the main tree species in hemiboreal forest zone could be used for a more accurate understanding of their actual and potential role in climate change mitigation and impacting data-driven policy and multi-purpose forest management decisions in achieving forest-related climate and biodiversity policy goals.

SATURS / *CONTENTS*

PUBLIKĀCIJU SARAKSTS / *LIST OF PUBLICATIONS*

Promocijas darbā iegūtie rezultāti apkopoti sešās publikācijās, uz kurām atsauces tekstā veidotas, izmantojot romiešu ciparus:

The thesis is based on six publications, referred in the text with Roman numerals:

I **Ķēniņa L.**, Elferts D., Bāders E., Jansons Ā. (2018) Carbon pools in a hemiboreal over-mature Norway spruce stands. Forests, 9, 435. 10.3390.f9070435

II **Ķēniņa L.**, Jaunslaviete I., Liepa L., Zute D., Jansons Ā. (2019) Carbon pools in old-growth Scots pine stands in hemiboreal Latvia. Forests, 10, 911. 10.3390/f10100911

III **Ķēniņa L.**, Mača S., Jaunslaviete I., Jansons Ā. (2019) Carbon pools in old-growth Scots pine stands on organic soils and its concentration in deadwood: cases study in Latvia. In: Proceedings of the 9th International Scientific Conference "Rural Development 2019". Vytaitas Magnus University, Agriculture Academy, Lithuania, p. 284–288. 10.15544/RD.2019.054

IV **Ķēniņa L.**, Jaunslaviete I., Liepa L., Straupe I., Bickovskis K. (2020) Tree biomass in over-mature unmanaged coniferous forests in Latvia. In: Proceedings of the XX International Multidisciplinary Scientific Geo-Conference Surveying, Geology and Mining, Ecology and Management – SGEM 2020, Albena. 10.5593/sgem2020/3.1/s14.099

V **Ķēniņa L.**, Elferts D., Jaunslaviete I., Bāders E., Jansons Ā. (2022) Sustaining carbon storage: lessons from hemiboreal old-growth coniferous and deciduous forest stands. Forest Science, 2022, 1–9. 10.1093/forsci/fxac055

VI **Ķēniņa L.**, Elferts D., Jaunslaviete I., Bāders E., Šņepsts G., Jansons Ā. (2022) Tree biomass – a fragile carbon storage in old-growth birch and aspen stands in hemiboreal Latvia. Baltic Forestry, 28(2), id654. 10.46490/BF654

Autoru ieguldījums / The contribution of the authors

	I	II	III	IV	V	VI
Ideja / *Original idea*	JĀ, **ĶL**	JĀ, **ĶL,** LL	JĀ, MS	**ĶL**, JĀ	**ĶL**	JĀ, **ĶL**
Pētījuma plāns / *Study design*	**ĶL**, JĀ	**ĶL**, ZD	**ĶL**, JĀ	**ĶL**, LL, SI	JĀ, **ĶL**	JĀ, **ĶL**
Datu ievākšana / *Data collection*	**ĶL**, BE	JI, **ĶL**	JI, MS	JI, **ĶL**, BK	JI, **ĶL**	JI, ŠG
Datu analīze / *Data analysis*	ED, **ĶL**, BE	**ĶL**	**ĶL**, JĀ	**ĶL**, JĀ	ED, **ĶL**	ED, BE, **ĶL**
Manuskripta sagatavošana / *Manuscript preparation*	**ĶL**, JĀ	**ĶL**, JĀ	**ĶL**, JĀ	**ĶL**, JĀ	**ĶL**, JĀ	**ĶL**, JĀ
Promocijas darba autora ieguldījums, % / *Contribution of author of the thesis, %*	80	85	50	80	75	70

BE – Endijs Bāders, BK – Kārlis Bičkovskis, ED – Didzis Elferts, JĀ – Āris Jansons, JI – Ieva Jaunslaviete, ŠG – Guntars Šņepsts, **ĶL – Laura Ķēniņa**, LL – Līga Liepa, MS – Santa Mača, SI – Inga Straupe, ZD – Daiga Zute.

PROMOCIJAS DARBA REZULTĀTU APROBĀCIJA / *APPROBATION OF RESEARCH RESULTS*

Ziņojumi par pētījuma rezultātiem prezentēti deviņās starptautiskajās konferencēs:

Results of the study have been pressented in nine international scientific conferences:

1. Zute D., **Ķēniņa L.**, Jaunslaviete I., Samariks V., Jansons Ā. (2021) Old-growth coniferous stands on fertile drained organic soils: first results of tree biomass and deadwood carbon stocks. 6th International conference “Sustainable management of natural resources – a basic condition for successful socio-economic development in the period of implementation of the new environmental policy of the European Union”, 25 November 2021, Jelgava, Latvia, stenda referāts / *poster*.
2. **Ķēniņa L.** (2021) Carbon stock in old-growth Scots pine (*Pinus sylvestris* L.) forests on wet peat soils in Latvia. 16th International Peatland Congress 2021 – IPC 2021, 3–6 May 2021, Tallinn, Estonia, prezentācija / *oral presentation*.
3. **Ķēniņa L.** (2020) Tree biomass and deadwood volume in old un-managed coniferous hemiboreal forests in Latvia. XX International Multidisciplinary Scientific GeoConference Surveying, Geology and Mining, Ecology and Management – SGEM 2020, 16–25 August 2020, Albena, Bulgaria, prezentācija / *oral presentation*.
4. **Ķēniņa L.** (2020) Biomass distribution in over-mature Scots pine and Norway spruce forest stands. International Scientific Events, Ecology & Safety, 26– 29 August 2020, Burgas, Bulgaria, prezentācija / *oral presentation*.
5. **Ķēniņa L.**, Mača S., Jaunslaviete I., Jansons Ā. (2019) Carbon pools in old-growth Scots pine stands on organic soils and its concentration in deadwood: cases study in Latvia. 9th International Scientific Conference “Rural Development 2019: Research and Innovation for Bioeconomy”, 26– 28 September 2019, Kaunas, Lithuania, prezentācija / *oral presentation*.
6. Jansons Ā., Bārdulis A., **Ķēniņa L.**, Lazdiņa D., Džeriņš E., Kāpostiņš R. (2018) Carbon content of below-ground biomass of young Scots pines in Latvia. Biosystems Engineering 2018, 9–11 May 2018, Tartu, Estonia, stenda referāts / *poster*.
7. **Ķēniņa L.**, Straupe I., Liepa L., Bigača Z., Jansons Ā. (2018) Carbon storage in tree biomass in old Norway spruce and Scots pine dominated hemiboreal forests, Latvia. Forestry Conference for Baltic PhD students, 26–27 April 2018, Sokka, Estonia, prezentācija / *oral presentation*.

8. **Ķēniņa L.**, Donis J., Šņepsts G., Bigača Z., Krišāns O., Jansons J., Jansons Ā. (2017) Characteristics of over-mature Norway spruce stands in hemiboreal forests, Latvia. International scientific conference “Environment and sustainable forest management in the Baltics. The Earth and human- in balanced interaction”, 9 November 2017, Daugavpils, Latvia, stenda referāts / *poster*.
9. Jansons Ā., **Ķēniņa L.**, Šēnhofa S., Bigača Z., Džeriņa B., Jansons J. (2017) Carbon in aboveground biomass of old Norway spruce stands in hemiboreal forests, Latvia. Natural Disturbance Dynamics Analysis for Forest Ecosystem Management FORDISMAN conference 2017, 12–13 October 2017, Šķēde, Latvia, stenda referāts / *poster*.

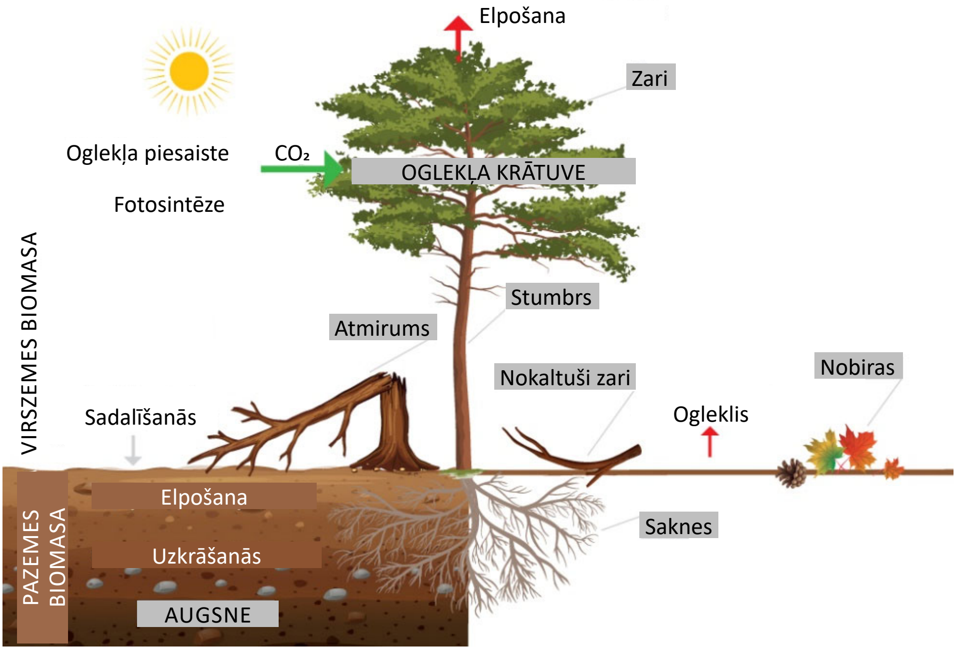
1. IEVADS

Mežam ir būtiska loma bioloģiskās daudzveidības nodrošināšanā meža ainavā, kā arī klimata pārmaiņu mazināšanā un citu ekosistēmas pakalpojumu nodrošināšanā (Seedre et al. 2015; Bernáldez 2017; Badalamenti et al. 2019; Kulha et al. 2020). Eiropā veci meži ir reti sastopami, tomēr lielā daļā Eiropas, arī Latvijā, ir novērojama mežaudžu novecošanās tendence, kā rezultātā ir izveidojies nozīmīgs biomasas un līdz ar to oglekļa uzkrājums, kas tuvojas piesātinājuma līmenim (Vilén et al. 2012; Nabuurs et al. 2013; Senf et al. 2021). Līdztekus darbam Eiropas Savienības (ES) Klimata politikas ietvarā, vecu mežu loma bioloģiskās daudzveidības uzturēšanā uzsvērta arī ES Bioloģiskās daudzveidības stratēģijā 2030 (O'Brien et al. 2021). ES Bioloģiskās daudzveidības stratēģija paredz noteikt stingrus aizsardzības pasākumus – aizsargāt 30% ES sauszemes teritorijas, stingri aizsargāt 10% ES sauszemes teritorijas, kā arī stingri aizsargāt visus pārējos ES pirmatnējos un senos mežus, kuros iekļauti arī veci meži (Eiropas Komisija 2020; O'Brien et al. 2021). Tāpēc, lai maksimāli efektīvi izmantotu ierobežoto meža platību dažādo mērķu sasniegšanā, svarīga ir zinātniskā informācija par veciem mežiem un par oglekļa uzkrājuma potenciālu vecās mežaudzēs, kas atrodas abu stratēģiju interešu lokā.

Latvija ir ratificējusi Kioto protokolu (2002. gads) un Parīzes nolīgumu (2017. gads), un – kā Apvienoto Nāciju Organizācijas (ANO) un ES dalībvalsts – ir uzņēmusies saistības ES Klimata politikas ietvarā samazināt ikgadējo siltumnīcefekta gāzu (SEG) emisiju apjomu, tādā veidā mazinot klimata pārmaiņas. Oglekļa uzkrājums mežā sniedz ievērojamu ieguldījumu ceļā uz ES līmeņa klimata mērķu sasniegšanu, kas katrai valstij noteikti Zemes lietošanas, zemes izmantošanas maiņas un mežsaimniecības (ZIZIMM) sektora regulas ietvaros (ES Regula 2018/841, 2018 ; ES Regula 2018/842, 2018). Jaunā ES ZIZIMM regula pirmo reizi paredz noteikt obligātas saistības samazināt SEG emisijas ZIZIMM sektorā, tajā skaitā aramzemēm un zālājiem, papildus izveidojot meža references līmeņa metodiku saistību noteikšanai. Jaunajā pieejā paredzēts, ka, aprēķinot meža sektora SEG samazināšanas saistības 2021.–2025. gados, noteikta CO_2 piesaiste, kas veidotos koksnes krājas ikgadējā pieauguma rezultātā un citās oglekļa krātuvēs, no tās atņemot koksnes atmiruma un mežizstrādes radītos oglekļa zudumus, kā arī SEG emisijas no augsnes, meža ugunsgrēku un meža mēslošanas rezultātā, ja meža apsaimniekošana turpinātos kā references periodā (2000.–2009. gads). Nākošajam periodam (2026.–2030. gads) piedāvāta citāda metodika, nosakot kopīgu mērķi visam ZIZIMM sektoram, kas Latvijā vairākkārt palielinātu emisiju samazināšanas mērķi. Papildus tam, ES ir noteikusi principu, ka ZIZIMM sektora devumu klimata politikā ir nepieciešams zinātniski pamatot, lai to akceptētu ANO klimata konvencijas pārstāvji, ikgadēji izvērtējot katras valsts progresu, kā arī atspoguļot ikgadējos ziņojumos. Tādēļ ir svarīgi iegūt zinātniski pamatotus oglekļa uzkrājuma un tā dinamikas datus hemiboreālajos mežos, kurus tālāk izmantot, sagatavojot ziņojumus par valsts progresu dažādu ES mēroga stratēģiju mērķu īstenošanā, tā virzoties uz klimatneitralitāti un nenodarot ekonomiskus zaudējumus Latvijas tautsaimniecībai neprecīzu metožu pielietošanas radīto sankciju rezultātā. Turklāt, ES elastības mehānismu ietvaros, meža nozare var palīdzēt sasniegt citu tautsaimniecības nozaru (lauksaimniecība, transports) mērķus gadījumā, ja tā jau ir īstenojusi savu mērķi.

Informācija par oglekļa uzkrājumu vecās audzēs Eiropā ir fragmentāra, tomēr šādu audžu platība kā Latvijā, tā Eiropā kopumā pieaug (Vilén et al. 2012; EFE State and trends 2016; Badalamenti et al. 2019; Sabatini et al. 2020). Tajā pašā laikā pieejamais empīriskais datu materiāls par vecajās audzēs esošo oglekļa uzkrājumu, īpaši boreālajos un hemiboreālajos mežos, kuri ir būtisks Eiropas meža resurss, nav visaptverošs. Tas ir viens no iemesliem, kāpēc Eiropā šobrīd notiek tik spraigas diskusijas par veco audžu ietekmi klimata un ar to saistīto politiku balansa nodrošināšanā starp dažādiem ekosistēmas pakalpojumiem, radot iespējami lielāku ieguvumu sabiedrībai (Högbom et al. 2021; Molina-Valera et al. 2021). Lai iegūtu precīzus datus par oglekļa uzkrājumu vecās audzēs, nepieciešama zinātniski pamatotu datu ievākšana, tādējādi izvairoties no oglekļa uzkrājuma pārvērtēšanas un dodot iespēju pamatot veco audžu lomu ES mērķu sasniegšanā.

Mežā kopējo oglekļa uzkrājumu nosaka dažādu oglekļa krātuvju (*carbon pools*) lielums un to izmaiņu dinamika – koku biomasa, atmirums, augsne, un zemsega, kā arī zemsedzes augi, kas ir dinamiska un maz pētīta daļa (1.1. att.). Oglekļa krātuve (*carbon pool*) ir dabas sistēma vai tās daļa, kurā ir uzkrāts ogleklis (*carbon storage*), jebkāds oglekli saturošas siltumnīcefekta gāzes prekursors vai jebkāda



1.1. att. **Oglekļa krātuves un tā aprite meža ekosistēmā** oglekli saturoša siltumnīcefekta gāze. Katra oglekļa krātuve vai krātuvju kopa (*carbon pool*) glabā noteiktu oglekļa masu jeb oglekļa uzkrājumu (*carbon stock*). Meža ekosistēmās nosaka oglekļa uzkrājumu, kā arī tā dinamiku/bilanci (*carbon budget*), ko novērtē, analizējot oglekļa piesaisti (*carbon sequestration*) un oglekļa emisijas (*carbon emissions*). Neto primārajā ražošanā (*net primary production*) notiek oglekļa dioksīda (CO_2) piesaiste (*carbon sequestration*) no atmosfēras CO_2 piesaistītājos. Fotosintēzes procesā koki no atmosfēras piesaista (*carbon sequestration*) CO_2, akumulējot oglekli koksnes biomasā, un atbrīvo skābekli. Oglekļa piesaistītājs (*carbon sink*) ir jebkas, kas CO_2 no atmosfēras spēj absorbēt vairāk nekā atbrīvot (pozitīva ekosistēmas produktivitāte) – koku biomasa, augi, okeāns vai augsne. Un pretēji, oglekļa avots (*carbon source)* ir jebkas, kas atbrīvo/emitē vairāk CO_2 atmosfērā nekā to absorbē un tam ir negatīva ekosistēmas produktivitāte. Oglekļa bilance var būt gan pozitīva (*carbon sink*) (piesaista vairāk oglekli nekā emitē), gan negatīva (*carbon source*) (emisijas ir lielākas par oglekļa piesaisti), un šī bilance dinamiski mainās atkarībā no audzes produktivitātes un dabisko traucējumu ietekmes. Meža ekosistēmās pēc dabiskā traucējuma (piemēram, ugunsgrēka) vai koku ciršanas mežaudze noteiktu laika posmu var būt ar negatīvu ekosistēmas produktivitāti (*carbon source*), bet pēc laika, mežam aktīvi augot un ražojot biomasu, audze atkal uzrāda pozitīvu oglekļa bilanci (*carbon sink*) (Taylor et al. 2014).

Pētījumā vērtēts oglekļa uzkrājums (*carbon stock*, *carbon storage in carbon pools*) vecās mežaudzēs, bet ne tā piesaistes dinamika. Veci meži uzskatāmi nodrošina nozīmīgu oglekļa uzkrājumu un piesaisti koku biomasā un citos šīs ekosistēmas komponentos (Brockerhoff et al. 2017; Gundersen et al. 2021). Klimats, tā pārmaiņas, augšanas apstākļi, valdošā koku suga, audzes vecums, atmiruma veidošanās – gan dabiskā atmiršana, gan dabisko traucējumu izraisītā – ietekmē katras oglekļa krātuves lielumu (Jandl et al. 2007; Jacob et al. 2013; Kumpu et al. 2018; Clarke et al. 2021). Atkarībā no dažādiem ietekmējošajiem faktoriem un to mijiedarbības konkrētajā vietā, konkrēta mežaudze attiecīgā dzīves cikla posmā var būt gan oglekļa avots (*carbon source*), gan oglekļa piesaistītājs (*carbon sink*) un spēj saglabāt pozitīvu oglekļa bilanci ilgstošu laika periodu (Framstad et al. 2013).

Audzes vecums ir viens no faktoriem, kam ir nozīmīga ietekme uz kopējo oglekļa bilanci konkrētajā vietā, un to apliecina arī iepriekšējos pētījumos iegūtie secinājumi (Pregitzer & Euskirchen 2004; Wei et al. 2013; Yuan et al. 2016; Martin et al. 2018). Pieaugot audzes vecumam, oglekļa uzkrājums koku biomasā zināmu laika periodu pieaug, tomēr šis process ir cieši saistīts ar audzes taksācijas rādītājiem un dabisko traucējumu ietekmi (Pukkala et al. 2017; Luyssaert et al. 2021; Gundersen et al. 2021). Igaunijā veiktā pētījumā secināts, ka uzkrātā oglekļa apjoms koku biomasā pieaug līdz 100 gadu vecumam, kad tas nostabilizējas (Uri et al. 2019; ; Uri et al. 2021). Arī Spānijā veiktā pētījumā konstatēts, ka oglekļa uzkrājums koku biomasā ir ļoti liels parastā dižskābarža (*Fagus sylvatica* L.) pieaugušās audzēs, bet vecākās audzēs tas variē atkarībā no dabisko traucējumu ietekmes, parādot, ka koksnes biomasa, līdz ar to oglekļa uzkrājums ne vienmēr ir nozīmīgi lielāks dabiskās, vecās mežaudzēs (Molina-Valero et al. 2021). Veca audze var saglabāt pozitīvu oglekļa piesaisti vairākus gadu simtus, ko apliecina arī Ziemeļamerikas boreālajos mežos pētītas *Pinus* sp. audzes, kur konstatēts, ka audze sasniedza oglekļa piesaistes un emisiju neitralitāti vairāk nekā 400–600 gadu vecumā (Framstad et al. 2013). Tieši vecu audžu spēja glabāt lielu oglekļa uzkrājumu un darīt to ilgstošu laika periodu ir iemesls, kāpēc vecās audzes kļuvušas aktuālas klimata pārmaiņu politiku kontekstā, tomēr, tā kā šo politiku mērķis ir samazināt CO_2 atmosfērā, vecām audzēm nav pozitīvas ietekmes uz klimata pārmaiņu mazināšanu ilgtermiņā (Kun et al. 2020).

Valdošā koku suga ir viens no faktoriem, kas ietekmē ne tikai oglekļa uzkrājumu koku biomasā, jo sugām ir atšķirīga produktivitāte, bet arī atmirušās koksnes un nobiru veidošanos un sadalīšanās procesu, kā arī ietekmē augsni un uzsūcošo sakņu veidošanos un sadalīšanās dinamiku (Hansson et al. 2011; Laganière et al. 2015; Błońska et al. 2019).

Dabisko traucējumu kopējais un kumulatīvais risks var būtiski mainīt oglekļa uzkrājumu vecās audzēs, jo līdz ar vecumu pieaug arī vēja un dendrofāgo kukaiņu radītie riski (Seidl et al. 2020). Laika gaitā ne vien samazinās mežaudzes noturība pret dažādiem dabiskajiem traucējumiem, bet arī palielinās nopietna dabiska traucējuma (piemēram, vētras) iestāšanās varbūtība (Jõgiste et al. 2017). Konstatēts, ka trupe, it īpaši neapsaimniekotajās audzēs, ir viens no faktoriem, kas ietekmē koku noturību, līdz ar to var atstāt arī ietekmi uz oglekļa uzkrājumu, sevišķi apšu audzēs, kur trupi konstatē biežāk nekā citām koku sugām (Latva-Karjanmaa et al. 2007). Tāpat prognozēts, ka dabisko traucējumu biežums un intensitāte klimata pārmaiņu ietekmē pieaugs, tādējādi nozīmīgi ietekmējot oglekļa uzkrāšanos un audzes noturību ilgā laika periodā (Seidl et al. 2020; Högbom et al. 2021). Vislielākās oglekļa uzkrājuma izmaiņas konstatē koksnes biomasā, kā rezultātā nozīmīgi tiek izmainīta dzīvo koku biomasas un atmiruma proporcija, samazinot kopējo ekosistēmas oglekļa uzkrājumu pat par 39% (Thom & Seidl 2016). Vecās audzēs konstatēta ievērojama oglekļa uzkrājuma variācija atkarībā no dabiskā traucējuma intensitātes ilgstošā laika periodā (Palviainen et al. 2020). Arī dabiskās sukcesijas procesā vecās audzēs novēro individuālu koku atmiršanu, kā rezultātā pieaug CO_2 emisijas, sadaloties atmirušajai koksnei (Kuuluvainen & Gauthier 2018; Jones et al. 2019; Šēnhofa et al. 2020). Tomēr kopumā audze var palikt pozitīva oglekļa krātuve (*carbon sink*) arī pēc dabiskā traucējuma, kaut arī oglekļa emisijas visās oglekļa krātuvēs pieaug. Tas pierāda, ka nepieciešams detalizēti pētīt oglekļa plūsmas (*carbon fluxes*) mežaudzēs, īpaši vecās audzēs, kur notiek nepārtrauktas strukturālās un ainaviskās izmaiņas dabiskās sukcesijas, dabisko traucējumu un citu faktoru ietekmē (Kuuluvainen & Gauthier 2018; Nord-Larsen et al. 2019; Palviainen et al. 2020).

Klimats nosaka ne tikai biomasas augšanu (tajā skaitā koku), bet arī organisko vielu sadalīšanās ātrumu, līdz ar to atstājot būtisku ietekmi uz oglekļa uzkrājuma veidošanās dinamiku (Khan et al. 2019). Dažādi klimatiskie faktori – gaisa temperatūra un gaisa mitrums (Khan et al. 2019; Sullivan et al. 2020), augsnes temperatūra un mitruma režīms (Lim et al. 2019), kā arī nokrišņu daudzums (Hasper et al. 2016), ir faktori, kas analizēti, lai izvērtētu klimata ietekmi uz koku biomasas veidošanos. Saistībā ar klimatiskajiem faktoriem arī konkrētās vietas ģeogrāfiskajam platumam ir ietekme uz oglekļa uzkrājumu parastās priedes audzēs (66–178 gadi) – tas konstatēts, analizējot audzes teritorijā no Polijas dienvidiem līdz Somijas ziemeļiem (Vucetich et al. 2000). Papildus minētajiem t.s. “dabiskajiem faktoriem” liela nozīme ir arī audzes noturību sekmējošam meža apsaimniekošanas veidam, kas tādējādi nodrošina ilgtspējīgu ieguvumu klimata pārmaiņu mazināšanā, veicinot oglekļa piesaisti meža ekosistēmā.

Var secināt, ka meža ekosistēmas oglekļa uzkrājuma un piesaistes potenciāls ir atkarīgs no daudziem ietekmējošajiem faktoriem un šo faktoru mijiedarbībām, kas atšķiras ne tikai starp klimata zonām, bet pat viena klimatiskā reģiona ietvaros, līdz ar to nepieciešams ievākt plašu lokālu empīrisko materiālu, lai būtu pamats secinājumu izdarīšanai par veco audžu oglekļa uzkrājumu un tā dinamiku.

Veco audžu precīza definēšana ir noteicoša, lai nošķirtu vairākus atšķirīgus jēdzienus un lai tādējādi neveidotos dažādas interpretācijas, un salīdzinājums konkrētajā situācijā būtu korekts (O’Brien et al. 2021). Analizētās vecās audzes pētījumā atbilst ANO Pārtikas un lauksaimniecības organizācijas jeb FAO klasifikācijas n6 kategorijai – *old-growth forest* (Buchwald 2005). Šajos mežos raksturīgi veci, lieli koki un novērojami arī ar tiem saistītie ekosistēmas struktūras elementi, kas var būtiski atšķirties starp klimatiskajām joslām, kā arī pat starp specifiskiem augšanas apstākļiem, kas veidojušies konkrēta dabisko traucējumu režīma vai pagātnē notikušas cilvēku darbības ietekmē. Kā būtiskākos ekosistēmas struktūras elementus vecās audzēs min: 1) lielu dimensiju koki (atbilstoši konkrētajiem augšanas apstākļiem un koku sugai); 2) lielu dimensiju un salīdzinoši liela apjoma atmiruma klātbūtne; 3) starp audzēm un audzes ietvaros liela koku dimensiju un audzes biezuma dažādība; 4) dabisko traucējumu ietekmes elementi – lauztas galotnes, stumbra un sakņu bojājumi; 5) dažādstāvu audze; 6) atvērumi audzes vainagu klājā, mozaīkstruktūra (Buchwald 2005). Tātad, veca kokaudze var būt vecs mežs, bet ne vienmēr vecu mežu veido veca kokaudze. Eiropā aplēsts, ka tikai 0,7% no kopējās mežu platības ir veci meži (Sabatini et al. 2020), atbilstoši FAO klasifikācijai (n10–n5). Sākotnēji šajā pētījumā lietots termins “pāraugusi audze”, ko pētījuma gaitā ir papildinājis/nomainījis termins “veca mežaudze”. **Veca mežaudze** ir mežaudze, kurā valdošās koku sugas koki ir pārsnieguši atjaunošanas cirtes vecuma robežvērtību par vismaz divām vecumklasēm. Šajā pētījumā analizēts konkrēts mežaudzes stāvoklis, kad vecā mežā (ilgstoši antropogēni maz traucēts mežs ar dabisko traucējumu ietekmi) dominējošais meža elements vēl joprojām ir veci koki, t.i., tā ir veca audze.

Eiropā līdz šim veikts maz pētījumu par kopējo oglekļa uzkrājumu vecās mežaudzēs, pārsvarā analizējot parasto dižskābardi (Nord-Larsen et al. 2019; Molina-Valero et al. 2021), parasto egli (*Picea abies* (L.) Karst.) (Mund et al. 2002; Jacob et al. 2013; Seedre et al. 2015) vai ozolu (*Quercus* sp.) (Badalamenti et al. 2019; Nord-Larsen et al. 2019), lielākoties Vidusjūras kalnu reģionos. Dānijā veiktā ilglaicīgā pētījumā par veciem (līdz 142 gadiem) platlapjiem (*Fagus sylvatica*, *Quercus robur* L.) mistraudzē, secināts, ka šīs audzes ir lielas oglekļa krātuves (arī atmirusī koksne veido nozīmīgu un stabilu oglekļa krātuvi, 35 t C ha^{-1}), bet oglekļa piesaiste (ekosistēmas produktivitāte) ir ļoti zema (Nord-Larsen et al. 2019). Ziemeļeiropas hemiboreālajā un boreālajā zonā nav pieejami visaptveroši pētījumi par oglekļa uzkrājumu vecās mežaudzēs, kaut arī tieši šajā reģionā koncentrēti nozīmīgi meža resursi. Pieejamās meta-analīzes, kurās salīdzināts oglekļa uzkrājums tropiskajos, mērenās joslas un boreālajos mežos, norāda, ka boreālajā reģionā audzes agrāk sasniedz oglekļa uzkrājuma maksimumu un tas ir salīdzinoši mazāks nekā mērenās joslas vai tropiskajos mežos (Pregitzer & Euskirchen 2004). Boreālajos mežos Somijas austrumdaļā salīdzinoši nabadzīgā meža tipā (*Vaccinium-Myrtillus*) vecā (140 gadi) mistrotā audzē, kurā valdošā suga ir parastā egle, kopējais ekosistēmas oglekļa uzkrājums ir 175 t C ha^{-1} (60% konstatēts koku biomasā) (Finér et al. 2003). Augsne kā ļoti liela oglekļa krātuve, īpaši boreālajā un hemiboreālajā reģionā (Deluca & Boisvenue 2012; Bradshaw & Warkentin 2015; Mayer et al. 2020), ir bieži pētīta, tomēr nav pētījumu par situāciju vecās mežaudzēs. Igaunijā, analizējot 70 līdz 139 gadus vecas audzes (parastā priede (*Pinus sylvestris* L.), parastā egle, bērzi (*Betula pendula* Roth un *Betula pubescens* Ehrh.), parastā apse (*Populus tremula* L.), parastais ozols (*Quercus robur* L.), melnalksnis (*Alnus glutinosa* (L.) Gaerth.), baltalksnis (*Alnis incana* (L.) Moench)), konstatēts, ka meža tipam un sugu sastāvam ir nozīmīga ietekme uz oglekļa uzkrājumu, un tas būtiski variē starp objektiem no 10 līdz 152 t C ha^{-1} (Lutter et al. 2019).

Latvija atrodas hemiboreālajā zonā, kas ir pāreja starp mērenās joslas un boreālajiem mežiem (Ahti et al. 1968). Hemiboreālā mežu zona nošķir tipisko skujkoku boreālo mežu zonu no mērenās joslas tipisko lapu koku mežu zonas. Hemiboreālajā zonā atrodamas skujkoku un lapu koku mistraudzes, kas nodrošina daudzveidīgu sugu sastāvu (Lõhmus & Kraut 2010). Eiropas hemiboreālo mežu zona ir unikāla Eiropā, jo šeit mežs klāj nozīmīgu daļu valstu teritoriju jau ļoti ilgi laiku – Latvijā un Igaunijā pusi teritorijas klāj meži, Lietuvā – trešdaļu (Jõgiste et al. 2018). Turklāt potenciāli Latvijas teritoriju varētu klāt līdz pat 90% mežu, un tikai antropogēnās ietekmes (it īpaši – lauksaimniecības vajadzībām veiktās atmežošanas) rezultātā meža zemes īpatsvars ir mazāks (Jõgiste et al. 2018). Ņemot vērā stipri variējošo dabisko traucējumu režīmu, kā arī tradicionālo cilvēka darbības ietekmi, augsnes dažādību un šo faktoru savstarpējās mijiedarbības, hemiboreālajā mežu zonā ir sarežģīti raksturot dabisku meža attīstību jeb sukcesijas procesu (Lõhmus & Kraut 2010; Nigul et al. 2015). Parastās priedes un parastās egles mistrojums ar lapu kokiem – bērziem, parasto apsi un alkšņiem – ir bieži sastopams hemiboreālajā zonā, kur lapu koki lielākoties sastopami sākotnējās sukcesijas stadijās līdz sukcesijas vidusposmam (European Environment Agency 2007). Kopumā Latvijā ir 3239,7 tūkst. ha meža, kas aizņem vairāk nekā 50% no Latvijas valsts sauszemes platības. Saskaņā ar Meža statistiskās inventarizācijas (MSI 2016–2020) datiem, Latvijā četras galvenās koku sugas – priede, egle, bērzi un apse – aizņem 80,6% no kopējās mežaudžu platības un 85,7% no kopējās mežaudžu krājas.

Puse no mežiem Latvijā atrodas sausieņu meža tipos, galvenokārt damaksnī (*Hylocomniosa*) un vērī (*Oxalidosa*), kuru kopējais īpatsvars ir 39,5% no kopējās mežu platības (MSI, 2016–2020). Oglekļa uzkrājuma novērtēšana Latvijā tieši meža tipos ar augstāko īpatsvaru no kopējās meža platības un plašāk pārstāvētajām koku sugām ir īpaši nozīmīga, raksturojot veco mežaudžu potenciālo lomu klimatneitralitātes mērķu sasniegšanā.

1.1. Promocijas darba mērķis

Pētījuma mērķis ir novērtēt oglekļa uzkrājumu vecās, saimnieciskās darbības ilgstoši neietekmētās priežu, egļu, bērzu un apšu audzēs sausieņu mežos.

1.2. Promocijas darba uzdevumi

Lai sasniegtu pētījuma mērķi, izvirzīti šādi darba uzdevumi:

1. novērtēt vecu mežaudžu taksācijas rādītājus;
2. raksturot vecu audžu galveno oglekļa krātuvju (dzīvo koku biomasa, atmirums, augsne un zemsega) un kokaudžu parametru sakarības;
3. izpētīt audzes vecuma ietekmi uz oglekļa uzkrājumu.

1.3. Promocijas darba tēzes

Promocijas darbā izvirzītas divas tēzes:

1. Damaksnī un vērī kopējais ekosistēmas oglekļa uzkrājums, palielinoties audzes vecumam (priedei virs 97 gadiem, eglei virs 79 gadiem, bērzam virs 69 un apsei virs 58 gadiem), turpina pieaugt, savukārt oglekļa uzkrāšanās efektivitāte (oglekļa uzkrājums gadā) samazinās;
2. Dzīvo koku oglekļa krātuve vecās, saimnieciskās darbības ilgstoši neietekmētās priežu, egļu, bērzu un apšu mežaudzēs damaksnī un vērī veido lielāko daļu no kopējā oglekļa uzkrājuma.

1.4. Pētījuma novitāte

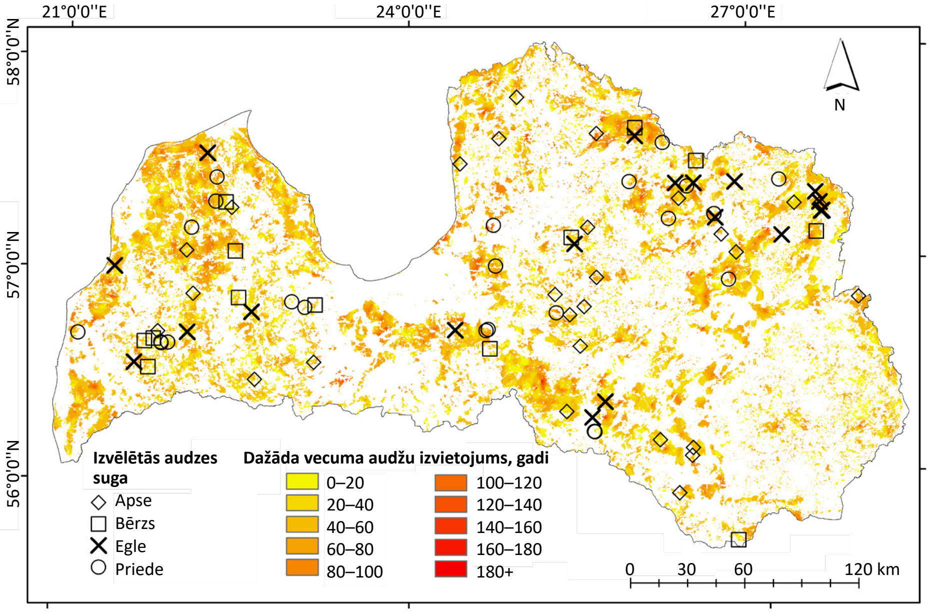
Pētījumā pirmo reizi Eiropā iegūti dati par oglekļa uzkrājumu vecās bērzu un apšu mežaudzēs. Pirmo reizi Eiropas hemiboreālajos mežos raksturots oglekļa uzkrājums vecās skuju un lapu koku mežaudzēs un veikts tā atšķirību novērtējums (vecuma starpība lapu koku audzēs 58 gadi un skuju koku audzēs 93 gadi no kontroles līdz veco audžu vecumam) sausieņos.

2. MATERIĀLS UN METODES

Pētījuma īstenošanai ievākti un analizēti dati 84 vecās parastās priedes (*Pinus sylvestris*), parastās egles (*Picea abies*), bērzu (*Betula pendula* Roth un *Betula pubescens* Ehrh.) un parastās apses (*Populus tremula*) mežaudzēs damaksnī (Dm; *Hylocomiosa*) un vērī (Vr; *Oxalidosa*) visā Latvijas teritorijā (2.1. att.). Saskaņā ar Meža statistiskās inventarizācijas (MSI) datiem, gan parastās priedes, gan bērzu audzes aizņem 26% no kopējās mežu platības, kam seko parastās egles audzes ar 19% un parastās apses ar 8% no kopējās mežu platības.

