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OGLEKĻA UZKRĀJUMA ILGTERMIŅA IZMAIŅAS HIDROMELIORĀCIJAS IETEKMĒ MEŽOS AR KŪDRAS AUGSNĒM

CARBON STOCK CHANGES AFTER LONG-TERM DRAINAGE IN FORESTS ON ORGANIC SOILS

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ANOTĀCIJA

Meža ekosistēmas ar organiskām augsnēm ir nozīmīgas oglekļa krātuves, kuru loma klimata pārmaiņu mazināšanā hemiboreālajā reģionā ir saistīta ar hidroloģisko režīmu un apsaimniekošanas vēsturi. Turklāt liela daļa mežu ar organiskām augsnēm vēsturiski ir meliorēti, lai uzlabotu produktivitāti, tomēr zinātniskajā literatūrā informācija par meliorācijas ilgtermiņa ietekmi uz dažādām oglekļa krātuvēm, īpaši vecos mežos, ir fragmentāra. Tāpēc oglekļa uzkrājuma un emisiju kvantificēšanas nozīme ir neatsverama hidrotehniskās meliorācijas ilgtermiņa ietekmes novērtējumam klimata pārmaiņu mazināšanā. Promocijas darba mērķis ir novērtēt hidrotehniskās meliorācijas ilgtermiņa ietekmi uz augsnes siltumnīcefekta gāzu emisijām un oglekļa uzkrājuma dinamiku galvenajās oglekļa krātuvēs vecās skuju koku audzēs mežos ar mezotrofām organiskām augsnēm.

Hemiboreālos skuju koku mežos ar organiskām augsnēm pirms 54 gadiem izveidotas meliorācijas sistēmas ilgtermiņa ietekme būtiski mainīja ekosistēmas dinamiku. Lai gan meliorācija izraisīja augsnes nosēšanos (vidēji par 26 cm), tā neveicināja augsnes oglekļa zudumus. Turpretim uzlabotā augsnes aerācija un pazemūtais gruntsūdens līmenis ievērojami uzlaboja koku augšanu un tādējādi palielināja oglekļa uzkrājumu koku biomasā. Vecās mežaudzēs kūdreņos koku biomasas oglekļa uzkrājums ir 162.0 ± 25.0 t C ha^{-1} un 167.0 ± 24.6 t C ha^{-1}, attiecīgi egļu un priežu audzēs. Savukārt purvaiņos oglekļa uzkrājums koku biomasā priežu mežaudzēs ir 74.0 ± 20.6 t C ha^{-1}, bet egļu mežaudzēs – 121.1 ± 7.6 t C ha^{-1}. Atmirušās koksnes oglekļa uzkrājums priežu audzēs purvaiņos un kūdreņos, kā arī egļu audzēs kūdreņos bija līdzīgs (8–10 t C ha^{-1}), bet egļu audzēs purvaiņos – būtiski mazāks. Meliorācija, nodrošinot augsnes aerāciju, ietekmēja siltumnīcefekta gāzu emisijas no augsnes, organiskām augsnēm piesaistot CH_4, ja gruntsūdens līmenis bija zemāks par 30–40 cm. Savukārt augsts gruntsūdens līmenis veicināja CH_4 emisijas. Augsnes CO_2 emisijas galvenokārt bija saistītas ar augsnes temperatūru nevis meliorāciju; heterotrofā elpošana veidoja 41% no kopējām augsnes CO_2 emisijām. Meliorācija ietekmēja sīko sakņu oglekļa uzkrājuma dinamiku. Sīko sakņu biomasa bija būtiski lielāka purvaiņos, iespējams, kā veģetācijas adaptēšanās pārmitriem apstākļiem. Tā kā sīko sakņu veidošanās kūdreņos un purvaiņos bija līdzīga, tad mazāka to biomasa kūdreņos, visticamāk, bija straujākas sīko sakņu aprites rezultāts. Zemsedzes veģetācijas biomasas un nobiru oglekļa uzkrājumi, lai gan mazāki nekā citās oglekļa krātuvēs, bija līdzīgi gan kūdreņos, gan purvaiņos.

Novērtētie oglekļa uzkrājumi liecina, ka vecas mežaudzes kūdreņos un purvaiņos ir nozīmīgas, taču ierobežotas oglekļa krātuves hemiboreālo mežu ekosistēmās. Novērtētās atšķirības norāda uz labi funkcionējošu meliorācijas sistēmu kā priekšnosacījumu oglekļa uzkrājumam mežos ar dziļām organiskām augsnēm, nodrošinot to pienesumu globālo klimata pārmaiņu mazināšanā.

ABSTRACT

Forest ecosystems with organic soils are major carbon stores, and their role in climate change mitigation in the hemiboreal region is linked to the hydrological regime and management history. Moreover, a large proportion of forests on organic soils have historically been drained to improve forest productivity. Scientific literature provides only fragmentary information on the long-term impact of drainage on various carbon pools, especially in old-growth forests. Therefore, quantification of carbon stock and emissions is essential for the assessment of the long-term impact of drainage on climate change mitigation. The aim of the study is to assess the long-term impact of forest drainage on soil greenhouse gas emissions and the dynamics of carbon stock in major carbon pools in old-growth forests with organic soils.

In hemiboreal old-growth coniferous forest stands on organic soils, the long-term effect of forest drainage (established 54 years ago) substantially altered ecosystem dynamics. While drainage caused soil subsidence (by an average of 26cm), it did not deplete soil carbon stock. Instead, the improved soil aeration and lowered groundwater level (GWL) significantly improved tree growth and consequently expanded the carbon pool. Old-growth forest stands on drained organic soils reached tree biomass carbon stock at 162.0 ± 25.0 t C ha^{-1} and 167.0 ± 24.6 t C ha^{-1} in spruce and pine-dominated stands, respectively. Contrastingly, in undrained pine stands, the carbon stock was 74.0 ± 20.6 t C ha^{-1}, but in spruce stands, it was 121.1 ± 7.6 t C ha^{-1}. Deadwood was a moderate carbon pool, reaching 8–10 t C ha^{-1} in drained sites, which was lower in undrained spruce stands. Drainage affected soil greenhouse gas emissions, with organic soils functioning as CH_4 sinks when the GWL was lower than 30-40 cm, providing soil aeration. However, high GWL or poorly functioning drainage resulted in CH_4 emissions. Soil CO_2 emissions were primarily driven by soil temperature, not by the presence of drainage; heterotrophic respiration accounted for 41% of total soil CO_2 efflux. Drainage altered the belowground dynamics of the fine-root carbon pool. Fine-root biomass was significantly higher in undrained sites, likely as an adaptation of vegetation to waterlogged conditions. Since the production of fine-roots was similar in drained and undrained sites, the lower fine-root biomass in drained sites was most likely the result of a faster fine-root turnover. Ground vegetation biomass and litter carbon stocks, though smaller than other carbon pools, were similar between drained and undrained stands.

The estimated carbon stocks highlight old-growth forest stands on organic soils as significant, yet limited carbon stores, in the hemiboreal forest ecosystem. The observed differences highlight well-functioning drainage systems as paramount for sustaining increased carbon stock and the contribution of drained forests to climate change mitigation goals.

SATURS / *CONTENTS*

PUBLIKĀCIJU SARAKSTS / *LIST OF PUBLICATIONS*

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

The thesis is based on seven papers, referred in the text with Roman numerals:

I Ķēniņa, L., Zute, D., Jaunslaviete, I., **Samariks, V.**, Jansons, Ā. (2022) Old-Growth Coniferous Stands on Fertile Drained Organic Soil: First Results of Tree Biomass and Deadwood Carbon Stocks in Hemiboreal Latvia. Forests, 13, 279. DOI: 10.3390/f13020279

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Autoru ieguldījums / *The contribution of the authors*

Autora ieguldījums	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
Ideja / *Original idea*	ĀJ	ĀJ, **VS**	ĀJ	ĀJ, **VS**	ĀJ	ĀJ, **VS**	ĀJ, **VS**
Pētījuma plāns / *Study design*	LĶ, ĀJ, DZ	KJ, FV, ĀJ	AB, IL	ĀJ, LĶ, VS,	ĀJ, **VS**	ĀJ, **VS**	KA, MV, ĀJ
Datu ievākšana / *Data collection*	IJ, **VS**	**VS**	DP, AL	**VS**, NĪ, KO	**VS**, KB	IJ, AA, SD	**VS**, LĶ, AAL
Datu analīze / *Data analysis*	LĶ	**VS**, EB	**VS**, SD	**VS**, KK	**VS**, KB	**VS**	MK, KA, MV
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VS – Valters Samariks, ĀJ – Āris Jansons, LĶ – Laura Ķēniņa, IJ – Ieva Jaunslaviete, DZ – Daiga Zute, KJ – Kalev Jõgiste, FJ – Floortje Vodde, EB – Endijs Bāders, SD – Stefānija Dubra, IL – Ieva Līcīte, AB – Aldis Butlers, DP – Dana Purviņa, AL – Ainārs Lupiķis, NĪ – Nauris Īstenais, KO – Kristaps Ozoliņš, KK – Kajar Köster, KB – Kārlis Bičkovskis, AA – Andis Adamovičs, SD – Sabīne Ieviņa (ex. Dubašinska), MK – Māra Kitenberga, KA – Kristiina Aun, MV – Mats Varik, AAL – Agnese Anta Liepiņa.

PROMOCIJAS DARBA REZULTĀTU APROBĀCIJA / *APPROBATION OF RESEARCH RESULTS*

Ziņojumi par pētījuma rezultātiem prezentēti divpadsmit starptautiskās zinātniskās konferencēs:

Results of the study have been presented in twelve international scientific conferences:

I **Samariks, V.,** Zute, D., Jansons, Ā. (2021) Long-term impact of forest hydro melioration on carbon storage and emissions (Is it good to wet in the forest?). 6th International conference "Sustainable management of natural resources – a basic condition for successful socioeconomic development in the period of implementation of the new environmental policy of the European Union", 25 November, 2021, Jelgava, Latvia. Poster / Stenda referāts

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IX **Samariks, V.** (2023) Can prolonged rotation in combination of forest drainage be a solution to increased carbon storage in Scots pine forests on organic soils of hemiboreal region? 5th International Congress on Planted Forests, 5–13 November, 2023, Nairobi, Kenya. Presentation / Prezentācija

X **Samariks, V.**, Ozoliņš, K., Jansons, Ā. (2024) Is establishment of drainage systems a long-term climate smart forestry measure in hemiboreal Scots pine forests on deep organic soils? 26th IUFRO World Congress, 23–29 June, 2024, Stockholm, Sweden. Poster / Stenda referāts

XI **Samariks, V.**, Jaunslaviete, I., Zute, D., Jansons, Ā. (2024) Prolonged rotation in combination of forest drainage – a solution to increased carbon storage in hemiboreal coniferous forests on organic soils? 26th IUFRO World Congress, 23–29 June, 2024, Stockholm, Sweden. Poster / Stenda referāts

XII **Samariks, V.**, Ozoliņš, K., Ķēniņa, L., Bāders, E., Jansons, Ā. (2025) Groundwater level driving the dynamics of soil greenhouse gas fluxes in old-growth hemiboreal birch (*Betula* spp.) stands on organic soils. 12th INTERCOL Wetland Conference, 29 June– 4 July, 2024, Tartu, Estonia. Presentation / Prezentācija

1. IEVADS

Mežu ekosistēmas ir būtiskas globālā oglekļa cikla sastāvdaļas, kas darbojas gan kā nozīmīgas oglekļa krātuves, gan kā dinamiski regulētāji, veicot oglekļa piesaisti un siltumnīcefekta gāzu (SEG) apmaiņu starp biosfēru un atmosfēru (Pan et al. 2011; Friedlingstein et al. 2022). Pēdējās desmitgadēs mežu nozīme klimata pārmaiņu mazināšanā un bioloģiskās daudzveidības saglabāšanā ir arvien vairāk uzsvērta starptautiskos un reģionālos politikas dokumentos (FAO 2020; IPCC 2021). Eiropas Savienība ir izvirzījusi mērķus mazināt klimata pārmaiņas un pielāgoties tām, kā arī sasniegt un uzturēt klimatneitralitāti līdz 2050. gadam un turpmāk (Fetting 2020; Erback 2021). Meža oglekļa krātuvju kvantificēšana reģionālā un nacionālā mērogā ir būtiska zinātniski pamatotu apsaimniekošanas un politikas stratēģiju izstrādei, tādējādi uzlabojot oglekļa uzskaites precizitāti, veicinot adaptīvu mežu apsaimniekošanu un sekmējot bioloģiskās daudzveidības un klimata mērķu sasniegšanu.

Ziemeļeiropas hemiboreālais reģions, kurā ietilpst Latvija, Igaunija, Dienvidzviedrija un daļa Somijas, ir pārejas zona starp boreālajiem skuju koku un mērenā klimata lapu koku mežiem (Ahti et al. 1968). Latvija ir Baltijas reģiona valsts ar vislielāko mežu platību, kas nodrošina ievērojamus koksnes resursus, un prognozēts, ka pieprasījums pēc tiem nākotnē pieaugs. Meži klāj 53% Latvijas sauszemes teritorijas. Parastā egle un parastā priede ir galvenās mežsaimniecības sugas, kas kopā veido 45% no kopējās meža platības (NFI 2023). Piejūras klimata, pēcleduslaikmeta reljefa un augsta augsnes mitruma mijiedarbība ir veicinājusi plašu organisko augšņu un purvu veidošanos. Latvijā 23% mežu ir ar organiskām augsnēm (NFI 2023).

Ogleklis meža ekosistēmās atrodas vairākās savstarpēji saistītās krātuvēs, kas kopā nosaka kopējo oglekļa bilanci un meža kā oglekļa piesaistes vai emisiju avota lomu. Galvenās oglekļa krātuves meža ekosistēmās ir koku biomasa (virszemes un pazemes daļa), atmirusī koksne (sausokņi un kritalas), nobiras, zemsedzes veģetācija un augsne (īpaši organiskā augsne), un katra no tām darbojas atšķirīgos laika un telpas mērogos oglekļa aprites ciklā. Koku biomasa ir visdinamiskākā oglekļa krātuve, kuru nosaka audzes vecums, produktivitāte, apsaimniekošanas intensitāte un sugu sastāvs. Atmirusī koksne ir gaistoša oglekļa krātuve, kas sadaloties pakāpeniski atbrīvo oglekli, vienlaikus veicinot bioloģisko daudzveidību un organisko vielu uzkrāšanos augsnē ilgtermiņā. Koku nobiras, ko veido nokritušās skujas, lapas un zari, nodrošina nepārtrauktu organisko vielu ienesi augsnē, uzturot barības vielu apriti un mikrobioloģisko aktivitāti. Augsnes oglekļa uzkrājums, īpaši organiskās augsnēs, ir lielākā un stabilākā oglekļa krātuve, kas bieži pārsniedz virszemes oglekļa uzkrājumu. Sīkās saknes un zemsedzes veģetācija, pateicoties to nepārtrauktajai nomaiņai, sekmē augsnes organisko vielu veidošanos un veicina ilgtermiņa oglekļa uzkrāšanu.

Laikā no 1960. līdz 1980. gadam Baltijas valstīs veikti plaši mežu hidrotehniskās meliorācijas pasākumi, lai uzlabotu koku augšanu un palielinātu mežu produktivitāti teritorijās ar dabiski augstu gruntsūdens līmeni (Paavilainen & Päivänen 1995; Šņore 2004). Rezultātā aptuveni 54% mežu ar organiskām augsnēm Latvijā ir meliorēti (NFI 2023). Meliorācijas sistēmām nepieciešama periodiska atjaunošana, lai nodrošinātu to funkcionēšanu un uzturētu vēlamo koku augšanas potenciālu (Nieminen et al. 2018; Bičkovksis et al. 2025). Pēdējā desmitgadē Latvijā jaunu meliorācijas sistēmu izbūve meža zemēs praktiski nav notikusi; apsaimniekošanas pasākumi galvenokārt vērsti uz esošo sistēmu uzturēšanu un atjaunošanu, vai pretēji – uz meliorācijas grāvju slēgšanu un gruntsūdens līmeņa paaugstināšanu.

Organiskās augsnes var būt nozīmīgs SEG emisiju avots salīdzinājumā ar minerālaugsnēm, tādēļ, lai nodrošinātu precīzu oglekļa bilances novērtējumu, ir būtiski kvantitatīvi novērtēt emisiju apjomu no meliorētam un nemeliorētam organiskām augsnēm. Organisko augšņu meliorēšana var veicināt organisko vielu aerobo sadalīšanos, kas var rezultēties ar CO_2 emisiju palielināšanos (Von Arnold et al. 2005; Wüst-Galley et al. 2016), savukārt nemeliorētās mežaudzēs augsts gruntsūdens līmenis var samazināt CO_2 emisijas no augsnes, jo ierobežota skābekļa pieejamība kavē organiskās vielas noārdīšanos, bet vienlaikus

veicina CH_4 emisijas anaerobos apstākļos (Matthews & Fung 1987). Turpretī, zems gruntsūdens līmenis parasti veicina CH_4 piesaisti, jo aerētajos augsnes slāņos palielinās metanotrofā aktivitāte (Le Mer & Roger 2001).

Latvijā vecu mežaudžu platības uzrāda pakāpeniski pieaugošu tendenci (NFI 2023), kamēr lielākajā daļā Eiropas šādas mežu platības samazinās (O'Brien et al. 2021). Vecām mežaudzēm ir būtiska loma bioloģiskās daudzveidības uzturēšanā ainavas mērogā un klimata pārmaiņu mazināšanā, tādēļ ir svarīgi kvantificēt dažādu oglekļa krātuvju apjomu šajās ekosistēmās un novērtēt meliorācijas ilgtermiņa ietekmi uz kopējo oglekļa uzkrājumu. Līdzšinējie pētījumi par vecām mežaudzēm Latvijā galvenokārt veikti mežos ar minerālaugsnēm, akcentējot koku biomasas un atmirušās koksnes oglekļa uzkrājumu reģionā saimnieciski nozīmīgām koku sugām (Ķēniņa et al. 2018, 2019). Savukārt iepriekšējie pētījumi par mežiem ar organiskām augsnēm galvenokārt vērsti uz atsevišķām oglekļa krātuvēm (Bičkovskis et al. 2023) un SEG emisiju novērtējumu mežaudzēs dažādās attīstības stadijās (Butlers 2023), bet ne ciršanas vecumu pārsniegušās audzēs. Tāpēc būtiskāko oglekļa krātuvju un plūsmu novērtējums meliorācijas ilgtermiņa ietekmē vecos hemiboreālos mežos Latvijā ir nepieciešams, lai aizpildītu esošo zināšanu trūkumu un nodrošinātu uzticamus pamatdatus ilgtspējīgas mežsaimniecības un klimata politikas plānošanai.

1.1. Promocijas darba mērķis

Promocijas darba mērķis ir novērtēt hidrotehniskās meliorācijas ilgtermiņa ietekmi uz augsnes siltumnīcefekta gāzu emisijām un oglekļa uzkrājuma dinamiku galvenajās oglekļa krātuvēs vecās skuju koku audzēs mežos ar mezotrofām organiskām augsnēm.

1.2. Promocijas darba uzdevumi

Mērķa sasniegšanai izvirzīti šādi darba uzdevumi:

1. Novērtēt hidrotehniskās meliorācijas ietekmi uz kokaudzes biomasas un atmirušās koksnes oglekļa uzkrājumu.
2. Raksturot hidrotehniskās meliorācijas ietekmi uz augsnes oglekļa uzkrājumu un SEG emisijām.
3. Novērtēt hidrotehniskās meliorācijas ietekmi uz zemsedzes veģetācijas, sīko sakņu un nobiru oglekļa uzkrājumu.

1.3. Promocijas darba tēze

Hemiboreālajos skuju koku mežos ar mezotrofām organiskām augsnēm hidrotehniskā meliorācija ilgtermiņā palielina oglekļa uzkrājumu koku biomasā, neatstāj negatīvu ietekmi uz oglekļa uzkrājumu augsnē un samazina metāna emisijas.

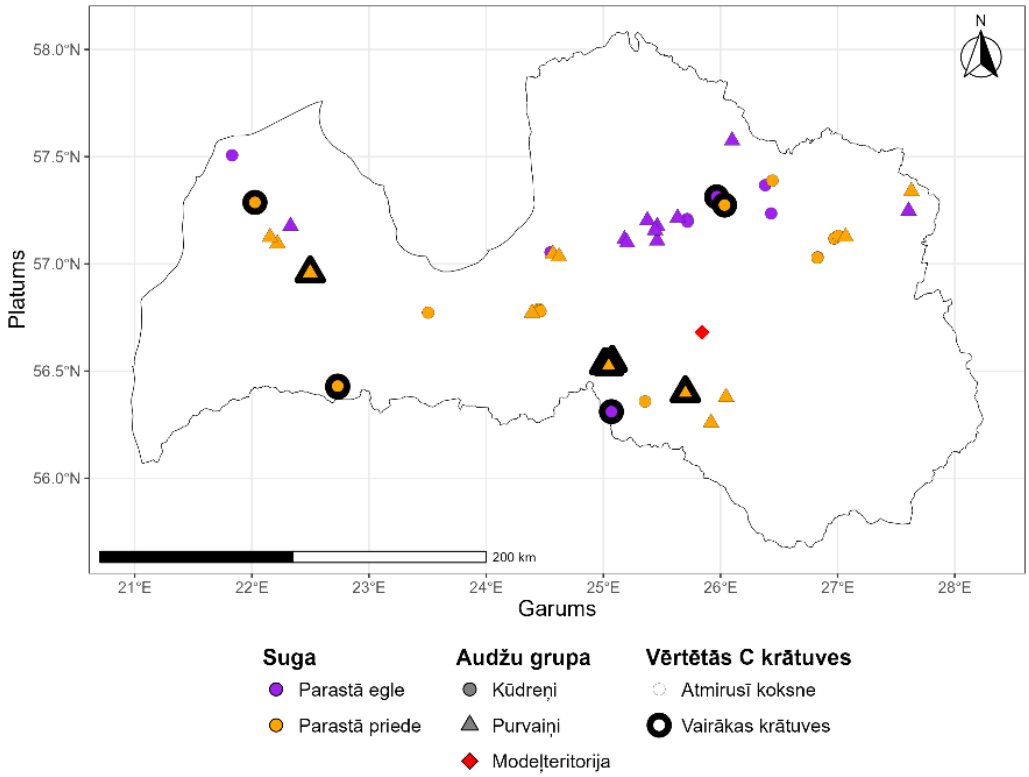
1.4. Pētījuma novitāte

Pirmo reizi Eiropas hemiboreālajos mežos novērtētas un kvantificētas galvenās meža ekosistēmas oglekļa krātuves hidrotehniskās meliorācijas ilgtermiņa ietekmē vecās skuju koku mežaudzēs (122–218 gadi) kūdreņos un purvaiņos. Pētījums sniedz zināšanas par šādu ekosistēmu stabilitāti un oglekļa uzkrājuma izmaiņām ilgtermiņā, pēc meliorācijas sistēmu izveides.

2. MATERIĀLI UN METODES

2.1. Pētījuma objekts

Pētījuma galvenais objekts ir vecas skuju koku audzes mežos ar organiskām augsnēm hemiboreālajā reģionā, Latvijā (2.1. att.; Ahti et al. 1968). Koku biomasas, atmirušās koksnes, nobiru, zemsedzes veģetācijas, sīko sakņu oglekļa uzkrājuma un SEG emisiju novērtējumam atlasītas meliorētas un nemeliorētas audzes mežos ar organiskām augsnēm, bez nesenām saimnieciskās darbības pazīmēm, audžu vecums ir vismaz divas vecumklases virs ciršanas vecuma (egle > 120 gadi, priede > 140 gadi) un valdošās koku sugas šķērslaukums pārsniedz 50% no audzes šķērslaukuma. Izvēle veikta, balstoties uz stratificētu audžu atlasi no Valsts meža dienesta datubāzes. Koku biomasas oglekļa (C) uzkrājums vērtēts 23 vecās (131– 179 gadi) priežu un egļu mežaudzēs šaurlapju kūdrenī (*Myrtillosa turf. mel.*, turpmāk tekstā – kūdreņi) un niedrājā (*Caricoso-phragmitosa*, turpmāk tekstā – purvaiņi; I publikācija). Atmirušās koksnes C uzkrājums vērtēts 52 vecās (122–218 gadi) priežu un egļu mežaudzēs purvaiņos un kūdreņos (II publikācija). SEG emisijas un sīkās saknes vērtētas sešās vecās priežu mežaudzēs kūdreņos un purvaiņos (IV un VII publikācija). Koku nobiras un zemsedzes veģetācija vērtēta 12 vecās priežu un egļu mežaudzēs kūdreņos un purvaiņos (V– VI publikācija). Ilgtermiņa meliorācijas ietekme uz organisko augšņu C uzkrājumu vērtēta modeļteritorijā, Meža pētīšanas stacijas Kalsnavas mežu novadā (Zālītis, 2012), kur augsnes C uzkrājums kūdreņos salīdzināts ar nemeliorētu (kontroles) teritoriju purvaiņos (III publikācija). Pirms meliorācijas sistēmu izveidošanas teritorija bija pārejas purvs. Mežaudžu vecums modeļteritorijā variē no 40 līdz 110 gadiem. Daļā modeļteritorijas 1960. gadā izveidota meliorācijas sistēma. Meliorējot niedrāju, meža tips visbiežāk mainās uz šaurlapju kūdreni (Bušs 1976).