Damaksnis (Dm) un vēris (Vr) ir sausieņu meži, kur pirmā stāva valdošā koku suga ir priede, egle, kā arī šo sugu mistrojums ar bērzu un apses piejaukumu. Vērī bieži sastopamas arī bērzu un apses tīraudzes (Bušs 1976). Saskaņā ar Meža statistiskās inventarizācijas (MSI) datiem, damaksnis un vēris kopā aizņem 40% no Latvijas meža kopējās platības, un tie ir piemēroti visu vērtēto koku sugu augšanai: priedes audzes tajos aizņem 37%, egles 22%, bērzu 26% un apses 7%. Pēc MSI datiem, mežaudzes, kas vecākas par 120 gadiem, aizņem 4% no Latvijas meža kopējās platības. Lielāko daļu (90%) no vecajām audzēm veido parastā priede.

Sākotnēji saskaņā ar meža inventarizācijas informāciju (Meža valsts reģistra datu bāzē) tika atlasītas vecas audzes, kuras atbilda šādiem kritērijiem: 1) valdošā suga – priede, egle, bērzi, apse; 2) audzes vecums – priede > 160 gadi, egle > 160 gadi, bērzi > 120 gadi, apse > 100 gadi; 3) meža tips – Dm, Vr; 4) valdošās



2.1. att. **Pētījuma objektu izvietojums vecās mežaudzēs pa valdošajām koku sugām** sugas īpatsvars audzes sastāva formulā > 50% no pirmā stāva krājas; 5) nav pieejama dokumentāla informācija par saimniecisko darbību audzē vismaz pēdējos 30 gadus; 6) atrašanās vieta vismaz 5 km no apdzīvotām vietām un 1 km no autoceļiem); 7) nogabala platība vismaz 0,5 ha. Audzes vecuma ietekmes raksturošanai (salīdzinājumam) izmantoti MSI III cikla (laika periods no 2014. līdz 2018. gadam) dati no priedes (vecumā 80–120 gadi), egles (60–100 gadi), bērzu (60–90 gadi) un apses (40–80 gadi) audzēm (definējot tās kā "kontroles audzes"), kas iegūti no kopumā 447 parauglaukumiem (2.1., 2.2. tab.).

2.1. tabula

Veco un kontroles audžu vecuma raksturojums

	Vecās audzes		Kontroles audzes		Vidējā vecuma starpība starp audžu grupām
	PL * skaits	Vecums (amplitūda)	PL skaits	Vecums (amplitūda)	
Apse	146	112 ± 3 (104–135)	86	58 ± 3 (39–80)	54 ± 4
Bērzi	67	131 ± 4 (123–148)	114	69 ± 1 (61–80)	62 ± 4
Egle	102	182 ± 2 (170–205)	117	79 ± 2 (61–100)	103 ± 6
Priede	148	179 ± 6 (163–218)	130	97 ± 2 (81–120)	82 ± 6

± 95% ticamības intervāls;
* izmantoti tikai tie parauglaukumi un parauglaukumu sektori, kuru platība ir > 400 m^2.

Atlasītās potenciālās audzes, izvēloties nejaušā secībā, tika apsekotas dabā, lai pārliecinātos par faktiskās situācijas sakritību ar taksācijas datos norādīto un to, ka nav konstatējamas saimnieciskās darbības pazīmes (nav celmu un pievešanas ceļu, nav pazīmju, ka būtu izvākta atmirusī koksne). Atbilstošās audzēs ierīkoti parauglaukumi, līdz sasniegts katrai sugai izvēlētais kopējais audžu skaits. Kopumā uzmērīti 463 apļveida parauglaukumi.

2.2. tabula

Kontroles audžu I stāva raksturojums

Taksācijas rādītāji	Apse	Bērzs	Egle	Priede
Vidējais caurmērs D *, cm	37 ± 2,3	30 ± 1,0	32 ± 1,3	36 ± 0,9
Vidējais augstums H *, cm	30 ± 1,1	29 ± 0,6	26 ± 0,7	29 ± 0,5
Vidējais šķērslaukums, m^2 ha^{-1}	24 ± 2,2	23 ± 1,4	26 ± 1,8	30 ± 1,9
Vidējā krāja, m^3 ha^{-1}	343 ± 36,1	296 ± 20,2	326 ± 26,7	396 ± 27,1
Vidējais audzes biezums, koki ha^{-1}	358 ± 50	352 ± 27	381 ± 40	326 ± 25

* D – vidējais kvadrātiskais caurmērs, cm; H – vidējā kvadrātiskā caurmēra kokam atbilstošais augstums pēc augstumlīknes, m.

2.1. Datu ievākšanas metodika

Datu ievākšana organizēta pa posmiem. Laikā no 2016. līdz 2017. gadam uzmērītas vecās skujkoku audzes, novērtējot 19 egļu audzes vecumā no 167 līdz 213 gadiem (Ķēniņa et al. 2018 / I publikācija) un 25 priežu audzes vecumā no 163 līdz 218 gadiem (Ķēniņa et al. 2019a / II publikācija). Datu ievākšana vecās lapu koku audzēs organizēta no 2018. līdz 2019. gadam. Šajā laika periodā ievākti dati par 15 bērzu audzēm vecumā no 123 līdz 148 gadiem un 25 apšu audzēm vecumā no 104 līdz 135 gadiem (Ķēniņa et al. 2022 / VI publikācija).

Katrā atlasītajā audzē ierīkoti 6–8 parauglaukumi regulārā tīklā atbilstoši audzes konfigurācijai, izvairoties no netipiskām ieplakām, paaugstinājumiem, kā arī vismaz 10 m attālumā no audzes malas. Katrā parauglaukumā (R = 12,62 m; S = 500 m^2) uzmērīta kokaudze, kā arī atmirusī koksne (sausokņi, stumbeņi, kritalas). Parauglaukuma platībā fiksē koka krūšaugstuma caurmēru (caurmērs ≥ 6,1 cm, parauglaukuma sektorā (R = 5,64 m; 0°–90° sektorā) fiksē kokus ar caurmēru ≥ 2,1 cm). Katram kokam fiksē arī atrašanās vietu (attālumu, virzienu), sugu, piederību audzes stāvam, kā arī piešķir numuru. Pirmajā stāvā apvieno visus audzes augstākos kokus, kuru augstuma atšķirības nepārsniedz 20%. Pārējie koki veido II stāvu, ja to augstums nav mazāks par vienu ceturtdaļu no I stāva koku augstuma. Katram meža elementam (valdošajam elementam pieciem kokiem, pārējiem meža elementiem diviem dažādu dimensiju kokiem) uzmēra koku augstumu un vainaga sākuma augstumu, kā arī ievāc pieauguma urbumu krūšu augstumā. Augstumu un caurmēru uzmēra arī nedzīvajiem sausstāvošajiem kokiem – stumbeņiem (st) un sausokņiem (sa) (caurmērs ≥ 6,1 cm; parauglaukuma sektorā caurmērs ≥ 2,1 cm). Parauglaukumā nosaka kritalas atrašanās vietu, caurmēru tievgalī un resgalī kritalām, kuru resgaļa caurmērs ir lielāks par 14,0 cm (parauglaukuma sektorā caurmērs > 6 cm). Visiem nedzīvajiem kokiem nosaka sadalīšanās pakāpi piecās kategorijās (saskaņā ar Sandström et al. 2007).

Katram kokam aprēķināts augstums pēc Naslunda augstumlīknes:

$$H = 1{,}3 + \left(\frac{D}{k \cdot D \cdot c}\right)^3 , \qquad (1)$$

kur:

H – vidējā kvadrātiskā caurmēra kokam atbilstošais augstums pēc augstumlīknes, m;
D – koku caurmērs, cm;
k, c – koeficienti.

Pētījuma objektā atsevišķa augstumlīkne aprēķināta katram meža elementam, bet, ja augstums mērīts mazāk nekā 5 kokiem, tad meža elementa augstums aprēķināts, izmantojot Gafreja vispārīgo augstumlīkni (Šņepsts 2020).

Vidējais audzes caurmērs 1,3 m augstumā aprēķināts kā vidējais kvadrātiskais caurmērs (MSI metodika 2013):

$$D = \sqrt{\frac{4000 \cdot G}{\pi \cdot N}} \;, \tag{2}$$

kur:
D – vidējais kvadrātiskais caurmērs, cm;
G – šķērslaukums, $m^2\ ha^{-1}$;
N – koku skaits, gab. ha^{-1}.

Dzīvo koku un sausstāvošo koku krāja aprēķināta pēc L. Liepas (1996) formulas:

$$V = \psi \cdot L^{\alpha} d^{\beta \lg L + \varphi} \;, \tag{3}$$

kur:
V – koka tilpums, m^3;
L – stumbra garums, m;
d – koku krūšaugstuma caurmērs, cm;
$\psi, \alpha, \beta, \varphi$ – koku sugas atkarīgi koeficienti.

Stumbeņu un kritalu krāja aprēķināta, izmantojot Hubert formulu (MSI metodika 2013):

$$V = \frac{L \pi d_m^2}{4} \;, \tag{4}$$

kur:
V – krāja, m^3;
L – kritalas garums/stumbeņa augstums, cm;
d_m – vidējais nogriežņa diametrs, cm.

Atmirušās koksnes paraugi oglekļa satura koeficientu vērtību noteikšanai ievākti 4 nejauši izvēlētās veco bērzu mežaudzēs (Ķēniņa et al. 2019b / III publikācija). Katrā audzē ierīkoti 6 līdz 8 parauglaukumi. Kopā ierīkoti 26 parauglaukumi, kuros pētījumā analizētajām valdošajām koku sugām katrā no piecām sadalīšanās pakāpēm ievākti 5 koksnes paraugi (kopā 76 koksnes paraugi). Pirmās un otrās sadalīšanās pakāpes atmirušās koksnes paraugi iegūti ar zondi (diametrs = 13 mm), bet trešās līdz piektās sadalīšanās pakāpes atmirušās koksnes paraugi iegūti ar lielāku zondi (diametrs = 50 mm). Koksnes paraugi nogādāti pēc ISO 17025:2017 standarta akreditētajā LVMI Silava Meža vides laboratorijā, kur noteikts oglekļa saturs pa koku sugām un sadalīšanās pakāpēm. Augsnes (100 cm^3) un zemsegas paraugi ievākti daļā no veco un kontroles audžu kopas (pavisam 157 audzēs) trijos punktos ārpus parauglaukuma ārējās robežas atbilstoši meža augšņu monitoringa metodikai. Augsnes paraugus ievāca četros dziļumos (0–10 cm, 10–20 cm, 20–40 cm, 40–80 cm). Ievāktie augsnes un zemsegas paraugi nogādāti analīžu veikšanai LVMI Silava Meža vides laboratorijā, kur noteikts augsnes blīvums un oglekļa saturs augsnes un zemsegas paraugos.

2.2. Datu analīze

Oglekļa uzkrājums aprēķināts galvenajām oglekļa krātuvēm (kokaudze, augsne, atmirusī koksne un zemsega). Oglekļa uzkrājums koku biomasā aprēķināts, izmantojot individuālus koku biomasas modeļus galvenajām koku sugām (Liepiņš et al. 2017) un standartizētu oglekļa satura koeficienta (0,5) vērtību koksnē, ko noteikusi Klimata pārmaiņu starpvaldības padome (IPCC) (Eggleston et al. 2006).

Oglekļa uzkrājums atmirušajā koksnē individuāliem kokiem aprēķināts, izmantojot koksnes blīvuma vērtības un oglekļa satura koeficienta vērtības pa koksnes sadalīšanās pakāpēm un koku sugām. Veicot novērtējumu Latvijā ierobežotam paraugu skaitam galvenajām koku sugām (Ķēniņa et al. 2019 / III publikācija), Igaunijā un Latvijā iegūtajām oglekļa satura koeficientu vērtībām būtiskas atšķirības netika konstatētas, kas ļāva pētījumā izmantot Igaunijā Köster et al. (2015) izstrādātas parametru vērtības. Ņemot vērā, ka MSI dati par atmirušo koksni iegūti trijās sadalīšanās pakāpēs, pētījuma ietvaros noteiktās sadalīšanās pakāpes attiecinātas šādi: svaiga koksne – iekļauj 1. un 2. sadalīšanās pakāpi veco mežaudžu datos un aprēķinus veic pēc 2. sadalīšanās pakāpes; vidēji sadalījusies koksne – iekļauj 3. sadalīšanās pakāpi veco mežaudžu datos un aprēķinus veic pēc 3. sadalīšanās pakāpes; stipri sadalījusies koksne – iekļauj 4. un 5. sadalīšanās pakāpi veco mežaudžu datos un aprēķinus veic pēc 4. sadalīšanās pakāpes.

Valdošās koku sugas, audzes biezuma, krājas un šo parametru mijiedarbības ietekme uz oglekļa uzkrājumu koku biomasā un atmirušajā koksnē vecās mežaudzēs novērtēta ar lineāru jaukta efekta modeli (LMER). Parametri, kas ietverti t.s. noslēdzošajos modeļos oglekļa uzkrājuma visprecīzākajai raksturošanai, izvēlēti pēc statistiski nebūtisko (pie 95% ticamības līmeņa) mainīgo parametru un parametru mijiedarbību izslēgšanas no modeļa un salīdzinot modeļus pēc Akaike informācijas kritērija vērtības (AIC). Visos modeļos objekts definēts kā nejaušais (*random*) parametrs, jo vienā audzē bija vairāki parauglaukumi. Lai novērtētu saistības starp analizētajiem faktoriem un oglekļa uzkrājumu augsnē un zemsegā, izmantota dispersijas analīze (ANOVA). Lai salīdzinātu veco audžu kokaudzes parametrus – šķērslaukumu (I un II stāvs), biezumu (I un II stāvs), krāju (I un II stāvs), caurmēru (I un II stāvs), atmirušās koksnes krāju pa atmiruma veidiem – starp valdošajām koku sugām, kā arī, lai noteiktu kokaudžu parametru atšķirības starp veco audžu un kontroles audžu grupām, izmantota dispersijas analīze (ANOVA). Lai samazinātu atkarīgo mainīgo heterogenitāti, oglekļa uzkrājuma vērtības atmirušajā koksnē, augsnē un zemsegā tika logaritmizētas pirms modeļu veidošanas. Ja konstatēta būtiska faktoru vai to mijiedarbības ietekme, tad grupu jeb parametru gradācijas klašu savstarpējai salīdzināšanai izmantots PostHoc tests. Visi aprēķini veikti R programmā (v. 4.1.0., R Core Team 2021), izmantotas paketes *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), *emmeans* (Lenth 2021).

3. REZULTĀTI UN DISKUSIJA

3.1. Veco mežaudžu taksācijas rādītāji (I, II, IV, V un VI publikācija)

Valdošā koku suga statistiski būtiski ietekmē audzes vidējo I un II stāva caurmēru, šķērslaukumu un krāju, koku skaitu I un II stāvā, kā arī atmirušās koksnes apjomu vecajās mežaudzēs (3.1. tab.). Veco audžu kopā netika konstatēta statistiski būtiska vecuma ietekme uz kokaudzi raksturojošajiem rādītājiem, liecinot, ka gadījumos, kad veci koki ir saglabājušies kā dominējošais meža elements, līdzīga maksimālā krāja iespējama plašā vecuma diapazonā (pētījumā iekļautas skujkoku audzes no 163 līdz 218 gadiem, lapu koku audzes no 104 līdz 148 gadiem). Citos pētījumos, vērtējot valdošā meža elementa vecuma ietekmi audzēs, kas jaunākas nekā šajā pētījumā ietvertās vecās mežaudzēs, secināts, ka tas ir ļoti nozīmīgs kokaudzes parametrus, kā arī oglekļa uzkrājumu ietekmējošs faktors (Carey et al. 2001; Pregitzer & Euskirchen 2004; Lee et al. 2016; Martin et al. 2018). Tomēr manā pētījumā analizēta konkrēta audzes attīstības stadija, un šajā stadijā vecuma ietekme nav izteikta. Līdzīgi rezultāti iegūti arī, analizējot ekosistēmas produktivitāti vecās audzēs pēc ugunsgrēka (Taylor et al. 2014).

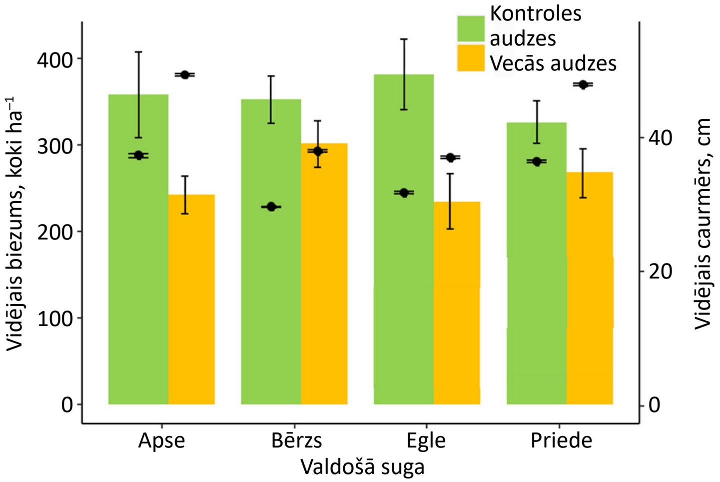
3.1. tabula

Veco audžu I stāva raksturojums

Taksācijas rādītāji	Apse	Bērzs	Egle	Priede
Vidējais caurmērs, cm	49 ± 1,1	38 ± 1,5	37 ± 1,6	48 ± 1,1
Vidējais augstums, m	37 ± 0,4	30 ± 0,7	29 ± 0,7	31 ± 0,4
Vidējais šķērslaukums, m^2 ha^{-1}	39 ± 2,4	30 ± 2,9	24 ± 3,1	36 ± 2,8
Vidējā krāja, m^3 ha^{-1}	666 ± 48,0	411 ± 53,0	319 ± 53,0	495 ± 41,0
Vidējais audzes biezums, koki ha^{-1}	242 ± 22	301 ± 27	235 ± 32	268 ± 28
Vidējais valdošās koku sugas īpatsvars (amplitūda)	9 ± 0,2 (5–10)	7 ± 0,4 (5–10)	7 ± 0,7 5–10	7 ± 0,1 (5–10)
Valdošās koku sugas caurmērs, cm	49	38	35	47
Valdošās koku sugas augstums, m	37	30	28	31
Atmirusī koksne, m^3 ha^{-1}	103 ± 11,0	65 ± 10,5	90 ± 14,2	97 ± 14,0

* valdošās koku sugas īpatsvars – valdošās koku sugas sastāva vienības pēc I stāva krājas.

Vidējais caurmērs ir būtiski atšķirīgs ($p < 0,001$) dažādu valdošo koku sugu vecajās audzēs gan I stāva, gan II stāva kokiem. I stāva caurmērs vecās apšu (49 ± 1,1 cm) un priežu (48 ± 1,1 cm) audzēs ir būtiski lielāks nekā bērzu (38 ± 1,5 cm) un egļu (37 ± 1,6 cm) audzēs (3.1. att.). Arī audzes biezums (I stāva, II stāva, kopējais) dažādu valdošo koku sugu vecās audzēs ir būtiski ($p < 0,001$) atšķirīgs (3.1. att.). Vecās bērzu audzēs I stāva biezums (301 ± 27 koki ha^{-1}) ir bū-

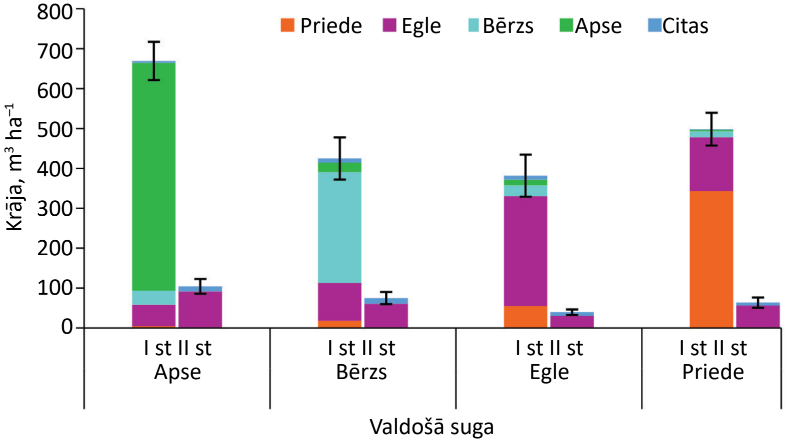


3.1. att. **Audzes I stāva biezuma (stabiņi) un I stāva vidējā kvadrātiskā caurmēra (punkti) salīdzinājums apšu, bērzu, egļu un priežu vecās un kontroles mežaudzēs (± 95% ticamības intervāls)**

tiski lielāks nekā apšu (242 ± 22 koki ha^{-1}) un egļu (235 ± 32 koki ha^{-1}) audzēs un līdzīgs kā priežu (268 ± 28 koki ha^{-1}) audzēs. Visu valdošo koku sugu vecās mežaudzēs gan I stāva, gan II stāva biezums ir būtiski ($p < 0{,}001$) mazāks nekā kontroles audzēs (kuru vecums priedei ir 97 ± 2 gadi, eglei 79 ± 2, bērziem 69 ± 1 un apsei 58 ± 3 gadi). Dati liecina par zemu oglekļa uzkrājuma stabilitāti vecās mežaudzēs: atsevišķu I stāva koku bojāeja dabisko traucējumu un/vai vecuma ietekmē var nozīmīgi samazināt kopējo oglekļa uzkrājumu. Iegūtie rezultāti apliecina iepriekšējos pētījumos secināto, ka reti, bet lieli koki I stāvā veido galveno dzīvo koku krāju vecās mežaudzēs (Nilsson et al. 2002).

Analizējot mežaudžu krājas datus, secināts, ka valdošā koku suga būtiski ($p < 0{,}001$) ietekmē audzes I stāva krāju, II stāva krāju, kā arī kopējo audzes krāju. Vecās apses audzēs ir būtiski ($p < 0{,}001$) lielāka I un II stāva krāja, salīdzinot ar pārējo valdošo koku sugu audzēm. I stāva krāja vecās bērzu un priežu audzēs ir līdzīga, bet egļu audzēs tā ir būtiski mazāka nekā vecās priežu audzēs. Savukārt II stāvā vecās egļu audzēs krāja ir būtiski ($p < 0{,}01$) mazāka nekā pārējo valdošo koku sugu audzēs (3.2. att.). Analizējot II stāva krāju pa koku sugām, secināts, ka egle ir dominējošā koku suga veco mežaudžu II stāvā, aizņemot 77–89% no kopējās II stāva krājas visās vecajās mežaudzēs.

Krāju ietekmē arī veco audžu sugu sastāvs: vecās priežu un bērzu audzēs konstatēts relatīvi augsts egles īpatsvars I stāvā. Visu valdošo koku sugu vecās audzēs novērotā egles dominance II stāvā liecina par notiekošu sukcesiju veco audžu grupā – gan skuju koku audzēs (vecumā no 163 līdz 218 gadiem), gan lapu koku audzēs (vecumā no 104 līdz 148 gadiem). Rezultāti atbilst klasiskajai izpratnei par sukcesijas norisi audzēs, kuras ilgstoši nav skāruši nozīmīgi dabiskie traucējumi: notiek pakāpeniska atjaunošanās ar ēncietīgu koku sugu – egli (Drobyshev et al. 1999).



3.2. att. **Pirmā (I st) un otrā (II st) stāva krāja vecās apšu, bērzu, egļu un priežu mežaudzēs pa koku sugām (± 95% ticamības intervāls)**

Kopējā un I stāva krāja priežu, bērzu un apšu vecajās mežaudzēs ir ievērojami (I stāva – par 99–323 m^3 ha^{-1}) un būtiski lielāka, bet vecajās egļu audzēs – līdzīga kā attiecīgo sugu kontroles audzēm (vecuma starpība 54 ± 4 gadi apsei, 62 ± 4 bērziem, 82 ± 6 priedei un 103 ± 6 gadi eglei).

Atmirušās koksnes krāja ir līdzīga (64–103 m^3 ha^{-1}) dažādu valdošo koku sugu vecajās audzēs. Audzes krājai un biezumam ir būtiska ($p < 0{,}01$) ietekme uz atmirušās koksnes apjomu šajā vecuma posmā. Lai gan kopējais atmiruma apjoms ir liels, tas ir 13–24% no dzīvo koku krājas. Kontekstā ar krājas sadalījumu (neliels biezums lielu dimensiju koku) iegūtie rezultāti liecina, ka šī audžu kopa ir vairāk pakļauta dabiskā traucējuma riskam nākotnē (Jõgiste et al. 2017; Seidl et al. 2020; Öder et al. 2021). Atmiruma apjoms atsevišķos veco audžu parauglaukumos, kā arī starp audzēm ievērojami atšķiras (3.2. tab.). Līdzīgas sakarības, ka atmirušas koksnes apjomu ietekmē koku sugu sastāvs, kā arī audzes krāja, audzes biezums un tas stipri variē starp parauglaukumiem, konstatētas arī citos veco audžu pētījumos (Öder et al. 2021). Vērtējot atmirušās koksnes krāju pa atmiruma veidiem, konstatēts, ka sausokņu krāja vecās audzēs ir atkarīga no valdošās koku sugas ($p < 0{,}001$), savukārt audzes krāja, šķērslaukums un biezums būtiski ($p < 0{,}001$) ietekmē kritalu krāju vecās audzēs (3.2. tab.). Vecās priežu audzēs sausokņu krāja (42 m^3 ha^{-1}) ir būtiski lielāka nekā pārējo valdošo koku sugu audzēs (12–18 m^3 ha^{-1}). Kritalas veido lielu daļu no kopējā nedzīvās koksnes apjoma vecās mežaudzēs. Atšķirības atmirušās koksnes apjomā pa atmiruma veidiem apstiprina audzes sugu sastāva ietekmi – egle ātrāk veido kritalas, bet priede ilgāku laiku ir sausoknis/stumbenis, pirms nokrīt (Šēnhofa et al. 2020). Lielāko daļu no atmirušās koksnes vecās mežaudzēs (3.2. tab.) veido vidēji sadalījušies koki (2. un 3. sadalīšanās pakāpes), ko ietekmē arī atšķirības starp koku sugu koksnes īpašībām (Šēnhofa et al. 2020).

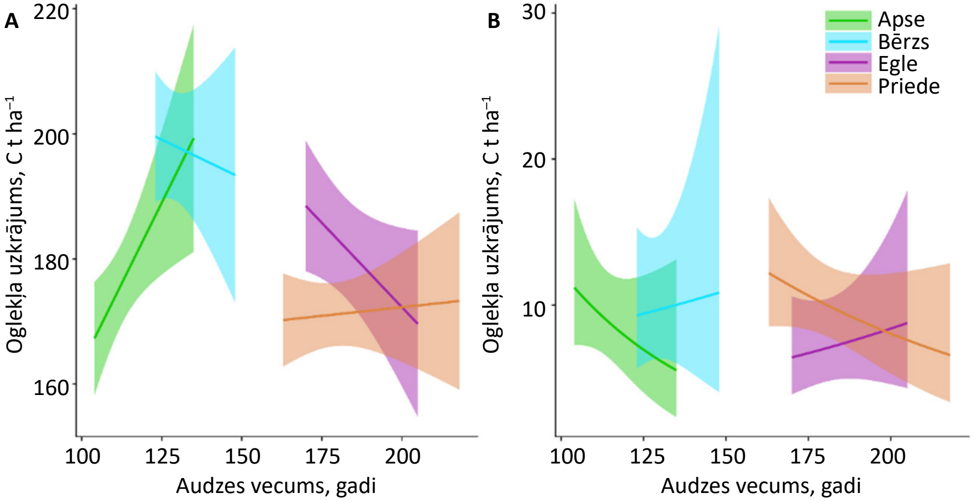
3.2. tabula

Atmirušās koksnes vidējā krāja pa atmiruma veidiem un sadalīšanās pakāpēm (± 95% ticamības intervāls)

	Apse	Bērzs	Egle	Priede
Atmirušās koksnes krāja pa atmiruma veidiem, m^3 ha^{-1} (amplitūda)				
Kritalas	73 ± 9,4 (0–302,4)	45 ± 8,4 (1,5–167,4)	61 ± 10,4 (0–226,2)	43 ± 10,6 (0–405,0)
Sausokņi	18 ± 4,2 (0–145,8)	12 ± 4,2 (0–95,3)	18 ± 7,3 (0–246,1)	42 ± 6,5 (0–210,5)
Stumbeņi	12 ± 2,6 (0–90,4)	8 ± 2,8 (0–55,4)	10 ± 4,6 (0–132,6)	11 ± 2,7 (0–77,7)
Atmirusī koksne kopā	103 ± 11,0 (2,0– 363,1)	64 ± 10,5 (3,2–222,8)	89 ± 14,2 (1,6–437,1)	97 ± 14,0 (0–483,2)
Atmirušās koksnes krāja pa sadalīšanās pakāpēm, m^3 ha^{-1} (proporcija no kopējās atmirušās koksnes krājas)				
1. sadalīšanās pakāpe	17 ± 4,2 (16%)	15 ± 6,3 (3%)	3 ± 1,8 (3%)	3 ± 2,6 (3%)
2. sadalīšanās pakāpe	38 ± 6,1 (37%)	24 ± 6,1 (38%)	39 ± 10,4 (44%)	64 ± 8,9 (66%)
3. sadalīšanās pakāpe	23 ± 4,1 (22%)	14 ± 3,9 (22%)	20 ± 4,8 (22%)	19 ± 5,4 (19%)
4. sadalīšanās pakāpe	16 ± 3,7 (15%)	8 ± 1,8 (12%)	16 ± 4,2 (18%)	9 ± 5,0 (9%)
5. sadalīšanās pakāpe	10 ± 2,6 (10%)	3 ± 1,7 (5%)	12 ± 3,6 (13%)	3 ± 1,5 (3%)

3.2. Oglekļa uzkrājums vecās mežaudzēs (II, III, IV, un VI publikācija)

Koku biomasa ir nozīmīgākā oglekļa krātuve vecās mežaudzēs, kas tieši ietekmē arī oglekļa uzkrājumu atmirušajā koksnē un zemsegā. Tā veido vidēji 59% no kopējā oglekļa uzkrājuma, un augsne sastāda vidēji 31% no kopējā oglekļa uzkrājuma. Arī pētījumos Somijā un Eiropas centrālajā daļā konstatēts, ka koku biomasa ir lielākā oglekļa krātuve vecās mežaudzēs (Finér et al. 2003; Seedre et al. 2015). Kaut arī pētījumam atlasīta specifiska veco mežu daļa – situācija, kur vecie koki vēl joprojām ir dominējošais meža elements (t.i., vecās mežaudzes), – arī šo audžu atsevišķos punktos (parauglaukumos) novērojamas izteiktas oglekļa uzkrājuma atšķirības: apšu audzēs no 70 līdz 318 t C ha^{-1}, priežu audzēs no 73 līdz 245 t C ha^{-1} un bērzu audzēs – no 88 līdz 272 t C ha^{-1}, egļu audzēs – no 60 līdz 292 t C ha^{-1}. Šo heterogenitāti visticamāk ietekmē dažādu audžu vēsturisko attīstību nosakošo faktoru mijiedarbības – augsnes īpašības, mitruma režīma svārstības, atšķirības sukcesijas procesā (Jandl et al. 2007; Hansson et al. 2011; Uri et al. 2012; Lutter et al. 2019).

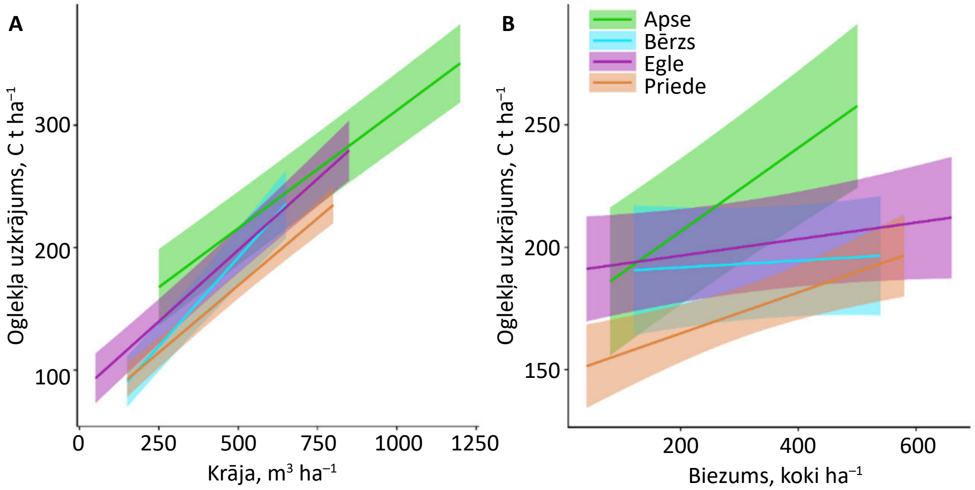


3.3. att. **Oglekļa uzkrājuma izmaiņas koku biomasā (A) un atmirušajā koksnē (B) atkarībā no audzes vecuma (± 95% ticamības intervāls)**

Vecās audzēs valdošās koku sugas vecumam ir būtiska, sugai specifiska ietekme ($p < 0{,}01$) uz oglekļa uzkrājumu koku biomasā un atmirušajā koksnē (3.3. att.). Vecuma ietekme uz oglekļa uzkrājumu koku biomasā būtiski ($p < 0{,}01$) atšķiras starp egļu un apšu mežaudzēm. Iespējams, ka pētījumā vērtētais vecuma posms egļu audzēs ietver arī stadiju, kurā dabiski notiek paaudžu nomaiņa, kamēr apšu audzēm pētījuma ietvaros ir izdevies atrast ekstrēmus to saglabāšanās ilglaicības gadījumus.

Vērtējot kokaudzes parametru ietekmi uz oglekļa uzkrājumu, secināts, ka vecās audzēs valdošā koku suga ($p < 0{,}01$), audzes I stāva krāja ($p < 0{,}001$), I stāva biezums ($p < 0{,}001$) būtiski ietekmē oglekļa uzkrājumu dzīvo koku biomasā. Oglekļa uzkrājumu koku biomasā būtiski ietekmē arī mijiedarbības starp faktoriem: gan I stāva krājas, gan I stāva biezuma ietekme uz oglekļa uzkrājumu ir statistiski būtiski atšķirīga atkarībā no valdošās koku sugas (abos gadījumos $p < 0{,}001$) (3.4. att.). Kā parāda iepriekšējie pētījumi, līdz ar audzes vecumu oglekļa uzkrājums koku biomasā turpina pieaugt, līdz tas sasniedz maksimumu (piesātinājumu) un turpmāk saglabājas relatīvi stabils noteiktu laiku (Pregitzer & Euskirchen 2004; Jones et al. 2019). Šī stabilā posma ilgums atkarīgs no dabisko traucējumu ietekmes, pašizretināšanās un sukcesijas procesa ātruma dažādu koku sugu vecās mežaudzēs (Pregitzer & Euskirchen 2004; Taylor et al. 2014; Jones et al. 2019).

Vecās apšu audzēs konstatēts vislielākais oglekļa uzkrājums koku biomasā (vidēji 205 ± 7,0 t C ha^{-1}). Tāpat salīdzinoši augsts (un savstarpēji līdzīgs) vidējais oglekļa uzkrājums koku biomasā novērots vecās bērzu un priežu audzēs, attiecīgi 175 ± 10,0 t C ha^{-1} un 172 ± 7,0 t C ha^{-1}. Nozīmīgi mazāks oglekļa uzkrājums dzīvo koku biomasā konstatēts vecās egļu audzēs (140 ± 9,0 t C ha^{-1}).



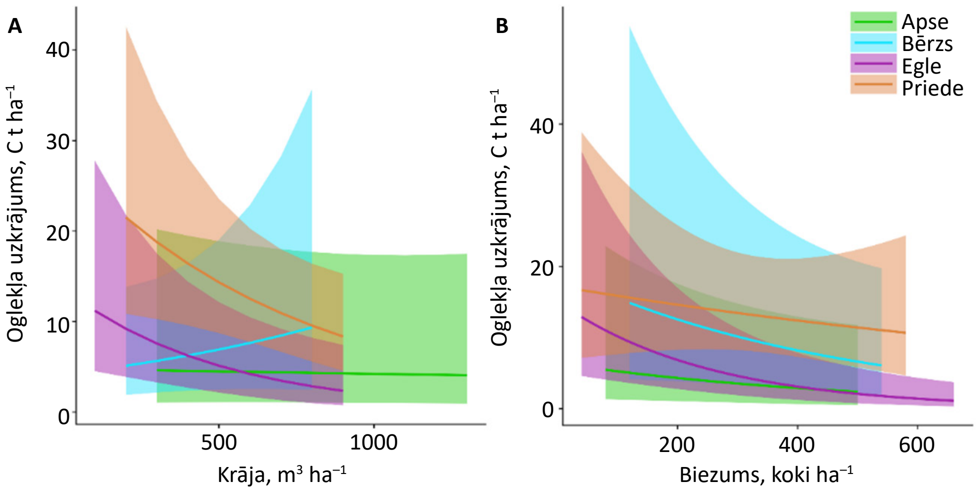
3.4. att. **Oglekļa uzkrājuma izmaiņas koku biomasā dažādu valdošo koku sugu vecajās mežaudzēs atkarībā no I stāva krājas (A), I stāva biezuma (B) (± 95% ticamības intervāls)**

Oglekļa uzkrājums koku biomasā I stāva krājas ietekmē būtiski atšķiras starp vecām apšu un bērzu audzēm, bet I stāva biezuma ietekmē būtiskas atšķirības ir starp apšu un bērzu, kā arī starp apšu un egļu audzēm.

Vērtējot oglekļa uzkrājumu koku biomasas frakcijās, konstatēts, ka lielākā oglekļa krātuve ir stumbrs (47–73% no kopējā oglekļa apjoma koku biomasā), bet pazemes biomasa, kuru veido balstsaknes, uzsūcošās un sīkās saknes, kā arī celms, veido 16–25% no kopējā oglekļa apjoma koku biomasā.

Atmirusī koksne pakāpeniski sadalās, tādēļ tā ir relatīvi neliela oglekļa krātuve vecajās mežaudzēs, kam var būt nozīmīga loma citu meža ekosistēmas pakalpojumu nodrošināšanā (Nord-Larsen et al. 2019; Ruel & Gardiner 2019; Stakėnas et al. 2020), kā arī oglekļa dzīves cikla paildzināšanā (Johnston & Radeloff 2019). Oglekļa uzkrājums atmirušajā koksnē ir līdzīgs visu valdošo koku sugu vecajās audzēs (10–15 t C ha^{-1}), tomēr tas variē plašā amplitūdā starp parauglaukumiem (no 0,3 līdz 75 t C ha^{-1}).

Oglekļa uzkrājumu atmirušajā koksnē būtiski ietekmē audzes kopējās krājas un valdošās koku sugas mijiedarbība ($p < 0{,}05$) (3.5. att.). Tāpat audzes I stāva biezums būtiski ($p < 0{,}001$) ietekmē oglekļa uzkrājumu atmirušajā koksnē (3.5. att.). Tātad, vecās mežaudzēs, kurās ir lielāka krāja – lielāki koki (lielāks caurmērs) un vairāk koku audzē (lielāks audzes biezums) – ir lielāks koksnes apjoms, kas var pāriet atmirušajā koksnē. Tas saskan ar iepriekšējiem pētījumiem, kur vecās audzēs atmirušās koksnes oglekļa krātuves lielumu nosaka tas, cik daudz dzīvo koku un cik ilgi tie papildina šo oglekļa krātuvi (Pregitzer & Euskirchen 2004). Līdz ar to, jo vairāk būs koku audzē (lielāks audzes biezums), jo stabilāka atmirušās koksnes oglekļa krātuve būs ilgtermiņā.

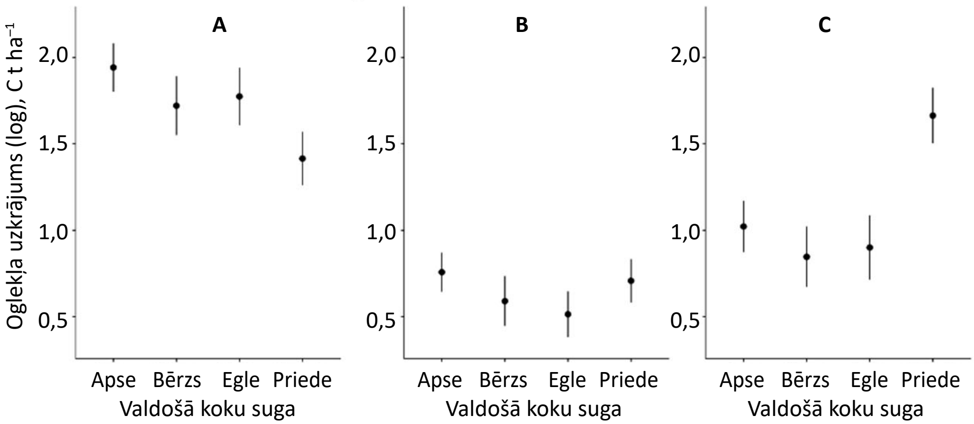


3.5. att. **Oglekļa uzkrājuma izmaiņas atmirušajā koksnē atkarībā no kopējās kokaudzes krājas (A) un I stāva biezuma (B) (± 95% ticamības intervāls)**

Nelielais oglekļa uzkrājums atmirušajā koksnē, kā arī ļoti vājā korelācija starp oglekļa uzkrājumu koku biomasā un atmirušajā koksnē liecina, ka analizētajā audžu kopā dabisko traucējumu ietekme ilgstoši ir bijusi neliela. Tātad iegūtie dati raksturo oglekļa uzkrājuma potenciālu (maksimumu) vecās audzēs. Iegūtās atziņas sakrīt ar iepriekšējos pētījumos izvirzītajiem apgalvojumiem, ka veco audžu stadijā, kur oglekļa uzkrājums ir sasniedzis savu maksimumu, atmirušās koksnes apjoma izmaiņas galvenokārt ietekmē laiks, kad noticis pēdējais dabiskais traucējums, kā arī tā intensitāte un biežums konkrētajā punktā (Martin et al. 2021).

Oglekļa uzkrājumu atmirušajā koksnē ietekmē atmiruma veids un koksnes sadalīšanās pakāpes, ko nosaka/ietekmē dažādi abiotiskie faktori – gaisa temperatūra un gaisa mitrums, augsnes īpašības un mitruma režīms, tāpat biotiskie faktori – sēnes un kukaiņi, kā arī koksnes īpašības dažādām koku sugām, koku dimensijas un novietojums (stāvošs, nokritis koks) (Yatskov et al. 2003; Ruel & Gardiner 2019). Lielākais atmirušās koksnes oglekļa uzkrājums ir kritalās vecās apšu (vidēji 9 ± 1,2 t C ha^{-1}), bērzu (vidēji 6 ± 1,3 t C ha^{-1}) un egļu (vidēji 7 ± 1,2 t C ha^{-1}) audzēs, un tas ir līdzīgs starp šīm sugām (3.6. att.). Sausokņos lielākais oglekļa uzkrājums ir vecās priežu audzēs (vidēji 7 ± 1,5 t C ha^{-1}), un tas ir būtiski lielāks nekā pārējo valdošo koku sugu vecajās audzēs (vidēji 3 ± 0,5 t C ha^{-1}). Tas saistīts ar priedes koksnes sadalīšanās īpašībām un sausokņu noturību pret vēju pēc koka bojāejas (Kuuluvainen et al. 2017). Stumbeņos uzkrātais oglekļa apjoms ir līdzīgs visu valdošo koku sugu vecās mežaudzēs (vidēji 2 ± 1,0 t C ha^{-1}).

Augsne ir otra lielākā oglekļa krātuve aiz koku biomasas vecās mežaudzēs sausieņos (21–37% atkarībā no valdošās koku sugas, vidēji 31% no kopējā ekosistēmas uzkrājuma). Vecās lapu koku audzēs konstatēts būtiski ($p < 0,001$)



3.6. att. **Oglekļa uzkrājums atmirušajā koksnē vecās mežaudzēs pa atmiruma veidiem – kritalas (A), stumbeņi (B), sausokņi (C) (logaritmizētas vērtības ± 95% ticamības intervāls)**

augstāks oglekļa uzkrājums augsnē (apšu audzēs vidēji 101 ± 17,6 t C ha^{-1} un bērzu audzēs 117 ± 26,3 t C ha^{-1}) nekā vecās skuju koku audzēs (priežu audzēs vidēji 72 ± 30,6 t C ha^{-1} un egļu audzēs 58 ± 21,2 t C ha^{-1}). Augsnes oglekļa uzkrājuma datiem novērota ļoti augsta variācija, īpaši bērzu un egļu audzēs, ko iespējams skaidrot ar lielāku sugu daudzveidību un audzes struktūras atšķirībām (Hansson et al. 2013; Laganière et al. 2015). Turklāt, daļa no ievāktajiem augsnes paraugiem priežu audzēs nebija analīzei derīgi, bet iegūtie rezultāti atšķīrās pat simtkārtīgi, līdz ar to iegūtās vērtības sniedz tikai aptuvenu priekšstatu par oglekļa uzkrājumu augsnē. Arī Cindy & Vesterdal (2013) konstatēja lielu oglekļa uzkrājumu augsnē variāciju neatkarīgi no valdošās koku sugas, kas norāda uz citu faktoru – augsnes sastāva, augsnes mitruma, kā arī audzes vēsturiskās attīstības ietekmi uz oglekļa uzkrājumu (Jandl et al. 2007; Hansson et al. 2011; Lutter et al. 2019). Analizējot oglekļa uzkrājumu pa augsnes slāņu dziļumiem, secināts, ka virsējā augsnes slānī (0– 10 cm) koncentrējas vairāk kā 30% no kopējā tā apjoma šajā krātuvē. Līdzīgi rezultāti iegūti arī, analizējot 60 gadus vecas bērzu audzes mežos ar auglīgu minerālaugsni, kur virsējā augsnes slānī (0–30 cm) konstatēts 38% no kopējā augsnes oglekļa uzkrājuma (Uri et al. 2012). Kā parāda iepriekšējie pētījumi, oglekļa uzkrājumu virsējā augsnes slānī, salīdzinot ar dziļākajiem slāņiem, nozīmīgi ietekmē ūdens iztvaikošana no augsnes, gaisa temperatūras svārstības, kam savukārt ir ietekme arī uz mikroorganismu aktivitāti šajā slānī (Hansson et al. 2011). Zemsega ir procentuāli neliela oglekļa krātuve no kopējā oglekļa uzkrājuma, tomēr tai ir galvenā loma oglekļa pārnesē no virszemes oglekļa krātuvēm uz augsni (Jandl et al. 2007).

Oglekļa uzkrājums zemsegā arī būtiski atšķiras starp bērzu un priežu audzēm ($p < 0,05$). Vidējais oglekļa uzkrājums zemsegā vecās priežu audzēs ir 21 ± 5,3 t C ha^{-1} un egļu audzēs 25 ± 12,0 t C ha^{-1}, bet lapu koku audzēs tas ir zemāks – apšu audzēs 17 ± 4,8 t C ha^{-1} un bērzu audzēs 14 ± 5,2 t C ha^{-1}. Šīs tendences apliecina arī citās analīzēs konstatēto, ka valdošā koku suga, audzes sastāvs, kā arī citi šajā pētījumā nevērtēti parametri, piemēram, zemsedzes veģetācija, būtiski ietekmē zemsegas oglekļa krātuvi (Hansson et al. 2011; Cindy & Vesterdal 2013; Lutter et al. 2019). Oglekļa uzkrājums skuju koku audzēs ir lielāks, jo skujas sadalās lēnāk nekā lapas, kā arī atšķirības starp priežu un egļu audzēm, visticamāk, ietekmē atšķirīgie nobiru ikgadējie apjomi un sadalīšanās ātrums – priedēm skujas sadalās divu gadu laikā, bet eglēm – pat sešu gadu periodā (Hansson et al. 2011).

Kopējais oglekļa uzkrājums audzē ir četru galveno oglekļa krātuvju vidējo vērtību summa, jo novērojumu skaits dažādās oglekļa krātuvēs ievāktajiem datiem ir atšķirīgs. Koku biomasa iekļauj virszemes (stumbrs, zari) un pazemes (sīkās saknes, balstsaknes, uzsūcošās saknes un celms) biomasu. Tā ir lielākā oglekļa krātuve visu analizēto valdošo koku sugu audzēs (55–61%). Augsne ir otra lielākā un visplašāk variējošā oglekļa krātuve vecās mežaudzēs, kas veido 25–37% no kopējā oglekļa uzkrājuma atkarībā no valdošās koku sugas. Atmirusī koksne (3–5% atkarībā no valdošās koku sugas) un zemsega (4–11% atkarībā no valdošās koku sugas) veido nelielu daļu no kopējā oglekļa uzkrājuma. Vidēji koku biomasa veido 59%, augsne 30%, bet atmirusī koksne un zemsega attiecīgi 4% un 7% no kopējā ekosistēmas oglekļa uzkrājuma. Arī citos pētījumos dažādās Eiropas vietās ir iegūti līdzīgi rezultāti par oglekļa uzkrājumu mežā galvenajās oglekļa krātuvēs (Krankina & Harmon 1995; Finér et al. 2003; Seedre et al. 2015; Nord-Larsen et al. 2019). Tomēr kopējais oglekļa uzkrājums vecās mežaudzēs sausieņos ievērojami atšķiras pat starp vienas valdošās sugas audzēm, liecinot par lielu oglekļa uzkrājuma variāciju un dažādu audzes vēsturisko attīstību ietekmējošajiem faktoriem (Lutter et al. 2019; Krasnova et al. 2019).

3.3. Oglekļa uzkrājuma salīdzinājums kontroles un vecās mežaudzēs (V publikācija)

Oglekļa uzkrājums koku biomasā un atmirušajā koksnē vecās audzēs visām koku sugām ir būtiski lielāks nekā par 54–103 gadiem jaunākās (kontroles) audzēs (3.3. tab.). Vecās audzēs, kur vecie koki ir dominējošais meža elements, oglekļa uzkrājums koku biomasā ir par 19% (priežu un egļu audzēs) līdz 42% (apšu audzēs) lielāks nekā kontroles audzēs.

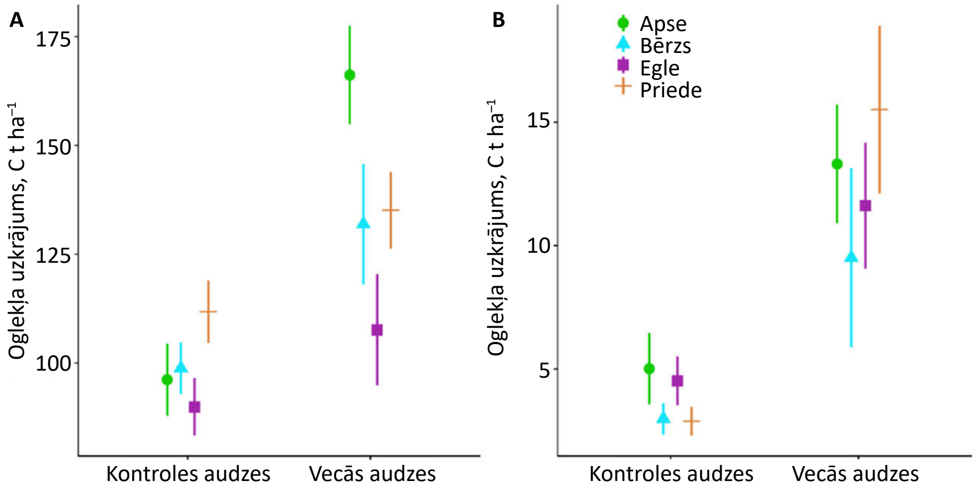
3.3. tabula

Oglekļa uzkrājums (t C ha^{-1}) oglekļa krātuvēs vecās un kontroles audzēs (vidējais ± 95% ticamības intervāls)

	Koku biomasa	Atmirusī koksne	Augsne *	Zemsega *	Kopējais oglekļa uzkrājums
Apse					
Vecās audzes	205 ± 7,0	14 ± 1,5	101 ± 17,6	17 ± 4,8	337
Kontroles audzes	119 ± 10,0	5 ± 1,5	104 ± 16,4	24 ± 8,4	252
Bērzs					
Vecās audzes	175 ± 10,0	10 ± 1,8	117 ± 26,3	14 ± 5,2	316
Kontroles audzes	124 ± 7,2	3 ± 0,6	89 ± 13,5	15 ± 11,3	231
Egle					
Vecās audzes	140 ± 9,0	12 ± 2,0	58 ± 21,2	25 ± 12,0	235
Kontroles audzes	113 ± 8,1	5 ± 1,0	96 ± 23,4	30 ± 5,3	244
Priede					
Vecās audzes	172 ± 7,0	15 ± 2,1	72 ± 30,6	21 ± 5,3	280
Kontroles audzes	139 ± 8,8	3 ± 0,9	91 ± 23,6	21 ± 2,1	254

* vidējās vērtības aprēķinātas tikai tiem objektiem, kuros iegūti kvalitatīvi rezultāti kopējā uzkrājuma aprēķināšanai. Statistiskajā analīzē parametru ietekmes vērtēšana un salīdzināšana veikta logaritmizētām vērtībām atmirušās koksnes, augsnes, zemsegas oglekļa uzkrājumu vērtēšanā.

Vecās apšu audzēs, kur koku dimensijas ir nozīmīgi lielākas nekā pārējo koku sugu audzēs, oglekļa uzkrājums ir būtiski ($p < 0,001$) lielāks nekā egļu un priežu audzēs (3.7. att.). Turpretī kontroles audzēs lielākais oglekļa uzkrājums ir priežu audzēs (139 ± 8,8 t C ha^{-1}) un tas ir būtiski ($p < 0,001$) lielāks nekā apšu (119 ± 10,0 t C ha^{-1}) un egļu (113 ± 8,1 t C ha^{-1}) audzēs, bet līdzīgs kā bērzu audzēs (124 ± 7,3 t C ha^{-1}) (3.7. att.). Secināts, ka oglekļa uzkrājuma atšķirības starp kontroles un vecām audzēm nosaka valdošā koku suga ($p < 0,001$), vecuma grupa ($p < 0,001$), kā arī valdošās koku sugas un vecuma grupas mijiedarbība ($p < 0,001$). Kontroles audzēs oglekļa uzkrājums atmirušajā koksnē atkarībā no valdošās koku sugas ir par 58–80% mazāks nekā vecās audzēs. Tāpat kontroles audzēs novēro būtiskas oglekļa uzkrājuma atšķirības atmirušajā koksnē starp egļu (5 ± 1,0 t C ha^{-1}) un priežu (3 ± 0,6 t C ha^{-1}) audzēm (3.7. att.). Kopumā damaksnī un vērī oglekļa uzkrājums koku biomasā un atmirušajā koksnē, palielinoties audzes vecumam virs kontroles audžu vecuma vērtībām, turpina pieaugt. Šī tendence turpinās tik ilgi, kamēr tiek sasniegts uzkrājuma maksimums. Līdzīgi secinājumi iegūti arī, analizējot audžu ilgtermiņa attīstību pēc dabiskā traucējuma (ugunsgrēka) boreālajos mežos Kanādā un konstatējot, ka pēc stabilā maksimuma posma kopējais uzkrājums samazinās neatkarīgi no valdošās sugas (Gao et al. 2018). Iespējams, ka vērtētajā vecuma intervālā egļu mežaudzēs maksimālā uzkrājuma posms noslēdzas.



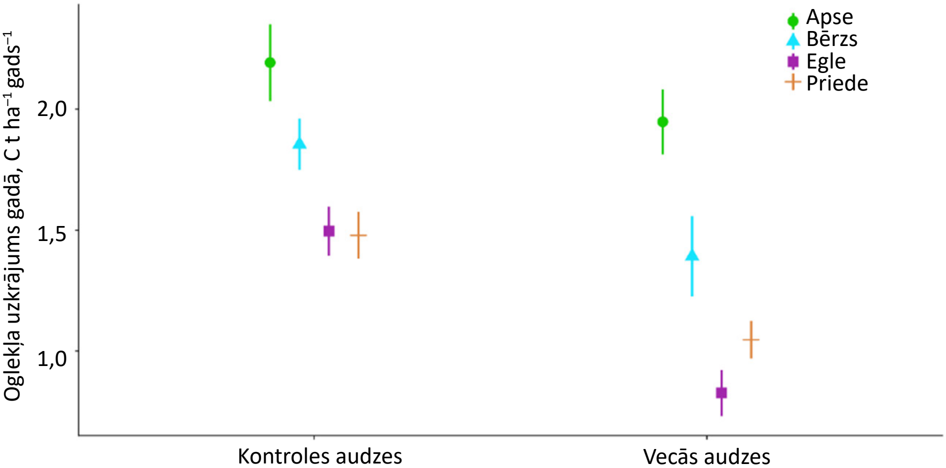
3.7. att. **Oglekļa uzkrājums koku biomasā (A) un atmirušajā koksnē (B) vecās un kontroles audzēs (± 95% ticamības intervāls)**

Izvērtējot pieejamos datus par oglekļa uzkrājumu augsnē un zemsegā, secināts, ka kontroles audzēs oglekļa uzkrājums augsnē visām koku sugām ir līdzīgs. Kontroles audzēs oglekļa uzkrājums zemsegā būtiski atšķiras starp bērzu un egļu audzēm ($p < 0{,}01$). Vecās audzēs oglekļa uzkrājums augsnē ir līdzīgs apšu un bērzu audzēs, bet tas būtiski ($p < 0{,}01$) atšķiras no uzkrājuma skujkoku – vecās priežu un egļu audzēs. Veco audžu grupā, skuju koku audzēm oglekļa uzkrājums zemsegā ir lielāks nekā lapu koku audzēm – būtiskas atšķirības ($p < 0{,}05$) novērotas starp vecām bērzu un vecām priežu audzēm. Salīdzinot oglekļa uzkrājumu augsnē pa valdošajām koku sugām starp vecuma grupām, konstatēts, ka augsnes oglekļa uzkrājums ir līdzīgs starp vecām un kontroles audzēm apšu un bērzu audzēs, bet skujkokiem novēro būtiskas atšķirības ($p < 0{,}01$). Egļu audzēs oglekļa uzkrājums zemsegā būtiski ($p < 0{,}01$) atšķiras starp vecām un kontroles audzēm. Kopumā kontroles audzēs zemsegas oglekļa krātuve ir lielāka nekā vecās audzēs, kas apliecina, ka audzes pēc 58–97 gadiem (atkarībā no koku sugas) jau ir sasniegušas savu augšanas potenciālu (maksimumu) un tāpēc vairs neveidojas tik liela nobiru masa kā jaunākās audzēs (Hansson et al. 2011).

Pētījumā par parastā dižskābarža un parastā ozola audzēm vecumā no 30 līdz 142 gadiem, secināts, ka oglekļa uzkrājums augsnē nav atkarīgs no audzes vecuma (Nord-Larsen et al. 2019). Izmaiņas augsnes oglekļa krātuvē var notikt, augsnes virskārtā zemsegas sadalīšanās rezultātā ieskalojoties organiskajām daļām (Angst et al. 2018), kamēr augsnes dziļākos slāņos oglekļa noturības laiks ir nozīmīgi lielāks, līdz ar to augsne tiek uzskatīta par stabilu ilgtermiņa oglekļa krātuvi (Deluca & Boisvenue 2012; Angst et al. 2018). To apliecina arī pētījumā iegūtie augsnes oglekļa uzkrājuma dati dziļākajos augsnes slāņos vecajās un kontroles audzēs.

Pētījumā iegūtie rezultāti apliecina, ka jau kontroles audžu vecumā zemsega atrodas oglekļa piesātinājuma punktā un augsne tam tuvojas, tāpēc vecajās mežaudzēs nav sagaidāms oglekļa apjoma kāpums šajā krātuvē. Turklāt nozīmīgāku dabisko traucējumu ietekmē ne tikai virszemes biomasā, bet arī augsnes virskārtā un zemsegā oglekļa uzkrājums noteiktu laika posmu var sarukt pat par 50–100% (Palviainen et al. 2020). Tāpat, neviennozīmīgie zemsegas oglekļa uzkrājuma dati kontroles un veco audžu grupā norāda arī uz citiem nobiru sadalīšanos ietekmējošiem faktoriem, kas saistīti ar lapu, skuju, čiekuru un citu nobiru sadalīšanās procesa atšķirībām (Hansson et al. 2011; Lutter et al. 2019), audzes mistrojumu (Laganière et al. 2015), kā arī atmirušās koksnes apjomu (Błońska et al. 2019) un dabisko traucējumu ietekmi konkrētajā audzē (Palviainen et al. 2020).

Novērtēta oglekļa uzkrāšanās efektivitāte starp kontroles un vecām audzēm, aprēķinot oglekļa uzkrājumu gadā koku biomasā un atmirušajā koksnē. Oglekļa uzkrājumu gadā būtiski ietekmē valdošā koku suga ($p < 0{,}001$) un vecuma grupa ($p < 0{,}001$). Kontroles audžu grupā būtiskas atšķirības oglekļa uzkrājumam gadā nav konstatētas tikai starp priežu (vidēji 1,5 ± 0,10 t C ha^{-1} gadā) un egļu (vidēji 1,5 ± 0,11 t C ha^{-1} gadā) audzēm (3.8. att.). Kontroles vecuma grupā lielākais oglekļa uzkrājums gadā konstatēts apšu audzēs (vidēji 2,2 ± 0,16 t C ha^{-1} gadā) un bērzu audzēs (vidēji 1,9 ± 0,10 t C ha^{-1} gadā). Veco mežaudžu grupā apšu audzēm ir būtiski lielāks oglekļa uzkrājums gadā (vidēji 2,0 ± 0,14 t C ha^{-1} gadā), salīdzinot ar pārējām koku sugām, kur līdzīgs uzkrājums gadā ir bērzu (vidēji 1,4 ± 0,16 t C ha^{-1} gadā) un priežu (vidēji 1,1 ± 0,08 t C ha^{-1} gadā), kā arī priežu un egļu (vidēji 0,8 ± 0,10 t C ha^{-1} gadā) audzēm (3.8. att.). Audzes vecumam palielinoties 1,9– 2,3 reizes (apsēm par 54 ± 4 gadiem, bērziem par 62 ± 4, priedēm par 82 ± 6 un eglēm par 103 ± 6 gadiem), oglekļa uzkrājums gadā koku biomasā un atmirušajā koksnē vecās audzēs ir ievērojami un būtiski (bērziem, priedēm, eglēm $p < 0{,}001$; apsēm $p = 0{,}06$) mazāks



3.8. att. **Oglekļa uzkrājums gadā koku biomasā un atmirušajā koksnē vecās un kontroles audzēs (± 95% ticamības intervāls)** nekā kontroles audzēs: par 10% mazāks apšu audzēs, par 27% – priežu un bērzu, par 47% egļu audzēs. Gan kontroles, gan veco audžu grupā oglekļa uzkrājums gadā koku biomasā un atmirušajā koksnē lielāks ir lapu koku sugu audzēs (3.8. att.). Jāatzīmē, ka kontroles audzes vecumi izvēlēti subjektīvi – tātad kontroles vecums neatbilst kādai specifiskai situācijai, piemēram, kad konkrētā koku suga sasniedz maksimālo tekošo vai vidējo krājas pieaugumu.

Iegūtie rezultāti kopumā saskan ar Gundersen et al. (2021) pētījumu, kur secināts, ka oglekļa uzkrājums laika vienībā vecās, saimnieciskās darbības neietekmētās audzēs ir mazāks nekā apsaimniekotās mežaudzēs. Turklāt jāņem vērā, ka liela daļa kontroles audžu atrodas saimnieciskajos mežos, un koksne, kas no tām iegūta kopšanas cirtēs, jau ir izmantota koksnes produktu ražošanā: tātad to faktiskā ietekme uz klimata pārmaiņu mazināšanu ir lielāka nekā konstatējams šajā pētījumā (Pukkala 2017; Holmgren 2021). Kopumā var secināt – kaut arī oglekļa uzkrājums turpina pieaugt līdz ar audzes vecumu (Luyssaert et al. 2021), tomēr šī pieauguma temps ievērojami palēninās, un tādēļ vecas audzes nenodrošina efektīvu klimata pārmaiņu mazināšanu.

SECINĀJUMI

Veco audžu kopējā un pirmā stāva krāja priežu, bērzu un apšu audzēs ir būtiski lielāka (I stāva – par 99–323 m^3 ha^{-1}), bet egļu audzēs – līdzīga kā kontroles audzēm. Pirmā stāva biezums ir atšķirīgs ($p < 0,001$) dažādu valdošo koku sugu vecajās audzēs (vidēji no 235 ± 32 koki ha^{-1} egļu līdz 301 ± 27 koki ha^{-1} bērzu audzēs), un tas ir zemāks ($p < 0,001$) nekā kontroles audzēs, liecinot par zemu oglekļa uzkrājuma stabilitāti: atsevišķu pirmā stāva koku bojāeja dabisko traucējumu un/vai vecuma ietekmē var nozīmīgi samazināt kopējo oglekļa uzkrājumu.

Oglekļa uzkrājumu analizētajās audzēs būtiski ietekmē valdošā koku suga. Oglekļa uzkrājumu vecās priežu un bērzu mežaudzēs palielina relatīvi liels egļu īpatsvars pirmajā stāvā un tās dominance otrajā stāvā, liecinot par jau šajā vecumā (163–218 gadi skuju koku audzēs, 104– 148 gadi lapu koku audzēs) notiekošu sukcesiju.

Nozīmīgākās oglekļa krātuves vecās mežaudzēs ir koku biomasa (55– 61%, vidēji 59% no kopējā ekosistēmas uzkrājuma) un augsne (25–37%, vidēji 30% no kopējā ekosistēmas uzkrājuma).

Saimnieciskās darbības ilgstoši neietekmētās vecās mežaudzēs (104–218 gadi), kur vecie koki ir dominējošais meža elements, kopējais oglekļa uzkrājums ir vidēji par 20% lielāks nekā par 54–103 gadiem jaunākās (kontroles) audzēs: atšķirības atkarīgas no valdošās koku sugas.

Oglekļa uzkrāšanās efektivitāte (oglekļa uzkrājums gadā) koku biomasā un atmirušajā koksnē vecās priežu, bērzu un egļu mežaudzēs ir būtiski (par 27% līdz 47%, atkarībā no koku sugas) mazāka nekā vidēji divas reizes jaunākās kontroles audzēs.

Nelielais oglekļa uzkrājums atmirušajā koksnē, kā arī ļoti vājā korelācija starp oglekļa uzkrājumu koku biomasā un atmirušajā koksnē liecina, ka analizētajā audžu kopā dabisko traucējumu ietekme ilgstoši ir bijusi neliela. Tātad iegūtie dati raksturo oglekļa uzkrājuma potenciālu (maksimumu) vecās audzēs.

REKOMENDĀCIJAS

Apzinoties, ka dzīvo koku biomasa ir lielākā dinamiskā oglekļa krātuve, rekomendējams meža platībās, kurās ietekme uz klimata pārmaiņu mazināšanu ir galvenais mērķis, pielietot tādu mežsaimniecības modeli, lai veidotu iespējami ražīgas un pret dabiskajiem traucējumiem noturīgas audzes, tādējādi veicinot arī oglekļa uzkrājuma palielināšanās efektivitāti.

Meža platībās, kurās primārais mērķis ir dabas aizsardzība, jāņem vērā, ka oglekļa uzkrāšanās efektivitāte (oglekļa uzkrājums gadā) koku biomasā un atmirušajā koksnē laika periodā starp jaunākām kontroles audzēm, un veco audžu stadiju būtiski samazinās. Vecās mežaudzes (vecas kokaudzes) turpina lēni uzkrāt oglekli koku biomasā tik ilgi, kamēr koku vecuma un/vai dabisko traucējumu ietekmē nemainās dominējošais meža elements. Tādēļ, plānojot šādu teritoriju izvietojumu, ieteicams rīkoties tā, lai atstātu iespējami mazāku negatīvo ietekmi uz ES līmeņa klimata politikas realizāciju.

Rekomendējams turpināt pētījumus, iegūstot datus par veco audžu struktūru un tās elementiem, nosakot bioloģiskās vērtības indikatorus, izstrādājot zinātniski pamatotas pieejas bioloģiskās daudzveidības saglabāšanai kombinācijā ar bioekonomikas mērķiem platībās, kur tas ir iespējams.

Nepieciešams turpināt pētījumus, raksturojot dabisko traucējumu un sukcesijas ietekmi uz oglekļa uzkrājumu vecās mežaudzēs (vecā mežā), veicot ciklisku objektu pārmērīšanu. Tāpat nozīmīgi vērtēt oglekļa uzkrājumu un siltumnīcefekta gāzu bilanci vecās audzēs oligotrofos purvaiņos un kūdreņos, kā arī turpināt papildināt datus par oglekļa uzkrājumu un tā dinamiku (īpaši: uzsūcošo sakņu apjoma dinamiku) augsnē.

PATEICĪBAS

Autore pateicas darba vadītājam Ārim Jansonam par pētījuma ideju, kā arī sniegto atbalstu un iedrošinājumu promocijas darba izstrādes gaitā. Izsaku pateicību tuvākajiem LVMI Silava kolēģiem par iedrošinājumu un uzmundrinājumu promocijas darba tapšanas gaitā. Vēlos izteikt pateicību Didzim Elfertam par palīdzību datu statistiskajā apstrādē un Endijam Bāderam par kartogrāfiskā materiāla vizualizācijām. Izsaku pateicību kolēģiem, īpaši Ievai Jaunslavietei, par lielo darbu datu ievākšanā mežā. Paldies ģimenei par atbalstu un iedrošinājumu visa studiju procesa laikā.

1. INTRODUCTION

Forest ecosystems provide habitats for a diverse range of species and play an important role in climate change mitigation, as well as providing essential provisioning, cultural and supporting ecosystem services (Seedre et al. 2015; Bernáldez 2017; Badalamenti et al. 2019; Kulha et al. 2020). In Europe, old-growth forests are rare. However, in the last few decades, areas of old-growth forest stands have continued to grow, reaching biomass and carbon-stock maxima, as forest management intensity has decreased and forest protection has increased (Vilén et al. 2012; Nabuurs et al. 2013; Senf et al. 2021). Along with climate policy of the European Union (EU), the role of old-growth forests has also been emphasized in the EU Biodiversity Strategy for 2030 (O'Brien et al. 2021), which has set the targets of protecting 30% of the EU's land and sea, 10% of which will be under strict protection, including all primary and old-growth forests (European Commission 2020; O'Brien et al. 2021). Therefore, contributions to the knowledge base that will allow the most efficient use of the limited forest area in serving various purposes are very valuable, including data on the carbon storage potential of old-growth forests.

Latvia has ratified the Kyoto Protocol (2002) and the Paris Agreement (2017) and, as a member of the United Nations (UN) and the EU has committed itself to reducing greenhouse gas (GHG) emissions within the framework of the EU Climate Policy in order to reach its climate change mitigation targets. The high carbon storage potential in forest ecosystems can make a significant contribution towards achieving climate neutrality in Europe in accordance with the activities set for each EU Member State under the Land Use, Land-Use Change and Forestry (LULUCF) regulation (EU Regulation 2018/841, 2018; EU Regulation 2018/842, 2018). This new LULUCF regulation sets a binding commitment for each Member State to ensure that accounted emissions from land use are entirely compensated for by an equivalent accounted removal of carbon dioxide (CO_2) from the atmosphere through action in that sector. This is known as the 'no debit' rule. Moreover, regulations have set forest reference levels for accounting net emissions from the existing forests in each EU country (divided into two compliance periods – 2021–2025 and 2026–2030). Based on this new approach, reduction targets of GHG emissions for Latvia will increase by several times. In this context, the contribution of the LULUCF sector needs to be scientifically justified in order to ensure that annual inventories and review reports would be approved under the UN Framework Convention on Climate Change secretariat. Therefore, it is crucial to obtain local scientific data on carbon stocks and sequestration rates in hemiboreal forests that can serve as a reference in reports on national progress towards defined targets within different EU policy frameworks. This way ensuring climate neutrality, as well as making sure there were no losses to the Latvian economy as a result of sanctions that would be levied if inaccurate methods or measures were applied. In addition, proposed flexibility mechanisms allow the forest sector to support other sectors in order to achieve set climate targets.

Only few studies have assessed carbon stock in old-growth stands in Europe. However, areas of old-growth forests will now be allowed to continue to grow because of an increased forest protections under the EU Biodiversity Strategy for 2030 and changing management priorities towards closer-to-nature and more-continuous-cover forestry in Europe (Vilén et al. 2012; EFE State and trends 2016; Badalamenti et al. 2019; Sabatini et al. 2020). Consequently, research interest in old-growth European (especially boreal and hemiboreal) forests is increasing, given that these are an essential forest resource in Europe. Moreover, now they are being viewed as having a large carbon storage potential while also being sensitive to the balance of tree growth and mortality (Högbom et al. 2021; Molina-Valera et al. 2021). This potential is one of the reasons why the role of old-growth stands in carbon sequestration and carbon storage in Europe have been discussed so intensely during the development of the EU policy framework for biodiversity protection and climate change mitigation, also providing the greatest possible benefit to the society. To obtain accurate information on carbon storage in old-growth stands, and thus avoid overestimation of the carbon stocks, and to evaluate possible management practices aimed at climate change mitigation versus biodiversity targets – the collection of science-based empirical data is required.

There are four major forest carbon pools–tree biomass, soil, deadwood, and litter (Fig. 1.1). Each carbon pool has its own dynamics, which can be highly variable

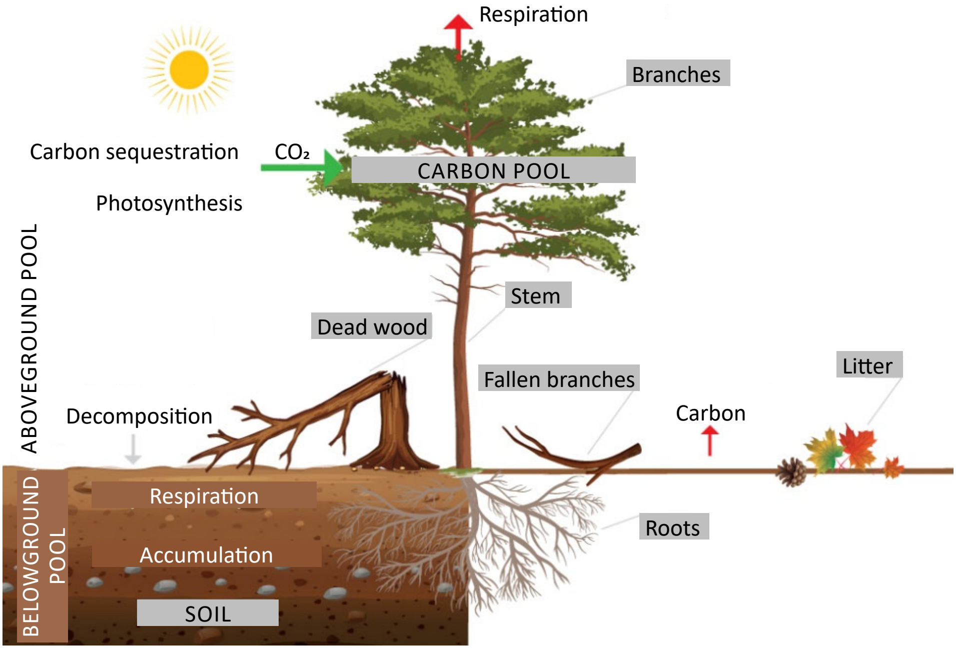


Fig. 1.1. **Carbon pools in a forest ecosystem**

depending on certain factors. Therefore, their share in the total ecosystem carbon differs during different stages of forest development (Seedre et al. 2015; Triviño et al. 2015). A carbon pool is a natural system, or part of such, in which carbon, any precursor to a GHG containing carbon, or any GHG containing carbon, is stored. Each carbon pool or pools store a certain amount of carbon or carbon stock. Data on carbon stocks have been assessed for forest ecosystems, while carbon budgets and carbon sequestration rates have been estimated, and carbon fluxes measured. Net primary production represents the flux of carbon (carbon sequestration and emissions) into the ecosystem. Through photosynthesis, trees sequester CO_2 from the atmosphere and store it as biomass. A carbon sink is anything that absorbs CO_2 from the atmosphere – tree biomass, vegetation, oceans, or soil. A carbon source refers to any organic or inorganic source that releases CO_2 into the atmosphere. A carbon balance is the difference between the CO_2 uptake and loss by a forest ecosystem, and it depends on the stand productivity and the impact of natural disturbances. A forest stand may have a negative ecosystem productivity resulting from a decline in the carbon stock after a forest fire or cutting for a certain period of time, but over time that changes (Taylor et al. 2014).