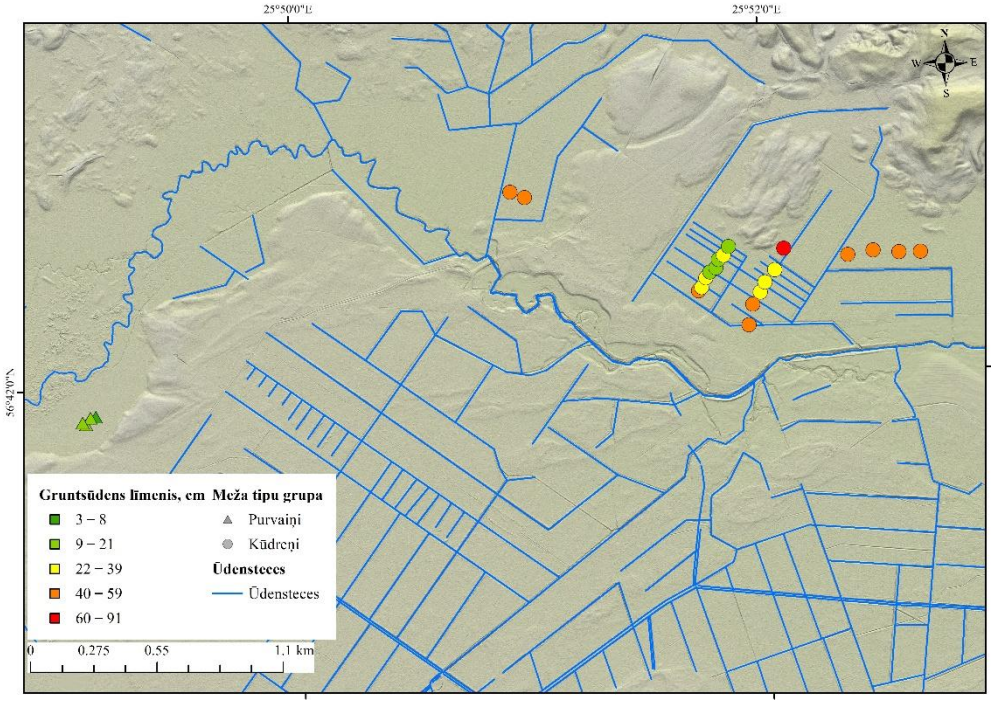
2.1. att. **Pētījuma objektu atrašanās vietas Latvijas teritorijā. Krāsa apzīmē valdošo koku sugu. Simbols apzīmē pētījumā iekļauto audžu grupu. Simbola melnā kontūra apzīmē vairākas vērtētās oglekļa krātuves vienā mežaudzē**

2.2. Datu ievākšana

Koku biomasas C uzkrājuma novērtējumam kopā izveidoti 133 parauglaukumi. Katrā audzē ierīkoti četri līdz seši apļveida parauglaukumi (R = 12.62 m, 500 m^2), atkarībā no audzes platības, kur katrā parauglaukumā visiem dzīvajiem kokiem uzmērīts caurmērs krūšaugstumā (DBH ≥ 6.1 cm) un noteikta koku suga. Koku augstums katrā parauglaukumā mērīts pieciem dzīviem pirmā stāva kokiem un trim otrā stāva kokiem, izveidojot augstumlīknes. Tajos pašos parauglaukumos izveidots mazāka rādiusa sektors (R = 5.64 m, 0°–90°, 25 m^2), kurā mērīts caurmērs dzīvajiem kokiem (2.1 ≤ DBH ≤ 6.0 cm; I publikācija).

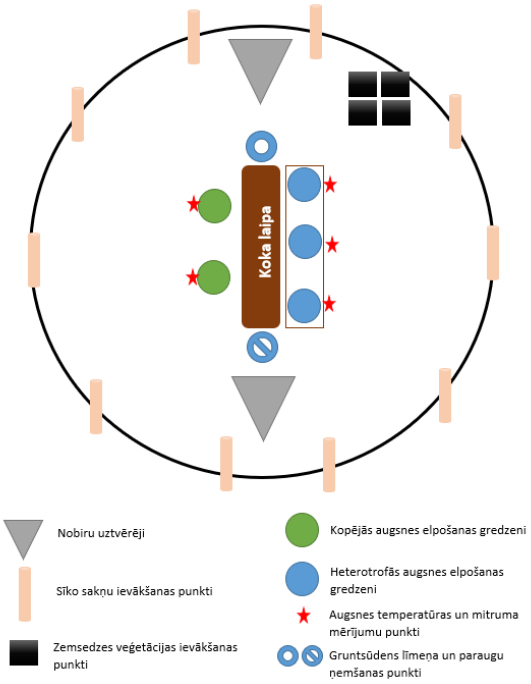
Atmirušās koksnes C uzkrājuma novērtējumam kopā izveidoti 317 parauglaukumi, kuros 12.62 m rādiusā uzmērīta visa atmirusī koksne ar caurmēru ≥ 14.1 cm, un 5.64 m rādiusā – ar caurmēru ≥ 6.1 cm. Atmirusī koksne iedalīta divās kategorijās: kritalas un sausokņi (ieskaitot arī stumbeņus). Kritalām uzmērīts kopējais garums un caurmērs abos galos. Sausokņiem caurmērs mērīts krūšaugstumā un augstums līdz galotnei vai lūzuma vietai (II publikācija). Atmirušās koksnes sadalīšanās pakāpe novērtēta vizuāli un ar "naža metodi", iedalot piecās sadalīšanās pakāpēs (Stokland 2001; Köster et al. 2015).

Modeļteritorijā 24 parauglaukumos vērtēts C uzkrājums augsnē (2.2. att.). Zemes virsmas augstums noteikts 20 parauglaukumos kūdreņos, izmantojot SEOP DS32 optisko nivelieri (Shanghai Sursup Precision Instrument Co., Ltd., Tianjin, China). Mērījumi atkārtoti 1960., 1966., 1970., 1972., 1975. un 2014. gadā. Katrā apsekošanā zemes virsmas augstuma mērījumi veikti konsekventi gar tiem pašiem meliorācijas grāvjiem. Augsnes paraugi ievākti 2014. gadā trīs atkārtojumos katrā parauglaukumā četros dziļuma intervālos: 0–10 cm, 10–20 cm, 20– 40 cm un 40–80 cm. Katra parauga tilpums 100 cm^3. Zemsedzes paraugi (augsnes O horizonts), kas sastāv no augu un dzīvnieku atliekām, ievākti trīs atkārtojumos, izmantojot 10 × 10 × 10 cm metāla kubu. Lai novērtētu augsnes sausu biomasu (kg m^{-3}) un oglekļa koncentrāciju (g C kg^{-1}), augsnes paraugi žāvēti krāsnī 105°C temperatūrā līdz konstantam svaram un pēc tam nosvērti. Izžāvētie paraugi izsijāti un samalti, izmantojot IKA A 11 analītiskās dzirnavas. Oglekļa saturs noteikts ar LECO CR analizatoru temperatūrā, kas pārsniedz 900°C (III publikācija).



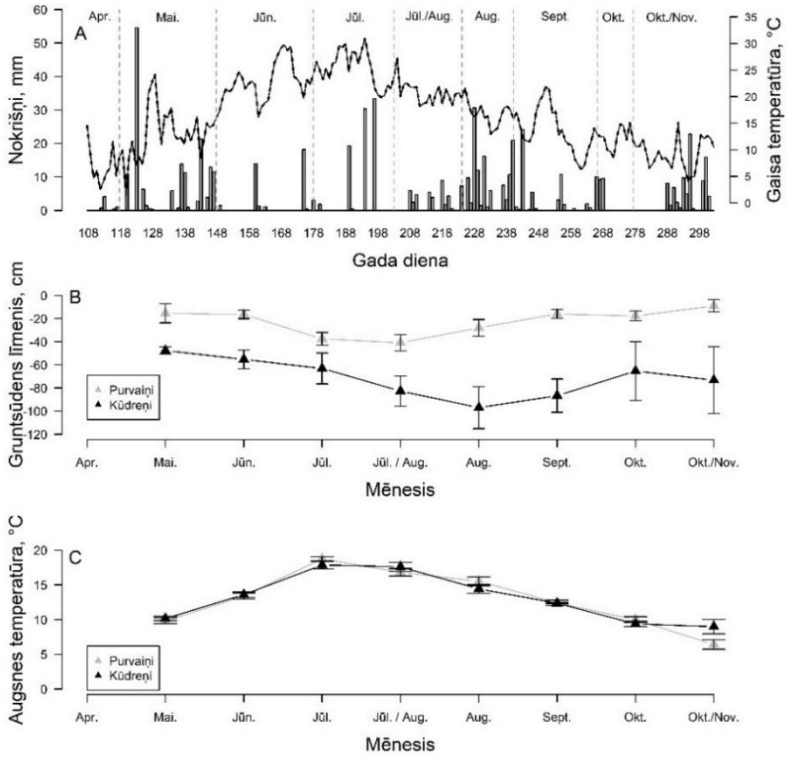
2.2. att. **Modeļteritorija Kalsnavas mežu novadā**

Koku nobiras, zemsedzes veģetācija, sīkās saknes un SEG emisijas vērtētas, ierīkojot katrā audzē trīs kompleksus parauglaukumus ($R = 12.62$ m, 500 m^2) mērījumu un paraugu ievākšanai (2.3. att.).



2.3. att. **Parauglaukuma shēma, kurā vērtētas SEG emisijas, nobiras, sīkās saknes un zemsedzes veģetācija**

SEG emisiju mērījumi veikti reizi trijās nedēļās bezsniega periodā no aprīļa līdz oktobrim. Vērtētās SEG ietvēra kopējo augsnes elpošanu ($RtCO_2$), heterotrofo elpošanu ($RhCO_2$) un metāna (CH_4) emisijas. Vienlaicīgi ar SEG emisiju mērījumiem mērīti dažādi vides parametri, piemēram, gruntsūdens līmenis, gaisa temperatūra, augsnes temperatūra (2.4. att.; IV publikācija).



2.4. att. **Nokrišņi (mm) un vidējā gaisa temperatūra gada dienās (A), vidējais gruntsūdens līmeņa dziļums (B) un augsnes temperatūra (C) siltumnīcefekta gāzu emisiju mērījumu laikā. Pelēkās pārtrauktās līnijas atdala mērījumu ciklus (A), vidējais gruntsūdens līmeņa dziļums (B) un augsnes temperatūra 10 cm dziļumā (C) 2021. gada mērījumu periodā purvaiņos un kūdreņos; ± 95% ticamības intervāls.**

Nobiru C uzkrājums vērtēts, katrā parauglaukumā 1.3 m augstumā virs zemes uzstādot divus apgriezta konusa formas nobiru uztvērējus ar 110 cm diametru augšdaļā. Katra uztvērēja apakšdaļā piestiprināts nobiru savākšanas maiss. Paraugi ievākti visa kalendārā gada laikā: pavasarī, vasarā un rudenī reizi trīs nedēļās, ziemas perioda nobiras ievāktas vienu reizi agrā pavasarī. Visi paraugi žāvēti 70°C temperatūrā līdz konstantam svaram un pēc tam nosvērti, lai iegūtu parauga sausas biomasas svaru (V publikācija).

Zemsedzes veģetācijas C uzkrājums vērtēts, katrā parauglaukumā vienu reizi sezonā ievācot zemsedzes veģetācijas biomasas paraugus, izveidojot 1 m^2 lielus laukumus, no kuriem ievākti četri $25 \times 25 \times 25$ cm ($0.0156\ m^3$) lieli paraugi. Katrs paraugs sadalīts divās daļās: virszemes un pazemes daļa. Virszemes biomasa sašķirota trīs funkcionālās grupās: lakstaugi, sīkkrūmi un sūnas. Pazemes paraugi klasificēti lakstaugu sakņu, sīkkrūmu sakņu un koku sakņu grupās. Sakņu klasifikācija veikta pēc caurmēra kritērijiem (caurmērs no 2–20 mm) saskaņā ar ICP Forest protokoliem (Cools et al. 2010). Šis izmēru diapazons specifiski izslēdza smalkās saknes (caurmērs < 2 mm), vienlaikus izvairoties no resnajām strukturālajām saknēm (caurmērs > 20 mm), tādējādi koncentrējoties uz vidējā izmēra sakņu klasi, kas reprezentē aktīvās barības vielu un ūdens uzņemšanas sistēmas. Visi ievāktie paraugi sistemātiski sašķiroti un žāvēti krāsnī 70°C temperatūrā līdz konstantam svaram un pēc tam nosvērti, lai noteiktu parauga sausu masu. Izžāvēto paraugu oglekļa saturs analizēts ar LECO CR analizatoru temperatūrā, kas pārsniedz 900°C (VI publikācija).

Sīko sakņu (FR) biomasas un veidošanās novērtēšanai izmantota secīgā augsnes urbšanas metode (Ostonen et al. 2005; Brunner et al. 2013). Paraugu ievākšana veikta 2021. gada maijā, augustā un oktobrī, kā arī 2022. gada martā. Katrā no sešām audzēm FR paraugi ievākti no trim apļveida parauglaukumiem. Katrā parauglaukumā nejauši izvēlētas vietās ar cilindrisku augsnes zondi (iekšējais diametrs 50 mm) ievākti 10 paraugi (monolīti) 40 cm dziļumā. Katrs

paraugs sadalīts 10 cm sekcijās (0–10, 10–20, 20–30, 30–40 cm). Visi FR paraugi šķiroti 4 frakcijās: priežu, egļu, sīkkrūmu un lakstaugu sīkās saknes, kopumā iegūstot 2880 FR paraugus. Sašķirotie paraugi žāvēti krāsnī 70°C temperatūrā līdz konstantam svaram un pēc tam nosvērti (VII publikācija).

2.3. Datu analīze

Uzmērītajiem parauglaukumiem aprēķināti mežaudžu taksācijas rādītāji: šķērslaukums, vidējais caurmērs un augstums, koksnes krāja, koku skaits uz hektāru, atmirušās koksnes apjoms. Koku biomasa aprēķināta, izmantojot lokāli izstrādātos koku biomasas vienādojumus saimnieciski nozīmīgākajām koku sugām (Liepiņš et al. 2018, 2021). Oglekļa uzkrājums koku biomasā aprēķināts, izmantojot lokāli izstrādātos oglekļa koncentrācijas koeficientus galvenajām koku sugām (Bārdule et al. 2021a). Atmirušās koksnes C uzkrājums aprēķināts, izmantojot C koncentrācijas koeficientus dažādām atmirušās koksnes sadalīšanās pakāpēm (Stokland 2001; Köster et al. 2015). Sīko sakņu veidošanās (FRP) un sīko sakņu aprites (FRT) aprēķins balstās uz sīko sakņu biomasas datiem (FRB). Ikgadējais FRP aprēķināts, izmantojot lēmumu matricu, iekļaujot tajā sīko sakņu biomasu un nekromasu no katra secīgā parauga (Fairley & Alexander 1985). Ikgadējais FRT aprēķināts, dalot kopējo FRP apjomu ar vidējo FRB (McClaugherty et al. 1982; Gill & Jackson 2000). Koku nobiru un sīko sakņu oglekļa uzkrājums aprēķināts, pieņemot, ka parauga sausās masas oglekļa koncentrācija ir 50%.