In this study, the carbon stocks instead of the carbon sequestration rates were assessed in old-growth forest stands. Old-growth forests are of particular interest because they can represent a reference level of carbon-carrying capacity (tree biomass being the largest contributor to the total carbon). This information can be used in decision-support tools for evaluating the influence of an increased share of unmanaged areas and for possible management practices that can make progress towards climate change mitigation versus biodiversity targets (Brockerhoff et al. 2017; Gundersen et al. 2021). Such information is even more topical, given that climate change mitigation depends on carbon stocks not sequestration rates (Kun et al. 2020). Particular factors, such as climate, tree species, site type, stand age, stand tree-growth dynamics, and tree replacement patterns in response to natural disturbances, have the strongest impact on carbon pools in old-growth stands (Jandl et al. 2007; Jacob et al. 2013; Kumpu et al. 2018; Martin et al. 2018; Ruel & Gardiner 2019; Clarke et al. 2021). Specific forest stands may act as carbon sinks or carbon sources for a certain period during stand development, depending on particular factors affecting a specific place (Framstad et al. 2013).

Stand age is one of the main factors influencing the dynamics of carbon in old-growth stands, but the age used to describe the old-growth stage differs between regions (Pregitzer & Euskirchen 2004; Wei et al. 2013; Yuan et al. 2016; Martin et al. 2018; Molina-Valero et al. 2020). The total ecosystem carbon storage results from the cumulative increase in tree biomass with stand age, thus it is closely related to the impact of natural disturbances and the stand structure (Pukkala et al. 2017; Gundersen et al. 2021; Luyssaert et al. 2021). Studies have shown the carbon stock of tree biomass is peaking till 100 years old, at which point the carbon budget is almost balanced (Uri et al. 2019; Uri et al. 2022). A carbon stock maximum has been reported in the tree biomass of mature European beech (*Fagus sylvatica* L.) stands, suggesting that the maximum live carbon stock can be reached in earlier stages than the old-growth stage, where it depends on the occurrence of past natural disturbances (Molina-Valero et al. 2021). Thus, old-growth stands may maintain positive carbon uptake due to an increase in biomass stock, even in stands older than 400 years, according to previous studies on *Pinus* sp. old-growth stands in North America (Framstad et al. 2013). Due to the ability of old-growth to store large amounts of tree biomass for a long time while continuing to grow, old-growth stands have become one of the key elements in meeting climate change mitigation goals (Kun et al. 2020). As climate policy aims to reduce CO_2 emissions into the atmosphere, then old-growth stands do not contribute to climate change mitigation over the long term due to carbon sequestration rates and the effects of natural disturbances on such stands.

Dominant tree species is one of the factors that affect carbon storage in tree biomass because different species exhibit different productivity, produce different amounts of deadwood, and differ in their litter formation and its decomposition. They also have an impact on soil and turnover rates in their fine roots (Hansson et al. 2011; Laganière et al. 2015; Błońska et al. 2019).

Natural disturbance regimes can significantly change the carbon stock in old-growth stands, especially with climate change as the risks from wind and insect outbreaks increases (Seidl et al. 2020). The susceptibility to natural disturbances increases in older stands due to tree aging. Therefore, the damage sustained in serious disturbance events (such as storms) also increases in older stands (Jõgiste et al. 2017). Stem rot, especially in unmanaged stands, is one of the factors affecting large tree resistance to disturbances, and it also has an impact on carbon storage in old-growth stands due to the decomposition of stem parts and hollows (Latva-Karjanmaa et al. 2007). Overall, in the context of the increasing influence of natural disturbances due to climate change (primarily storms), both the formation of deadwood and the decrease of the period, during which old trees are healthy and dominate the stand, strongly influence carbon storage in the long term (Gregow et al. 2017; Seidl et al. 2020; Högbom et al. 2021). Tree biomass is the carbon pool in which the greatest changes have been observed during disturbance events, which can reduce the total carbon stock by up to 39% of the carbon in the forest ecosystem (Thom & Seidl 2016). Old-growth stands may have larger deadwood volumes than younger stands (Šēnhofa et al. 2020), and this plays an important role in both biodiversity and carbon cycling (Nord-Larsen et al. 2019). The persistence of the deadwood carbon pool depends on tree species, time since the last disturbance, and the characteristics of the disturbance, as well as microhabitat activity, tree size, and site type (Mäkinen et al. 2006; Kuuluvainen & Gauthier 2018; Šēnhofa et al. 2020). Even so, stand can remain a positive carbon sink after a natural disturbance. However, carbon emissions from all carbon pools are still increasing. This demonstrates the need for more research on carbon fluxes, especially those in old-growth stands where continuous structural and landscape changes are taking place due to natural succession, natural disturbances, and other factors (Kuuluvainen & Gauthier 2018; Nord-Larsen et al. 2019; Palviainen et al. 2020).

Climate not only determines tree growth, but also impacts the decomposition rates of deadwood and organic matter (litterfall, etc.), thus exerting a significant effect on the carbon dynamics (Khan et al. 2019). Various climatic factors, such as air temperature and humidity (Khan et al. 2019; Sullivan et al. 2020), soil temperature and moisture regime (Lim et al. 2019), and precipitation (Hasper et al. 2016) have been analyzed in order to assess the effects of climate on tree biomass production. In addition, latitudinal gradient is one of the factors that has been linked to nutrient cycling and soil richness, and it has been found to impact the carbon stock in Scots pine stands (aged 66 to 178 years) from southern Poland to northern Finland (Vucetich et al. 2000). Applied forest management strategies have also contributed significantly to stand resilience, providing long-term stand persistence and carbon storage in forest ecosystems that benefits climate change mitigation.

Forest ecosystems' carbon storage potential and sequestration rates depend on many factors and their interactions, which differ between both climatic zones and within regions. Therefore, local data are more reliable for modeling carbon storage and its changes.

The absence of a generally accepted definition for old-growth forests makes it challenging to compare the available knowledge from different European countries and organizations (O'Brien et al. 2021). There is no consistent system of stand age class or naturalness level, or different tree-species life spans that represent the old-growth stage, which makes it difficult to even make comparisons between studies from one region (O'Brien et al. 2021). Old-growth forest is an ecosystem distinguished by old trees and structural attributes that typically differ from earlier stages in a variety of characteristics, which may include tree size, accumulation of large dead woody material, number of canopy layers, species composition, and ecosystem function (Buchwald 2005). Accordingly, old trees can form old-growth stands, but old-growth stands do not always contain old trees because the old-growth stage may have developed after an anthropogenic disturbance in the past, while the ages of the trees in such forest stands can vary widely due to climate, forest type, site conditions, and the severity and frequency of natural disturbances (Buchwald 2005). The known primary forests of Europe (Classes n10 to n5, according to Buchwald (2005)) cover only 0.7% of Europe's forested area (Sabatini et al. 2020). In our study, specific subgroups of old-growth forest stands, in which old target-species trees still formed the dominant cohort and which had reached the old-growth stage, were analyzed.

There have only been few case studies on baseline main carbon pool sizes for different forest ecosystems in Europe, and these have primarily examined European beech (Nord-Larsen et al. 2019; Molina-Valero et al. 2021), Norway spruce (*Picea abies* (L.) Karst.) (Mund et al. 2002; Jacob et al. 2013; Seedre et al. 2015), or oak (Badalamenti et al. 2019; Nord-Larsen et al. 2019) dominated stands in Mediterranean mountainous regions. The long-term study of semi-natural deciduous tree stands (*Fagus sylvatica*, *Quercus robur* L.) has confirmed that old-growth stands represent large and persistent carbon storage (with the deadwood carbon pool also being 35 t C ha^{-1}), with carbon sequestration (ecosystem productivity) being low (Nord-Larsen et al. 2019). There is an important knowledge gap in our understanding of how carbon pools vary in later stages of forest successional and in old-growth forest stands, where great heterogeneity has been observed between stands, and this is one of the greatest shortcomings in current data analysis (Seedre et al. 2015; Yuan et al. 2016), especially in the European boreal and hemiboreal regions, which represent some of the most important forest resources. A meta-analysis of the main carbon pools for the boreal, temperate, and tropical biomes of both managed and unmanaged forests by age class showed that the live tree biomass carbon peaked at an early age in the boreal forests and was relatively lower than in the temperate and tropical forests (Pregitzer & Euskirchen 2004). In eastern Finland, the total ecosystem carbon pool in old-growth (140 years) Norway spruce dominated stands was around 175 t C ha^{-1}, of which 60% was stored in tree biomass (Finér et al. 2003). Soil also accounts for a high amount of the carbon pool in boreal ecosystems (Deluca & Boisvenue 2012; Bradshaw & Warkentin 2015; Mayer et al. 2020). However, the estimates are highly uncertain and there is a lack of research on old-growth stands that would allow a comprehensive assessment of the carbon storage potential (Uri et al. 2012; Seedre et al. 2015). For example, a nationwide study in hemiboreal Estonia found that forest site type and tree species, as well as humus layer, soil trophic conditions, and moisture regime, had a significant effect on the ecosystem's carbon stocks, especially on the soil carbon (Lutter et al. 2019).

The forests in Latvia belong to the European hemiboreal forest zone, which represents the transition from temperate deciduous to boreal coniferous forests, and host a mixture of coniferous and deciduous trees at various scales, and a diverse biota (Lõhmus & Kraut 2010). The hemiboreal countries, including Latvia, Estonia, and Lithuania, are unique in Europe, with large areas of their landscapes having remained under forest cover for a long time – half of Estonia and Latvia and one-third of Lithuania are covered by forests (Jõgiste et al. 2018). Furthermore, potentially, up to 90% of the region could be covered by forests, anthropogenic deforestation (mainly extensive agrarian slash-and-burn agriculture) being the reason for the proportion of open land (Jõgiste et al. 2018). Due to diverse disturbance regimes, soils, and land-use by humans, it has been difficult to describe and analyze the successional dynamics in the landscapes of hemiboreal forests (Lõhmus & Kraut 2010; Nigul et al. 2015). Mixtures of Scots pine and Norway spruce with deciduous tree species, such as birch, European aspen, and alder, are common in hemiboreal forests. The deciduous trees generally characterize the early- to mid-successional stages (European Environment Agency 2007). According to Latvian National Forest Inventory (NFI) data, more than half of Latvia is covered by forests (53% of the land, 3.21 M ha). The most abundant tree species are Scots pine, Norway spruce, birch, and European aspen, which make up 80.6% of the total forest area and 85.7% of the total forest growing stock (NFI 2016–2020). The forest growing conditions are highly variable – 51% of the total forest area grows on dry mineral soils, 9% on wet mineral soils, 11% on peat soils, and 29% is drained. Our study focused on the most prevalent conditions – fertile mineral soils with a normal moisture regime (forest types *Hylocomniosa* and *Oxalidosa*, based on Bušs (1976)), which are found in 40% of the total forest area (NFI 2016–2020). Comprehensive carbon stock data from the forest stands with the most abandoned tree species in common forest types were especially important to be studied in order to provide a more accurate understanding of their actual and potential roles in climate change mitigation towards achieving the climate neutrality goals.

1.1. Aim of the study

The aim of the study was to evaluate the carbon stocks in old-growth Scots pine, Norway spruce, birch, and European aspen stands in which old trees still formed the dominant cohort, and which were growing on dry mineral soils.

1.2. Study objectives

The specific objectives of the study were to:

1. describe forest inventory data for the analyzed old-growth stands;
2. characterize the relationships between the main carbon pools (live tree biomass, deadwood, soil, and litter) and stand parameters; and
3. assess the age effect on carbon storage in forest stands.

1.3. Thesis statements

1. The total ecosystem carbon stock is increasing with stand age, but the mean annual difference in carbon is gradually decreasing over time, from two-times-younger (pine 80 to 120 years, spruce 60 to 100 years, birch 60 to 90 years, aspen 40 to 70 years) to old-growth stands.
2. The largest carbon pool in all the dominant-tree-species old-growth stands, where old trees still formed the dominant cohort, was tree biomass.

1.4. Scientific novelty

For the first time in European hemiboreal forests, the carbon pools of old-growth European aspen and birch stands have been characterized, and the carbon stocks of old-growth coniferous and deciduous stands have been described and compared with younger (age difference 58 years in deciduous stands and 93 years in coniferous stands) control stands.

2. MATERIALS AND METHODS

Data for this study were collected from 84 old-growth Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies*), birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.), and European aspen (*Populus tremula* L.) stands situated on fertile mineral soils (*Hylocomiosa* and *Oxalidosa* forest types, based on Bušs (1976)) occurring throughout the territory of Latvia (Fig. 2.1).

Hylocomniosa and *Oxalidosa* are dry forest types on mineral soil, where the herbaceous layer is dominated by common wood sorrel (*Oxalis acetosella* L.) and European blueberry (*Vaccinium myrtillus* L.), with the moss layer occupied by glittering woodmoss (*Hylocomium splendens* Hedw.) and wind-blown mosses (*Dicranum* spp.) (Bušs 1976). According to Latvian NFI data, *Hylocomniosa* and *Oxalidosa* forest types occupy 40% of the total forest area. Both forest types include stands dominated by Scots pine (16%), Norway spruce (24%), birch (25%), and European aspen (12%), with the common share of these tree species being 78% of the total *Hylocomniosa* and *Oxalidosa* forest areas. According to the NFI data, forest stands older than 120 years cover 4% of the total forest area in Latvia, the majority (90%) forming old Scots pine stands. Old-growth stands were preselected from the forest inventory database according the following criteria: target tree species (Scots pine, Norway spruce, birch, European aspen); stand age group (for pine, > 160 years, spruce > 160 years, birch > 120 years, aspen > 100 years); forest type (*Hylocomniosa*, *Oxalidosa*); dominance of target tree species (> 50% of the volume);

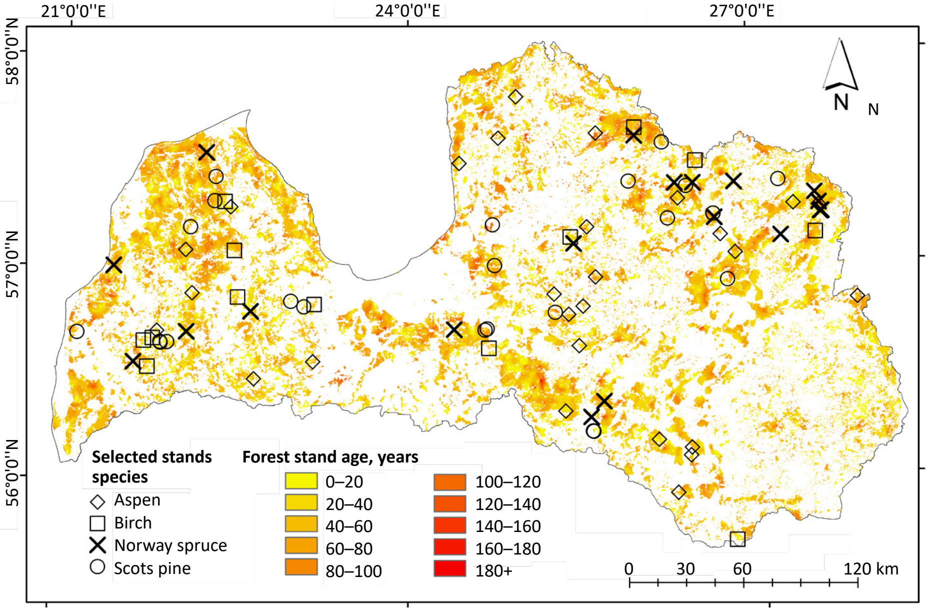


Fig. 2.1. **Distribution of old-growth stands in Latvia**

no documented information on forest management activities for the last 30 years; no signs of former logging; remote location (> 5 km from any villages and > 1 km from any roads) on state-owned forest property; and stand area at least 0.5 ha. Control data, characterizing younger managed mature stands, were selected from the NFI (2014–2018) database, based on the criteria: overstory dominated by target species; stand age (pine 80–120 years, spruce 60–100 years, birch 60–90 years, aspen 40–80 years; and *Hylocomniosa* and *Oxalidosa* forest types. Altogether, data from 447 NFI sampling plots were selected for the study (Tables 2.1 and 2.2).

Table 2.1

Age characteristics of control and old-growth stands

Target tree species	Old-growth stand		Control stand		Age difference [c]
	No. SP [a]	Age [b] (amplitude)	No. SP *	Age (amplitude)	
Aspen	146	112 ± 3 (104–135)	86	58 ± 3 (39–80)	54 ± 4
Birch	67	131 ± 4 (123–148)	114	69 ± 1 (61–80)	62 ± 4
Spruce	102	182 ± 2 (170–205)	117	79 ± 2 (61–100)	103 ± 6
Pine	148	179 ± 6 (163–218)	130	97 ± 2 (81–120)	82 ± 6

[a] sampling plots,

[b] mean stand age ± 95% confidence interval,

[c] mean age difference between control and old-growth stands.

Table 2.2

Characteristics of the first layer trees of the control stands by dominant tree species (mean ± 95% confidence interval)

Parameters	Aspen	Birch	Spruce	Pine
Mean tree DBH, cm	37 ± 2.3	30 ± 1.0	32 ± 1.3	36 ± 0.9
Mean tree height, m	30 ± 1.1	29 ± 0.6	26 ± 0.7	29 ± 0.5
Mean basal area, m^2 ha^{-1}	24 ± 2.2	23 ± 1.4	26 ± 1.8	30 ± 1.9
Mean volume, m^3 ha^{-1}	343 ± 36.1	296 ± 20.2	326 ± 26.7	396 ± 27.1
Mean stand density, trees ha^{-1}	358 ± 50	352 ± 27	381 ± 40	326 ± 25

The potential sample stands were visited and following aspects were examined on site: occurrence of forest type, dominance of the chosen tree species, and low human intervention (no signs of former logging, such as remains of strip roads, stumps) so as to ensure the most accurate deadwood records. Random samples from the stands that met all the eligibility criteria were selected and included in the study. Altogether, 463 sampling plots were systematically established in these stands.

2.1. Data collection

The data collection was performed from 2016 to 2019. In total, data from 19 spruce stands (167–213 years old: Ķēniņa et al. 2018 / Paper I), 25 pine stands (163–218 years old: Ķēniņa et al. 2019a / Paper II), 15 birch stands (123–148 years old: Ķēniņa et al. 2022 / Paper VI), and 25 aspen stands (104–135 years old: Ķēniņa et al. 2022 / Paper VI) were included.

In each stand, there were six to eight sampling plots of 500 m^2 (R = 12.62 m). In each of these, the tree species were recorded and the diameter at breast height (DBH ≥ 6.1 cm) of all the live trees was measured. The heights of five live trees in the first layer of the dominant tree species, and three live trees from each of the tree species in the second layer, were recorded. For the deadwood, the decay stage (five classes – fresh to almost complete decay), based on Sandström et al. (2007), was noted and the tree species (if identifiable) was recorded. The heights of all the standing dead trees (≥ 6.1 cm) were measured. For the standing deadwood (snags), the height and DBH were measured. For the lying deadwood, the diameters of both ends (≥ 14.1 cm at the thicker end) and the lengths were measured. At the center of the large sampling plots (500 m^2), smaller subplots (25 m^2) were placed where live trees and deadwood with smaller diameters were recorded (2.1–6.0 cm for the standing trees and 6.1–14.0 cm for the lying deadwood). The locations of all live and dead trees were determined. Three dominant trees in each sample plot were cored using a Pressler increment corer in order to determine stand age. The tree heights of all the trees were estimated based on the measured trees by correlating the height to the quadratic mean diameter using Näslund's model:

$$H = 1.3 + \left(\frac{D}{k \cdot D \cdot c}\right)^3 , \tag{1}$$

where:

H – tree height;

D – tree DBH, cm;

k, c – coefficients.

A separate height curve was calculated for each forest element, although in cases where fewer than five trees were measured, tree height was estimated according to the Gaffrey model (Šņepsts 2020). The DBH was estimated as the quadratic mean diameter, based on NFI (2013) methodology:

$$D = \sqrt{\frac{4000 \cdot G}{\pi \cdot N}} , \tag{2}$$

where:

D – mean quadratic diameter, cm;

G – basal area, $m^2\ ha^{-1}$;

N – number of trees per ha.

The volume of the live trees and dead standing trees was calculated, based on DBH and tree species, in accordance with Liepa (1996):

$$V = \psi \cdot L^{\alpha} d^{\beta \lg L + \varphi} \;, \tag{3}$$

where:
V – the stem volume, m^3;
L – stem length, m;
d – tree DBH, cm;
$\psi, \alpha, \beta, \varphi$ – coefficients for tree species.

The volume of the snags and the lying dead wood was calculated using Huber’s formula:

$$V = \frac{L \pi d_m^2}{4} \;, \tag{4}$$

where:
V – snag, lying dead wood volume, m^3;
L – snag height/log lenght, cm;
d_m – mid-diameter of the snag/lying deadwood, cm.

To test the carbon content in the deadwood, samples were taken from each of the five decay stages in all analyzed tree species (pine, spruce, birch, aspen) in four randomly selected old-growth birch stands (26 sampling plots in total) (Ķēniņa et al. 2019b / Paper III). Five samples were collected from each tree species (76 cores in total). Samples from wood exhibiting Class 1 and 2 decay were obtained using a 13-mm-inner-diameter sample corer, whereas samples of more degraded wood (Classes 3–5) were taken using 50-mm-inner-diameter) corer. These samples were transported to the LVS EN ISO/IEC 17025:2017-accredited Laboratory of the Forest Environment of the Latvian State Forest Research Institute Silava, where they were prepared and analyzed in accordance with the corresponding ISO standard, and the carbon content was determined. Soil and litter samples were collected together from 157 control and old-growth stands at three systematically located points. At these three points, soil samples and litter samples were taken at least 2 m from any large trees in the first layer. At each point, single soil samples were taken at fixed depths (0–10, 10–20, 20–40, 40–80 cm) using a 100-cm^3 metal cylinder. Litter (organic layer (O horizon) made of undecomposed, fresh and wholly decayed plant or animal debris without mineral material (IPCC 2000)) samples (10 × 10 cm) were taken at each point from the soil organic horizon, and included all litter and decomposed wood. These samples were prepared and analyzed at the same laboratory as above, according to the LVS ISO 10694:2005 standard. The physicochemical parameters of the soil samples, including soil bulk density, coarse fragment fraction, total carbon content, and inorganic-carbon content, were determined according to the corresponding ISO standard. The organic-carbon content in the soil was calculated as the difference between the total carbon and the inorganic-carbon content.

2.2. Data analysis

The carbon stocks of the main carbon pools (tree biomass, deadwood, soil, litter) were calculated. The individual tree biomass was estimated for the above- and belowground components using DBH and calculated tree height as input data. For the calculations, local biomass models for the main tree species in Latvia, developed by Liepiņš et al. (2017), were used. A carbon content of 50% was used to convert tree biomass into carbon to estimate the tree biomass carbon stock (Eggleston et al. 2006).

The individual deadwood mass and carbon stock were estimated from the volume, decay-class-specific density, and carbon content of the main tree species in hemiboreal forests, following Köster et al. (2015) and tested in Latvia (Ķēniņa et al. 2019b / Paper III). To compare the control- and old-growth-stand deadwood carbon pools, we used adjusted decay stages: 1) recently dead (Classes 1 and 2); 2) weakly decayed (Class 3); and 3) moderately to almost completely decomposed (Classes 4 and 5).

Linear mixed-effects models (LMERs) were used to test the effect of species, stand density, standing volume, species unit, and all two-way interactions between species (independent variables) on the dependent variables – the carbon stocks in the tree biomass (including separate models for the above- and belowground biomass) and deadwood. To reduce the heterogeneity of the dependent variables, the carbon stocks of the deadwood, soil, and litter were log-transformed before inputting them into the models. After removing the non-significant interaction terms or main variables (at a significance level of 0.05), the final models were chosen using the Akaike information criterion. In all the models, the stand identification was used as a random factor, as there were multiple plots per stand. If there was a significant effect of factor, or interaction with more than two levels, a Post Hoc test was used to compare the estimated marginal means. Analysis of variance (ANOVA) was used to test the effect of dominant tree species, stand age group, and interaction between those variables on the dependent variable – the carbon stocks of the tree biomass, deadwood, soil, and litter and the mean annual difference between tree biomass and deadwood carbon. Prior to the ANOVA, all dependent variables were averaged for each stand for the old-growth stands so as to have the data at the same level as the NFI data. All data analyses were performed using R 4.1.0. software (R Core Team 2021). The R libraries *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017) were used to implement the LMER. The R library *emmeans* (Lenth 2021) was used to calculate and compare the estimated marginal means.

3. RESULTS AND DISCUSSION

3.1. Stand parameters of the old-growth stands (Papers I, II, IV–VI)

In the old-growth stands, the dominant tree species had a significant impact on DBH, basal area, volume, stand density of the first and second layers, and deadwood volume (Table 3.1). Stand age had no impact on the analyzed stand parameters, indicating that, in cases where old trees still formed the dominant cohort, across a wide age range (including coniferous stands from 163 to 218 years and deciduous stands from 104 to 148 years), a similar volume could be observed. Previous studies on younger stands have shown that stand age is an important factor in influencing stand growth and, therefore, carbon storage (Carey et al. 2001; Pregitzer & Euskirchen 2004; Lee et al. 2016; Martin et al. 2018). Thus, as only one specific age group was analyzed in this study, the effect of stand age was not strongly expressed. Similar results were obtained when analyzing ecosystem productivity in the old stands after fire (Taylor et al. 2014).

Table 3.1

Characteristics of the first layer trees of the old-growth stands by dominant tree species (mean ± 95% confidence interval)

Parameters	Aspen	Birch	Spruce	Pine
Mean tree DBH, cm	49 ± 1.1	38 ± 1.5	37 ± 1.6	48 ± 1.1
Mean tree height, m	37 ± 0.4	30 ± 0.7	29 ± 0.7	31 ± 0.4
Mean basal area, m^2 ha^{-1}	39 ± 2.4	30 ± 2.9	24 ± 3.1	36 ± 2.8
Mean volume, m^3 ha^{-1}	666 ± 48.0	411 ± 53.0	319 ± 53.0	495 ± 41.0
Mean stand density, trees ha^{-1}	242 ± 22	301 ± 27	235 ± 32	268 ± 28
Mean proportion of dominant tree species (amplitude) [a]	9 ± 0.2 (5–10)	7 ± 0.4 (5–10)	7 ± 0.7 (5–10)	7 ± 0.1 (5–10)
Mean dominant tree species DBH, cm	49	38	35	47
Mean dominant tree species height, m	37	30	28	31
Deadwood volume, m^3 ha^{-1}	103 ± 11.0	65 ± 10.5	90 ± 14.2	97 ± 14.0

[a] based on first layer volume.

The mean DBH and stand density (both in the first and second layers) were significantly ($p < 0.001$) different among all analyzed old-growth stands for each dominant tree species. The mean first layer DBH was 49 ± 1.1 cm in the old-growth aspen stands, 48 ± 1.1 cm in the old-growth pine stands, 38 ± 1.5 cm in the old-growth birch stands, and 37 ± 1.6 cm in the old-growth spruce stands (Fig. 3.1). The

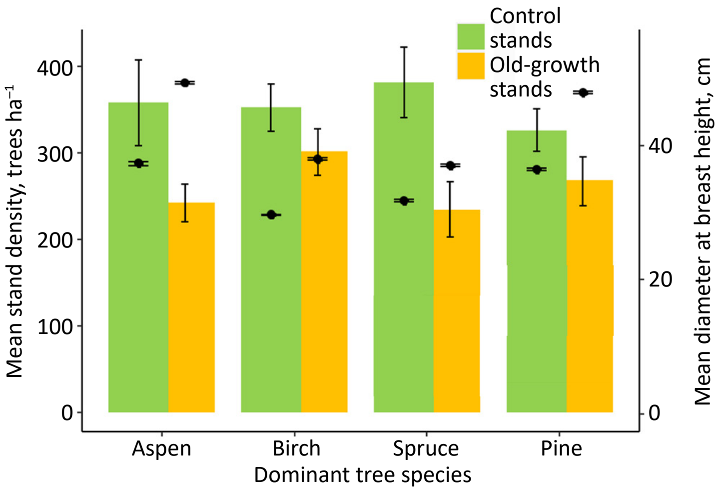


Fig. 3.1. **Mean stand density (columns) and DBH (dots) of the first layer trees by dominant tree species and age group (control and old-growth stands) (error bars show ± 95% confidence intervals)**

old-growth birch and spruce stands first layer had significantly thinner mean DBH than the aspen and pine stands. The mean stand density of the first layer trees in the old-growth birch stands (301 ± 27 trees ha^{-1}) was significantly greater than in the old-growth aspen (242 ± 22 trees ha^{-1}) and spruce (235 ± 32 trees ha^{-1}) stands, but similar to the old-growth pine stands (268 ± 28 trees ha^{-1}). In the old-growth stands, stand density in both the first and second layers for all analyzed tree species was significantly lower ($p < 0.001$) than in the control stands, which were 1.9–2.3 times younger, depending on tree species (in absolute values, 97 ± 2 years for pine, 79 ± 6 years for spruce, 69 ± 1 years for birch, and 58 ± 3 years for aspen). The results suggest that only a few tree losses from the first layer, due to natural disturbances and/or aging, can significantly reduce the total carbon storage in old-growth stands, indicating the low stability of long-term carbon storage. Also, previous studies have reported that the majority of the carbon stock in tree biomass in old-growth stands forms rare, but large, first layer trees (Nilsson et al. 2002).

Dominant tree species ($p < 0.001$) had a significant impact on the volume of the first and second layer and the total stand volume. The old-growth aspen stands had significantly ($p < 0.001$) larger stand volumes and first- and second layer volumes compared to the other species. The old-growth birch and pine stand first layers had similar volumes, but in the spruce stands, this was significantly smaller than in pine stands. However, the volume of the second layer in the old-growth spruce stands was significantly ($p < 0.01$) smaller than in the other old-growth stands (Fig. 3.2). Thus, the analysis showed that spruce was the dominant tree species in the second layer in all the old-growth stands, forming 77–89% of the total volume of the second layer.

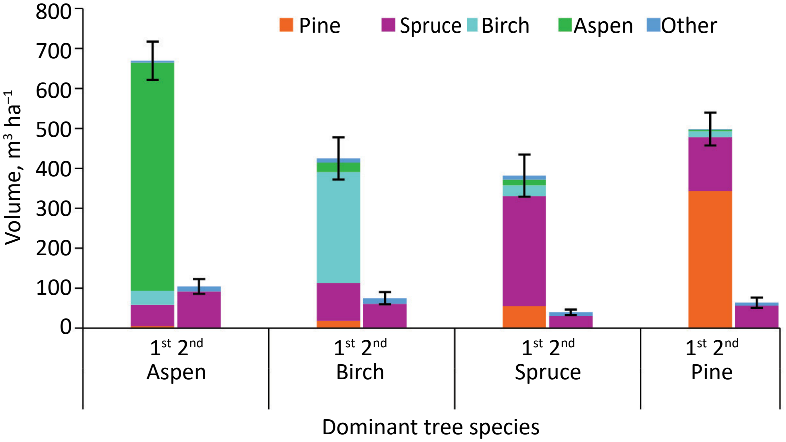


Fig. 3.2. **Mean stand volume of first (1st) and second (2nd) layers by dominant tree species of old-growth stands (error bars show ± 95% confidence intervals)**

Stand composition also had an impact on stand volume, with a relatively high proportion of spruce being found in both the old-growth pine and birch stands. Spruce dominance in the second layer in all the analyzed old-growth stands indicates ongoing succession in both the old-growth coniferous (aged 163 to 218 years) and deciduous (aged 104 to 148 years) stands. This finding is supported by knowledge of the forest succession process, in which stands that have not experienced natural disturbances in a long time regrow through natural regeneration, mostly occurring with shade-tolerant spruce (Drobyshev et al. 1999).

The total and first layer volumes of the old-growth pine, birch, and aspen stands were significantly larger (by 99 to 323 m^3 ha^{-1}) than in the control stands (mean age differences: aspen 54 ± 4 years, birch 62 ± 4 years, pine 82 ± 6 years), whereas the old-growth spruce and control stands were similar (mean age difference 103 ± 6 years).

The mean deadwood volume was similar (64–103 m^3 ha^{-1}) in all the old-growth stands, constituting 13–24% of the live tree volume. Stand volume and density had a significant ($p < 0.01$) impact on deadwood volume in the old-growth stands, suggesting that there will be a high impact from natural disturbances on these old-growth stands in the future (Jõgiste et al. 2017; Seidl et al. 2020; Öder et al. 2021). A huge heterogeneity was apparent between deadwood volume within and between the stands (Table 3.2). Similarly, a large heterogeneity was found between stand volume, stand density, and tree species composition, and their impact on deadwood volume has been reported in previous old-growth studies (Öder et al. 2021). The quantity of dead standing trees in the old-growth stands was determined by the dominant tree species ($p < 0.001$), while stand volume, basal area, and density significantly ($p < 0.001$) impacted the volume of lying deadwood (Table 3.2). The dead standing trees in the old-growth pine stands (42 m^3 ha^{-1}) constituted a significantly higher deadwood volume than that in the other dominant-tree-species old-growth stands (12–18 m^3 ha^{-1}). A large part of the deadwood volume in the old-growth stands was from lying deadwood (Table 3.2). Differences in the amount of deadwood by deadwood type confirmed the effect of species composition on the stand, with spruce become a lying deadwood more rapidly and pine persisting as dead standing trees for a longer time before falling (Šēnhofa et al. 2020). Most of the deadwood was in decay-stage Classes 2–3 (moderately decomposed trees), which was also affected by the differences between the wood properties of specific species (Šēnhofa et al. 2020).

Table 3.2

Characteristics of deadwood volume according to deadwood type and decay stages (mean ± 95% confidence interval)

	Aspen	Birch	Spruce	Pine
Deadwood according to deadwood type, m^3 ha^{-1} (amplitude)				
Lying deadwood	73 ± 9.4 (0–302.4)	45 ± 8.4 (1.5–167.4)	61 ± 10.4 (0–226.2)	43 ± 10.6 (0–405.0)
Dead standing trees	18 ± 4.2 (0–145.8)	12 ± 4.2 (0–95.3)	18 ± 7.3 (0–246.1)	42 ± 6.5 (0–210.5)
Snags	12 ± 2.6 (0–90.4)	8 ± 2.8 (0–55.4)	10 ± 4.6 (0–132.6)	11 ± 2.7 (0–77.7)
Total deadwood	103 ± 11.0 (2.0–363.1)	64 ± 10.5 (3.2–222.8)	89 ± 14.2 (1.6–437.1)	97 ± 14.0 (0–483.2)
Deadwood according to decay stage, m^3 ha^{-1} (proportion of the total deadwood volume)				
Decay stage 1	17 ± 4.2 (16%)	15 ± 6.3 (3%)	3 ± 1.8 (3%)	3 ± 2.6 (3%)
Decay stage 2	38 ± 6.1 (37%)	24 ± 6.1 (38%)	39 ± 10.4 (44%)	64 ± 8.9 (66%)
Decay stage 3	23 ± 4.1 (22%)	14 ± 3.9 (22%)	20 ± 4.8 (22%)	19 ± 5.4 (19%)
Decay stage 4	16 ± 3.7 (15%)	8 ± 1.8 (12%)	16 ± 4.2 (18%)	9 ± 5.0 (9%)
Decay stage 5	10 ± 2.6 (10%)	3 ± 1.7 (5%)	12 ± 3.6 (13%)	3 ± 1.5 (3%)

3.2. Carbon storage in old-growth stands (Papers II–IV, VI)

Tree biomass formed the greatest percentage of the total carbon stocks in the old-growth stands, which also directly impacted the carbon stocks in the deadwood and litter. Tree biomass constituted 59%, while soil accounted for 31% of the total carbon stock. Other European studies have also shown that tree biomass is the dominant carbon pool in old-growth stands (Finér et al. 2003; Seedre et al. 2015). However, specific subgroups of old-growth forest stands, in which old target-species trees still formed the dominant cohort and which had reached the old-growth stage, indicated that there were also significant differences in carbon stocks between the sampling plots – in the aspen stands, from 70 to 318 t C ha^{-1}, 73 to 245 t C ha^{-1} in the pine stands, 88 to 272 t C ha^{-1} in the birch stands, and 60 to 292 t C ha^{-1} in the spruce stands. This heterogeneity was most likely influenced by interactions between the factors that determined the historical development of the different stands, including soil properties, moisture regime fluctuations, and differences in the succession process (Jandl et al. 2007; Hansson et al. 2011; Uri et al. 2012, Lutter et al. 2019).

Stand age had a species-specific significant ($p < 0.01$) impact on carbon storage in live tree biomass and deadwood (Fig. 3.3). The significant ($p < 0.01$) impact of the age effect on tree biomass carbon stock was observed between spruce and aspen old-growth stands. It appears that the assessed age group of the old-growth spruce stands may also include stands in which natural regeneration has already started, whereas extreme cases of longevity were found in the aspen stands.

According to the LMERs, the tree biomass carbon was determined by dominant tree species ($p < 0.01$), standing volume of the first layer ($p < 0.001$), and stand density of the first layer ($p < 0.001$). Moreover, dominant tree species interactions with stand density and stand volume were significant for tree biomass carbon (both $p < 0.001$) (Fig. 3.4). As previous studies have shown, the carbon stock in tree biomass continues to increase with stand age until it reaches a maximum, and then it remains relatively stable for some time (Pregitzer & Euskirchen 2004; Jones et al. 2019). This time period is mostly determined by the effect of natural disturbances and self-thinning of different tree species in the succession process (Pregitzer & Euskirchen 2004; Taylor et al. 2014; Jones et al. 2019).

The significantly highest tree biomass carbon stock was found in the old-growth aspen stands (mean 205 ± 7.0 t C ha^{-1}). Relatively high and similar mean

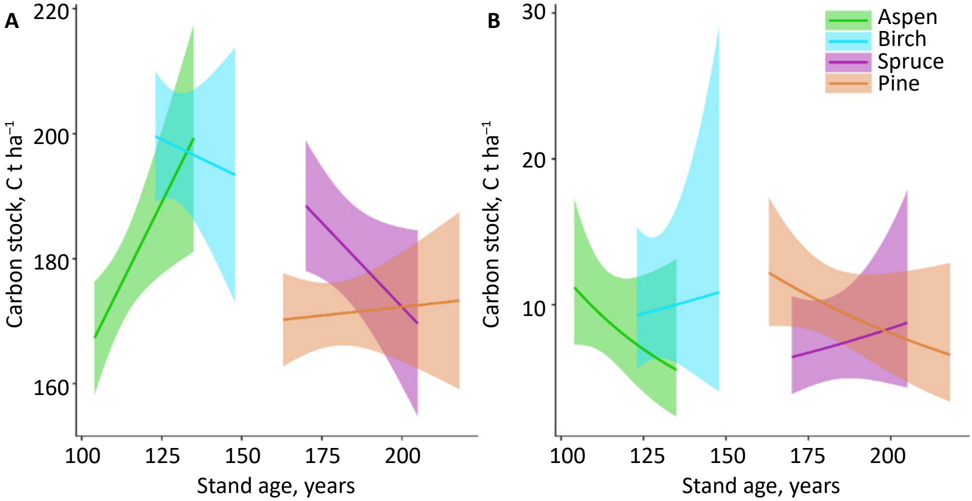


Fig. 3.3. **Model predicted carbon stock changes according to stand age (years) in tree biomass (A) and deadwood (B) (± 95% confidence band)**

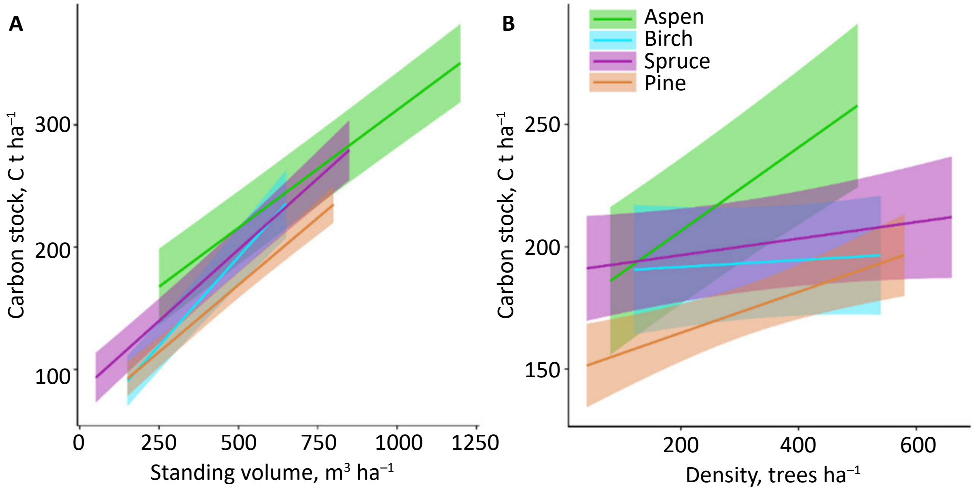


Fig. 3.4. **Model of predicted change in the tree biomass carbon stock by species in response to: standing volume (A); stand density (B) (± 95% confidence band)**

tree biomass carbon stocks were observed in the birch and pine old-growth stands (175 ± 10.0 t C ha^{-1} and 172 ± 7.0 t C ha^{-1}, respectively). Significantly lower tree biomass carbon stocks were found in the old-growth spruce stands (140 ± 9.0 t C ha^{-1}). The size of the tree biomass carbon stock differed significantly between the old-growth aspen and birch stands under the influence of stand volume of the first layer, although stand density of the first layer caused significant differences in tree biomass carbon storage between the aspen and birch old-growth stands. The largest share of the mean tree biomass carbon stock for all tree species in the old-growth stands was stored in the stem (47–73% of the total tree carbon), whereas only 16–25% of the total tree biomass carbon accounted for the belowground biomass, which consisted of small roots, course roots, and stump biomass.

According to the results of this study, deadwood contributed only in a minor way to the total carbon pool in the old-growth stands, but it is an important component of forests in terms of biodiversity and providing other ecosystem services (Nord-Larsen et al. 2019; Ruel & Gardiner 2019; Stakėnas et al. 2020), such as extending the life cycle of carbon in forest ecosystems (Johnston & Radeloff 2019). The carbon storage in deadwood was similar among all analyzed tree species (10–15 t C ha^{-1}), although it was highly variable (0.3– 75 t C ha^{-1}) across the sampling plots.

The size of the deadwood carbon stock in the old-growth stands was determined using the stand density ($p < 0.001$), interactions between the dominant tree species in the stand, and total stand volume ($p < 0.05$) (Fig. 3.5). Consequently, old-growth stands with larger stand volumes – that is, larger trees and more trees (i.e., higher stand density) – had greater amounts of wood that could be transformed into deadwood. Similar observations were made by Pregitzer and Euskirchen (2004),

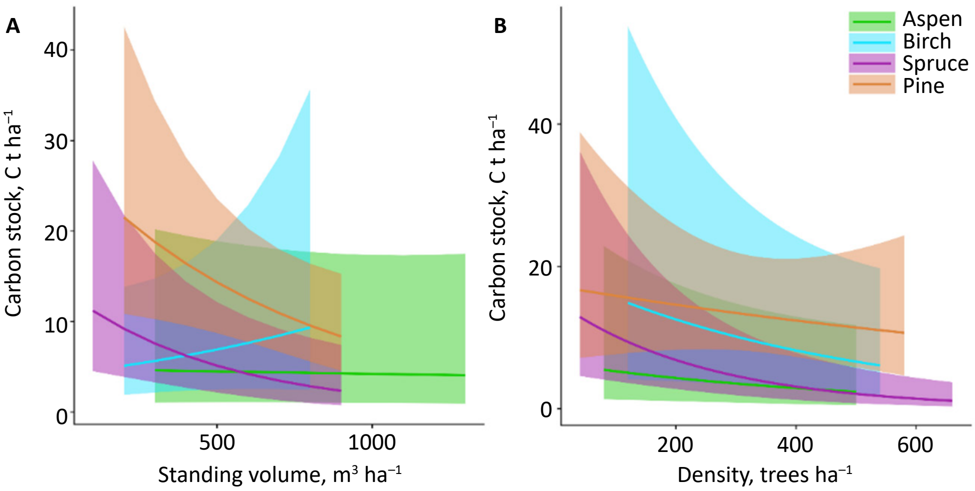


Fig. 3.5. Model of predicted change in the deadwood carbon stock by species in response to: standing volume (A) and stand density (B) (± 95% confidence band)

who also noted that the deadwood carbon stock in old-growth stands could be determined by the number of live trees and the length of time they complemented this carbon pool for. Consequently, the more trees growing in a stand (i.e., higher stand density), the more stable the deadwood carbon pool would be in the long term.

The small amount of carbon stored in the deadwood, as well as the very weak correlation between the tree biomass and deadwood carbon stocks, suggests that the impact of natural disturbances on the old-growth stands has been limited for a long time. Thus, the results obtained from these stands represent the potential maximum carbon storage for old-growth stands. The estimates provided herein support the previous understanding that changes in deadwood carbon stock in old-growth stands, where old trees still form the dominant cohort, are mainly influenced by the tree replacement pattern based on the intensity and frequency of natural disturbances in the specific stand (Martin et al. 2021).

Abiotic factors (air temperature, humidity, and soil properties), biotic factors (fungi and insects), and wood properties (tree species, tree dimensions, and dead tree position (downed/standing) in the stand) are the main aspects affecting deadwood type and the decomposition of dead trees in a stand (Yatskov et al. 2003; Ruel & Gardiner 2019). The mean deadwood carbon stock was 49 ± 1.1 cm in the old-growth aspen stands, 48 ± 1.1 cm in the old-growth pine stands, 38 ± 1.5 cm in the old-growth birch stands, and 37 ± 1.6 cm in the old-growth spruce stands (Fig. 3.1). Lying deadwood constituted the greater part of the total deadwood in the old-growth aspen (mean 9 ± 1.2 t C ha^{-1}), birch (mean 6 ± 1.3 t C ha^{-1}), and spruce (mean 7 ± 1.2 t C ha^{-1}) stands, and these values were similar among these species (Fig. 3.6). In the old-growth pine stands, dead standing trees had the highest share

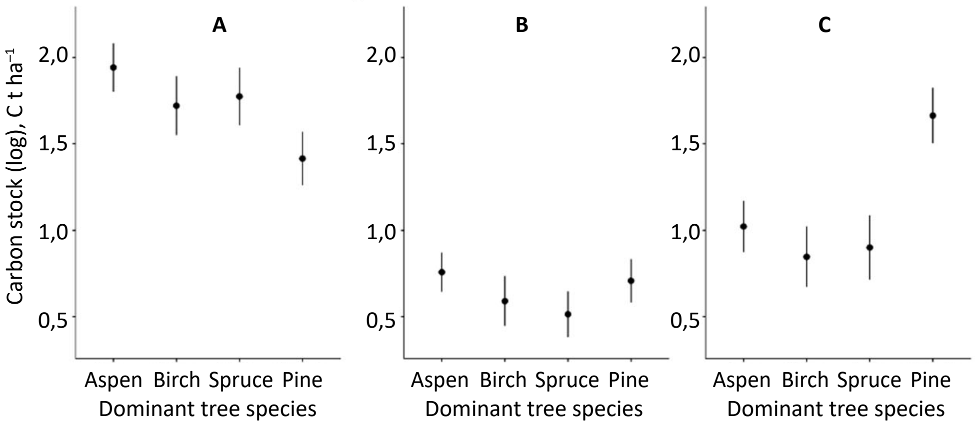


Fig. 3.6. **Deadwood carbon stock in old-growth stands according to deadwood types: lying deadwood (A); snags (B); dead standing trees (C) (logarithmic values; error bars show ± 95% confidence intervals)**

of the total deadwood carbon pool (mean 7 ± 1.5 t C ha^{-1}), and this was significantly higher than in the other old-growth stands (mean 3 ± 0.5 t C ha^{-1}). It is assumed that resistance to wind and the wood properties of pine could be the main reasons for the larger carbon stock being in dead standing trees compared to the other tree species (Kuuluvainen et al. 2017). The smallest mean carbon pool in the deadwood was in the snags subgroup (2 ± 1.0 t C ha^{-1}), and this was similar among all the old-growth stands.

Mineral soil (0–80 cm depth) is the second largest repository for carbon after tree biomass in old-growth stands, varying between 21 and 37% depending on the dominant tree species (mean 31% of the total carbon storage). In the old-growth stands, the soil carbon stock was similar between the aspen (mean 101 ± 17.6 t C ha^{-1}) and birch (117 ± 26.3 t C ha^{-1}) stands, but was significantly ($p < 0.001$) lower in the pine (mean 72 ± 30.6 t C ha^{-1}) and spruce (mean 58 ± 21.2 t C ha^{-1}) stands. The obtained data showed high variability among the stands, which may be a result of species structure and site differences (Hansson et al. 2013; Laganière et al. 2015). In addition, some of the soil samples from the old-growth pine stands were not suitable for further analysis, and variability in the other data was characteristic of the soil carbon pool size in the old-growth stands. Similarly, high carbon-stock variability has been reported by Cindy and Vesterdal (2013) who suggested that soil properties (moisture regime, soil composition, and site history) could be factors responsible for differences in the carbon storage (Jandl et al. 2007; Hansson et al. 2011; Lutter et al. 2019). The upper 0–10 cm soil layer stored more than 30% of the total soil carbon, supporting the findings of a previous study on 60-year-old birch stands, in which the upper 30 cm accumulated 38% of the total forest carbon pool (Uri et al. 2012). Also, Hansson et al. (2011) reported that the upper soil layer was more affected by different natural processes, such as high microbial activity and soil respiration, which affected the carbon stock (Hansson et al. 2011). The litter carbon pool, although numerically small, is considered to be an important transfer point between the surface and soil carbon pools (Jandl et al. 2007). The forest-litter carbon stocks were significantly higher ($p < 0.05$) in the old-growth pine stands (mean 21 ± 5.3 t C ha^{-1}) than in the old-growth birch stands (mean 14 ± 5.2 t C ha^{-1}). The old-growth pine and spruce stands (25 ± 1.0 t C ha^{-1}) had similar litter carbon stocks, and these were higher than in the deciduous old-growth aspen (mean 17 ± 4.8 t C ha^{-1}) and birch stands. In most cases, the litter carbon stock in coniferous stands is higher than in deciduous stands due to slower needle decomposition compared to leaf decomposition, although the differences between pine and spruce litter carbon storage are likely to be affected by different annual litter rates and needle decomposition rates – pines decompose in two years, spruce in six years (Hansson et al. 2011). Moreover, 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 litter carbon stock (Hansson et al. 2011; Cindy & Vesterdal 2013; Lutter et al. 2019).

The total carbon stock was taken as the sum of the mean values of the carbon pools of the live tree biomass, deadwood, soil, and litter from the data obtained. The tree biomass carbon stock included the above- and belowground biomass. The tree biomass represented the largest carbon pool in all the analyzed old-growth stands, comprising 55 to 61% of the total carbon stock. The mineral soil was the second-largest, and most variable, carbon pool (25–37% of the total carbon stock, depending on tree species). Both litter and deadwood were marginal carbon pools, contributing 4–11% and 3–5% of the total carbon stock, respectively. The tree biomass formed the greatest percentage of the mean total carbon stock (mean 59%), followed by the mineral-soil carbon pool (mean 30%), litter (mean 7%), and deadwood (mean 4%). Other studies on Europe have also shown that tree biomass is the dominant carbon pool (Krankina & Harmon 1995; Finér et al. 2003; Seedre et al. 2015; Nord-Larsen et al. 2019). Nevertheless, the total carbon stocks differed notably among stands with the same dominant tree species and between species, indicating a wide variation in the carbon storage in old-growth stands, and reflecting great diversity in the historical development of the stands (Krasnova et al. 2019; Lutter et al. 2019).

3.3. Comparison of the carbon storage in old-growth and younger stands (Paper V)

In the old-growth stands, in which old trees still formed the dominant cohort, the tree biomass carbon stock for all analyzed species was significantly higher (from 19% in the pine and spruce stands to 42% in the aspen stands) than in the younger than 54 to 103 years (1.9 to 2.3 times younger) control stands (Table 3.3).

Table 3.3

Carbon pool size (t C ha^{-1}) of control and old-growth aspen, birch, pine, and spruce stands (mean ± 95% confidence interval)

	Tree biomass	Deadwood	Soil *	Litter *	Total carbon
			Aspen		
Old-growth stands	205 ± 7.0	14 ± 1.5	101 ± 17.6	17 ± 4.8	337
Control stands	119 ± 10.0	5 ± 1.5	104 ± 16.4	24 ± 8.4	252
			Birch		
Old-growth stands	175 ± 10.0	10 ± 1.8	117 ± 26.3	14 ± 5.2	316
Control stands	124 ± 7.2	3 ± 0.6	89 ± 13.5	15 ± 11.3	231
			Spruce		
Old-growth stands	140 ± 9.0	12 ± 2.0	58 ± 21.2	25 ± 12.0	235
Control stands	113 ± 8.1	5 ± 1.0	96 ± 23.4	30 ± 5.3	244
			Pine		
Old-growth stands	172 ± 7.0	15 ± 2.1	72 ± 30.6	21 ± 5.3	280
Control stands	139 ± 8.8	3 ± 0.9	91 ± 23.6	21 ± 2.1	254

* mean values calculated only for those forest stands, from which reliable results were observed.

In the old-growth aspen stands, where individual tree height was significantly ($p < 0.001$) greater compared to the other tree species (Table 3.1), the tree biomass carbon stock (mean 205 ± 7.0 t C ha^{-1}) was significantly higher than that of the spruce and pine stands (Fig. 3.7). In the control stands, the highest tree biomass carbon stock was detected in the pine stands (mean 139 ± 8.8 t C ha^{-1}), where it was significantly ($p < 0.001$) larger than the aspen (mean 119 ± 10.0 t C ha^{-1}) and spruce (mean 113 ± 8.1 t C ha^{-1}) stands, but similar to the control birch stands (mean 124 ± 7.3 t C ha^{-1}) (Fig. 3.7). The tree biomass carbon stocks differed significantly between the dominant tree species and age groups (both $p < 0.001$). The effect of the interaction between the dominant tree species and age groups also had a significant impact on the carbon storage in the live-tree biomass ($p < 0.001$). The deadwood carbon pool, depending on the dominant tree species, was 58–80% smaller in the control stands than in the old-growth stands. The deadwood carbon pool size differed significantly between the control stands, with the pine stands (3 ± 0.6 t C ha^{-1}) having significantly smaller carbon stocks than the spruce stands (5 ± 1.0 t C ha^{-1}) (Fig. 3.7).

The carbon stock in the tree biomass and deadwood continued to increase with increasing stand age, from the control to the old-growth stage, on mineral soils. It is assumed that this trend will continue until the carbon stocks reach their maximum. A similar observation has been reported from a Canadian fire study, in which an analysis of long-term stand development following a natural disturbance revealed that, after reaching a stable carbon-stock maximum, the total carbon stor-

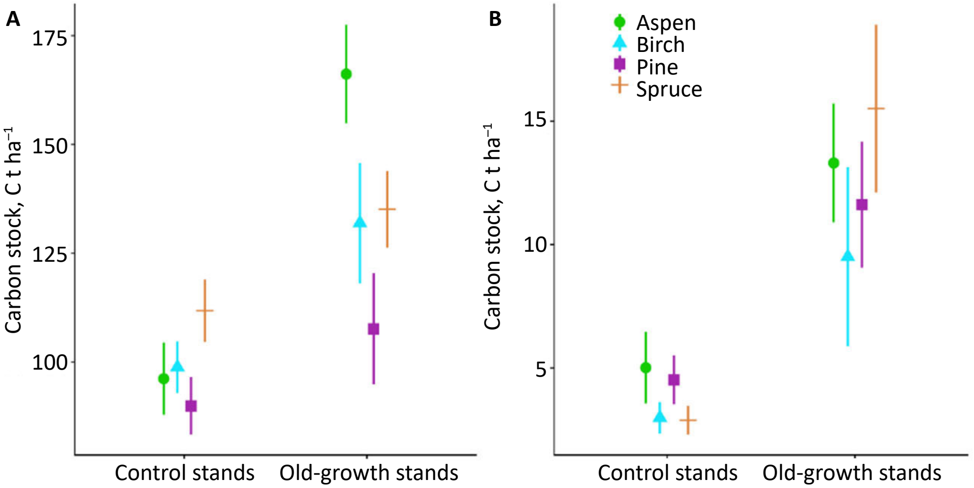


Fig. 3.7. **Mean carbon stocks in control and old-growth aspen, birch, spruce, and pine stands on mineral soil in hemiboreal Latvia from: tree biomass (A) and deadwood (B) (error bars show ± 95% confidence intervals)**

age decreased in all analyzed tree-species stands (Gao et al. 2018). Moreover, in this study, it is more than likely that the peak carbon-storage period in the analyzed spruce stands had already ended.

The soil carbon stock was significantly affected by dominant tree species ($p < 0.001$) and the interaction between dominant tree species and age group ($p < 0.05$), whereas the litter carbon stock was affected by dominant tree species ($p < 0.001$) and age group ($p < 0.05$). In the control stands, the carbon stock in the soil was similar among all tree species, whereas the carbon storage in the litter was significantly different ($p < 0.01$) between the birch and spruce stands, it being twice as large in the spruce stands. In the old-growth stands, the soil carbon stock was similar between the aspen and birch stands, but was significantly ($p < 0.01$) lower in the pine and spruce stands. The litter carbon stock was significantly different ($p < 0.001$) between the birch (mean 14 ± 5.2 t C ha^{-1}) and pine (mean 21 ± 5.3 t C ha^{-1}) stands in the old-growth stands. Based on dominant tree species, the soil carbon stocks significantly differed between the control and old-growth stands in the pine ($p < 0.05$) and spruce ($p < 0.001$) stands, while the litter carbon stock differed between the spruce ($p < 0.05$) control and old-growth stands. The obtained results showed that, in the younger (control) stands, the litter carbon had already reached its maximum. Therefore, in the old-growth stage (after 58 to 97 years, depending on the dominant tree species), the litter production rates and carbon stocks did not increase, which is in line with the findings of previous studies (Hansson et al. 2011). Similar results have been reported on soil carbon stocks, with stands between the ages of 30 and 142 years showing no increases in carbon stocks with increasing age (Nord-Larsen et al. 2019). Most of the changes in the carbon stocks were observed in the upper layers of the soils of both the control and old-growth stands, as a result of organic-matter decomposition and leaching into the soil (Angst et al. 2018), while the carbon stock in the deeper soil layers are considered to represent a stable long-term carbon pool, albeit with a significantly smaller carbon store (Deluca & Boisvenue 2012; Angst et al. 2018).

The data presented herein confirm the hypothesis that, in the younger (control) stands, the litter carbon pool has already reached it maximum and the soil carbon pool is approaching it. Therefore, no significant increase in the carbon stocks in either pool can be expected in the old-growth stands. In addition, in the upper soil layer and litter, the carbon stocks after severe natural disturbance (fire) may decline from 50 to 100%, primarily a result of the decline in the litter carbon pool (Palviainen et al. 2020). Also, high variability in the litter carbon stock data from both the control and old-growth stands indicates a significant impact from the effect of dominant tree species (Hansson et al. 2011; Lutter et al. 2019), together with other overlooked factors, such as stand structure, ground vegetation (Laganière et al. 2015), the amount of deadwood (Błońska et al. 2019), and the natural disturbance regime, all of which have a significant impact on litter production and decomposition (Palviainen et al. 2020).

In order to assess the efficiency of the intensity of carbon storage in the old-growth stands, the mean annual difference between the sums of the tree biomass and deadwood carbon was calculated. Dominant tree species ($p < 0.001$) and age group ($p < 0.001$) had a significant impact on this value. In the control stands, the mean annual difference between the sums of the tree biomass and deadwood carbon was similar in pine and spruce (1.5 ± 0.10 and 1.5 ± 0.11 t C ha^{-1} yr^{-1}, respectively) (Fig. 3.8). Large mean annual differences in carbon in the control stands were found in the aspen (2.2 ± 0.16 t C ha^{-1} yr^{-1}) and birch (1.9 ± 0.10 t C ha^{-1} yr^{-1}) stands (Fig. 3.8). In the old-growth stage, the aspen stands had significantly higher (2.0 ± 0.14 t C ha^{-1} yr^{-1}) than the mean annual differences in carbon compared to the other tree species, with the values being similar between the birch (1.4 ± 0.16 t C ha^{-1} yr^{-1}) and pine (1.1 ± 0.08 t C ha^{-1} yr^{-1}), and the pine and spruce (0.8 ± 0.10 t C ha^{-1} yr^{-1}) stands (Fig. 3.8). The mean annual difference in carbon gradually significantly ($p < 0.001$) decreased (except for in the spruce stands ($p = 0.06$)) over time (82 ± 6 years for pine, 103 ± 6 years for spruce, 62 ± 4 years for birch, and 58 ± 3 years for aspen), from the control to the old-growth stage. A major decrease (47%) in carbon was detected from the mature to old-growth stage in the spruce stands, followed by pine (27%), birch (27%), and aspen (10%). Overall, both in the control and old-growth stands, the mean annual difference in the sum of the tree biomass and deadwood carbon was higher in the deciduous tree stands (Fig. 3.8). It should be noted that the age of the control stand was chosen subjectively, and thus the age did not correspond to a specific situation –for example, when a particular tree species reached the maximum growing stock.

The annual difference values from the younger control to the old-growth stands indicate that forests continue to accumulate carbon into old age, as sug-

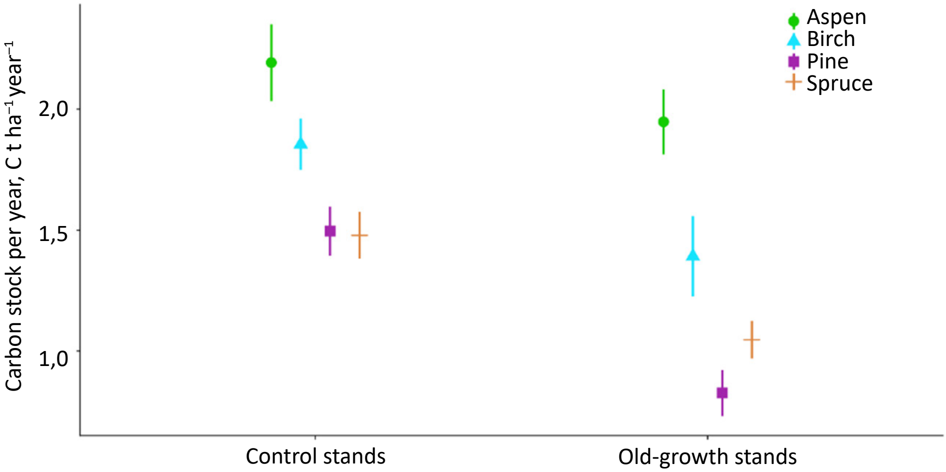


Fig. 3.8. **Mean annual difference in the sum of tree biomass and deadwood carbon in the control and old-growth pine, spruce, birch, and aspen stands (error bars show ± 95% confidence intervals)**

gested by Luyssaert et al. (2021). However, according to Gundersen et al. (2021), carbon uptake decreases over time in old-growth stands, with unmanaged forests having lower carbon-sequestration rates than managed forests. Additionally, most of the control stands have come from commercial forests, where commercial thinning has been performed, and part of this timber has already been used in wood-based products in order to avoid carbon emissions (Pukkala 2017; Holmgren 2021). Thus, the actual impact of younger stands on climate change mitigation could be greater than that found in this study. Nevertheless, the mean annual difference in carbon gradually decreased over time, from the two-times-younger control to the old-growth stage, in all analyzed tree species. Therefore, old-growth stands do not provide an effective use of forestland for climate change mitigation purposes in the long term.

CONCLUSIONS

The total stand and first layer volumes of the pine, birch, and aspen old-growth stands were significantly larger (by 99 to 323 m^3 ha^{-1} in first layer) than in the control stands, but there was similarity between the old-growth and control spruce stands. The mean stand density of the first layer trees was significantly different ($p < 0.001$) among the old-growth stand species (from 235 ± 32 trees ha^{-1} in spruce to 301 ± 27 trees ha^{-1} in spruce stands), and was significantly lower ($p < 0.001$) than in the control stands for all analyzed tree species. The obtained results showed that only a few tree losses in the first layer, due to natural disturbance and/or aging, could significantly reduce the total carbon storage in the old-growth stand, indicating low stability of the carbon storage for the long term.

Dominant tree species ($p < 0.001$) had a significant impact on the carbon stock. A relatively high proportion of spruce had an impact on carbon storage in the tree biomass both in the old-growth pine and birch stands. Moreover, spruce dominance in the second layer in all the analyzed old-growth stands, indicated ongoing succession both in the old-growth coniferous (aged 163 to 218 years) and deciduous (aged 104 to 148 years) stands.

Tree biomass (51–61% depending on the dominant tree species, and mean 59% of the total carbon stock) and the mineral soils (25–37%, mean 30% of the total carbon stock) together accounted for the largest carbon stock in the old-growth stands on mineral soils.

In the old-growth stands (104 to 218 years), in which old target-species trees still formed the dominant cohort, the total carbon stock was, on average, 20% larger than in the younger (than 54 to 103 years) control stands, the difference depending on the dominant tree species.

The carbon storage efficiency (i.e., mean annual difference in the carbon stock) of tree biomass and deadwood carbon in the old-growth pine, birch and spruce stands was significantly (by 27 to 47% depending on dominant tree species) lower than in the two-times-younger control stands.

The small amount of carbon stored in the deadwood, as well as the very weak correlation between the tree biomass and deadwood carbon stocks, suggests that there had been limited impact from natural disturbances on the old-growth stands for a long time. Thus, the results obtained from these stands represent the potential maximum carbon storage in old-growth stands.

RECOMMENDATIONS

In recognizing that tree biomass is the largest and most dynamic carbon pool in old-growth stands, it is recommended that in forest areas where climate change mitigation is the main management objective, a forest model be used that ensures stands that are the most productive and highly resistant to natural disturbances. This would also result in contributing to increased carbon storage efficiency.

In forest areas where the primary management objective is the protection of nature, it should be taken into consideration that the carbon storage efficiency (mean annual difference in carbon stock) in tree biomass and deadwood decreases significantly between the younger (control) and old-growth stands. Old-growth forests continue to accumulate carbon in old age, but their uptake decreases over time, until the dominant forest element changes due to tree aging and/or the impact of the natural disturbance. Therefore, when planning the locations of such forest areas, it is recommended that the impact on EU-level climate change mitigation initiatives be minimized in long the term.

In order to develop science-based approaches to the conservation of biological diversity in combination with achieving bioeconomic objectives in forest areas, where possible, obtaining data on the stand structure and elements of old-growth stands, and determining indicators of biological values, should be continued.

More research is needed to describe the effect of natural disturbance and succession on carbon stocks in old-growth stands by performing periodic re-measurements of the studied stands. It is also important to assess the carbon storage and carbon balance on old-growth stands in oligotrophic peat soils, as well as to further supplement the data-set on the soil carbon stock and it dynamics (including the fine roots).

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Carbon Pools in a Hemiboreal Over-Mature Norway Spruce Stands

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Abstract: Old unmanaged forests are commonly assumed to be carbon neutral; however, there is still a lack of reference studies available to increase the recognition of carbon stock changes in these forests. Studies of old forest carbon storage from hemiboreal regions are very rare compared to temperate and boreal forests in Europe; therefore, the aim of this study was to quantify the carbon stock in hemiboreal over-mature (167–213 years) Norway spruce (*Picea abies* (L.) Karst.) stands. To explore the total ecosystem carbon pool, the carbon stock of tree biomass, deadwood, and soil in unmanaged (for at least the last 40 years) spruce stands was calculated and compared between different forest site types on dry, wet, and drained mineral soils. Total carbon stock of hemiboreal over-mature spruce stands ranged from 164.8 Mg C ha^{-1} to 386.7 Mg C ha^{-1}, and 238.5 Mg C ha^{-1} on average, with no significant differences ($p > 0.05$) between the forest site types. The carbon stock of tree biomass was significantly affected by the basal area of the upper tree layer ($p < 0.0001$) and the interaction between the forest site type and proportion of spruce in the stand composition ($p = 0.002$). Tree biomass was the dominant carbon pool, followed by soil and deadwood in over-mature spruce stands.

Keywords: carbon stock; *Picea abies* (L.) Karst.; old-growth forests; aboveground and belowground biomass; soil organic carbon; deadwood

1. Introduction

Climate change has been increasingly recognised as one of the greatest environmental issues and the international community is facing these challenges by implementing the United Nations Framework Convention on Climate Change (UNFCCC), Kyoto Protocol, and Paris Agreement [1]. Boreal forests are one of the biggest terrestrial carbon pools on Earth [2,3], storing carbon in the tree biomass and releasing it through decomposition, therefore playing a significant role in global climate change mitigation [4,5]. With increasing interest to promote carbon sequestration in forests, various new forest management practices are employed in managed even-aged stands [6–9] to meet the climate change targets and to reduce the carbon dioxide emissions in land use, land use change, and forestry (LULUCF) sector [1,10]. However, there is still a lack of reference studies of unmanaged over-mature forests [2].

Under unmanaged conditions, ageing forests slowly develop stand structures that are typical for old-growth forests [11]. In these conditions, species and age composition as well as the occurrence of natural disturbances play a key role in the formation of carbon stock and carbon fluxes [12–14]. Thus, only very limited review studies in old forests with a mixed-species, multi-cohort structure under various past-management practices are available to understand the carbon stock changes [7,15].

Old unmanaged forests are commonly assumed to be carbon neutral due to the decline of net primary productivity with increasing stand age [16,17]. However, some studies suggest that over-mature forests may serve as important carbon sinks [18,19]. Recent data of over-mature boreal forests revealed that when managed forests are left unmanaged, they become weak carbon sinks due to very low carbon accumulation in soil and living biomass [20].

Tree biomass comprised the largest carbon pool in forests along with soil organic matters [17,20]. Through the development of the stand, carbon is reallocated between the pools [12,21]; thus, it is still challenging to estimate soil and litter carbon stocks [3,21]. The analysis of carbon in the tree biomass shows that stands with older trees have lower carbon uptake rates, yet they have a large carbon stock [18–20], giving just a partial understanding of the total ecosystem carbon. Moreover, in the hemiboreal region, there are just a few studies of birch stands dealing with carbon stock estimations [4,22], where boreal and temperate forest species form a large heterogeneity in forest stands [23].

Hemiboreal forests, which occur in north and northeast Europe, are dominated by the mixture of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) with deciduous trees [24]. According to the national forest inventory, Norway spruce forests constitute 20% of the forest standing volume in Latvia, also being one of the most economically important and intensively managed tree species [25]. As sustainable forest management is considered the most efficient way to increase the forest carbon stock [9,20], there is a growing need for reference data from unmanaged spruce stands. Therefore, the aim of this study was to quantify hemiboreal old unmanaged Norway spruce forests carbon stock in the main carbon pools: tree biomass, deadwood, and soil organic carbon.

2. Materials and Methods

2.1. Study Area

The study was conducted in the hemiboreal mixed ageing Norway spruce (*Picea abies* (L.) Karst.) forests among various site types in Latvia between 56°14′ and 57°34′ between 21°3′ and 27°17′. The climate in Latvia is moderately cool and moist due to western winds, which bring cool and moist air masses from the Baltic Sea and Atlantic Ocean. According to the data from the Latvian Environment, Geology and Meteorology Centre, the mean annual temperature is +5 °C, ranging from around −5 °C in January to +17 °C in July. The mean annual precipitation is 550–850 mm; about 500 mm falls during the summer months. The vegetation period usually extends from late April to October.

Most common soil types in Latvia are podzols and gley soils [26]. In general, the forest site types vary from oligotrophic to meso-eutrophic and eutrophic site types, with different water regimes and species structures according to the Latvian forest ecosystem classification [26,27]. Forest site types used in this study were: *Hylocomniosa*, *Oxalidosa* (dry forests; fertile minerals with a normal moisture regime), *Myrtilloso-sphagnosa*, *Myrtilloso-polytrichosa* (wet mineral soils), *Myrtillosa mel.* (drained mineral soils). The forest types according to Bušs [27] are mostly dominated by Norway spruce stands.

2.2. Sampling and Measurements

Prior to the fieldwork, the potential sample stands were randomly selected from protected forests based on age limit (>160 years), dominance of Norway spruce (>50% from basal area), and location (>5 km from villages and >1 km from roads). Selected stands were inspected in the field for conformity of the dominated species occurrence. In the case of any signs of former logging (strip roads, stumps, etc.), they were discarded.

In total, 26 over-mature spruce dominated stands between 167 years and 213 years were sampled (Table 1). Altogether, 178 sample plots (6–8 sample plots in each stand) of 500 m^2 were systematically established in these stands in 2016.

Table 1. Characteristics of over-mature spruce stands of each forest site type. The forest site types included dry (*Hylocomniosa*, *Oxalidosa*), wet (*Myrtilloso-sphagnosa*, *Myrtilloso-polytrichosa*), and drained (*Myrtillosa mel.*) mineral soils.

Parameters ± CI [1]	**Dry Mineral Soil**	**Wet Mineral Soil**	**Drained Mineral Soil**
Mean tree dbh [2], cm	41.2 ± 4.2	32.9 ± 4.8	31.1 ± 5.5
Mean tree height, m	29.7 ± 1.8	25.9 ± 2.3	26.7 ± 3.3
Mean stand basal area, m^2 ha^{-1}	37.9 ± 3.4	32.7 ± 3.8	33.4 ± 8.9
Mean basal area in upper tree layer, m^2 ha^{-1}	29.9 ± 3.6	25.6 ± 3.2	26.4 ± 7.2
Mean stand volume, m^3 ha^{-1}	462.0 ± 66.5	357.4 ± 51.4	389.4 ± 121.4
Site index, m	27	23	25
Mean stand age, years	181.1 ± 6.2	179 ± 11.5	185 ± 23.4
Number of sample plots	98	42	38

[1] CI: 95% confidence interval; [2] dbh: diameter at breast height.

The diameter at the breast height (dbh) of all living trees ≥6.1 cm was measured. For all standing dead trees ≥6.1 cm, the dbh and length of the snags were recorded. The tree height for three to five living trees of each species and the layer of stand (upper tree layer, second tree layer) in each sample plot was measured to estimate tree height [28]. The site index (the height at age 100 years) for spruce in each of the forest site types was estimated [29]. The total (above- and belowground) tree biomass was calculated using dbh and height with equations for the main tree species in Latvia developed by Liepiņš et al. [30]. The carbon content of 50% was used for the tree biomass carbon stock estimation [5,31]. Lying deadwood with a diameter at the thicker end ≥14.1 cm was measured at both ends within the area of the sample plot. The decay stages of lying and standing dead trees were set using a five-class decay classification and 'knife method' (modified from Sandström et al. [32] and Köster et al. [33]). The volume of the lying deadwood and dead trees with broken tops was calculated using a truncated cone formula and converted to mass using the decay class-specific density. The values of the deadwood basic density and carbon content for the main tree species (Norway spruce, Scots pine (*Pinus sylvestris* L.), birch sp. (*Betula pendula* Roth. and *Betula pubescens* Ehrh.), European aspen (*Populus tremula* L.), grey alder (*Alnus incana* (L.) Moench.), and black alder (*Alnus glutinosa* (L.) Gaertn.)) were applied from recent studies in Estonia [33,34].