Augsnes C uzkrājums aprēķināts, izmantojot iegūto paraugu oglekļa satura un blīvuma rādītājus. Augsnes C uzkrājuma aprēķinos ņemta vērā kūdras sablīvēšanās. Kontroles (nemeliorētajos) parauglaukumos C uzkrājuma aprēķins vērtēts 0–80 cm dziļumā. Meliorētās mežaudzēs C uzkrājums aprēķināts 0–(80–x) cm slānim, kur "x" apzīmē kūdras sablīvēšanās dziļumu centimetros.

SEG emisijas aprēķinātas, izmantojot lineārās regresijas slīpuma koeficientu gāzu koncentrāciju izmaiņām laikā mērījumu kamerā. Mērījums atzīts par nederīgu, ja lineārās regresijas determinācijas koeficienta (R^2) vērtība bija zemāka par 0.8 ($p < 0.01$). Emisiju aprēķināšanai izmantotā lineārās regresijas slīpuma koeficienta (*slope*) noteikšanai izmantoti tikai tie mērījumi, kas atbilda kvalitātes kritērijiem.

$$flux = \frac{M \times P \times V \times slope}{R \times T \times A \times 1000}, \quad (1)$$

kur:
flux – augsnes SEG emisijas (mg GHG m^{-2} h^{-1});
M – SEG gāzes molmasa (g mol^{-1});
R – universālā gāzu konstante (m^3 Pa K^{-1} mol^{-1});
P – gaisa spiediens mērījumu kambarī (Pa);
T – gaisa temperatūra (K);
V – kambara tilpums (0.0094 m^3);
Slope – SEG koncentrācijas izmaiņu slīpuma koeficients kambarī;
A – mērījuma laukums (0.0314 m^2).

Atkarīgo mainīgo (koku biomasas, atmirušās koksnes, augsnes, zemsedzes veģetācijas, sīko sakņu un SEG emisiju) normālā sadalījuma novērtēšana veikta ar vienkāršotu pieeju, izmantojot Shapiro-Wilk testu. Lai nodrošinātu neparametrisko datu normālo sadalījumu, veikta logaritmiska transformācija. T-tests izmantots, lai salīdzinātu divu grupu vidējos rādītājus (kūdreņi pret purvaiņiem, priedes pret eglēm) mainīgajiem, kas atbilst normālajam sadalījumam, bet Mann Whitney – U tests mainīgajiem, kas neatbilst normālajam sadalījumam. Tukey HSD tests izmantots mainīgajiem, kas atbilst normālajam sadalījumam, lai novērtētu, vai vairākas grupas būtiski atšķiras viena no otras. Kruskal-Wallis tests izmantots datiem, kas

neatbilda normālajam sadalījumam, lai salīdzinātu vidējās vērtības starp vairākām grupām. Dispersijas analīze (ANOVA) izmantota, lai novērtētu tādu faktoru, kā valdošās koku sugas, šķērslaukuma, koksnes krājas, atmirušās koksnes ietekmi uz atkarīgo mainīgo – koku nobiru C uzkrājumu.

Lineārie jauktā efekta modeļi izmantoti, lai pārbaudītu audzes taksācijas rādītāju, augsnes un vides parametru saikni ar atkarīgajiem mainīgajiem (dažādu C krātuvju C uzkrājums, SEG emisijas). Sākotnēji visi pieejamie parametri tika iekļauti modelī kā fiksētie efekti, bet parauglaukums un mežaudzes ID izmantoti kā nejaušie efekti. Pēc tam, pamatojoties uz vispārināto variācijas inflācijas faktoru (GVIF), izslēgti savstarpēji korelējoši mainīgie, ja GVIF vērtība bija lielāka par 5. Labākais modelis tika izvēlēts, pamatojoties uz mazāko Akaike informācijas kritērija (AIC) vērtību. Modeļu fiksētie un nejaušie efekti tika novērtēti ar ANOVA tipa III Wald χ^2 testu. Datu analīze veikta ar statistikas programmu R (R Core Team 2025), izmantojot bibliotēkas lme4 (Bates et al. 2015), emmeans (Lenth 2025).

3. REZULTĀTI UN DISKUSIJA

3.1. Koku biomasas un atmirušās koksnes oglekļa uzkrājums (I, II un III publikācija)

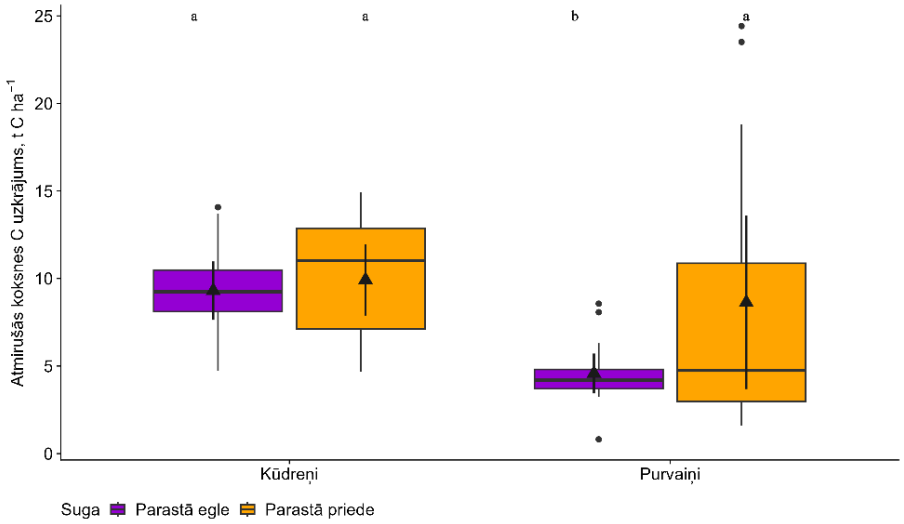
Klimata pārmaiņas un vidējās gaisa temperatūras paaugstināšanās ir raisījušas diskusijas par meliorācijas grāvju nepieciešamību un to lomu klimata pārmaiņu mazināšanā. Pētījumos hemiboreālajā un boreālajā reģionā pēc meliorācijas konstatēta uzlabota koku augšana un lielāks oglekļa uzkrājums koku biomasā (Skaggs et al. 2016; Jansone et al. 2020). Līdzīgi rezultāti iegūti arī šajā pētījumā – mežos ar organiskajām augsnēm Latvijā, meliorācija ilgtermiņā rezultējās ar uzlabotu koku augšanu (vidējais caurmērs, augstums un šķērslaukums) meliorētās mežaudzēs kūdreņos salīdzinājumā ar nemeliorētām mežaudzēm purvaiņos.

Vecās skuju koku mežaudzēs kūdreņos taksācijas rādītāji priežu un egļu mežaudzēs bija līdzīgi ($p > 0.05$). Uzmērītajos parauglaukumos novērota augsta koku biomasas C uzkrājuma heterogenitāte, kas variēja no 84 līdz 270 t C ha^{-1} vecās priežu mežaudzēs un no 103 līdz 237 t C ha^{-1} vecās egļu mežaudzēs. Augstā variācija norāda uz sasniegto koku biomasas C uzkrājuma maksimumu vecās mežaudzēs. Vecās priežu mežaudzēs kūdreņos vidējais C uzkrājums koku biomasā ir 167.0 ± 24.6 t C ha^{-1} (šeit un turpmāk norādītas vidējās vērtības ± 95% ticamības intervāls), turklāt līdzīgas vērtības (162.0 ± 25.0 t C ha^{-1}) novērotas arī vecās egļu mežaudzēs (I publikācija). Ievērojami zemāks koku biomasas C uzkrājums novērots vecās priežu mežaudzēs purvaiņos, sasniedzot no 61.1 līdz 81.3 t C ha^{-1}, vidēji 74.0 ± 20.6 t C ha^{-1} (IV publikācija). Savukārt vecās egļu mežaudzēs purvaiņos vidējais C uzkrājums koku biomasā sasniedza 121.1 ± 7.6 t C ha^{-1}. Meliorācijas ilgtermiņa ietekme uz koku biomasas C uzkrājumu rezultējās būtiskās atšķirībās ($p < 0.05$) starp meža tipu grupām, kur kūdreņos novērotas augstākas vērtības, salīdzinot ar purvaiņiem. Atšķirības koku biomasas C uzkrājumā starp kūdreņiem un purvaiņiem skaidrojamas ar gruntsūdens līmeni, kas purvaiņos tipiski ir augstāks, samazinot skābekļa pieejamību koku saknēm un tādējādi limitējot koku augšanu (Glenz et al. 2006; Sikström & Hökkä 2016). Iegūtie rezultāti kūdreņos ir līdzīgi kā vecās priežu (171.0 ± 6.1 t C ha^{-1}) un egļu (149.2 ± 18.9 t C ha^{-1}) mežaudzēs sausieņos hemiboreālajā reģionā, Latvijā (Ķēniņa et al. 2018, 2019).

Meža tipu grupai un koksnes krājai novērota būtiska ietekme uz C uzkrājumu ($p < 0.01$), taču audzes vecumam un valdošajai koku sugai nav novērota būtiska saikne ar koku biomasas C uzkrājumu vecās mežaudzēs.

Atmirušās koksnes daudzumu nosaka kompleksa mijiedarbība starp meža novecošanu, koku savstarpējo konkurenci, dabiskajiem traucējumiem un apsaimniekošanas ietekmi, turklāt tas nodrošina oglekļa uzkrājumu gaistošā C krātuvē, kas pakāpeniski sadalās (Mäkinen et al. 2006). Vidējais atmirušās koksnes C uzkrājums variēja no 4.6 līdz 9.7 t C ha^{-1} (3.1. att.; II publikācija). Zemākās vērtības novērotas egļu mežaudzēs purvaiņos (4.6 ± 1.1 t C ha^{-1}), kas bija būtiski ($p < 0.05$) mazākas nekā priežu mežaudzēs (7.9 ± 2.9 t C ha^{-1}) tādā pašā meža tipā. Kūdreņos C uzkrājums priežu mežaudzēs bija 9.7 ± 1.9 t C ha^{-1}, kas ir par 9% vairāk nekā egļu mežaudzēs (9.0 ± 1.6 t C ha^{-1}), taču atšķirības nav statistiski būtiskas ($p > 0.05$). Atmirušās koksnes C uzkrājumu būtiski ($p < 0.05$) ietekmēja audzes vidējais caurmērs, šķērslaukums un meža tipu grupa, turpretī audzes vecums, koku suga, augstums un skaits uz hektāru neuzrādīja būtisku saikni ($p > 0.05$).

Novērtētais atmirušās koksnes C uzkrājums vecās skuju koku mežaudzēs ir līdzīgs tam, kāds citos pētījumos novērtēts minerālaugsnē augošās vecās lapu koku mežaudzēs (6.7– 12.5 t C ha^{-1}; Šēnhofa et al. 2020, 2021) un organiskā augsnē augošās skuju koku mežaudzēs (7.0–11.2 t C ha^{-1}; Jonsson et al. 2016). Vienlaikus mūsu pētījumā konstatētais C uzkrājums atmirušā koksnē ir zemāks par to, kas novērtēts vecās egļu mežaudzēs Čehijā (13 t C ha^{-1}; Seedre et al. 2015) un pieaugušās egļu mežaudzēs Igaunijā (14.5–20.6 t C ha^{-1}; Rosenvald et al. 2025). Augstā atmirušās koksnes C uzkrājuma mainība starp vērtētajām mežaudzēm, parauglaukumiem un dažādiem pētījumiem norāda uz būtisku citu faktoru (piemēram, dabisko traucējumu) ietekmi uz atmirušās koksnes C uzkrājumu.



3.1. att. **Vidējais atmirušās koksnes oglekļa uzkrājums pa meža tipu grupām egļu un priežu mežaudzēs. Trijstūri apzīmē vidējās vērtības (± 95% ticamības intervāls), katram taisnstūrim attēlota mediāna, vērtību 25% un 75% procentiles un maksimālās un minimālās vērtības; dažādi burti norāda uz būtiskām ($p < 0.05$) atšķirībām**

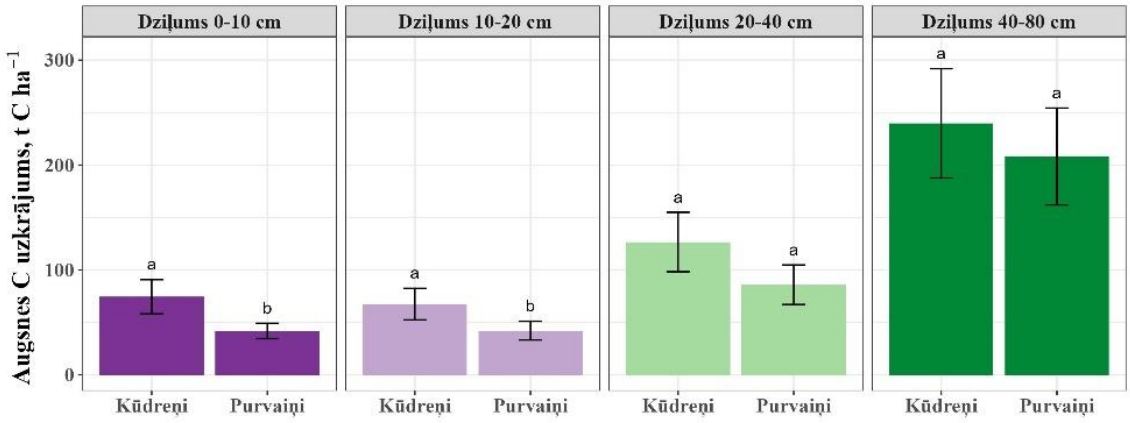
3.2. Organisko augšņu oglekļa uzkrājums un SEG emisijas (III un IV publikācija)

Augsnes sablīvēšanās ir tipiska parādība pēc kūdras augšņu meliorācijas (Lazdiņš et al. 2024). Ilgtermiņā augsnes vidējā sablīvēšanās meliorācijas ietekmē novērtēta no 22 līdz 25 cm Somijas boreālajā reģionā (Minkkinen & Laine 1998). Kalsnavas mežu novada modeļteritorijā laika posmā no 1960. gada līdz 2014. gadam zemes virsmas augstums samazinājās vidēji par 25.7 ± 3.5 cm salīdzinājumā ar sākotnējo augstumu. Visizteiktākā sablīvēšanās notika pirmajos desmit gados pēc meliorācijas, un turpmākajās desmitgadēs sablīvēšanās temps samazinājās (III publikācija).