Soil samples (organic layer and four mineral soil layers 0–10 cm, 10–20 cm, 20–40 cm, and 40–80 cm) were taken from 16 stands at systematically located points outside the sample plots from the forests on dry and wet mineral soils. Obtained samples were returned to the Forest Environment Laboratory at the Latvian State Forest Research Institute Silava, where physical and chemical analyses were carried out following the reference methods outlined in Part X of the International Co-operative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests Manual on Sampling and Analysis of Soil [35]. The soil samples were prepared for analyses according to the LVS ISO 11646: 2005 standard. In the soil samples, the following parameters were determined: bulk density (kg m^{-3}) according to LVS ISO 11272:1998, total carbon content using elementary analysis (dry combustion) according to LVS ISO 10694:2006, and carbonate content using the Eijkelkamp calcimeter according to ISO 10693:1995. The organic carbon concentration (g kg^{-1}) in the soil was calculated as the difference between the total carbon content and the inorganic carbon content.

2.3. Data Analysis

The carbon stock of the tree biomass and deadwood was studied using a linear mixed-effects model analysis as implemented in the program R 3.4.3 [36] library lme4 [37]. The predictor variables (forest site type, basal area of upper tree layer, proportion of spruce in stand composition, and interactions between forest site type and each of the factors) in the model were treated as fixed effects. The stand was treated as a random effect to account for possible correlation between plots of one stand. Linear mixed-effects models were used also to test the effect of forest site types on stand parameters. Pairwise comparison of estimated marginal means, as implemented in the library emmeans [38], was used as PostHoc test. To test the effect of the predictor variable on soil carbon, separate analysis of variance (ANOVA) or linear regression models were performed for each predictor, as there was only one sample per stand.

3. Results

3.1. Tree Biomass Carbon Stock

The carbon in the stems accounted for 59% of carbon stock in the tree biomass, followed by carbon stock in the roots (belowground biomass) and branches. The mean carbon stock in the tree biomass was not significantly ($F_{2,162.59} = 1.87$, $p > 0.05$) different between the forest site types: 149.2 ± 18.9 Mg C ha^{-1} in forests on dry mineral soils, 125.2 ± 14.0 Mg C ha^{-1} in forests on wet soils, and 130.9 ± 38.1 Mg C ha^{-1} in forests on drained mineral soil (Figure 1).

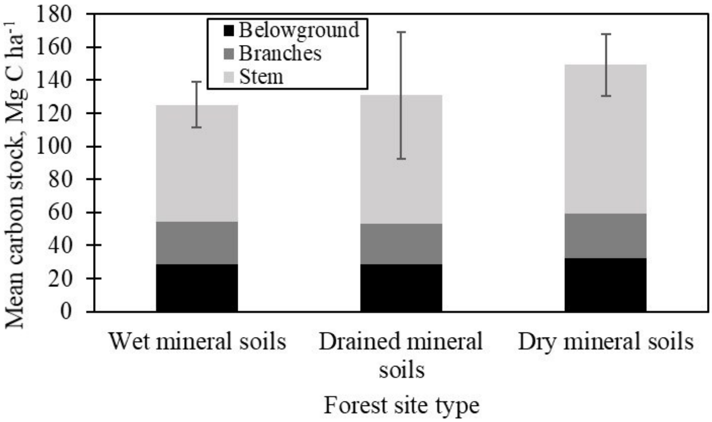

Figure 1. Mean carbon stock of tree biomass components (±95% confidence interval of mean total tree biomass carbon stock) between the forest site types.

Despite the similar carbon stock of the tree biomass, there were differences in tree species composition and stand parameters between the forest site types. The mean proportion of spruce in stand composition (69%) was similar between the forest site types ($F_{2,164.16} = 0.09$, $p > 0.05$). Scots pine had the second-largest mean proportion in stand composition after spruce, both in forests on dry (36%) and drained (25%) mineral soils. The second most represented species on wet mineral soils was birch (25%). Birch and Scots pine were common tree species, occurring in 43% of the studied stands. Along with the tree species composition, differences in stand parameters of the upper tree layer affected the carbon distribution of the tree biomass between forest site types. There were no significant differences ($p > 0.05$) of spruce parameters in the upper layer between the forests on wet (mean tree dbh of 30.4 cm, tree height of 25.0 m, density of 231 trees ha^{-1}, and volume of 208.5 m^3 ha^{-1}) and drained (mean tree dbh of 29.2 cm, tree height of 25.2 m, density of 270 trees ha^{-1}, and volume of 238.3 m^3 ha^{-1}) mineral soils. The upper layer spruces in forests on dry mineral soils had significantly higher mean tree dbh ($F_{2,165.32} = 26.13$, $p < 0.0001$; 36.7 cm), tree height ($F_{2,159.83} = 30.95$, $p < 0.0001$; 28.3 m), and volume ($F_{2,149.86} = 8.71$, $p < 0.0001$; 264.7 m^3 ha^{-1}), but significantly lower density ($F_{2,156.17} = 35.72$, $p < 0.0001$; 175 trees ha^{-1}).

The carbon stock in the tree biomass was significantly affected by the basal area (positively, $F_{1,156.15} = 1253.16$, $p < 0.0001$) and by the interaction between forest site type and proportion of spruce in the stand composition ($F_{2,153.68} = 6.37$, $p = 0.002$) (Figure 2). In forests on drained mineral soils, the carbon stock of the tree biomass significantly decreased with the increasing proportion of spruce in the stand composition; the opposite trend was observed in forests on dry and wet mineral soils.

Thus, the basal area (m^2 ha^{-1}) of spruces in the upper tree layer were similar ($F_{2,149.30}$ = 0.04, $p > 0.05$) between the forest site types because, in forests on dry mineral soils, a few large spruces (40–60 cm in dbh) comprised a great share of the total basal area. The basal area in the upper tree layer ranged from 3.8 to 55.5 m^2 ha^{-1}; the spruces made up the largest share (68%).

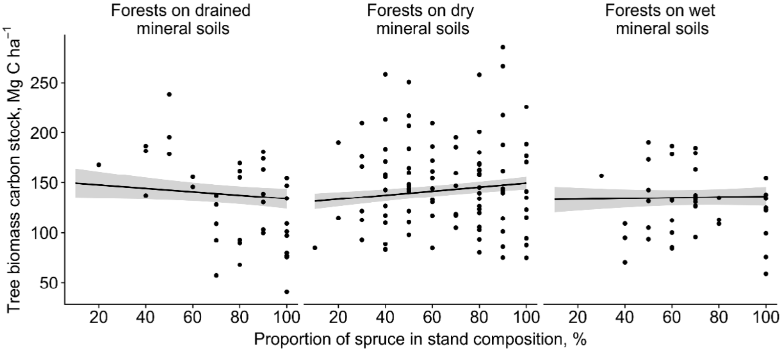

Figure 2. Influence of proportion of spruce in the stand composition on tree biomass (above- and belowground biomass) carbon stock (±95% confidence interval (grey area)) in different forest site types.

3.2. Deadwood Carbon Stock

The mean carbon stock of deadwood was 11.8 ± 2.3 Mg C ha^{-1} (ranging between 0.1 Mg C ha^{-1} and 71 Mg C ha^{-1}) in forests on dry mineral soils. Spruce trees (mean dbh 24.2 cm) formed the largest proportion of deadwood carbon stock (8.2 Mg C ha^{-1}), followed by pines (mean dbh 29.6 cm; 1.0 Mg C ha^{-1}) and different broadleaved tree species (mean dbh 16.4 cm; 2.4 Mg C ha^{-1}) in forests on dry mineral soils. In the forests on wet mineral soils, the mean deadwood carbon stock ranged between 1.4 Mg C ha^{-1} and 30.8 Mg C ha^{-1} with a mean of 11.8 ± 2.2 Mg C ha^{-1}. The largest deadwood carbon stock in forests on wet mineral soils consisted of spruces (mean dbh 21.3 cm; 8.2 Mg C ha^{-1}), followed by birches (mean dbh 26.7 cm; 1.4 Mg C ha^{-1}). In forests on wet mineral soils, birch (1.4 Mg C ha^{-1}) and black alder deadwood carbon stocks were significantly higher ($F_{2,173.00}$ = 5.03, $p < 0.008$) compared to both other forest site types. The smallest mean carbon stock of deadwood was in forests on drained mineral soils (10.6 ± 2.2 Mg C ha^{-1}, ranging from 0.8 Mg C ha^{-1} to 30.7 Mg C ha^{-1}). No significant differences ($F_{2,20.78}$ = 0.78, $p > 0.05$) in the total deadwood carbon stock were found between the forest site types due to the high variation of the studied stands (Figure 3).

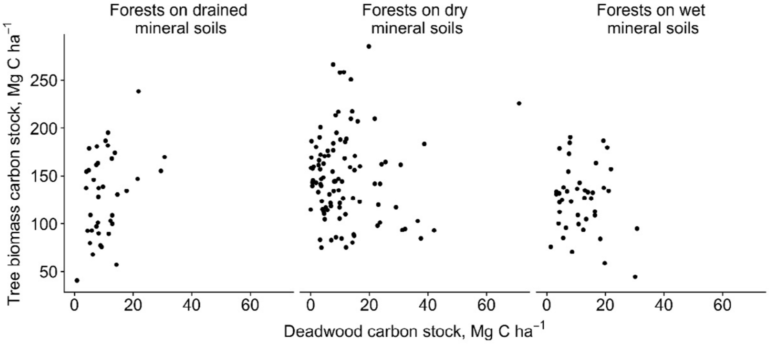

Figure 3. The tree biomass and deadwood carbon stocks of sample plots in different forest site types.

The downed logs contained, on average, 63% of the total carbon stored in the deadwood. The largest share of deadwood carbon stock accounted for 12.2% of the aboveground biomass carbon in forests on wet mineral soils, followed by forests on drained (10.3%) and dry (10.0%) mineral soils. The carbon stock in the deadwood was not significantly linked to any of the stand variables included in the analysis.

3.3. Soil Carbon

The carbon stored in the mineral soil (0–80 cm) of the studied stands ranged from 29.5 Mg C ha^{-1} to 214.3 Mg C ha^{-1} with an average carbon stock of 85.6 ± 26.1 Mg C ha^{-1} and did not differ ($F_{1,15} = 0.004$, $p > 0.05$) between forests on dry and wet mineral soils. The soil organic carbon content decreased with depths from 57 g kg^{-1} (0–10 cm) to 30 g kg^{-1} (40–80 cm). The mean carbon stock in the upper 0–10 cm layer ranged from 1.5 Mg C ha^{-1} to 60.1 Mg C ha^{-1}. However, in the 40–80 cm layer, it ranged from 1.5 Mg C ha^{-1} to 32.7 Mg C ha^{-1} in sampled stands. The mean soil organic carbon stock decreased with increasing depth and greatly varied between the observed depth intervals.

3.4. Total Carbon Stock in Over-Mature Spruce Forests

The total carbon stock (including the carbon stored both in live and dead trees and soil) in over-mature forests on dry mineral soils varied from 164.8 Mg C ha^{-1} to 386.6 Mg C ha^{-1} (Table 2). Less variation of the total carbon stock was found in forests on wet (205.9–245.6 Mg C ha^{-1}) and drained (188.3–259.8 Mg C ha^{-1}) mineral soils. The mean total carbon stock was 249.3 ± 31.8 Mg C ha^{-1} in forests on dry mineral soils, 225.1 ± 11.4 Mg C ha^{-1} in forests on wet mineral soils, and 227.0 ± 39.8 Mg C ha^{-1} in forests on drained mineral soils. No significant differences of the total carbon stock in over-mature spruce stands in the assessed forest site types were observed ($F_{2,25} = 0.92$, $p > 0.05$).

Table 2. Mean carbon stock (Mg C ha^{-1}) of live, dead trees and soil in over-mature spruce forests between the different forest site types.

Carbon Pools ± CI [1]	Dry Mineral Soil	Wet Mineral Soil	Drained Mineral Soil
Aboveground tree biomass	116.8 ± 15.4	96.8 ± 11.5	102.4 ± 30.3
Belowground tree biomass	32.3 ± 3.6	28.4 ± 2.6	28.5 ± 7.9
Total tree biomass carbon stock	149.2 ± 18.9	125.2 ± 14.0	130.9 ± 38.1
Lying deadwood	37.9 ± 3.4	32.7 ± 3.8	33.4 ± 8.9
Standing snags	29.9 ± 3.6	25.6 ± 3.2	26.4 ± 7.2
Total deadwood carbon stock	11.8 ± 2.3	11.8 ± 2.2	10.6 ± 2.2
Soil carbon stock	88.4 ± 23.8	88.0 ± 12.4	85.6 ± 26.1 *
Total carbon stock	249.3 ± 31.8	225.1 ± 11.4	227.0 ± 39.8

[1] CI: 95% confidence interval; * mean soil carbon stock was used.

4. Discussion

Latitudinal gradient is linked to nutrient cycling and soil richness, therefore, causing differences in carbon stock between the pools in forest ecosystem [39]. At present, the proportion of old-growth forest is very low [40]; therefore, many carbon stock studies have been conducted in young-to-mature managed temporal and boreal forests (e.g., [41–43]. However, few studies are available regarding the hemiboreal zone [4,22,23], which is the transition zone with diverse species and stand structures. Moreover, to our knowledge, there are no studies dealing with carbon stock estimations in over-mature spruce hemiboreal forests. Our study quantified the carbon stock of over-mature Norway spruce stands tree biomass, deadwood and soil, covering different forest site types in Latvia.

The tree biomass (above- and belowground) was the dominant carbon pool in over-mature spruce forests, ranging greatly between the stands from 41% to 74% of total carbon stock. This corresponds with the results found in other old-growth forest studies [2,17]. The mean carbon stock of the tree biomass in hemiboreal over-mature spruce stands, 139.2 Mg C ha^{-1}, was somewhat more than reported from mixed old-growth (140–170 years) spruce stands (*Vaccinium-Myrtillus* type) in eastern Finland (106.3 Mg C ha^{-1}) [2]. However, studies of old-growth spruce forests in central Europe found even more carbon stored in the tree biomass. In northeast Bavaria, Germany, 142-year-old spruce forests contained 162.5 Mg C ha^{-1} [44] and spruce stands (116–145 years) in the Bohemian Forest, Czech Republic, contained 150 Mg C ha^{-1} to 227 Mg C ha^{-1}, respectively [17].

The tree biomass carbon stock was not significantly different between the forest site types, although forests on dry mineral soils had, on average, 16% more carbon stored in the tree biomass compared to both other forest site types (Figure 1). Nevertheless, the decline in productivity during the stand ageing process aligned the differences of the tree biomass carbon stock between older trees in different growing conditions [43], revealing that the studied over-mature spruce stands had reached their biomass storage capacity [17].

The spruce upper layer tree parameters affected the carbon stock of the tree biomass between the forest site types. Although the tree species composition in stands may be a result of random natural processes, the variation of the present species structure and stand parameters between the studied forest site types could be associated with the fertility of the site type [15,45,46] and the successional stage (tree mortality) of each stand [40,47]. Gap dynamics were assumed to be the main natural disturbance regime in studied over-mature spruce stands [48]. However, Norway spruce is highly susceptible to insects, pathogens and wind, as well as interaction among those factors, reducing the life span of the trees and dominance of particular generation of spruces in a specific stand [49]. Data of the Latvian State forest service revealed that more than 25% of established Norway spruce stands do not reach mature age (80 years). Other studies have suggested increasing (high) susceptibility of ageing spruce stands to stand-replacing disturbances [48]. Most likely, this is the main reason we were not able to find older Norway spruce stands than the ones included in the study, deliberately selected for Norway spruce dominance. Therefore, we assume that the studied over-mature spruce stands represent the maximum carbon storage capacity and can be used as a reference for comparison with managed stands. However, further studies shall be conducted to evaluate the carbon storage dynamics in theses stands as the dominant age class and/or tree species are changing due to natural disturbances, as part of the decaying old trees is captured and kept in the soil [50].

Deadwood is a functionally and ecologically important component of old forest ecosystems, affecting the total carbon storage [40,51]. The deadwood carbon stock was not significantly different between forest site types, which varied greatly between 0.1 Mg C ha^{-1} and 71.1 Mg C ha^{-1}. Large differences in the amount of deadwood carbon stock occurred in the over-mature spruce stands even within the forest site type, revealing that the distribution of living trees and tree mortality within stands were the main factors explaining the variation in carbon stock [6,47]. The mean deadwood carbon stock in our sites was not very high, 11.5 Mg C ha^{-1}, but it coincides with those of other studies [2,17]. A very high mean deadwood carbon stock (49.0 Mg C ha^{-1}) was reported from northern Germany in old-growth (>200-year-old) spruce forests [42]. However, when comparing the mean proportion of the deadwood carbon stock of aboveground biomass in our study (10–12%) with results from northern Germany [42], Czech Republic [17], and Finland [2], comparable (12–15%) values were obtained. Although, we did not quantify dead roots (up to 3 Mg C ha^{-1}; [17]), the largest share (63%) of deadwood carbon comprised lying deadwood.

The soil carbon plays an important role in carbon cycling as it has a potential to be stored for a long time [50]; however, the quantitative estimates of soil stock in forest ecosystems for many regions are scare [15]. Contrary to the results of studies by Klein et al. [43], and Pukkala [20], in the current study, the soil organic carbon stock was smaller than the tree biomass carbon, at about 85 Mg C ha^{-1}. Thus, our results supported the evidence that the mean soil organic carbon stock decreased with increasing depth [52]. Nearly 30% of the soil organic carbon was concentrated in the soil surface (0–10 cm), which is more affected by different natural processes [52], although, due to the limited sample size, further analyses of the high variability of the soil organic carbon stock between the soil layers and forest site types were not possible.

The total carbon stock size of over-mature hemiboreal spruce stands was synthesised from forests where all three major carbon pools (tree biomass, deadwood, and soil) were directly measured (Table 2). By studying all major carbon pools in over-mature spruce forests, we determined that the total carbon stock was not different between the stand age of 167–213 years, which was in line with a previous study [17].

5. Conclusions

Some significant differences were observed in tree and deadwood carbon pools due to variations in stand structure (species composition and stand parameters) between the stands. Our results indicated that the total carbon stock in over-mature spruce stands between the forest site types was statistically insignificant. Overall, the carbon pools (above- and belowground biomass, deadwood, and soil) of over-mature unmanaged Norway spruce stands presented in our study may serve as a reference for further forest carbon studies in hemiboreal regions.

Author Contributions: Ā.J. conceived of the original research idea. Ā.J. and E.B. contributed to the experimental design. E.B. and L.Ķ. were responsible for data collection. L.Ķ. and D.E. analysed the data. L.Ķ. had the main responsibility for writing of the manuscript with contributions from other co-authors.

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

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forests

Article

Carbon Pools in Old-Growth Scots Pine Stands in Hemiboreal Latvia

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Abstract: Old-growth forests are widely recognised for the benefits they provide for biodiversity; however, a more comprehensive understanding of their role in climate change mitigation must still be established to find the optimal balance between different forest ecosystem services at a national or regional scale. Very few studies have assessed carbon pools in old-growth Scots pine (*Pinus sylvestris* L.)-dominated boreal forests, and none have been conducted in hemiboreal forests. Therefore, we assessed the carbon storage of the living tree biomass, deadwood, forest floor (soil organic horizon, including all litter and decomposed wood), and mineral soil in 25 hemiboreal old-growth (163–218 years) unmanaged Scots pine stands in Latvia. The studied stands were without known records of any major natural or human-made disturbance in the visible past. Our results show, that the total ecosystem carbon pool (excluding ground vegetation) was 291.2 ± 54.2 Mg C ha^{-1}, which was primarily composed of living tree biomass (59%), followed by mineral soil (31%), deadwood (5%), and the forest floor (5%). Within the studied stand age group, the total carbon pool remained stable; however, interchanges among the carbon pools, i.e., living biomass and laying deadwood, did occur.

Keywords: *Pinus sylvestris*; deadwood; above- and below-ground tree biomass; forest floor; mineral soil; semi-natural forest; over-mature forest

1. Introduction

Carbon sequestration and storage is one of the essential ecosystem services provided by forests, which has great potential to mitigate climate change [1,2]. Boreal forests store approximately one-third of global terrestrial carbon and therefore are highly important in this context [3]. The carbon sequestration in forests is affected by climate [4], soil [5], and natural disturbance [6], along with forest stand characteristics, such as tree species composition [7], age [8,9], and silviculture practices [10–13].

The total ecosystem carbon (TEC) is stored in different pools (above- and below-ground tree biomass, deadwood, forest floor, and soil), and the dynamics of these pools depend on forest development stage [14]. Generally, the TEC pool increases with stand age and is closely related to site productivity [4,5]. Dynamics of TEC pools can be abruptly altered following stand-replacing natural or human-made disturbances. Following windthrow or fire events, a large proportion of live tree biomass is turned into deadwood, while following clear-cut, a large proportion of live biomass is removed from the site [15,16].

The old-growth forests are important from ecosystem functioning and biodiversity aspects [17]. The long and intensive exploitation of European forests has heavily shaped the distribution, structure, and composition of these ecosystems. In Europe, old-growth forests with natural structures are rare, mainly preserved in distant areas, where forest management operations have been unprofitable due to challenging terrain or low productivity [17,18].

Globally, old-growth boreal and temperate forests serve as a major carbon sink [4]. In some specific conditions for a certain period, old-growth forests might become carbon neutral [19] or even a carbon source, when net carbon balance becomes negative [20]. In Europe, several studies have investigated ecosystem carbon pools in stands dominated by old-growth Norway spruce (*Picea abies* (L.) Karst.) [14,16,21,22]. These studies show that live tree biomass and soil are the largest carbon pools [14,16,21,22]. Among these studies, the lowest TEC (175 Mg ha^{-1}) was estimated in old-growth boreal forests [16], the highest TEC (> 400 Mg ha^{-1}) in Central European forests [14,22], and moderate estimates (240 Mg C ha^{-1}) in hemiboreal forests [21], implying that TEC pools change according to latitudinal position. Similar observations are reported from southern boreal forests in Canada, where depending on site productivity the TEC pools ranged from 120 to 725 Mg C ha^{-1} [23]. The soil organic carbon (SOC) pool in old-growth forests can increase over time [24] or remain rather stable [14,22], which likely depends on soil and climate conditions, as well as on forest stand characteristics. The deadwood carbon pool in old-growth forests is related to tree morality rates, and generally increases with stand age [22]. Forest floor carbon pools are usually one the of the smallest TEC pools, closely related to site productivity and decomposition rates [14,16,22].

The dominant tree species is a significant factor influencing TEC dynamics [25]. Scots pine (*Pinus sylvestris* L.) is a long-living common tree species in Northern Europe [26]. Yet, knowledge of TEC pools in old-growth Scots pine stands is scarce, as the majority of studies have assessed TEC in old-growth Norway spruce stands [14,16,21,22]. Therefore, the aim of our study was to assess the main carbon pools (living tree biomass, deadwood, forest floor, and mineral soil) in hemiboreal old-growth (>160 years) Scots pine forests in Latvia. Gained insight into the TEC of old-growth forests could be used to develop balanced management strategies for protected forests as well as to maximise climate change mitigation through adaptive forest management strategies [1,27,28].

Studies have shown that in old-growth Norway spruce-dominated stands, the total carbon pool remained stable between stand ages of 116 to 145 years [22]. Considering the low annual growth rates of Scots pine trees older than 100 years [29] and the absence of evidence of recent natural or human-made disturbances in studied stands, we hypothesised that the TEC pool of old growth Scots pine forests would not change in stands aged between 163 and 218 years.

2. Materials and Methods

2.1. Study Area

Latvia is located in the hemiboreal region within a moderately cool and moist climate [26]. According to data from the Latvian Environment, Geology and Meteorology Centre, the mean annual temperature is +5 °C, ranging from around −5 °C in January to +17 °C in July. The mean annual precipitation is 550–850 mm; about 500 mm falls during the growing season (April to October). According to the National Forest Inventory data, Scots pine is the second-most common tree species in Latvia, occurring in 874,000 ha or 26% of the total forest area. The largest proportion of Scots pine grows on sandy (19%) or sandy loam (37%) soils. The sampling plots were established in the *Hylocomniosa* forest site type, which is characterised by medium-rich sandy loam soils with a normal moisture regime [30]. In this forest site type, 36% of the area is occupied by pine-dominated forests. In Latvia, the majority (85%) of the forests older than 120 years are dominated by Scots pine.

2.2. Fieldwork

The methodology used for the fieldwork and the data analysis is the same as was published in 2018 by Ķēniņa et al. [21], where old-growth Norway spruce stands were analysed. In total, 25 stands were stratified from the set of potential areas using the following criteria: age > 160 years, dominance of Scots pine (> 50% out of the basal area), location (> 5 km from villages and > 1 km from roads), and no documented information or field observations indicating past management activities (e.g., stumps), and growing in mesotrophic soil conditions (*Hylocomniosa* forest type) in protected areas in Latvia (Figure 1). The mean stand age (± 95% confidence interval) in our study was 179 ± 7 years, ranging between 163 and 218 years.

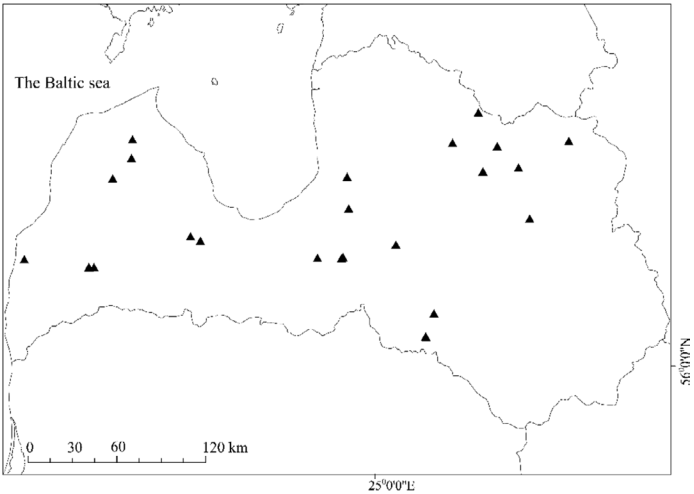

Figure 1. Location of the sampled old-growth Scots pine-dominated stands in the territory of Latvia.

Six to eight circular sampling plots of 500 m^2 (143 sample plots in total) were placed systematically in each stand. In these sampling plots, the tree species and diameter at breast height (DBH) were recorded for all the living and standing dead trees of DBH ≥ 6.1 cm and for lying deadwood of DBH ≥ 14.1 cm. In the centre of the large sampling plots (500 m^2), smaller subplots (25 m^2) were placed, where living trees of DBH 2.1 to 6.0 cm and laying deadwood of DBH 6.1 to 14.0 cm were recorded.

The tree height was measured for three to five living trees of each species in each canopy layer and for all snags (dead trees with broken tops). For lying deadwood sections within the sample plot, we recorded the tree species (if possible), stage of decay in five classes [31], diameter at both ends, and length.

Soil samples were taken outside the large sampling plot (500 m^2) at random location points, at least 2 m from large trees. At each stand, soil samples were taken from 3 points. In total, 18 stands were sampled. From the stands, which were located nearby, only a single stand was sampled. At each point, the forest floor (soil organic horizon, including all litter and decomposed wood) [12,15] and mineral soil samples were taken. At each place, a profile pit (60 cm × 120 cm × 90 cm) was created, where mineral soil samples at fixed depths (0–10 cm; 10–20 cm; 20–40 cm, and 40–80 cm) were taken using a metal cylinder (100 cm^3). A single soil sample was taken per each fixed depth. Physical and chemical analyses of the obtained samples (e.g., bulk density, total carbon content, and carbonate content) were conducted in the Forest Environment Laboratory at the Latvian State Forest Research Institute 'Silava', following the reference method by Fleck et al. [32].

2.3. Data Analysis

The height of living and standing dead trees was calculated using Näslund's and Gaffrey's models [33]. The volume of living trees and standing dead trees with the tops was calculated according to Liepa [34], using the measured tree height and DBH values with the respective coefficients for the tree species as follows:

$$v = \psi \times L^{\alpha} d^{\beta lg L + \varphi} \tag{1}$$

where v is the stem volume (m^3); L denotes stem length (m); d indicates tree diameter at breast height (DBH; cm); lg denotes the logarithm of base 10; and ψ, α, β, and φ are the coefficients for tree species. The coefficients for the Scots pine are the following: Ψ is 1.6541×10^4, α is 0.56582, β is 0.25924, and φ is 1.59689.

Snags and lying deadwood were calculated according to the formula for a cylinder. The living tree biomass (above- and below-ground) was estimated from the DBH and tree height for individual trees based on the local biomass equation [35]. The living tree biomass carbon pool was calculated using the living tree biomass values multiplied by the carbon content of 50% [36,37].

The deadwood carbon pool was calculated based on deadwood volume estimations, decay class-specific density, and carbon content for the main tree species in hemiboreal forests [31]. The mineral soil carbon/forest floor carbon was obtained by multiplying the organic carbon concentration (the difference between the total carbon content and inorganic carbon content) with the soil mass in the respective layers/mass of the forest floor [22,38].

Relationships between the living tree biomass and deadwood carbon pools were analysed using a linear mixed-effects (LME) model as implemented in R (3.5.0 library lme4) [39]. The total deadwood carbon and the lying deadwood carbon data were log transformed to meet assumptions of variance homogeneity and normality. The stand was treated as a random effect to account for the possible correlation between the plots of one stand.

3. Results

3.1. Volume

The mean standing volume of old-growth pine stands was 570.9 ± 22.2 m^3 ha^{-1} (ranging from 241.0 to 837.5 m^3 ha^{-1}), and the mean basal area was 45.3 ± 1.6 m^2 ha^{-1}. The height of the upper tree layer ranged from 23.9 to 34.8 m, with a mean value of 31.1 ± 0.4 m.

The tree DBH of the upper and second tree layers also had a considerable range with a mean of 48.0 ± 1.2 cm and 18.1 ± 0.6 cm, respectively. The mean stand density in the upper tree layer was 268 ± 15 ha^{-1}, of which 140 ± 11 ha^{-1} were pines. In the second tree layer, the mean stand density was 1084 ± 153 ha^{-1}; it was dominated by Norway spruce (630 ± 96 ha^{-1} on average) (Figure 2).

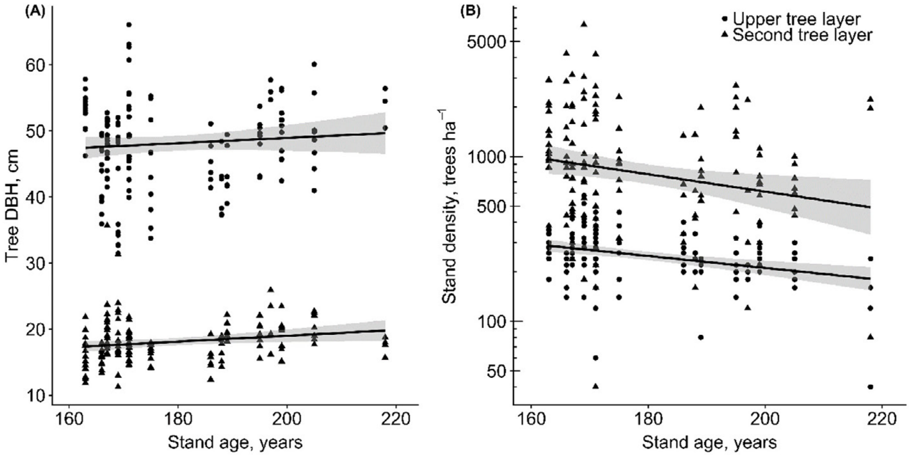

Figure 2. (**A**) The mean tree diameter at breast height (DBH) and (**B**) stand density versus stand age in the upper and second tree layers in old-growth Scots pine-dominated sampling plots (n = 143).

The mean stock of deadwood was 98.4 ± 14.4 m^3 ha^{-1} (ranging from 0 to 483.2 m^3 ha^{-1}) comprising 44.3 ± 10.9 m^3 ha^{-1} lying dead logs, 42.7 ± 6.8 m^3 ha^{-1} standing dead trees, and 11.5 ± 2.7 m^3 ha^{-1} snags.

3.2. Carbon Pools

The TEC pool was 291.2 ± 54.2 Mg C ha^{-1}, representing the sum of mean values for carbon pools of living tree biomass, deadwood, forest floor, and mineral soil pools delivered from the data obtained in this study, except ground vegetation, which was not addressed in this study (Table 1). Neither the carbon pool of living tree biomass nor deadwood was significantly related to the stand age, according to the LME model.

Table 1. Carbon pool size (Mg C ha^{-1}) ± 95% confidence interval (CI) with the percentage of the pool from the total ecosystem carbon.

Carbon Pool	Mean ± CI	%
Above-ground tree biomass	135.8 ± 4.9	47
Below-ground tree biomass	35.4 ± 1.2	12
Living tree biomass (n = 143)	171.2 ± 6.1	59
Lying deadwood	5.9 ± 1.5	2
Standing dead trees	7.1 ± 1.2	2
Snags	1.8 ± 0.4	1
Total deadwood (n = 143)	14.8 ± 2.1	5
Forest floor (n = 18)	15.2 ± 7.1	5
Mineral soil (0–80 cm; n = 18)	90.0 ± 38.9	31
Total ecosystem carbon[1]	291.2 ± 54.2	100

[1] Except ground vegetation.

The mean carbon pool of living tree biomass was 171.2 ± 6.1 Mg C ha^{-1}, 64% of which was found in the stem biomass. The carbon pool in the above-ground biomass varied between 57.6 Mg C ha^{-1} and 196.4 Mg C ha^{-1}. The share of the below-ground biomass carbon pool in the living tree biomass varied between 19% and 23%, with a mean of 21% ± 0.1%.

The total deadwood carbon pool was highly variable among the sample plots, ranging from 0.5 Mg C ha^{-1} to 74.6 Mg C ha^{-1} (mean 14.8 ± 2.1 Mg C ha^{-1}); deadwood was absent in four sample plots. The results show no relationship between carbon pools of living tree biomass and the total deadwood (slope = −0.003, t-value = −244, p = 0.151) using the LME model. The total carbon pools of living tree biomass were significantly negatively related to the total lying deadwood carbon pool (slope = −0.007, t-value = −3.279, p = 0.001; Figure 3).

Overall, the share of the carbon pool from the total deadwood carbon pool was higher in the standing dead trees than in the lying deadwood, approximately 48.0% vs. 40.0%, respectively. The smallest mean carbon pool of deadwood was in snags (1.8 ± 0.4 Mg C ha^{-1}).

Both forest floor and mineral soil (0–80 cm) carbon pool variability was high. The mean values were 15.2 ± 7.1 Mg C ha^{-1} and 90.0 ± 38.9 Mg C ha^{-1}, respectively. The carbon pool of mineral soil (0–80 cm) ranged from 33.8 Mg C ha^{-1} to 301.5 Mg C ha^{-1} with 15.2 ± 6.7 Mg C ha^{-1} in the upper 0–10 cm layer and 42.3 ± 38.3 Mg C ha^{-1} in the 40–80 cm layer. The mean bulk density in the upper 0–10 cm layer was 963 kg m^3 (ranging from 63 to 1481 kg m^3), in the 10–20 cm layer 1143 kg m^3 (ranging from 63 to 1657 kg m^3), in the 20–40 cm layer 1295 kg m^3 (ranging from 81 to 2061 kg m^3), and in the 40–80 cm layer 1485 kg m^3 (ranging from 865 to 2486 kg m^3).

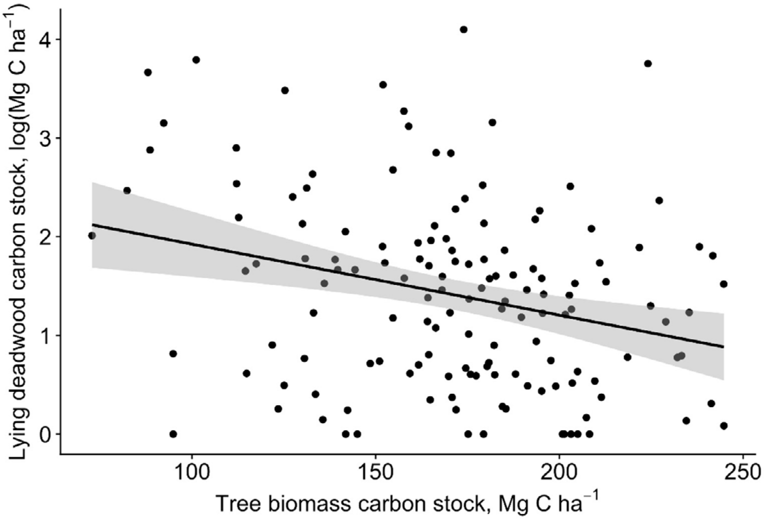

Figure 3. Changes in the lying deadwood carbon stock with the increasing carbon stock of the living tree biomass in the sampled old-growth pine stands ± 95% confidence interval (n = 143).

Almost 60% of the total ecosystem carbon in old-growth pine stands was found in the living tree biomass, which represented the largest forest carbon pool. Mineral soil was the second-largest carbon pool, comprising up to 31% of the total ecosystem carbon. Both the forest floor and deadwood were marginal carbon pools. Comparing stands within the studied stand age group (163–218 years) did not show any notable trend of changes in the size of forest carbon pools with ageing.

4. Discussion

Forest carbon pools generally vary with stand age [8,40,41]; however, in our study, we focused on the old-growth stands, specifically assessing the age range of 163–218 years. Our results showed that the forest carbon pools did not change significantly over the analysed period. Similar observations were reported by Seedre et al. [22] for a montane old-growth Norway spruce stand (116–145 years) in the Bohemian Forest in the Czech Republic. In our study, the lack of significant changes in the TEC pool, over the analysed stand age range, implies that these forests might be carbon neutral or even sources [22]. In old-growth forests, the net ecosystem productivity (NEP) is low due to the slow increase of living biomass [20], and combined with a rather large amount of decomposing deadwood [22] can lead to negative NEP. Yet, a carbon exchange study is needed to precisely assess the NEP balance in these sites.