Boreālajā reģionā organiskās meža augsnes satur vairāk oglekļa nekā koki (Gower et al. 1997), un šāda tendence novērota arī hemiboreālajā reģionā. Kopējais C uzkrājums augsnē bija 513.2 ± 49.7 t C ha^{-1} kūdreņos un 377.9 ± 126.5 t C ha^{-1} purvaiņos, taču atšķirības starp meža tipu grupām nebija statistiski būtiskas ($p > 0.05$; 3.1. tab.). Oglekļa uzkrājums vērtētajos virsējos (0–20 cm) augsnes slāņos norādīja uz būtiskām ($p < 0.05$) atšķirībām starp meliorētām un nemeliorētam augsnēm, taču dziļākajos slāņos (20–80 cm) atšķirības nav būtiskas ($p > 0.05$; 3.2. att.; III publikācija). Pēc meliorācijas augstāks oglekļa uzkrājums gan augsnē, gan koku biomasā ir konstatēts vairākos pētījumos, kas veikti hemiboreālajos un boreālajos reģionos (Minkkinen & Laine 1998; Lupikis & Lazdiņš 2017; Lazdiņš et al. 2024), kas iezīmē meža meliorācijas pozitīvo ietekmi uz C uzkrājumu.

3.1. tabula. **Oglekļa uzkrājums augsnē (vidējais, ± 95% ticamības intervāls)**

Oglekļa uzkrājums (t C ha^{-1})	**Kūdreņi**	**Purvaiņi**
O horizonts	5.1 ± 2.1	0
Augsnes dziļums 0–10 cm	74.4 ± 7.7	41.8 ± 11.6
Augsnes dziļums 10–20 cm	67.5 ± 7.0	42.1 ± 14.3
Augsnes dziļums 20–40 cm	126.6 ± 13.3	85.9 ± 30.0
Augsnes dziļums 40–80 cm	239.7 ± 24.4	208.1 ± 73.5
Kopā augsnē	513.2 ± 49.7	377.9 ± 126.5

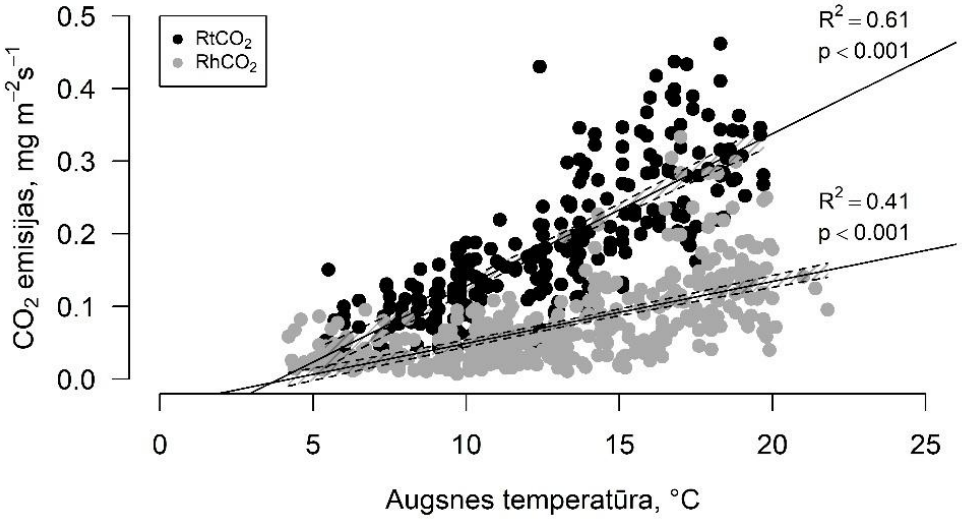


3.2. att. **Augsnes oglekļa uzkrājums dažādos dziļumos kūdreņos un purvaiņos. Atšķirīgi burti norāda uz būtiskām ($p < 0.05$) atšķirībām starp meža tipu grupām vērtētajā augsnes slānī**

Meliorācijas sistēmu ietekmē var mainīties augsnes siltumnīcefekta gāzu dinamika, gan pozitīvi, gan negatīvi ietekmējot emisijas un oglekļa piesaisti no augsnes (Strack & Waddington 2008; Butlers et al. 2025). Boreālajos mežos augsnes pēc meliorācijas parasti nodrošina neto oglekļa piesaisti (Minkkinen & Laine 1998; Lohila et al. 2011). Taču klimatiskie apstākļi un konkrētās vietas raksturojošie parametri ir galvenie faktori, kas nosaka, vai meliorētas organiskās augsnes darbojas kā emisiju avoti vai piesaistītāji (Butlers et al. 2025). Tāpēc ir svarīgi ņemt vērā šos faktorus un veikt konkrēto vietu raksturojošus mērījumus, lai precīzi novērtētu oglekļa dinamiku mainīgos vides apstākļos.

Oglekļa dioksīda plūsmai novērota sezonāla tendence, ar augstākiem emisiju rādītājiem vasaras sezonā un zemākiem pavasarī un rudenī. Vidējās $RtCO_2$ emisijas mērījumu sezonā bija 0.17 ± 0.01 mg m^{-2} s^{-1}, un tās bija līdzīgas kūdreņos (0.18 ± 0.018 mg m^{-2} s^{-1}) un purvaiņos (0.17 ± 0.015 mg m^{-2} s^{-1}). Savukārt $RhCO_2$ emisijas variēja no 0.007 līdz 0.33 mg m^{-2} s^{-1}, sezonas vidējās emisijas bija 0.07 ± 0.005 mg m^{-2} s^{-1}, un tās bija līdzīgas kūdreņos (0.08 ± 0.007 mg m^{-2} s^{-1}) un purvaiņos (0.07 ± 0.007 mg m^{-2} s^{-1}). Augsnes $RhCO_2$ emisijas veidoja 37–49% no kopējās augsnes CO_2 elpošanas, vidēji 41%. Līdzīgas $RhCO_2$ proporcijas (40–43%) ir novērotas apmežotos kūdrājos boreālajā reģionā (Berglund et al. 2011; Hermans et al. 2022).

Pētījumā konstatēta cieša un statistiski būtiska pozitīva saikne ($p < 0.001$) starp $RtCO_2$ plūsmu un augsnes temperatūru (T_soil). Determinācijas koeficients (R^2) bija 0.61 $RtCO_2$ un 0.41 $RhCO_2$ (3.3. att.), kas norāda uz ciešāku saikni kopējai augsnes elpošanai ($RtCO_2$) salīdzinājumā ar heterotrofo ($RhCO_2$) elpošanu. Lai gan parasti tiek prognozēts, ka augsnes CO_2 plūsmas samazināsies līdz ar gruntsūdens līmeņa paaugstināšanos (Von Arnold et al. 2005; Jungkunst et al. 2008), šajā pētījumā saikne bija būtiska, taču vāja ($R^2 = 0.06–0.08$), liecinot, ka citi faktori veido spēcīgāku ietekmi uz augsnes CO_2 emisijām (IV publikācija).

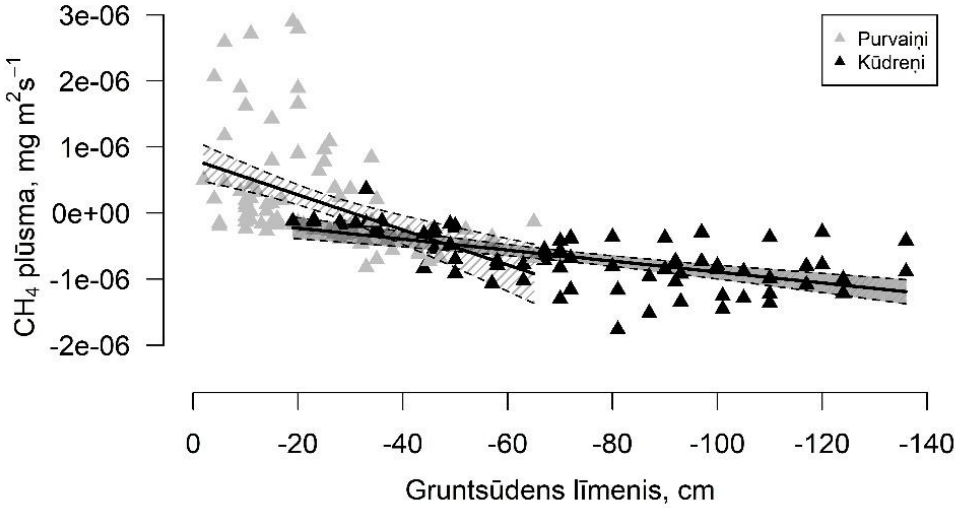


3.3. att. **Augsnes kopējās ($RtCO_2$) un heterotrofās ($RhCO_2$) elpošanas saikne ar augsnes temperatūru 10 cm dziļumā (°C). Pelēkais svītrotais laukums apzīmē ± 95% ticamības intervālu**

Augsnes CH_4 emisijas variēja no $-1.77 \cdot 10^{-6}$ līdz $2.90 \cdot 10^{-6}$ mg m^{-2} s^{-1}. Sezonas vidējās CH_4 emisijas bija $-3.67 \cdot 10^{-7} \pm 1.24 \cdot 10^{-6}$ mg m^{-2} s^{-1} kūdreņos un $8.81 \cdot 10^{-9} \pm 2.97 \cdot 10^{-6}$ mg m^{-2} s^{-1} purvaiņos, turklāt atšķirības bija statistiski būtiskas ($p < 0.001$).

Pētījumā konstatēta būtiska negatīva saikne ($R^2 = 0.39$, $p < 0.001$; 3.4. att.) starp $RtCH_4$ plūsmu un gruntsūdens līmeni. Augstāks gruntsūdens līmenis bija saistīts ar palielinātām CH_4 emisijām, savukārt zemāks gruntsūdens līmenis nodrošināja CH_4 piesaisti (IV publikācija).

Gruntsūdens līmeņa pazemināšana veicina skābekļa apjoma palielināšanos augsnes virsējos slāņos, tādējādi uzlabojot organisko vielu mineralizāciju, jo aerobā vidē sadalīšanās notiek ātrāk (Clymo 1984). Skābekļa pieejamība regulē arī CH_4 emisijas. Tādējādi, uzturot gruntsūdens līmeni 30–40 cm zem zemes virsmas, var samazināt CH_4 emisijas no augsnes (Elberling et al. 2011; Tong et al. 2022; Butlers et al. 2023) un vērtētās vecās priežu mežaudzes nodrošināja CH_4 piesaisti. Turpretī salīdzinoši augsts gruntsūdens līmenis (0–30 cm) un gandrīz piesātināti (anaerobi) augsnes apstākļi var veicināt CH_4 emisijas (Korkiakoski et al. 2019), un šāda sakarība ir novērota arī šajā pētījumā.