Our results suggest, that old-growth Scots pine-dominated forests are important carbon stores with a mean of 291 ± 54.2 Mg C ha^{-1}. Slightly lower TEC values have been obtained in old-growth hemiboreal Norway spruce stands (range of 225 to 249 Mg C ha^{-1}) [21]. Overall, TEC pools in old-growth hemiboreal forests are considerably larger than in old-growth boreal forests [16]. In our study, similar to other studies [16,21,22], the largest carbon pool was the living tree biomass. Our results showed that in older stands there were fewer but larger individual trees (Figure 2). Hence, in older stands the importance of individual tree contributions to TEC increases, and in the case of dieback of a few trees, the proportion between different carbon pools can be considerably altered.

The forest floor and deadwood were the two smallest carbon pools (each 5% of TEC). In our study, the estimated mean forest floor carbon pool (15.2 ± 7.1 Mg C ha^{-1}) was considerably lower than the estimated forest carbon pool in Scots pine-dominated forests (82–132 years) in Estonia (mean 80 Mg ha^{-1}, ranging from 5–120 Mg ha^{-1}) [42]. The huge variation of forest floor carbon pools in pine-dominated hemiboreal forests is likely driven by a large variation in litter production [22] and site ecological conditions [42].

In our study, the deadwood carbon pool was highly variable, with a mean of 14.8 ± 2.1 Mg C ha^{-1}. The mean deadwood carbon pool values corresponded well with the results (approximately 17 Mg C ha^{-1}) from old-growth boreal forests in northwest Russia [43], but considerably higher values were observed in over-mature Norway spruce stands in Central Europe (approximately 49 Mg C ha^{-1}) [14]. The basis for deadwood formation is stand yield and density, which most likely explains observed differences with Central European forests [13,40]. In our study, the lying deadwood carbon pool slightly ($p = 0.04$) decreased with an increasing living tree biomass carbon pool (Figure 3). We assume that a higher volume of long-lasting deadwood likely hinders the tree regeneration and growth. Studies show that dead standing Scots pine trees, in particular, can stand for several decades following their death [44,45], leaving a long-lasting effect on microsite conditions.

In our study, widely ranging SOC pools (34–302 Mg C ha^{-1}) were similar to other observations, which concluded, that these pools are highly variable, particularly within the boreal zone [40,46]. Studies show that soil organic carbon depends not only on climate conditions but also on the soil texture (physical and chemical properties), the time since the last disturbance (human-made/natural), the parent material, and the vegetation [5,47,48].

The assessed values of carbon pools in our study potentially represent the upper limit of carbon pools characterising undisturbed hemiboreal old-growth Scots pine stands (i.e., the situation where most of the dominated cohorts in the stand are old Scots pines). Studies show that Scots pines can reach a notably older age than those of our study, and such old stands are usually associated with slow growth determined by poor soil conditions (e.g., bogs) or harsh climatic conditions (e.g., northern boreal forests). Thus, the total biomass most likely is lower than that of our study. Succession in boreal forests, changing the dominant cohort of trees (old-growth to younger), can be a lengthy process associated with lower standing biomass [49]. Although living biomass might decline in old-growth forests, carbon accumulation continues in soil and deadwood pools [24,50].

5. Conclusions

In hemiboreal old-growth Scots pine stands on mesotrophic soils, the living tree biomass and mineral soil were estimated to be the main carbon pools, which, however, appeared unaffected by age (within the age range of 163–218 years). The carbon pool values in our study potentially represent the upper limit of carbon pools in undisturbed hemiboreal old-growth Scots pine stands, which can be used in carbon modelling and long-term silviculture management planning. Considering the large local/regional variance in different carbon pools (deadwood, forest floor and soil) in old-growth pine forests, more research is needed to assess the effect of ecological local/regional factors that control the carbon sequestration.

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CARBON POOLS IN OLD-GROWTH SCOTS PINE STANDS ON ORGANIC SOILS AND ITS CONCENTRATION IN DEADWOOD: CASES STUDY IN LATVIA

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Carbon sequestration is crucial to mitigate climate changes, therefore it is important to have accurate estimates of carbon pools in the forest. So far, data on carbon pools in old-growth forests are very scarce, therefore aim of the study was to assess the carbon pools in old-growth Scots pine stands on organic soil and carbon concentration in deadwood of different decay classes in Latvia. Carbon content in deadwood was test in samples, collected in 26 randomly selected over mature, unmanaged stands across Latvia (five samples per decay class and tree species). Carbon pools were assessed in 38 sample plots (size 500 m^2) in five Scots pine stands on wet organic soil (*Caricoso- phragmitosa* forest type) at the age of 167 to 203 years. Mean carbon concentration in deadwood across all species and decay classes was 46.6±1.57%. For aspen it did not change with progressing decay was found, but increase was observed for Scots pine, Norway spruce and birch. For these species difference in concentration between first three (more fresh) and last two decay classes (mean 45.9±0.9% and 49.9±1.6%, respectively) was statistically significant. Old-growth Scots pine stands on peat soils had rather large amount of deadwood: 100.6 ± 74.7 m^3ha^{-1}. However, its share in total carbon storage (290.0 ± 57.9 t ha-1) was small and most of carbon (57%) was found in soil. Mean annual carbon storage in tree biomass and deadwood decreased with stand age; its absolute value was similar in over-mature and mature (101-120 years) stands.

Keywords: *biomass, carbon storage, old growth, standing volume, wood decay*

INTRODUCTION

Carbon sequestration had become an important forest service. As numerous other forest service, so far also this has not been a source of income, rather than a potential obligation, for the forest owner. However, ta situation might change in future. Therefore it is important to quantify the carbon storage in old-growth forests and use it in decision support tools. Such information is important also at the state level, when assessing the influence of increased un-managed areas of reduced harvesting rates on the carbon pools. Largest carbon pools in forests are tree biomass and soil. Litter and deadwood plays a role in total carbon flow between the atmosphere and forest.

Biomass equations that are developed or adjusted, based on the local data, are important for accurate estimation of carbon in this pool (Jansons et al., 2017, Kenina et al., 2018, Lībiete et al., 2017). Additionally, information on forest inventory parameters are needed. Such data and/or estimates of carbon pools in old-growth forests are very scarce. Norway spruce had been studied in old-growth (116-145 years) mountain forests of Czech Republic (Seedre et al., 2015), single old growth (140 to 170 years) mixed forest in Finland (Finér et al., 2003), chronosequence (16-142 years) and natural over-mature spruce forest in Central Europe (Jacob et al., 2013, Mund et al., 2003). Old-growth Scots pine has been represented by a single stand (>150 years) in Estonia and Finland (Vucetich et al., 2000), and Mediterranean mountain forests (120 years) in Spain (Moreno et al., 2015) and (up to 177 years) Turkey (Lee et al., 2016). In Latvia the only analysis so far characterizes carbon stock in over-mature (167–213 years) Norway spruce stands (Ķēniņa et al., 2018). All of these studies deal with old-growth forests, where old trees are still the dominant cohort. However, such state is not permanent even in un-managed forests – due to natural disturbance, like storms and forest fires, young stands will be formed (Donis et al., 2017, 2018). Even so the most intensive forest management (whole tree biomass harvesting) does not leave permanent negative effect on forest ecosystem (Jansons et al., 2016) it still changes the dominant age class of trees and leaves a long-lasting impact on forest legacies (Jogiste et al., 2018). Both the growth of trees as well as frequency and severity of disturbances – thus tree mortality – will be (are) affected by climate changes (Katrevics et al., 2018, Matisone et al., 2019, Matisons et al., 2018). Large-scale natural disturbances as well as single-tree mortality is a source of deadwood. This pool retains carbon as long as it has not been completely decayed. For the accuracy of carbon assessment, it is important to know the concentration of it both in living biomass (Bardulis et al., 2017) as well as

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deadwood of different decay classes. Such analysis has been carried out in Estonia (Köster et al., 2015) but not in Latvia. Therefore we need to verify it and understand its applicability based on independent set of samples.

Carbon storage in soils are often regarded as relative independed from that in tree biomass. However, a study in China had demonstrated an substantial accumulation of this element in top-soil over 24 years in intact forests (Zhou et al., 2016). Soil carbon pool and its fluctuation would be soil and climate specific, therefore it is important to characterize them in each of the set of conditions of interest.

Aim of the study was to assess the carbon pools in old-growth Scots pine stands on organic soil and carbon concentration in deadwood of different decay classes in Latvia.

MATERIALS AND METHODS

Carbon content in deadwood was test in samples, collected in 26 randomly selected over mature, unmanaged stands across Latvia as part of the project “Assessment of greenhouse gas emission and CO2 sequestration in old forest stands” (unpubished project reports in Latvian in www.silava.lv). Five samples have been collected from each tree species (Scots pine, Norway spruce, birch, European aspen) at each of five decay classes (Köster et al., 2015; Sandström et al., 2007). Sampling core (cylinder) with 13 mm inner diameter was used for the harder wood (first two decay classes) and 50 mm for the softer (more degraded) wood (decay classes three to five). Fresh and dry mass (after drying in 105ºC for 3 days) of samples measured. Samples grained and burned at 1360ºC in ELTRA CS-530 analyser to obtain carbon content.

Assess of the carbon pools in old-growth Scots pine stands was done, based on similar method, as described in Ķēniņa et al., 2018. Namely, material was collected in five Scot pine (60-90% of standing volume) stands on wet peat soil, *Caricoso- phragmitosa* forest type. Prior to the fieldwork, the potential sample stands were randomly selected from protected (no documented management) forests across Latvia, based on age limit (>160 years). Selected stands were inspected in the field for conformity of the dominance of species and age group. In the case of any signs of former logging (strip roads, stumps, etc.), they were discarded. Altogether, 38 sample plots (6–8 sample plots in each stand) of 500 m^2 were systematically established in these stands at the age of 167 to 203 years.

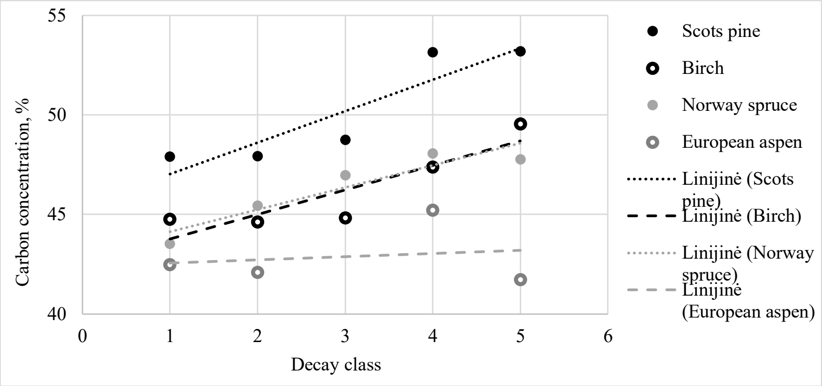
The diameter at the breast height (DBH) of all living trees ≥6.1 cm was measured. For all standing dead trees ≥6.1 cm, the DBH and length of the snags were recorded. The tree height for three to five living trees of each species and the layer of stand (upper tree layer, second tree layer) in each sample plot was measured to estimate tree height. The total (above- and belowground) tree biomass was calculated using DBH and height with equations for the main tree species in Latvia developed by Liepiņš et al. (2018). The carbon content of 50% was used for the tree biomass carbon stock estimation. Lying deadwood with a diameter at the thicker end ≥14.1 cm was measured at both ends within the area of the sample plot. The decay stages of lying and standing dead trees were set using a five-class decay classification and ‘knife method’ (modified from Köster et al., 2015). The volume of the lying deadwood and dead trees with broken tops was calculated using a truncated cone formula and converted to mass using the decay class-specific density. The values of the deadwood basic density and carbon content for the main tree species were applied after the testing (part of this study) from Köster et al. (2015).

Soil samples (litter layer and four depths: 0–10 cm, 10–20 cm, 20–40 cm, and 40–80 cm) were taken from each stands at systematically located points outside the sample plots. Obtained samples were returned to the Forest Environment Laboratory at the Latvian State Forest Research Institute Silava, where physical and chemical analyses were carried out following the reference methods outlined in Part X of the International Co-operative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests Manual on Sampling and Analysis of Soil (Fleck et al., 2016). The soil samples were prepared for analyses according to the LVS ISO 11646: 2005 standard. In the soil samples, the following parameters were determined: bulk density (kg m^{-3}) according to LVS ISO 11272:1998, total carbon content using elementary analysis (dry combustion) according to LVS ISO 10694:2006, and carbonate content using the Eijkelkamp calcimeter according to ISO 10693:1995. The organic carbon concentration (g kg^{-1}) in the soil was calculated as the difference between the total carbon content and the inorganic carbon content.

RESULTS AND DISCUSSION

Carbon concentration in deadwood increases with increasing its decay class (Figure 1): from fresh deadwood (decay class 1) to almost complete decay (class 5) it changes by 40 g kg^{-1} in pine deadwood, and by 58.9 and 52.2 g kg^{-1} for spruce and birch, respectively.

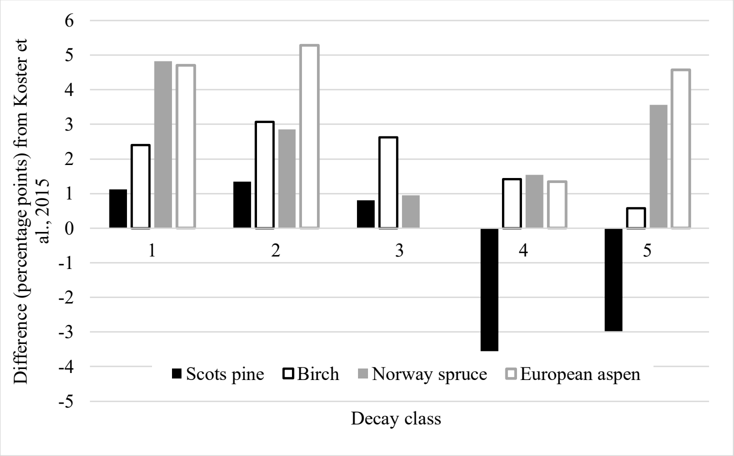
Our results follow the general patter, found also by Köster et al. (2015) and Sandström et al. (2007). Exception is decay of European aspen, where the trend in our data is not specifically clear, presumably due to small sample size and larger variation of carbon concentration in deadwood of this tree species. Scots pine and birch have rather similar tendency in changes of carbon concentration – slow in the first decay classes, followed by rather sharp rise in decay classes 4 and 5 (differences between these two groups of decay classes were statistically significant). For birch and spruce similar tendency is observed in Estonia (Köster et al., 2015); however, concentration in carbon with the decay class rises more gradually in this study. In Estonia, similarly than in our study, slight decline of carbon concentration in aspen wood in is observed, when comparing decay classes 1 and 2 with decay class 5. Tendency that for aspen carbon concentration is not significantly affected by changes in decay class, is in notable contract to that observed for other tree species and needs to be considered t ensure accurate carbon estimates.



Decay increases from class 1 (fresh deadwood) to 5 (almost complete decay); Köster et al., 2015, Sandström et al., 2007. Linear trendiness added to ensure visibility of tendencies.

Figure 1. Carbon concentration (%) in deadwood of different tree species depending on the decay class

Mean carbon concentration in deadwood across all species and decay classes in our study was on average by 1.9 percentage points lower than that, reported in Estonia (Köster et al., 2015): 46.6±1.57% vs.48.5±0.66, respectively. However, the differences were not statistically significant, mostly due to relative large variation within each of the species and decay class. When analysis each tree species and decay class separately, the only significant differences were found between estimates in decay class 2 for spruce and aspen and decay class 5 for spruce. Largest difference were found for carbon concentration in aspen deadwood (on average 4%), smallest – in pine deadwood (Figure 2). Considering the large heterogeneity of the carbon concentration in cross-section of even a single log classified as specific decay class due to e.g. contact to water from one side of the log, fungal, insect impact, resin concentration etc., the estimates based on largest set of samples shall be considered more accurate. Thus we conclude, that the estimates of carbon concentration in deadwood as set by Köster et al. (2015) can be used for deadwood carbon estimation in Latvia.



Decay increases from class 1 (fresh deadwood) to 5 (almost complete decay); Köster et al., 2015, Sandström et al., 2007.

Figure 2. Deadwood carbon concentration difference (percentage points) from the results in Köster et al., 2015

Old-growth Scots pine stands on peat soils had rather notable differences in all forest inventory parameters (Table 1). Men standing volume (both first and second layer trees together) of the stands was 311±131.0 m^3 ha^{-1}. It was significantly larger than that, found in mature stands (101-120 years) in the same forest type based on 12 National forest inventory sample plots: in first layer 276.9±122.3 and 170.2±36.1 m^3 ha^{-1}, respectively, in second layer 34.3±20.2 and 8.3±4.5 m^3 ha^{-1}, respectively; even so, the stand densities in any of the layer were not significantly different.

Table 1. Measured forest inventory parameters and carbon in selected old-growth Scots pine stands on wet peat soil

Age, years	I layer					No of sample plots	Carbon, t ha^{-1}, in:	
	DBH, cm	H, m	G, m^{2}ha^{-1}	M, m^{3}ha^{-1}	N, ha^{-1}		biomass	deadwood
177	31.4	20.0	14.7	136.2	240	6	57.8	3.8
167	28.7	21.7	41.1	401.9	800	8	116.9	18.7
177	31.1	25.4	29.4	328.6	480	8	125.4	17.5
203	31.3	19.3	28.8	253.4	430	8	92.0	5.0
187	25.9	21.9	26.7	264.6	575	8	110.6	18.7

DBH – diameter at breast height, H – height, G – basal area, M – standing volume, N – density

Above-ground biomass pool is on average 79.2 ± 26.3 t ha^{-1} (from 45.5 to 99.2 t ha^{-1}), in below ground (roots and stump) 21.3 ± 7.0 t ha^{-1} (from 12.3 to 26.2 t ha^{-1}). Old-growth Scots pine stands on peat soils had rather large amount of deadwood: 100.6 ± 74.7 m^{3}ha^{-1}; however, due to decay the amount of carbon in this pool was rather limited. Tree (biomass and deadwood) carbon was similar ($p=0.7$) in old-growth and mature stands 113.2 ± 41.9 and 104.8 ± 37.3 t ha^{-1}, respectively. Mean annual rate of changes in the tree biomass and deadwood carbon pool is decreasing over time (Figure 3).

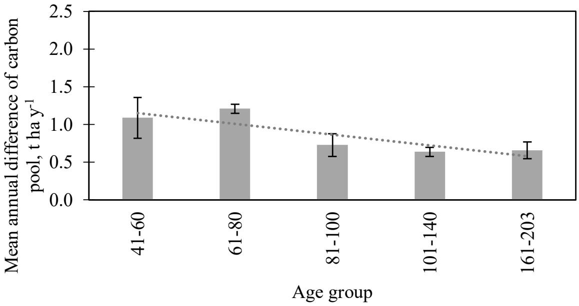


Figure 3. Mean annual increase of biomass and deadwood carbon pools (data of this study and National forest inventory)

Soil, especially organic soil, is a large carbon pool. In the old-growth pine stands in depth up to 80 cm there was 166.3 ± 78.6 t ha^{-1} – that is one third more in the wood (dead and alive). Additionally, in the litter layer there were 10.5 ± 6.2 t ha^{-1} carbon. Thus the total carbon storage in old-growth pine stands was 290.0 ± 57.9 t ha^{-1}.

CONCLUSIONS

Carbon concentration increased with increasing decay of deadwood for Scots pine, Norway spruce and birch and the differences between first three and last two decay classes were statistically significant. In contrast, for aspen no significant changes in deadwood carbon concentration with progressing decay was found. Mean carbon concentration in deadwood across all species and decay classes was not significantly different from that reported in Estonia and were rather variable within species and decay class; thus the estimates based on largest set of samples needs to be used for carbon assessment in deadwood. Total carbon storage in old-growth pine stands on peat soil was 290.0 ± 57.9 t ha^{-1} and its main component was carbon in soil (57%), followed by carbon in tree biomass (35%).

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TREE BIOMASS IN OVER-MATURE UNMANAGED CONIFEROUS FORESTS IN LATVIA

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ABSTRACT

Importance of unmanaged forests for biodiversity aspects in unquestionable, while their role in climate change mitigation is still unclear due to the large heterogeneity of these forests in different bioclimatic regions; therefore, requiring data of biomass distribution for their inclusion in national and regional carbon reporting systems.

The aim of our study was to assess the live biomass distribution and amount of dead wood in over-mature Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (K.) L.) dominated stands in Latvia without known records of disturbance both human-made and natural for at least last 40 years.

Live tree biomass and volume of dead wood in 44 over-mature (163 to 218 years) coniferous stands was determined based on tree measurements and local biomass equations on fertile sites (*Hylocomniosa*, *Oxalidosa* forest types). In our study, mean total tree biomass (± 95% confidence interval) in pine stands was significantly ($p=0.001$) higher compared to spruce stands, 343.1 ± 18.9 and 238.4 ± 48.2 t ha^{-1}. Largest pine trees (diameter at breast height, DBH $\leq$ 41 cm) formed greatest part of live biomass in unmanaged pine stands (41%), but not in spruce stands. In spruce stands medium (21 $\geq$ DBH $\leq$ 40 cm) and large trees were in similar proportions from total stand biomass (32 and 28%, respectively). Largest biomass of small (DBH $\leq$ 20 cm) and medium trees comprised spruce both in spruce- and pine-dominated stands. Also mean dead wood volume of over-mature pine- and spruce-dominated stands were similar, 95 and 89 m^3 ha^{-1}.

Keywords: above-ground biomass, below-ground biomass, *Pinus sylvestris, Picea abies,* hemiboreal zone

INTRODUCTION

International agreements on climate action seeks to mitigate the global climate change by setting binding greenhouse gas limitation requiring the carbon (C) stock estimations in different forest ecosystems. Beside natural disturbances and climatic factors, stand

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characteristics and forest management practices have a direct effect on forest growth [1].

Carbon sequestration is becoming an important goal of the forest management planning, therefore, it is necessary to address the variations in tree species composition, forest age structure as well as local conditions for tree biomass estimations, which is a critical assumption for C stock accounting based on inventory data [1], [2]. Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) are most widespread and economically important tree species in Northern Europe. Consequently, they have been intensively managed and numerous studies have addressed biomass and C stock in such even-aged, pure coniferous stands [3], [4]. In contrast, such data of semi-natural, over-mature forests, however, they contain large amount of biomass along with C are scare, and play important role in climate change mitigation in this region [5], [6].

Unmanaged over-mature forests compared to conventional forests preserves significantly higher proportion of dead wood and may store more live tree biomass [1]. However, due to the occurrence of natural disturbances and tree species structural development patterns or management regime used, amount of live tree and dead wood biomasses varies between sites [7].

Latvia is situated in the hemiboreal forest zone and according to the National forest inventory data, forests older than 120 years in Latvia are relatively rare and majority (96%) of them are Scots pine and Norway spruce dominated stands. Therefore, the aim of our study was to assess the live biomass and dead wood amount of unmanaged over-mature pine- and spruce-dominated forests in Latvia. Obtained understanding of biomass distribution of these species, will provide necessary information to calculate the C stock and its allocation for management considerations.

MATERIAL AND METHODS

Study material included in total of 44 over-mature and unmanaged (for at least 40 years) pine- and spruce-dominated stands growing on fertile mineral soils with normal moisture regime (*Hylocomniosa* and *Oxalidosa* forest types) in Latvia. The stands were randomly pre-selected from the forests in protected areas: (1) older than 160 years; (2) located at least 5 km from villages and 1 km from roads to minimised the probability of any human intervention. After the pre-selection, stands were checked in the field for signs of past management activities (cut stumps) and actual occurrence of a chosen forest type and old coniferous trees. Forest stands dominated by Scots pine or Norway spruce (> 50% from basal area) were included in this study. The selected over-mature stands were between 163 and 218 years (on average 177-year-old); age was non-significantly different between pine- and spruce-dominated stands (Table 1).

Table 1. Parameters of the sampled over-mature forest stands

	Scots pine	Norway spruce
Mean tree diameter at breast height, cm	32.7±4.4	25.9±3.7
Mean tree height, m	24.3±2.0	22.2±2.3
Mean stand basal area, m^2 ha^{-1}	45.1±2.4	32.4±2.9
Mean stand volume, m^3 ha^{-1}	567.2±36.6	381.6±52.4
Mean number of trees per ha	1358±181	2127±536
Mean stand age, years	178±6	175±6
Sampled stands (sampled plots)	25 (164)	19 (132)

Within each stand six to eight sample plots with an area of 500 m^2 (R=12.62 m) were systematically established, to measure:
(a) diameter at breast height (DBH) of live trees (≥ 6.1 cm);
(b) DBH of standing dead trees (≥ 6.1 cm) and length of snags (≥ stump height);
(c) diameter of both ends of lying dead wood (LDW) (diameter at thicker end ≥ 14.1 cm).

A smaller sub-plot (R=5.64 m; 100 m^2) in each of the pots was established, to measure:
(e) DBH of live trees (2.1-6.0 cm);
(f) DBH of standing dead trees (2.1-6.0 cm) and length of snags (≥ stump height);
(g) diameter of both ends of lying dead wood (LDW) (diameter at thicker end 6.1-14.0 cm).

Height (H) was measured for three to five trees of each species and layer of stand. Standing dead trees (b; f) were categorised as dead standing snags with tops (DST) – dead standing trees with and without tops (DSB).

Tree H for live trees and DST were estimated by Näslund's and Gaffrey models [8]. The stem volume of all living tree and dead standing snags (DST) was calculated based on DBH and tree species [9]. The volume of dead trees with broken tops (DSB) and lying dead wood (LDW) was calculated using formula for a cylinder. The biomass of each tree components (stem, total live and dead branches, small root as well as total below-ground biomass (including stump biomass)) was estimated using DBH and H based on best available local biomass models [3]. Using DBH of individual trees, biomass of each tree component in stand was estimated in three DBH groups (≤ 20 cm; 21–40 cm; ≥ 41 cm) to represent age structure of analysed over-mature coniferous stands.

Analysis of variance (ANOVA) and covariance (ANCOVA) as well as the Tukey Honest Significant difference (HSD) test were used to assess the differences of biomass between tree components, forest groups (pine- or spruce-dominated), forest types. Stand age was used as covariate for the analysis of stand live biomass differences. The differences of dead wood categories between forests were also estimated using ANOVA. Statistical analysis was made using the software R version 3.4.3.

RESULTS

We used both biomass estimation of tree compartments and combined DBH group and tree species data, as well as number of trees for characterising unmanaged over-mature pine- and spruce-dominated stands (Table 2).

Table 2. Distribution of mean biomass in tree components, tree biomass (sum of all components) (t ha^{-1}) for over-mature pine- and spruce-dominated stands by DBH groups (≤ 20 cm; 21–40 cm; ≥ 41 cm) (cm)

	Pinus sylvestris			*Picea abies*			Other species*		
	≤ 20	21–40	≥ 41	≤ 20	21–40	≥ 41	≤ 20	21–40	≥ 41
Pine forests									
Stem	0.12	22.88	100.45	11.65	44.58	25.36	3.79	6.29	4.02
Branch	0.02	3.31	15.52	6.92	15.64	7.87	1.03	1.45	1.26
Below-ground	0.03	6.05	27.44	5.18	17.65	9.57	1.39	2.06	1.79

	Pinus sylvestris			*Picea abies*			Other species*		
	≤ 20	21–40	≥ 41	≤ 20	21–40	≥ 41	≤ 20	21–40	≥ 41
Tree biomass ∑	0.16	30.53	139.73	22.92	75.92	44.95	7.39	10.23	7.39
Tree number	3	44	96	601	147	26	470	22	4
Spruce forests									
Stem	0.07	6.31	20.53	7.77	44.47	40.95	6.39	10.09	8.34
Branch	0.09	0.81	3.34	4.77	14.63	11.60	1.64	2.69	2.60
Below-ground	0.02	1.63	5.68	3.58	17.04	14.54	2.33	3.52	3.54
Tree biomass ∑	0.09	8.75	29.55	16.12	76.14	67.08	10.36	16.63	14.48
Tree number	347	133	35	1	16	28	632	28	8

*Other species – *Betula pendula*, *Alnus incana*, *Alnus glutinosa*, *Populus tremula* ect.

In pine stands the mean total biomass of *Pinus sylvestris* trees has increased significantly from small (DBH ≤ 20) to medium (21 ≥ DBH ≤ 40 cm) and large trees (DBH ≥ 41 cm). *Picea abies* comprised most biomass of small and medium trees both in pine- and spruce-dominated stands, 39 and 29% of total biomass. Moreover, large proportion of small trees biomass in spruce- and pine-dominated stands formed *Betula pendula* and other deciduous tree species (mostly *Alnus incana*, *Alnus glutinosa* and *Populus tremula).* The mean total tree biomass of small trees in absolute values were significantly smaller despite the significantly large amount of trees per hectare both in over-mature unmanaged pine- and spruce-dominated stands (Table 3).

Table 3. Total mean tree compartment's biomasses (± 95% confidence interval) (t ha^{-1}) of over-mature pine- and spruce-dominated stands within DBH groups (≤ 20 cm; 21–40 cm; ≥ 41 cm) (cm)

	Pine forests			**Spruce forests**		
	≤ 20	21–40	≥ 41	≤ 20	21–40	≥ 41
Stem biomass	15.57 ± 2.32	73.26 ± 12.27	129.9 ± 17.47	14.23 ± 2.60	60.82 ± 15.09	69.82 ± 25.23
Branch biomass	7.96 ± 1.29	20.44 ± 2.59	24.69 ± 3.37	6.42 ± 1.10	18.13 ± 3.54	17.54 ± 5.46
Below-ground biomass	6.61 ± 0.96	25.76 ± 3.59	38.86 ± 5.11	5.93 ± 0.99	22.20 ± 4.89	23.75 ± 7.71
Tree biomass ∑	30.14 ± 4.43	119.47 ± 17.94	193.49 ± 25.59	26.58 ± 4.45	101.15 ± 23.28	111.11 ± 37.96
Tree number	1039 ± 185	213 ± 31	126 ± 13	945 ± 366	172 ± 35	64 ± 19

Although the mean total biomass (± 95% confidence interval) also increased with increasing DBH class in spruce stands, there were no significant differences between biomass of medium and large trees, 101.15 ± 23.28 and 111.11 ± 37.96 t ha^{-1}, respectively. Hence, pine stands comprised significantly ($p < 0.001$) larger mean total tree biomass compared to spruce stands, 343.1 ± 18.9 and 238.4 ± 48.2 t ha^{-1} (standing volume 567.2 ± 36.6 and 381.6 ± 52.4 m^{3} ha^{-1}), respectively, due to the significantly ($p < 0.001$) higher biomass of the large trees in the pine stands. Neither the biomass of total tree nor tree component's was significant different for small and medium trees both in pine- and spruce-dominated stands (Table 2, Table 3).

Stem constituted 64% of the total tree biomass, followed by below-ground (21%) and branch (16%) biomass in pine stands. Obtained results were similar in spruce stands: stem biomass – 60%, below-ground biomass – 22% and branch biomass – 18% (Table 3).

Dead wood volume was highly variable both in pine- and spruce-dominated stands, but overall one third (28% and 30%) of live tree volume formed dead wood, 94.9 ± 13.3 and 89.0 ± 19.5 m^3 ha^{-1}, respectively. Independently from stand age, the mean total volume of dead wood between pine- and spruce-dominated stands were non-significantly (p=0.07) different due to similar (p=0.54) volume of LDW between pine- and spruce-dominated stands (Fig. 1). Largest proportion from total dead wood volume in spruce- and pine-dominated stands contributed LDW (64%) and DST (52%), respectively.

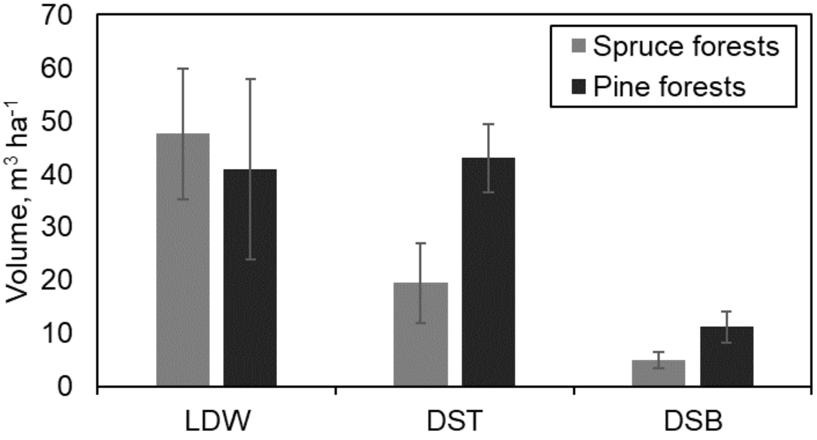

Figure 1. Dead wood volume (m^3 ha^{-1}) in three groups (lying dead woos (LDW), dead standing snags (DST), dead trees with broken tops (DSB)) for over-mature pine- and spruce-dominated stands. Error bars show 95% confidence intervals

In our study, stand parameters as biomass of tree compartments, tree number per hectare and dead wood volume were not related to the stand age.

DISCUSSION

Variation in forests productivity and stand structure in over-mature coniferous stands relived the heterogeneity of hemiboreal forests, however, data on unmanaged forests structure are scarce [7], [10]. In these forests trees had more variation in DBH impacted by disturbance-succession cycle [10]. Our results showed that contribution of small trees into total biomass amount is relatively low despite their large quantity in forest stands (Table 2). Similar to other studies [5], [11], sparse but large *Pinus sylvestris* trees formed the major part (41%) of live biomass in pine stands, confirming that over-mature trees are still dominant. By contrast, in spruce stands the dominance between biomass of medium and large *Picea abies* trees were not observed (Table 2), suggesting good shade tolerance in canopy gaps of this species [12]. Furthermore, biomass distribution between DBH groups of *Picea abies* were similar despite dominance or sub-dominance of the species in stand (Table 2), revealing different pine and spruce regeneration growth patterns [13].

In pine stands the mean total live biomass was significantly higher compared to spruce stands, likely due to greater resistance of *Pinus* species to decay [13], hence volume increment between both species and productivity of the study sites were considered similar [11]. Moreover, smaller dimension *Picea abies* trees contributed notable share to biomass in over-mature pine stands, but not vice versa. Consequently, to balance the biodiversity, economic and carbon storage functions in pine stands, periodic harvesting of ingrowth *Picea abies* trees can be applied. Such management approach, applied infrequent, will change the light-regime in the stands and boost the presence and/or density of light-demanding plant and animal specialists related to late-succession pine forest conditions [10]. Moreover, such management will break the fire-fuel vertical continuity, thus reducing the probability of stand-replacing crown fires.

Stem biomass contributed the largest proportion of total live biomass, followed by below-ground and branch biomass (Table 2). Although, proportion of the dead wood volume in pine- and spruce-dominated stands of live tree volume was similar, there were significant variations of dead wood compartments volume between them (Fig. 1). It appears that *Pinus sylvestris* has higher persistence to wind disturbance compared to *Picea abies* or other species [14].

In our study, stand age did not have a significant impact on stand parameters within the studied age group, as in this age class over-mature trees are still the dominant. However, generally age has been recognised as an important factor contributing to stand structure [7], [10], [13], for example, revealing that unmanaged over-mature coniferous stands stores higher amount of live and dead biomass compared to managed forests [15].

CONCLUSION

Mean total tree biomass in over-mature pine- and spruce-dominated stands growing on fertile mineral soils reached 343 and 238 t ha^{-1} (standing volume 567 and 381 m^3 ha^{-1}), respectively. The amount of tree biomass was significantly affected by dominated tree species in forest stand, but not by stand age (in range 163 to 218 years) in over-mature coniferous stands. Smaller dimension *Picea abies* trees contributed significantly to biomass in over-mature pine-dominated stands, but not vice versa. Smaller dimension *Picea abies* trees is an important factor determining the stand biomass, but not necessarily long term C storage. We suggest that management (periodic harvesting) of *Picea abies* trees in over-mature pine-dominated stands can be used for a better balance between economic and long-term carbon storage interests with additional benefit for structures important for biodiversity in these forests. Besides, large proportion of small trees biomass in pine- and spruce-dominated stands consisted of *Betula pendula* and other deciduous tree species. Stem represented the largest part (64%) of the total tree biomass, followed by below-ground (21%) and branch (16%) biomass in pine stands. Similar results were obtained in spruce stands: stem biomass – 60%, below-ground biomass – 22% and branch biomass – 18 % of the total tree biomass.

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Research Article

Forest Ecology

Sustaining Carbon Storage: Lessons from Hemiboreal Old-Growth Coniferous and Deciduous Forest Stands

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Abstract

For the last three decades, the area of old-growth forest stands in Europe has continued to increase as has their importance in achieving forest-related policy goals. This has triggered an increase in research interest in old-growth forests, both from climate change mitigation and biodiversity protection perspectives. However, carbon stock in old-growth stands in European hemiboreal forests had not been systematically studied. Therefore, in this article, we characterize differences in carbon stock between mature and old-growth stands on fertile mineral soils in hemiboreal Latvia to contribute to the understanding of carbon storage changes under different management strategies for forest lands. Carbon stock varied significantly both between old-growth stands of different dominant tree species and between mature (1.9–2.3 times younger) and old-growth stages of the same dominant species in forest stands. The carbon stock of tree biomass and deadwood was larger in old-growth stands, but their mean annual carbon stock change was significantly lower than in mature stands (27% to 47% depending on dominant tree species). Old-growth stands can serve as carbon reservoirs in areas with limited natural disturbances; however, for maintenance of climate neutrality, it is essential to expand the area of managed stands with larger annual carbon stock increase.

Study Implications: Forest ecosystems play a major role in regulation of global climate: They can store high quantities of carbon and also can gain or lose it rather quickly. For the last three decades, the area of old-growth forest stands in Europe has continued to increase as has their importance in achieving forest-related policy goals. Old-growth forests can represent the baseline carbon-carrying capacity in particular conditions. Therefore, we characterized differences in carbon stock between mature and old-growth stands on fertile mineral soils in hemiboreal Latvia to contribute to the understanding of carbon storage and for planning forest management activities.