3.4. att. **Augsnes metāna (CH_4) plūsmas saikne ar gruntsūdens līmeni (cm) kūdreņos un purvaiņos. Pelēkais svītrotais laukums apzīmē ± 95% ticamības intervālu**

3.3. Zemsedzes veģetācijas, nobiru un sīko sakņu oglekļa uzkrājums (V, VI un VII publikācija)

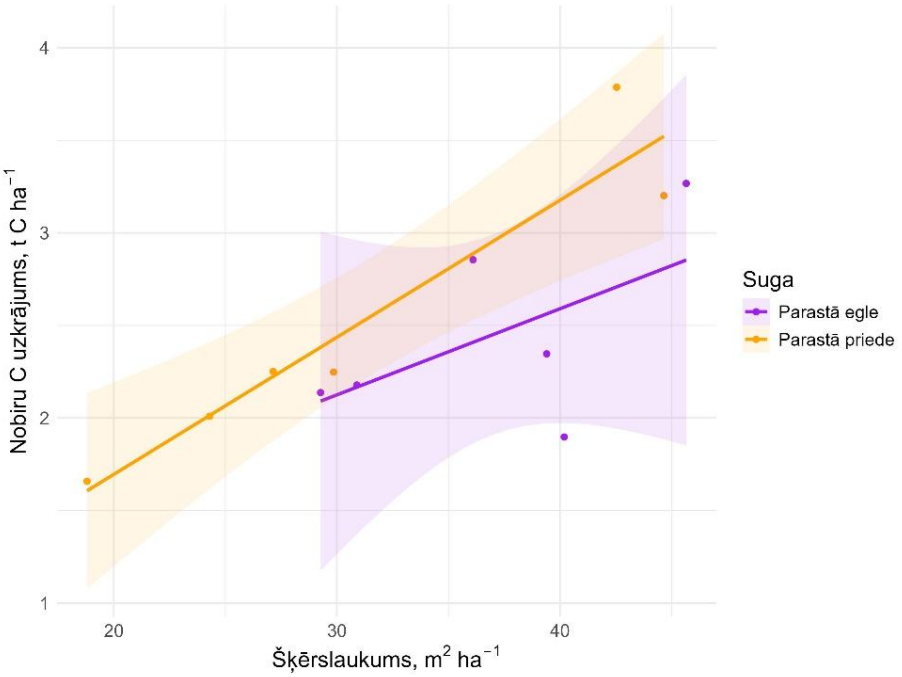
Koku nobiras ir nozīmīgs oglekļa un barības vielu avots augsnē, veidojot augsnes organiskos slāņus (Feng et al. 2019; Uri et al. 2022). Egļu audzēs nobiru oglekļa uzkrājums bija 2.53 ± 0.37 t C ha^{-1} g^{-1} kūdreņos un 2.37 ± 0.28 t C ha^{-1} g^{-1} purvaiņos. Priežu audzēs nobiru oglekļa uzkrājums bija 3.08 ± 0.45 t C ha^{-1} g^{-1} kūdreņos un 1.98 ± 0.28 t C ha^{-1} g^{-1} purvaiņos. Kopējais nobiru C uzkrājums kūdreņos un purvaiņos bija līdzīgs (3.2. tab.).

Ziemeļeiropas skuju koku mežos novērtēts, ka vidējais oglekļa daudzums, kas nonāk augsnē ar koku nobirām, ir 1.7 ± 1.1 t C ha^{-1} g^{-1} (Neumann et al. 2018). Igaunijā, hemiboreālajā reģionā, galvenajām mežsaimniecības koku sugām, kuru vecums variēja no 11 līdz 103 gadiem, ikgadējā nobiru dinamika bija no 0.06 līdz 3.37 t C ha^{-1} g^{-1} (Uri et al. 2022), kas atbilst šajā pētījumā novērtētajam nobiru apjomam. Salīdzinājumam, pētījumā Latvijā meliorētās organiskās augsnēs skuju koku jaunaudzēs un vidēja vecuma audzēs novērtētā oglekļa ienese augsnē no koku nobirām bija 1.82 ± 0.02 t C ha^{-1} g^{-1} (Bārdule et al. 2021b). Šajā pētījumā vecās skuju koku mežaudzēs novērots lielāks ikgadējais nobiru apjoms, un šādu atšķirību varētu izskaidrot ar papildu koku nobiru apjomu no otrā stāva kokiem (V publikācija).

3.2. tabula. **Koku nobiru biomasa un oglekļa uzkrājums vecās skuju koku mežaudzēs kūdreņos un purvaiņos**

Valdošā suga	Meža tipu grupa	Nobiru biomasa t C ha^{-1} g^{-1}	Nobiru C uzkrājums t C ha^{-1} g^{-1}
Parastā egle	Kūdreņi	5.1 ± 0.7	2.5 ± 0.4
	Purvaiņi	4.7 ± 0.6	2.4 ± 0.3
Parastā priede	Kūdreņi	6.2 ± 0.9	3.1 ± 0.5
	Purvaiņi	4.0 ± 0.4	2.0 ± 0.3

Vislielākā ietekme uz koku nobiru oglekļa uzkrājumu vecās skuju koku mežaudzēs bija audzes vidējam šķērslaukumam, neatkarīgi no meža tipu grupas ($p < 0.01$; 3.5. att.). Egļu audzēs modelis uzrādīja pozitīvu saikni starp koku nobiru C uzkrājumu un audzes šķērslaukumu ($R^2 = 0.31$). Priežu audzēs starp koku nobiru C uzkrājumu un audzes šķērslaukumu novērota vēl ciešāka pozitīva saikne ($R^2 = 0.9$; V publikācija). Audzes šķērslaukums tiek uzskatīts par tipisku neatkarīgo mainīgo koku nobiru daudzuma prognozēšanā, jo tas korelē ar audzes vainagu projekciju un skuju biomasu (Starr et al. 2005).

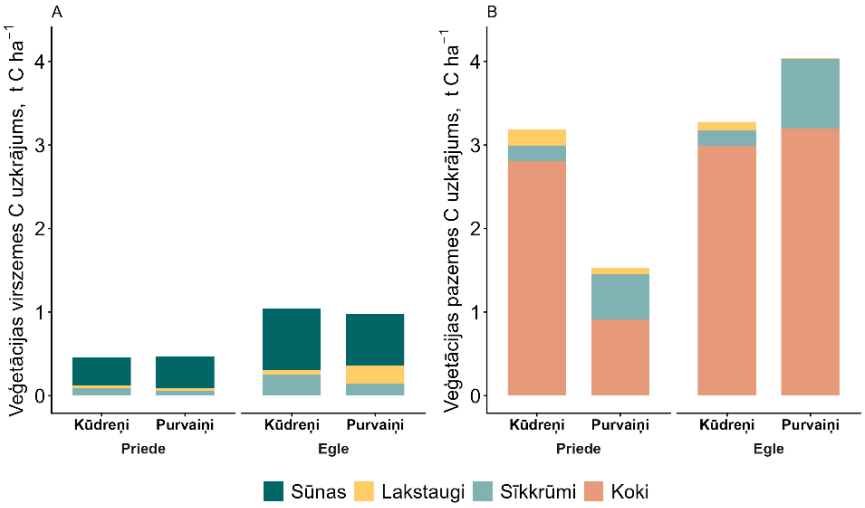


3.5. att. **Ikgadējais koku nobiru oglekļa uzkrājums vecās priežu un egļu mežaudzēs kūdreņos un purvaiņos atkarībā no audzes vidējā šķērslaukuma**

Zemsedzes veģetācijas biomasa ir atkarīga no gaismas pieejamības zem audzes vainagu klāja (Sigurdsson et al. 2005), un pēc pirmajām divām desmitgadēm tā vairs nav atkarīga no audzes vecuma (Peichl & Arain 2006).

Vecās priežu mežaudzēs zemsedzes veģetācijas virszemes daļas biomasas C uzkrājums bija 0.46 ± 0.32 t C ha^{-1} kūdreņos un 0.48 ± 0.43 t C ha^{-1} purvaiņos. Vecās egļu mežaudzēs zemsedzes veģetācijas virszemes daļas biomasas C uzkrājums bija 1.06 ± 0.74 t C ha^{-1} kūdreņos un 0.96 ± 0.78 t C ha^{-1} purvaiņos (3.6.A att.). Atšķirības ne starp meža tipu grupām, ne starp priežu un egļu audzēm nebija būtiskas ($p > 0.05$). Zemsedzes veģetācijas virszemes biomasas C uzkrājums atbilst boreālajā reģionā iepriekš novērtētajiem apjomiem (Ilvesniemi et al. 2009).

Vecās priežu mežaudzēs zemsedzes veģetācijas pazemes daļas biomasas C uzkrājums bija 3.19 ± 1.52 t C ha^{-1} kūdreņos un 1.52 ± 0.88 t C ha^{-1} purvaiņos. Vecās egļu mežaudzēs zemsedzes veģetācijas pazemes daļas biomasas C uzkrājums bija 3.27 ± 2.09 t C ha^{-1} kūdreņos un 4.04 ± 1.47 t C ha^{-1} purvaiņos (3.6.B att.). Statistiski būtiskas atšķirības ($p < 0.05$) konstatētas tikai starp pazemes biomasas C uzkrājumu priežu audzēs purvaiņos un pārējām vērtētajām grupām. Koku saknes (2–20 mm) visās mežaudzēs un meža tipu grupās veidoja lielāko daļu no zemsedzes veģetācijas pazemes daļas biomasas C uzkrājuma (VI publikācija).

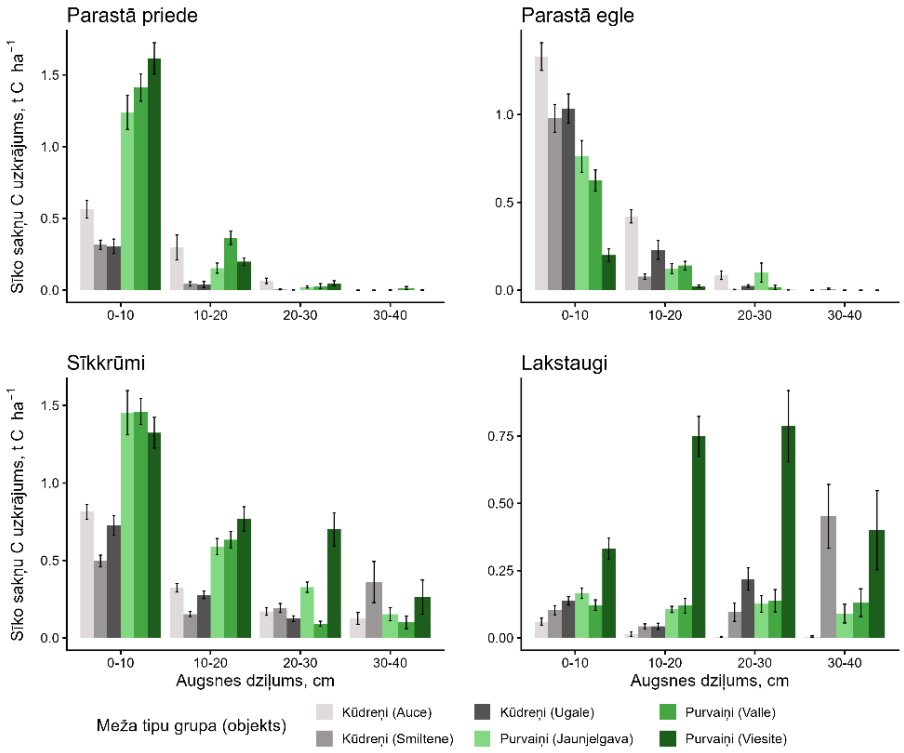


3.6. att. **Zemsedzes veģetācijas virszemes (A) un pazemes (B) biomasas oglekļa uzkrājums atkarībā no meža tipu grupas un valdošās koku sugas**

Vecās mežaudzēs kopumā purvaiņos bija būtiski lielāka sīko sakņu biomasa (FRB) salīdzinājumā ar kūdreņiem (attiecīgi, 3.4 un 2.0 t C ha^{-1}). Priežu FRB purvaiņos bija vairāk nekā trīs reizes lielāka nekā kūdreņos, norādot uz plašu barības vielu meklēšanas stratēģiju mitrākos, mazāk aerētos apstākļos. Novērotā tendence sakrīt ar novērojumiem boreālajos mežos, kur nemeliorētas mežaudzes priežu FRB biomasa bija lielāka (Lampela et al. 2023). Savukārt egļu FRB mūsu pētījumā lielāka bija kūdreņos, galvenokārt sugu sastāva un lielākas egļu krājas dēļ, kas novērots arī boreālajos mežos, kur egles parasti dominē meliorētās organiskās augsnēs (Finér & Laine 2000).

Abās meža tipu grupās lielākā daļa priežu, egļu un sīkkrūmu FRB bija koncentrēta organisko augšņu augšējā slānī (0–10 cm). Savukārt lakstaugu FRB bija augstāka dziļākos augsnes slāņos (20–40 cm), ar izteikti augstākām vērtībām atsevišķās mežaudzēs (3.7. att.), ko nosaka galvenokārt lakstaugu sastāvs, piemēram, grīšļi un graudzāles, kuri spēj uzturēt saknes anaerobos apstākļos, lai piekļūtu barības vielām dziļākos augsnes slāņos (Lampela et al. 2023). Sīkkrūmi veidoja lielāko FRB purvaiņos (2.4 t C ha^{-1}) un nozīmīgu FRB daļu arī kūdreņos (1.2 t C ha^{-1}). Tas norāda, ka lakstaugu un sīkkrūmu sīkās saknes ievērojami veicina oglekļa ienesi augsnē, kas ir uzsvērts arī pētījumos boreālajos mežos ar organiskām augsnēm (Bhuiyan et al. 2017).

Priežu FRB augsnes augšējā slānī (0–10 cm) purvaiņos un kūdreņos sastādīja, attiecīgi, 84% un 73%. Egļu FRB īpatsvars šajā slānī abās meža tipu grupās bija līdzīgs (~ 80%). Augšējā augsnes slānī purvaiņos un kūdreņos sīkkrūmu FRB sastādīja, attiecīgi, 54% un 51%, bet lakstaugu FRB – 19% un 21% (VII publikācija).



3.7. att. **Parastās priedes, parastās egles, sīkkrūmu un lakstaugu vidējās sīko sakņu biomasas vertikālais sadalījums organiskā augsnē līdz 40 cm dziļumam kūdreņos un purvaiņos**

Lai arī FRB atšķīrās starp meža tipu grupām, sīko sakņu veidošanās (FRP) bija līdzīga (*ca.* 1 t C ha^{-1} g^{-1}). Tas liecina, ka ikgadējā C ienese caur sīko sakņu veidošanos nav atkarīga no meliorācijas ietekmes, bet gan no audzes produktivitātes un konkrētās vietas raksturojošiem faktoriem, kas var izskaidrot arī novēroto variāciju starp pētījuma objektiem. Citi pētījumi boreālajā reģionā norāda, ka FRP ir cieši saistīta ar mežaudzes vecumu un augsnes auglību (Helmisaari et al. 2002; Yuan & Chen 2012).

Priežu sīko sakņu aprite (FRT) bija aptuveni divas reizes augstāka kūdreņos (0.61 g^{-1}) salīdzinājumā ar purvaiņiem (0.33 g^{-1}). Egļu sīko sakņu aprite kūdreņos un purvaiņos bija līdzīga. Tas norāda, ka, lai gan sīko sakņu biomasa kūdreņos ir zemāka, saknes tiek aizstātas ātrāk, paātrinot barības vielu un C apriti. Straujāka sīko sakņu aprite kūdreņos atbilst citu pētījumu rezultātiem, kas norāda, ka sīko sakņu aprite ir augstāka produktīvākās mežaudzēs (Kriiska et al. 2019). Uzlabota augsnes aerācija pēc meliorācijas sistēmu izveides, visticamāk, saīsina sīko sakņu dzīves ilgumu, un šāda tendence ir novērota arī citām sugām uzlabotos augšanas apstākļos (Förster et al. 2021).

SECINĀJUMI

Hidrotehniskā meliorācija ilgtermiņā (> 50 gadi) ievērojami palielina oglekļa uzkrājumu koku biomasā skuju koku mežos ar mezotrofām organiskām augsnēm, tādējādi sekmējot klimata pārmaiņu mazināšanu, kā arī būtiski palielina oglekļa uzkrājumu atmirušajā koksnē vecās egļu mežaudzēs, bet neietekmē vecās priežu mežaudzēs.

Augsne ilgtermiņā saglabājas kā stabila oglekļa krātuve, pēc hidrotehniskās meliorācijas mainoties zemes virsmas līmenim sablīvēšanās ietekmē, bet ne kopējam oglekļa uzkrājumam.

Hidrotehniskā meliorācija ilgtermiņā nodrošina no klimata pārmaiņu mazināšanas viedokļa vēlamu ietekmi uz siltumnīcefekta gāzu emisijām no augsnes. Kūdreņi nodrošina izteiktu metāna piesaisti, savukārt purvaiņi ir metāna emisiju avots. Metāna emisiju dinamika ir tieši saistīta ar gruntsūdens līmeni, norādot uz 30–40 cm dziļumu kā emisiju slieksni. Meliorācija neietekmē CO_2 emisijas, kas ir atkarīgas no augsnes temperatūras.

Zemsedzes veģetācijas biomasas un nobiru oglekļa uzkrājumi ir mazāki nekā citās oglekļa krātuvēs un līdzīgi gan kūdreņos, gan purvaiņos.

Hidrotehniskā meliorācija nodrošina straujāku sīko sakņu apriti, līdz ar to augstāku organiskā oglekļa ienesi augsnē, bet ne augstāku oglekļa uzkrājumu kopējā sīko sakņu biomasas komponentē.

REKOMENDĀCIJAS

Uzturēt un, kur iespējams, paplašināt hidrotehniskās meliorācijas sistēmas mežos ar mezotrofām organiskām augsnēm, veicinot šo teritoriju ieguldījumu klimata pārmaiņu mazināšanā.

Teritorijās, kur paredzēta gruntsūdens līmeņa kāpināšana, izmantot pašregulējošas sistēmas un nodrošināt, ka gruntsūdens līmenis nav augstāks par 30–40 cm no augsnes virskārtas, tādējādi novēršot papildus ilgtermiņa metāna emisijas. Veikt papildus pētījumus šādās teritorijās kritisko gruntsūdens līmeņa slieksni ietekmējošo faktoru noteikšanai.

Nodrošināt gruntsūdens līmeņa monitoringu faktiskā klimata pārmaiņu mazināšanas efekta noteikšanai mežos ar organiskām augsnēm.

Ierīkot demonstrācijas objektus ar brīvu reāllaika piekļuvi gruntsūdens līmeņa un emisiju mērījumiem, veicinot plašāku izpratni par hidrotehniskās meliorācijas ilgtermiņa ietekmi un iekļaujot šīs atziņas normatīvos aktos un oglekļa kredītu shēmās.

PATEICĪBAS

Autors pateicas darba vadītājiem, īpaši Ārim Jansonam, par pētījuma idejām, sniegtajiem padomiem un atbalstu promocijas darba izstrādes gaitā. Izsaku pateicību LVMI "Silava" kolēģiem, meža adaptācijas zinātniskajai grupai un līdzautoriem par palīdzību pētījuma datu ievākšanas un apstrādes procesā, ieteikumiem, uzmundrinājumu un, protams, arī konstruktīvo kritiku. Visbeidzot, es vēlos pateikties ģimenei, draugiem un radiniekiem par viņu atbalstu un iedrošinājumu visa studiju procesa gaitā.

1. INTRODUCTION

Forest ecosystems are significant global carbon cycle elements, functioning as both major carbon stores and dynamic regulators through their roles in carbon sequestration and greenhouse gas exchange between the biosphere and atmosphere (Pan et al. 2011; Friedlingstein et al. 2022). In recent decades, the role of forests in climate change mitigation and biodiversity conservation has been increasingly emphasized in international and regional policy frameworks (FAO 2020; IPCC 2021). The European Union has set objectives to mitigate and adapt to climate change, and to reach and maintain climate neutrality by 2050 and beyond (Fetting 2020; Erback 2021). Quantifying forest carbon pools at regional and national scales is essential for developing scientifically sound management and policy strategies, thereby enhancing the reliability of carbon accounting, supporting adaptive forest management, and advancing resilience, biodiversity, and climate objectives.

The hemiboreal region of Northern Europe, including Latvia, Estonia, southern Sweden, and parts of Finland, represents a transitional zone between boreal coniferous and temperate deciduous forests (Ahti et al. 1968). Latvia has the highest forest cover in the Baltic region, meanwhile providing significant amounts of timber resources, and the demand is projected to increase in the future. Forests cover 53% of Latvia's terrestrial area. Norway spruce and Scots pine are the main species for commercial forestry, together accounting for 45% of the forested area (NFI 2023). The interaction of maritime climate, post-glacial terrain, and high soil moisture has led to extensive formation of organic soils and peatlands. In Latvia, 23% of forests are growing on organic soils (NFI 2023).

Carbon in forest ecosystems is distributed across several interconnected pools that together determine the total carbon balance and the forest's role as a carbon sink or source. The main carbon pools in forest ecosystems are living tree biomass (above- and below-ground), deadwood (standing and lying), litter, ground vegetation biomass, and soil (especially organic soil), and each function on different temporal and spatial scales within the carbon cycle. Tree biomass represents the most dynamic carbon pool, shaped by stand age, productivity, management, and species composition. Deadwood is a transitional carbon reservoir, gradually releasing carbon through decomposition while supporting biodiversity goals and long-term organic matter accumulation. The litter layer formed by fallen needles, leaves, and twigs provides a continuous source of organic input to the soil, maintaining nutrient cycling and microbial activity. The soil carbon pool, especially in organic soils, is the largest and most stable carbon pool, often surpassing aboveground carbon stocks. Fine roots and ground vegetation contribute to belowground carbon accumulation through their continuous turnover, supporting the formation of soil organic matter and contributing to long-term carbon storage.

Between 1960 and 1980, extensive forest drainage initiatives were undertaken in the Baltic states to enhance tree growth and increase the productivity of forests in areas with water-table levels naturally close to the soil surface (Paavilainen & Päivänen 1995; Šņore 2004). This has resulted in approximately 52% of forests growing on organic soils in Latvia being drained (NFI 2023). The drainage systems need periodic cleaning and maintenance to ensure the drainage function and the desired tree growth rates (Nieminen et al. 2018; Bičkovskis et al. 2025). In the past decade, practically no new drainage systems have been established in Latvia; management efforts have focused either on maintaining and restoring existing systems or, in contrast, on the closure of drainage ditches to promote wetland restoration.

Organic soils can be a substantial source of greenhouse gas (GHG) emissions compared to mineral soils; therefore, quantifying the emission rate from drained and undrained organic soils is essential for accurate carbon balance assessments in the region. Drainage of organic soils can enhance aerobic decomposition of organic matter, leading to increased CO_2 emissions (Von Arnold et al. 2005; Wüst-Galley et al. 2016). In undrained forests, a high-water table level generally suppresses CO_2 efflux due to limited oxygen availability but promotes CH_4 emissions under anaerobic conditions (Matthews & Fung 1987). In contrast, low water-table levels

typically promote CH_4 uptake as methanotrophic activity increases in aerated soil layers (Le Mer & Roger 2001).

In Latvia, the area of overmature (including old-growth) forest stands shows a gradual increasing trend (NFI 2023), whereas across much of Europe, such forests are in decline (O'Brien et al. 2021). Old-growth forest stands can play a crucial role in maintaining biodiversity at the landscape scale and in mitigating climate change; therefore, it is essential to quantify the size of different carbon pools within these ecosystems and to assess the influence of drainage on total carbon stock. Previous studies of old-growth forest stands in Latvia have primarily focused on sites with mineral soils, emphasizing tree biomass and deadwood carbon pools for the region's dominant coniferous tree species (Ķēniņa et al. 2018, 2019). In contrast, research on forests on organic soils has mainly focused on individual carbon pools (Bičkovskis et al. 2023) and GHG emission assessments in forest stands at various stages of development (Butlers 2023), but not in stands that have exceeded the harvest age. Therefore, an assessment of the most significant carbon pools and fluxes in old-growth forests in hemiboreal Latvia under the long-term impact of drainage is necessary to fill the knowledge gaps and to provide robust baseline data for sustainable forestry and climate policy planning.

1.1. Aim of the study

The aim of the doctoral thesis is to assess the impact of forest drainage on soil greenhouse gas emissions and the dynamics of carbon stock in the main carbon pools in old-growth forest stands with mesotrophic organic soils.

1.2. Study objectives

To achieve the aim, the following tasks have been set:

1. To assess the effect of drainage on carbon stock in tree biomass and deadwood.
2. To characterize the effect of drainage on soil carbon stock and greenhouse gas (GHG) emissions.
3. To evaluate the effect of drainage on carbon stock in ground vegetation, fine roots, and litter.

1.3. Thesis statements

In hemiboreal coniferous forests with mesotrophic organic soils, forest drainage increases tree biomass carbon stock in the long-term, has no negative effect on soil carbon storage, and reduces methane emissions.

1.4. Scientific novelty

For the first time in European hemiboreal forests, the long-term impact of forest drainage on the main forest carbon pools of coniferous old-growth forest stands (122 to 218 years old) has been estimated and quantified in drained and undrained forests on organic soils. The study provides insights into the stability of hemiboreal old-growth forest ecosystems and fills the knowledge gap on the long-term impact of organic soil drainage on carbon storage in diverse carbon pools.

2. MATERIALS AND METHODS

2.1. Study objects

The main study object is old-growth coniferous forest stands on organic soils in the hemiboreal region of Latvia (Fig. 2.1; Ahti et al. 1968). To assess tree biomass, deadwood, litter, ground vegetation, and fine-root carbon stock and soil GHG emissions, forest stands with drained and undrained organic soils were selected, with no signs of recent human activity, where stand age is at least two age classes above the cutting age (spruce > 120 years, pine > 140 years), and the basal area of the dominant tree species exceeds 50% of the stands basal area, based on stratified stand selection from the State Forest Service database. Forest type corresponds to *Myrtillosa turf. mel.* (hereafter referred as Drained organic) and *Caricoso-phragmitosa* (hereafter referred as Undrained organic) based on the local classification system. Draining *Caricoso-phragmitosa* typically leads to *Myrtillosa turf. mel.* forest type (Bušs 1976). Tree biomass carbon (C) stock was assessed in 23 pine and spruce-dominated old-growth (131 to 179 years old) forest stands on drained and undrained organic soils (Paper I). Deadwood C stock was assessed in 52 pine and spruce-dominated old-growth (122 to 218 years old) forest stands on drained and undrained organic soils (Paper II). GHG fluxes and fine-roots were assessed in six pine-dominated old-growth forest stands on drained and undrained organic soils (Papers IV and VII). Tree litter and ground vegetation were estimated from twelve pine and spruce-dominated old-growth forest stands on drained and undrained organic soils (Papers V– VI). The long-term effect of drainage on organic soil C stock was assessed in a model territory at the Forest Research Station in the Kalsnava Forest District (Zālītis, 2012), where soil C stock in drained organic soils was compared to undrained organic soils (Paper III). The model territory prior to drainage was a transitional mire. A drainage system was established in part of the study area in the 1960s. Forest stand age in the model territory ranged from 40 to 110 years.