Keywords: carbon pools, mature managed stands, tree biomass, deadwood, soil

Forest ecosystems play a major role in regulation of global climate: They can store high quantities of carbon and also can gain or lose carbon rather quickly. Boreal forests store nearly half of the global forest carbon; however, the effect on the carbon cycle of various forest types, management, and forest age is poorly understood (Chen and Luo 2015). Wood is a valuable and versatile renewable material; therefore, sustainable use of forest resources could help to achieve the carbon neutrality targets set by the European Union (EU) and which the United Nations Member States adopted in the Kyoto Protocol and the Paris Agreement, overall adhering to a global environmental policy to replace fossil and nonbiomass materials (Högbom et al. 2021; Howard et al. 2021; Uri et al. 2022a. Nevertheless, in the last three decades, the area of old-growth forest stands in Europe has continued to increase as forest management intensity decreases and forest protection increases (Badalamenti et al. 2019; O'Brien et al. 2021). Old-growth forest is an ecosystem distinguished by old trees and structural attributes that typically differ from earlier stages in a variety of characteristics, which may include tree size, accumulation of large dead woody material, number of canopy layers, species composition, and ecosystem function. Old-growth forests can vary widely depending on forest type, climate, site conditions, and disturbance regime (Buchwald 2005). Old-growth forests provide a wide range of ecosystem services, such as biodiversity maintenance, an increased overall species richness of landscape, and coarse woody debris as essential habitat for a large number of decomposer fungi and invertebrates (Siitonen et al. 2000; Brockerhoff et al. 2017; Berglund and Kuuluvainen 2021; Martin et al. 2021). The term "old growth forest" is used differently in studies published about their effect in climate change mitigation, thereby resulting in contrasting (and even contradicting) conclusions. The absence of a generally accepted definition for old-growth forests makes the comparison of current knowledge across different European countries and organizations difficult (O'Brien et al. 2021).

To reduce this complexity, we here address a specific segment of old-growth forests—old-growth stands—where old trees still form the dominant cohort. Such stands can represent the baseline carbon-carrying capacity in particular conditions

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(Roxburgh et al. 2006; Chen and Luo 2015; Högbom et al. 2021; Molina-Valera et al. 2021).

Currently, relatively few forest stands in Europe have reached this stage (Lõhmus and Kraut 2010; Seedre et al. 2015; Molina-Valero et al. 2020). Information from these stands can be used to evaluate carbon storage capacity in defined conditions (forest type, dominant tree species) and, consequently, the influence of the increased proportion of unmanaged areas on climate change mitigation progress and to compare alternative land management strategies (Kun et al. 2020; Högbom et al. 2021; Gundersen et al. 2021). Factors including tree species, site type, stand-growth dynamics, natural disturbance regime (severity and frequency), and the pattern of tree replacement after disturbance have the strongest effect on carbon in old-growth stands (Martin et al. 2018; Ruel and Gardiner 2019). Tree age is typically used to define the old-growth stage, but age thresholds differ between tree species and regions, and possibly even within a region (O'Brien et al. 2021). Therefore, we cannot rely on studies from other forest zones for comparison and estimates (Pregitzer and Euskirchen 2004; Buchwald 2005; Molina-Valero et al. 2021).

Although the total ecosystem carbon storage reflects the cumulative increase in tree biomass, deadwood, and litter, with increasing stand age, the capacity to accumulate carbon from the atmosphere in biomass decreases after trees reach middle age (Taylor et al. 2014; Nord-Larsen et al 2019; Uri et al. 2022a). Old-growth forests do not have the large rates of carbon sequestration observed in younger stands (Uri et al. 2012; Taylor et al. 2014; Blaško et al. 2020; Nord-Larsen et al 2019).

Important gaps in our understanding of carbon pools are related to carbon stock dynamics over a longer period: comparing managed mature and old-growth forest stands (Badalamenti et al. 2019; Molina-Valero et al. 2021), where huge heterogeneity between stands has been observed (Seedre et al. 2015; Yuan et al. 2016). Maturity in managed stands is usually defined by the age after which the mean annual increment declines (Siitonen et al. 2000). In hemiboreal Latvia, it is 101 to 121 years for Scots pine (*Pinus sylvestris* L.), 81 years for Norway spruce (*Picea abies* L. Karst), 51 to 71 years for birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.), and 41 years for European aspen (*Populus tremula* L.). Managed stands are defined by reoccurring operations with an aim to increase productivity, decrease tree competition, reduce mortality, and remove the weakened or dead trees (Siitonen et al. 2000).

Important characteristics distinguishing old-growth from managed mature or overmature stands is the accumulation of deadwood and net primary production, and long-term net effect of these processes is best characterized by the total carbon stock changes (Siitonen et al. 2000; Gundersen et al. 2021). In boreal forests of Canada, annual net aboveground biomass changes of forest ecosystems decrease with tree age, reaching zero at approximately age 100–120 years due to the decrease of biomass growth and increase of tree mortality (Chen and Luo 2015). As the stand ages, the changes in carbon pools are affected by numerous factors, including dominant tree species, forest type, and climate. The net climate change mitigation effect as the stand ages is a topic of heated scientific debate, even when it concerns one eco-region and stands with one dominant species (Lõhmus 2022; Uri et al. 2022a, 2022b). Therefore, large local data pools are needed for informed policy and management decisions when balancing contrasting (or conflicting) goals for biodiversity, carbon storage, and wood supply (Högbom et al. 2021), especially in relation to old-growth stands. We aimed to characterize the differences in carbon stock between mature and old-growth stands in hemiboreal Latvia.

Based on trends of mean annual increment and yield as well as deadwood decay rates, we hypothesized that (1) total carbon stock would increase from mature to old-growth stands, whereas the mean annual carbon stock change would decline; and (2) both of these trends would be steeper in stands dominated by coniferous (Scots pine and Norway spruce) rather than broadleaved (birch and European aspen) trees.

Materials and Methods

Forests in Latvia belong to the European hemiboreal forest zone (N 55°40'–58°05', E 20°58'–28°14'), which encompasses the transition between temperate deciduous and boreal coniferous forests, hosting a variable mixture of coniferous and deciduous trees and a diverse biota (Lõhmus and Kraut 2010). According to data of the Latvian National Forest Inventory (NFI), more than a half of Latvia is covered by forest (53% of the land; 3.21 M ha). Forest growing conditions are highly variable: 51% of the total forest area is on fresh mineral soils, 9% on wet mineral soils, 11% on peat soils, and 29% on drained land. Our study focused on the most prevalent conditions, dry forests with mesotrophic soil conditions (forest types *Hylocomniosa* and *Oxalidosa* according to Bušs [1976]), found in 40% of the total forest area. In these forest types, the herbaceous layer is dominated by common wood sorrel (*Oxalis acetosella* L.) and European blueberries (*Vaccinium myrtillus* L.) and the moss layer by glittering woodmoss (*Hylocomium splendens* Hedw.) and wind-blown mosses (*Dicranum* spp.) (Bušs 1976). Both forest types include stands dominated by Scots pine (16%), Norway spruce (24%), birch (25%), and European aspen (12%); these tree species combined represent 78% of the total *Hylocomniosa* and *Oxalidosa* forest area. Scots pine, Norway spruce, and birch are the most economically important tree species, used for furniture, building, pulp and paper, veneer, and other purposes (Beck et al. 2016; Durrant et al. 2016). European aspen is an early-succession fast-growing species (Caudullo and Rigo 2016) that provides habitat for many endangered species (Šēnhofa et al. 2021). In Latvia, active cyclone circulations cause rapid changes in weather conditions (Ahti et al. 1968). The mean annual temperature in Latvia (1988–2017) is 7°C; the mean of the coldest month (January) is -3°C, and the mean of the warmest (July) is 18°C (Harris et al. 2020). The mean annual precipitation is 712 mm, with 345 mm falling during growing season in May–September (Harris et al. 2020).

Nearly all forests in Latvia have been managed for a long time. The main differences between managed mature and old-growth stands we determined to be management history, or the degree of previous thinning and selective logging, and stand age. Old-growth stands were preselected from the forest inventory database using the age of the dominant cohort, size (>0.5 ha), location (>5 km from any villages and > 1 km from any roads), and no information about management (supposedly unmanaged) as criteria. Then the stands were visited and the following aspects were examined on site: target tree species (>50% of the standing volume);

age (160 years for Norway spruce and Scots pine, 100 years for European aspen, and 120 for birch, checked by 12 increment cores of dominant trees of dominant species per stand); forest type (*Hylocomniosa, Oxalidosa*); signs of former logging, like stumps, sawn surfaces of logs etc. (if found, the stand was discarded from the study). Stands were visited in random order until the desired number meeting the criteria was reached. After this selection phase, sample plots were established in each of the selected stands. Data characterizing mature stands were obtained from the NFI (2014–2018) database according to these criteria: (1) dominated by target species; (2) age 80 to 120 years for pines, 60 to 100 years for spruces, 60 to 90 years for birches, or 40 to 80 years for aspens (stand age in the NFI determined as average from increment cores of three dominant trees of dominant species per plot); and (3) *Hylocomniosa* or *Oxalidosa* forest type (Table 1). A total of 447 NFI sample plots were used for the study (figure 1).

The data collection in old-growth stands was performed from 2016 to 2019. In total, data from 19 spruce stands (167–213 years old, Ķēniņa et al. 2018), 25 pine stands (163–218 years old, Ķēniņa et al. 2019), 15 birch stands (123–148 years old, unpublished data), and 25 aspen stands (104–135 years old, unpublished data) were collected throughout the territory of Latvia. Altogether, 463 sample plots were established in these forest stands (figure 1).

Six to eight regular sample plots were established across old-growth stands. In each sample plot (500 m^2; 12.62 m), tree species and the diameter at breast height (DBH ≥ 6.1 cm) were recorded for all the living trees. The height of five living dominant species trees in the first floor and three living trees from each tree species in the second floor was measured. The tree height and DBH of all the standing dead trees and snags (≥6.1 cm) were measured. If the height of the snag was < 1.3 m, the height and diameter at the root collar were measured. For lying deadwood, the diameter of both ends (≥14.1 cm at the thicker end) and the length were measured within the sample plot (500 m^2). If the piece of deadwood crossed the sample plot border, only the part of it inside the plot was measured. In the center of the sample plot, a smaller subplot (a quarter circle of 25 m^2) was placed, where 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). For deadwood, decay stage (ranked in five classes, fresh to almost complete decay, according to Sandström et al. [2007]) and tree species (if possible) were recorded.

Litter and mineral soil sampling were done (in 157 stands) both in old-growth and mature stands to assess the litter and mineral soil carbon pools. At three systematically located points at the edge of a sample plot, a single soil sample was taken at fixed depths (0–10 cm, 10–20 cm, 20–40 cm, and 40–80 cm) using a 100 cm^3 metal cylinder, and 10 × 10 cm litter samples (soil organic horizon, including all litter and decomposed wood) were taken. The obtained samples were prepared and analyzed in the Laboratory of Forest Environment of the Latvian State Forest Research Institute Silava according to the LVS ISO 10694:2005 standard.

The individual living tree biomass was calculated using local biomass models for the main tree species in Latvia according to Liepiņš et al. (2017). The model of the tree species with the most similar wood density was used to calculate biomass for the species that do not have such models (e.g., *Alnus incana* [L.] Moench, *Alnus glutinosa* [L.] Gaertn., *Quercus robur* L.). For converting tree biomass into the living tree biomass carbon stock, the carbon content of 50% was used (Eggleston et al. 2006). The mass of deadwood and the carbon stock for standing and lying logs was 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). To compare deadwood carbon pools between the managed mature stands and old-growth stands, we used adjusted decay stages: (1) recently dead, (2) weakly decayed, and (3) moderately to almost completely decomposed.

An analysis of variance (ANOVA) was used to test the effects of dominant tree species, stand age group, and interaction between tree species and age group on the dependent variables: the carbon stocks of tree biomass, deadwood, soil, and litter and the mean annual carbon stock change

Table 1. Stand characteristics by dominant tree species and stand age group. The mean volume and stand density were calculated at the first layer data. Mean values ± 95% confidence interval.

Variables	Birch	Aspen	Pine	Spruce
	Old-growth stands			
Mean tree diameter at breast height (cm)	38 ± 1.5	49 ± 1.1	48 ± 1.1	37 ± 1.62
Mean quadratic tree height (m)	30 ± 0.7	37 ± 0.4	31 ± 0.34	29 ± 0.72
Mean volume (m^3 ha^{-1})	411 ± 53.0	666 ± 48.0	495 ± 41.0	323 ± 28.88
Mean stand density (trees ha^{-1})	301 ± 27	242 ± 22	269 ± 28	268 ± 28
Mean stand age (years)	131 ± 4	112 ± 3	179 ± 6	182 ± 2
Number of sample plots	67	146	148	102
	Mature stands			
Mean tree diameter at breast height (cm)	30 ± 1.0	37 ± 2.3	36 ± 0.9	32 ± 1.3
Mean quadratic tree height (m)	29 ± 0.6	30 ± 1.1	29 ± 0.5	26 ± 0.7
Mean volume (m^3 ha^{-1})	296 ± 20.2	343 ± 36.1	396 ± 27.1	326 ± 26.7
Stand density (trees ha^{-1})	352 ± 27	358 ± 50	326 ± 25	381 ± 40
Mean stand age (years)	69 ± 1	58 ± 3	97 ± 2	79 ± 2
Number of sample plots	114	86	130	117

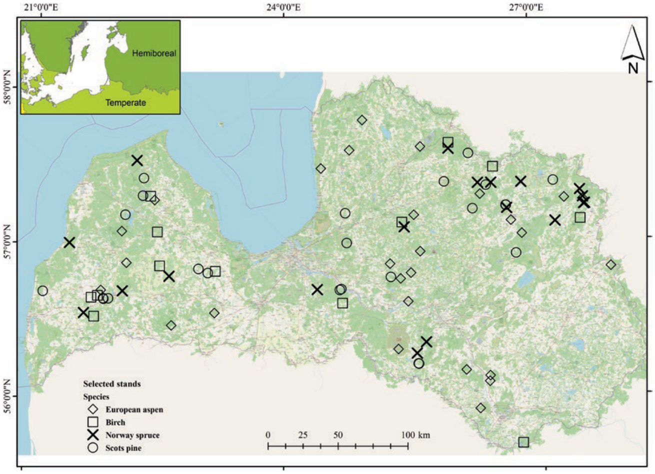

Figure 1 Distribution of old-growth stands in Latvia. Symbols indicate assessed old-growth stands by dominant tree species. OpenStreetMap has been used as background layer. In upper left corner the map of biogeographic regions (EEA 2022).

in tree biomass and deadwood carbon (separate model for each dependent variable). Before the ANOVA, all dependent variables were averaged for each old-growth stand, as the age group and dominant tree species were determined on the stand level, not on the plot level, as well as to standardize the data with the NFI data where only one observation per stand was done. As the data of the carbon stocks of deadwood, soil, and litter showed heterogeneity, they were log-transformed before they were put into models. After removing nonsignificant interactions or main variables (at a significance level of 0.05), the final models were chosen using the Akaike information criterion (AIC) (the lowest value). If a factor with more than two levels or interactions had a significant effect, a post hoc test comparing estimated marginal means was used. The estimated marginal means were calculated and compared in the R software version 4.1.0 (R Core Team 2021) using the *emmeans* package (Lenth 2021).

Results

The obtained carbon stock results from old-growth birch, aspen, pine, and spruce stands in *Hylocomniosa* and *Oxalidosa* forest types were compared with the NFI sample plot data from managed mature stands, which were 54–103 years younger and composed of the same tree species and forest types. Mature stands were 1.9–2.3 times (on average) younger than old-growth stands, depending on tree species; in absolute values, 97 ± 2 years for Scots pine, 79 ± 2 years for Norway spruce, 69 ± 1 years for birch, and 58 ± 3 years for European aspen.

Almost 60% (56%–61%, depending on dominant tree species) of the total ecosystem carbon in old-growth stands was found in the tree biomass, which represented the largest forest carbon pool. Mineral soil was the second-largest carbon pool, comprising up to 25%–37% of the total ecosystem carbon, whereas the litter (4%–11%) and deadwood (3%–5%) were marginal carbon pools in old-growth stands. In managed mature stands, the tree biomass was also the largest forest carbon pool, with 50% (46%–55%) of the total ecosystem carbon, but mineral soil comprised more (36%–41%) of the total ecosystem carbon. The smallest part of the total ecosystem carbon stock was deadwood (1%–2%), surpassed by forest litter (7%–12%).

The carbon stocks of tree biomass and deadwood differed significantly by dominant tree species and age group (all $P < 0.001$). The effect of interaction between dominant tree species and age groups also significantly affected carbon storage in living tree biomass ($P < 0.001$) and deadwood ($P < 0.05$) (Table 2).

In old-growth stands, where old trees still formed the dominant cohort, the carbon stock of tree biomass for all analyzed tree species was significantly higher (from 19% in Scots pine and Norway spruce to 42% in European aspen stands) than that in mature stands. Tree biomass carbon pools differed significantly between dominant tree species both in the mature and old-growth stands (figure 2A). In mature stands, the highest tree biomass carbon stock was detected in Scots pine stands (mean 139 ± 8.8 C t ha^{-1}), where it was significantly ($P < 0.001$) larger than that of European aspen (mean 119 ± 10.0 C t ha^{-1}) and Norway spruce (mean 113 ± 8.1 C t ha^{-1}) stands but similar to that of mature birch stands (mean 124 ± 7.3 C t ha^{-1}) (figure 2A; Table 3). In the old-growth stage, significantly higher carbon stock in tree biomass was found in aspen stands (mean 205 ± 7.0 C t ha^{-1}), where individual trees were significantly taller than other tree species (Table 1).

The deadwood carbon pool for all tree species in old-growth stands was significantly larger than in mature stands ($P < 0.001$). Depending on the dominant tree species, the difference was 58%–80% (Table 3; figure 2B). The size of deadwood carbon pool differed significantly between mature stands; Scots pine stands had significantly smaller carbon stocks than Norway spruce stands. In old-growth stands, the deadwood carbon stock between tree species was similar (Table 3; figure 2B).

The carbon stock in tree biomass and deadwood continued to increase from mature to old-growth stands as stand age increased for all analyzed tree species (figure 3).

The mean annual carbon stock change of tree biomass and deadwood carbon sum was evaluated to assess the changes in carbon storage intensity between mature and old-growth stands. Dominant tree species ($P < 0.001$) and age group ($P < 0.001$) significantly affected the annual carbon stock change of tree biomass and deadwood carbon sum (Table 2). The annual carbon stock change gradually decreased over time (over 82 ± 6 years for Scots pine, 103 ± 6 years for Norway spruce, 62 ± 4 years for birch, and 58 ± 3 years for European aspen) from the mature to the old-growth stage for all analyzed tree species (figure 4). All mature stands exhibited a significantly larger ($P < 0.001$) annual carbon stock change than old-growth stands, except for European aspen stands ($P = 0.06$), where the annual difference was similar in the mature (mean 2.2 ± 0.16 C t ha^{-1} year^{-1}) and old-growth stages (mean 2.0 ± 0.14 C t ha^{-1} year^{-1}). A major decrease (47%) of the annual carbon stock change from the mature to the old-growth stage was detected in spruce stands, from 1.5 to 0.8 C t ha^{-1} year^{-1}. Large and significantly different annual carbon stock change of carbon sum was found in mature European aspen and birch (1.9 ± 0.10 C t ha^{-1} year^{-1}) stands. A similar annual carbon stock change in the mature stands was found in Scots pine (1.5 ± 0.10 C t ha^{-1} year^{-1}) and Norway spruce (1.5 ± 0.11 C t ha^{-1} year^{-1}) stands (Figure 4). In the old-growth stage, European aspen stands exhibited a significantly higher annual carbon stock change than other tree species, although birch (1.4 ± 0.16 C t ha^{-1} year^{-1}) and Scots pine (1.1 ± 0.08 C t ha^{-1} year^{-1}) were similar, as were Scots pine and Norway spruce (0.8 ± 0.10 C t ha^{-1} year^{-1}) stands. Overall, in both mature and the old-growth stands, the mean annual carbon stock change of tree biomass and deadwood carbon sum was higher in deciduous tree stands.

Table 2. ANOVA model results of the effects of species, age, and their interaction on the carbon stocks of the tree biomass, deadwood, mean annual difference between tree biomass and deadwood, soil and litter carbon pools. Explanatory variables: species—birch, aspen, spruce, or pine; age—mature or old-growth stage. The *P*-value is shown as *: P < 0.05; (**): P < 0.01; (***): P < 0.001. Sum Sq—sum of squares; DF—degrees of freedom.

Carbon pool	Variable	DF	Sum Sq	*F* value (*P*-value)
Tree biomass	Species	3	60946	10.7 ***
	Age	1	161961	85.4 ***
	Age: species	3	41276	7.3 ***
	Residuals	523	991621	
Deadwood	Species	3	13.4	7.6 ***
	Age	1	115.4	195.1 ***
	Age: species	3	3.7	2.1
	Residuals	523	309.2	
Annual carbon stock change of tree biomass and deadwood	Species	3	46.7	49.2 ***
	Age	1	13.7	43.2 ***
	Age: species	3	1.6	1.7
	Residuals	523	165.4	
Soil	Species	3	4.6	5.3 **
	Age	1	0.8	2.9
	Age: species	3	3.9	4.5 **
	Residuals	160	46.3	
Litter	Species	3	8.3	6.1 ***
	Age	1	1.9	4.2 *
	Age: species	3	1.2	0.9
	Residuals	110	49.8	

The soil carbon stock was significantly affected by dominant tree species ($P < 0.001$) and by the interaction between dominant tree species and age group ($P < 0.05$), but the litter carbon stock was predominantly affected by dominant tree species ($P < 0.001$) and age group ($P < 0.05$) (Table 2). In mature stands, the soil carbon stock is similar for all tree species. In the old-growth stage, the soil carbon stock is similar between European aspen and birch stands, but it is significantly lower in Scots pine and Norway spruce stands. The litter carbon stock was significantly different ($P < 0.001$) between old-growth birch (mean 14 ± 5.2 t C ha^{-1}) and Scots pine stands (mean 21 ± 5.3 t C ha^{-1}). The carbon stock in forest litter was significantly different ($P < 0.01$) between mature birch and Norway spruce stands; it is twice as large in mature Norway spruce stands (Table 3). Soil carbon stocks also differed significantly between mature and old-growth Scots pine ($P < 0.05$) and Norway spruce ($P < 0.001$) stands, but litter carbon stock was significantly different between mature and old-growth Norway spruce ($P < 0.05$) stands.

Table 3. The carbon pool size of mature and old-growth (old) European aspen, birch, Scots pine, and Norway spruce stands. Marginal mean (C t ha-1) ± 95% confidence interval.

	Tree biomass	Deadwood	Soil *	Litter *	Total carbon
Aspen					
Old-growth stands	205 ± 7.0	14 ± 1.5	101 ± 17.6	17 ± 4.8	337
Mature stands	119 ± 10.0	5 ± 1.5	104 ± 16.4	24 ± 8.4	252
Birch					
Old-growth stands	175 ± 10.0	10 ± 1.8	117 ± 26.3	14 ± 5.2	316
Mature stands	124 ± 7.2	3 ± 0.6	89 ± 13.5	15 ± 11.3	231
Spruce					
Old-growth stands	140 ± 9.0	12 ± 2.0	58 ± 21.2	25 ± 12.0	235
Mature stands	113 ± 8.1	5 ± 1.0	96 ± 23.4	30 ± 5.3	244
Pine					
Old-growth stands	172 ± 7.0	15 ± 2.1	72 ± 30.6	21 ± 5.3	280
Mature stands	139 ± 8.8	3 ± 0.9	91 ± 23.6	21 ± 2.1	254

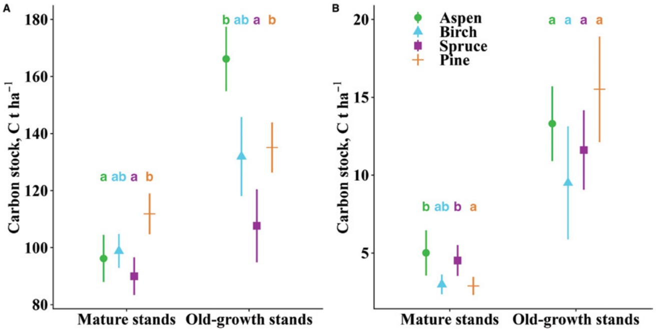

Figure 2 The mean carbon stocks (error bars show 95% confidence interval) of tree biomass (A) and deadwood (B) in mature and old-growth (old) European aspen, birch, Norway spruce, and Scots pine stands on mineral soils in hemiboreal Latvia. Letters above error bars shows results of species comparison within each age group. The same letters mean that difference is not significant.

Discussion

Our results supported the hypothesis that the carbon stock in tree biomass and deadwood continued to increase from mature to old-growth stands as the stand age increased (figure 3). This trend was gradually reduced with increasing stand age, consistent with findings of other studies in late-successional coniferous forests (Chen and Luo 2015). Additionally, an analysis of the long-term chronosequence after fire in the boreal forest of central Canada showed that carbon storage declined in late-succession stages (Gao et al. 2018). The carbon stock in tree biomass and deadwood in mature stands for all analyzed tree species was significantly lower than in old-growth stands (Table 3). Characteristics of tree species, like light demand and longevity, had a notable effect on the observed differences in carbon stock between mature and old-growth stands. Highest tree biomass carbon stock in younger managed mature stands was detected in Scots pine stands, but in the old-growth stage in European aspen stands (Table 3; figure 2). Deadwood, especially standing dead pine trees, remained longer in Scots pine stands. Other tree species fell more quickly and decayed rapidly, affecting deadwood carbon pool size and permitting pioneer species or a new generation of trees to regenerate in the opened gaps.

In our study, carbon pools were assessed only in forest stands that had reached the old-growth stage in which the target tree species still formed the dominant cohort. Nevertheless, possible disturbance and ongoing succession together with the dominant tree species effect—regeneration strategy and lifespan (Nilsson 1997; Martin et al. 2018; O’Brien et al. 2021)—affected tree biomass carbon stocks in stands between dominant tree species from the mature to the old-growth stage. We found that tree biomass and deadwood biomass carbon pools are highly variable between the sampled stands, which may be a result of species composition, site variability in soil properties, soil moisture, and site history effects (Jandl et al. 2007; Hansson et al. 2011; Uri et al. 2012; Gao et al. 2018; Lutter et al. 2018). Furthermore, old-growth European aspen stands had significantly higher tree biomass carbon stock; although especially large aspen trees are susceptible to wood-rotting fungi (Latva-Karjanmaa et al. 2007; Arhipova et al. 2011; Čakšs et al. 2022), the presence of rot in stems and hollowed stems was not calculated as carbon loss in our carbon stock estimations. Therefore, the obtained results supported our hypothesis only partially, as carbon stocks of tree biomass and deadwood were higher only in mature coniferous (Scots pine and Norway spruce) stands than in broadleaved (birch and European aspen) managed mature stands, but not in old-growth stands.

The mean annual carbon stock change of tree biomass and deadwood carbon sum was higher in deciduous tree stands both in the mature and the old-growth stage (figure 4). We observed that the annual carbon stock change gradually decreased over time from the mature stage to the two-times-older old-growth stage for all analyzed tree species: by 10% in European aspen stands, 27% in Scots pine and birch stands, and 47% in Norway spruce stands (figure 4). This shows that forests continue to accumulate carbon in old age, as Luyssaert et al. (2021) suggested. However, the carbon uptake decreased over time in old-growth stands; unmanaged forests had lower net ecosystem productivity, and thus, carbon sequestration rates, than managed forests (Gundersen et al. 2021; Uri et al. 2022, 2022a). This finding is consistent with Molina-Valero et al. (2021), who concluded that the maximum accumulation of live biomass can be reached in mature stands. Additionally, most of the mature stands were from commercial forests where commercial thinning has occurred and some of the timber has been used in wood-based products to substitute for fossil materials and contribute to climate change mitigation (Pukkala 2017; Holmgren 2021).

The soil carbon stock was similar among all tree species in mature stands, but in the old-growth stage, the soil carbon stock was similar between deciduous tree stands and significantly larger than in coniferous tree stands. No differences in soil carbon stocks were observed between mature and old-growth European aspen and birch stands, and carbon stocks were similar between mature and old-growth stands of European aspen, birch, and Scots pine. These findings align with previous reports on soil carbon stocks, stating that long-term soil carbon did not increase in unmanaged forests (Nord-Larsen et al. 2019). Moreover, the forest litter results from mature and old-growth stands confirm that this carbon pool reached its maximum in the younger managed stands and its maximum differs between tree species (Hansson et al. 2011). This aligns with the results of analyzed soil carbon

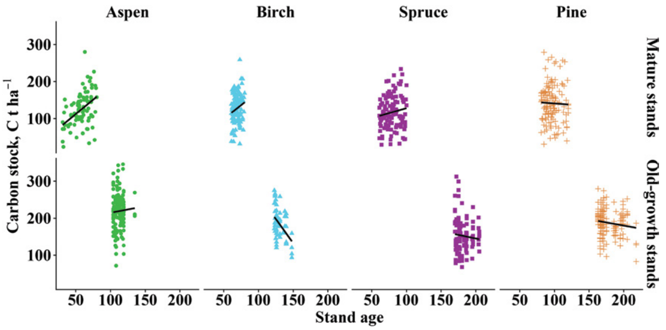

Figure 3 The mean carbon stock of tree biomass and deadwood in the Scots pine, Norway spruce, birch, and European aspen in mature to old-growth stands.

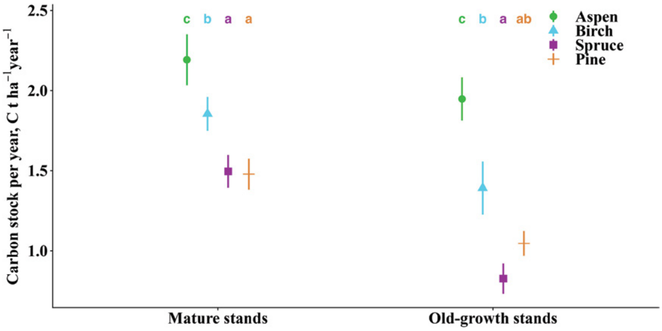

Figure 4 The mean annual carbon stock change of tree biomass and deadwood carbon sum (error bars show 95% confidence interval) in the Scots pine, Norway spruce, birch, and European aspen old-growth and mature stands on mineral soils in hemiboreal Latvia. Letters above error bars shows results of species comparison within each age group. The same letters mean that difference is not significant.

pool size in boreal forests, where carbon stock peaks in the 71-years-or-older age classes, thus being highly variable (Pregitzer and Euskirchen 2004). Therefore, more studies are required to analyze the species impact not only on the existing old-growth forest stands but also to understand the future old-growth stand ability to continue being carbon sinks with increasing age through tree biomass and soil, which is affected not only by the forest type and dominant tree species (Jandl et al. 2007; Lutter et al. 2018; Jones et al. 2019; Nord-Larsen et al. 2019) but also by other indirect factors such as the decomposition of deadwood (Błońska et al. 2019).

Conclusions

We assessed old-growth stands where old aspen (stands aged 104–135 years), birch (aged 123–148 years), spruce (aged 170–205 years), and pine (aged 163–218 years) are still the dominant cohorts, thus expanding current knowledge and contributing to a better understanding of old-growth forest carbon storage baseline in hemiboreal forests of Europe. The obtained main carbon pool sizes of old-growth stands can be used to evaluate various strategic and policy decisions regarding total ecosystem carbon in forests. Our data confirmed the hypothesis that carbon stocks in tree biomass and deadwood differed significantly between dominant tree species and age groups. In mature stands (two times younger than old-growth stands), the carbon pools for all analyzed tree species were significantly lower than those in old-growth stands, reaching 245 C t ha^{-1} and 292 C t ha^{-1}on average, respectively. However, the maximum of the mean annual carbon stock change was reached before the old-growth stage and gradually decreased over time from the mature to the old-growth stage for all analyzed tree species. The significantly smaller mean annual carbon stock change in old-growth stands cannot ensure the maintenance of climate neutrality; thus, they can serve as carbon reservoirs in areas with limited natural disturbance influence.

Author Contributions

Conceptualization: Āris Jansons; Methodology: Āris Jansons, Laura Ķēniņa; Data collection: Ieva Jaunsalviete, Laura Ķēniņa, Endijs Bāders; Formal analysis and investigation: Laura Ķēniņa, Didzis Elferts; Writing—original draft preparation: Laura Ķēniņa; Writing—review and editing: Laura Ķēniņa, Āris Jansons, Endijs Bāders, Didzis Elferts; Funding acquisition: Āris Jansons; Supervision: Āris Jansons.

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Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Consent for Publication

All authors gave their informed consent to this publication and its content.

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

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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

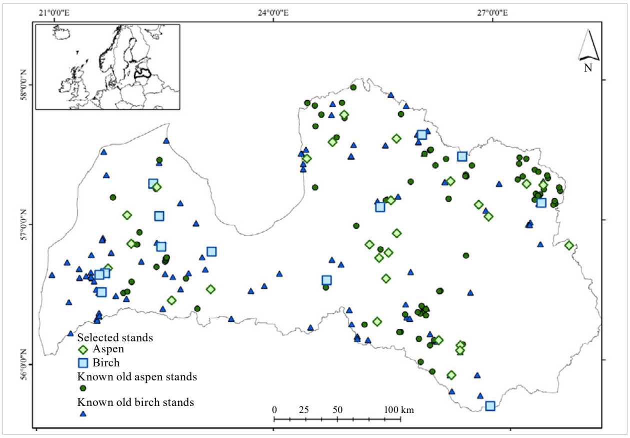

Figure 1. Distribution of known old-growth birch and aspen stands in Latvia

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.

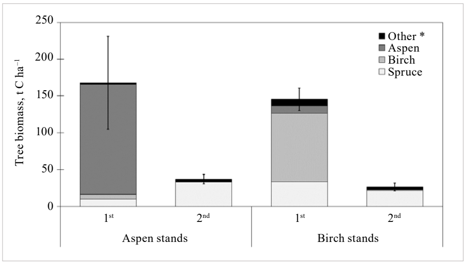

Figure 2. Mean tree biomass carbon stock of the first (1st) and second (2nd) layers by species in old-growth aspen and birch stands (error bars show ± 95% confidence intervals)

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

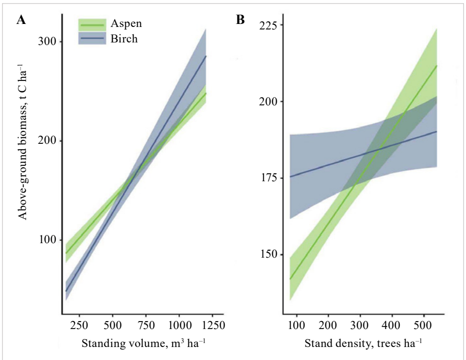

Figure 3. Model predicted change of the above-ground biomass carbon stock in response to (A) standing volume (M, m^3 ha^{-1}); (B) stand density (trees ha^{-1}) in old-growth birch and aspen stands. Mean (t C ha^{-1}) values ± 95% confidence interval

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 (*): $p < 0.05$; (**): $p < 0.01$; (***): $p < 0.001$.

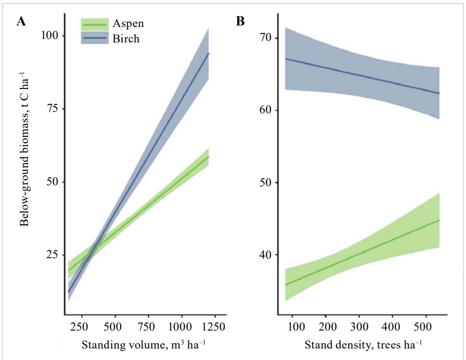

Figure 4. Model predicted change of the below-ground biomass carbon stock in response to (A) standing volume (M, m^3 ha^{-1}); (B) stand density (trees ha^{-1}) in old-growth birch and aspen stands. Mean (t C ha^{-1}) values ± 95% confidence interval

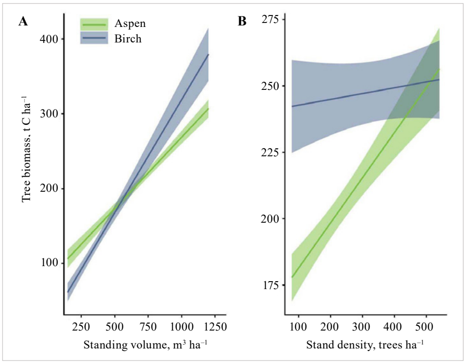

Figure 5. Model predicted change of the living tree biomass carbon stock in response to (A) standing volume (M, m^3 ha^{-1}); (B) stand density (trees ha^{-1}) in old-growth birch and aspen stands. Mean (t C ha^{-1}) values ± 95% confidence interval

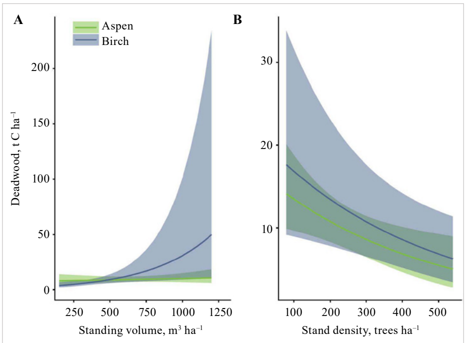

Figure 6. Predicted deadwood carbon stock in response to (A) standing volume (M, m³ ha⁻¹) and (B) stand density (trees ha⁻¹). Mean (t C ha⁻¹) values ± 95% confidence interval

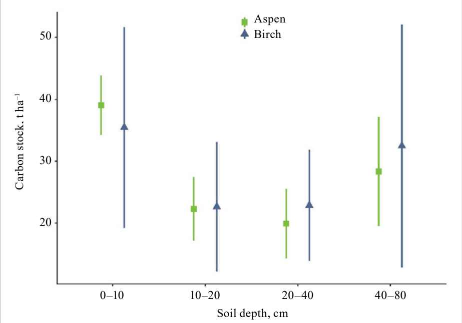

Figure 7. Differences in the mean soil carbon stock at different soil depths. Error bars show ± 95% confidence intervals

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.

Acknowledgements

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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).

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