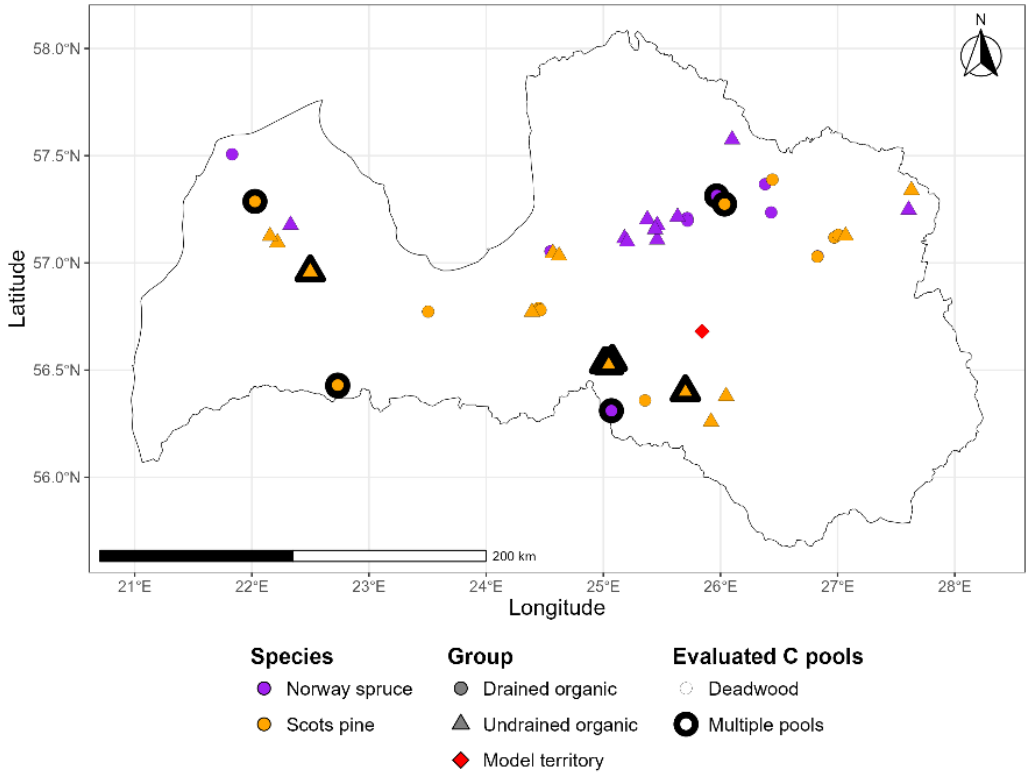


Fig. 2.1. **Study objects across the territory of Latvia. The colour represents dominant tree species. The symbol represents study object group. The black outline on symbols represents multiple C pools evaluated within a single forest stand**

2.2. Data collection

In total, 133 sample plots were established to estimate tree biomass C stock. In each forest stand, four to six circular sample plots were established ($R = 12.62$ m, 500 m^2), depending on the stand area, where in each sample plot, measurements of tree diameter at breast height (DBH) were performed and tree species recorded. Tree height was measured for five living I-layer trees and for three II-layer trees in each sample plot, which were used to construct height curves. In the same sample plot, a smaller sub-plot sector was established ($R = 5.64$ m, 0°–90°, 25 m^2) where the diameter of living trees was measured ($2.1 \leq \text{DBH} \leq 6.0$ cm; Paper I).

Deadwood C stock was estimated in 317 sample plots, where within $R = 12.62$ m, all deadwood with DBH ≥ 14.1 cm, and within $R = 5.64$ m, deadwood with DBH ≥ 6.1 cm was measured. Recorded deadwood types included downed logs and standing dead trees. For lying deadwood, the diameter was measured at both ends, and the total length was recorded. Standing dead trees were measured at breast height, with height recorded up to the top or breakage point (Paper II). Decay class was assessed visually and with the 'knife method,' categorized into five decay classes (Stokland 2001; Köster et al. 2015).

Soil C stock was estimated in 24 sample plots in model territory (Fig. 2.2). Peat subsidence was estimated in 20 sample plots in drained organic soils by measuring ground surface elevation using a SEOP DS32 optical level (Shanghai Sursup Precision Instrument Co., Ltd., Tianjin, China). Measurements were repeatedly taken in 1960, 1966, 1970, 1972, 1975, and 2014. Each survey consistently measured elevation along the same drainage ditches. Soil samples were collected in 2014 in tree replications at each sample plot ($R = 12.62$ m, 500 m^2) at four depth intervals: 0–10 cm, 10–20 cm, 20–40 cm, and 40–80 cm. Each soil sample's volume was 100 cm³. Litter (organic (O horizon) layer consisting of undecomposed, fresh and/or decayed plant or animal debris) samples were also collected in triplicate at the same locations, using 10 × 10 × 10 cm metal boxes. To determine soil dry bulk density (kg m³) and carbon content (g C kg^{-1}), soil samples were oven-dried at 105°C until they reached a constant mass and were weighed afterwards. Dried soil samples were sieved and ground using an IKA A 11 analytical mill. Carbon content was analyzed with a LECO CR analyzer at temperatures exceeding 900°C (Paper III).

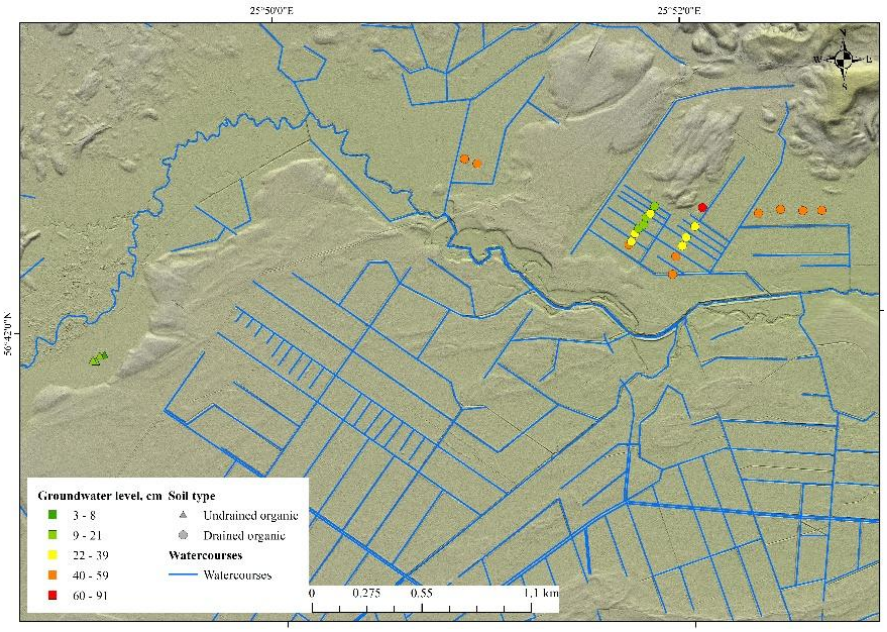


Fig. 2.2. **Model territory in Kalsnava Forest District**

Litter, ground vegetation, fine roots, and GHG emissions were estimated by establishing three complex sample plots ($R = 12.62$ m, 500 m^2) in each stand for measurements and sample collection (Fig. 2.3).

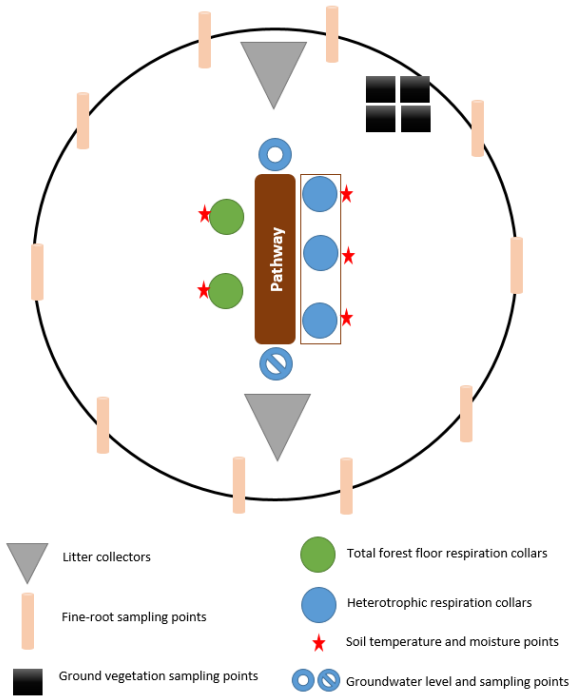


Fig. 2.3. **Sample plot scheme in which GHG emissions, litter, fine-root, and ground vegetation have been evaluated**

GHG emission measurements were performed every three weeks in the snow-free period from April to October. Evaluated fluxes included total forest floor respiration ($RtCO_2$), heterotrophic respiration ($RhCO_2$), and CH_4 flux. Simultaneously with flux measurements, environmental parameters were measured, such as groundwater level, air temperature, and soil temperature (Fig. 2.4; Paper IV).

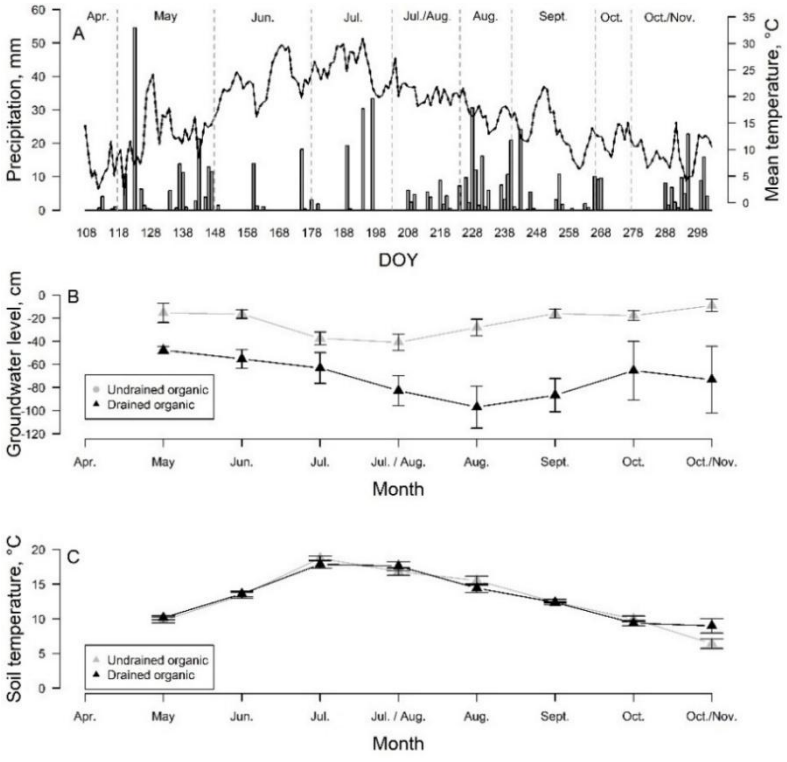


Fig. 2.4. **Precipitation and the mean air temperature per day of year (A); groundwater level (B), and soil temperature (C), during the greenhouse gas emission measurement**

campaign. The grey dashed lines separate measurement cycles (A), the mean groundwater level depth (B), and soil temperature at 10 cm depth (C), during the measurement period

Litter C stock was estimated by installing two inverted cone-shaped litter collectors 1.3 m above the ground level, each with a top diameter of 110 cm. A litter bag was attached to the bottom of each collector to capture all aboveground tree litter. Samples were collected throughout the calendar year, every three weeks during spring, summer, and autumn. Winter litter was collected once in early spring and combined with the spring samples. All samples were dried at 70°C until they reached a constant mass, then weighed (Paper V).

Ground vegetation C stock was estimated from collected samples in each sample plot sampling squares (area = 1 m^2) with four $25 \times 25 \times 25$ cm (0.0156 m^3) ground vegetation biomass samples extracted. Each collected sample was separated into aboveground and belowground biomass components. Aboveground biomass was sorted into three functional groups: herbaceous vegetation, dwarf shrubs, and bryophytes. Belowground samples were sorted into four functional groups: herbaceous roots, dwarf shrub roots, and tree root components. Root classification followed diameter-based criteria (diameter from 2 mm to 20 mm) according to ICP Forest protocols (Cools et al. 2010). This size range specifically excluded fine roots (< 2 mm diameter) while avoiding coarse structural roots (> 20 mm diameter), thereby focusing on the intermediate root size class representative of active nutrient and water uptake systems. All collected samples were systematically fractionated and oven-dried at 70°C until achieving constant mass, then weighed to determine the dry mass of the sample. The carbon content of the dried sample was analyzed using a LECO CR analyzer at a temperature exceeding 900°C (Paper VI).

Fine-root (FR) biomass and production were estimated with the sequential soil coring method (Ostonen et al. 2005; Brunner et al. 2013). Sampling was conducted in May, August, and October 2021, and in March 2022. From each plot, 10 soil cores (monoliths) were randomly extracted using a cylindrical soil corer (inner diameter 50 mm) to a depth of 40 cm. Each core was sectioned into 10 cm intervals (0–10, 10–20, 20–30, and 30–40 cm). All FR samples (< 2 mm diameter) were sorted into 4 groups: pine, spruce, shrub, and herbaceous plant fine-roots, acquiring a total of 2,880 FR samples. Sorted samples were oven-dried at 70°C until achieving constant mass and were weighed (Paper VII).

2.3. Data analysis

Forest stand parameters were calculated from the measured sample plots: basal area, mean diameter and height, growing stock, number of trees per hectare, and volume of deadwood. Individual tree biomass was estimated according to local biomass models (Liepiņš et al. 2017, 2021). The C stock of living trees was estimated based on locally developed C concentration coefficients for main tree species (Bārdule et al. 2021a). Deadwood C stock was estimated based on tree decay class C concentration coefficients (Köster et al. 2015). The calculation of fine-root production (FRP) and fine-root turnover (FRT) is based on fine-root biomass data (FRB). Annual FRP is calculated using a decision matrix, including fine-root biomass and necromass from each consecutive sample (Fairley & Alexander 1985). Annual FRT is calculated by dividing the annual FRP by the average FRB (McClaugherty et al. 1982, Gill & Jackson 2000). Ground vegetation C stock was estimated based on the actual C content. The C stock of aboveground litter and fine-roots was calculated assuming that the C concentration of the sample's dry mass is 50%.

The soil C stock was calculated using the obtained sample C content and density values. In soil C stock estimates, peat subsidence was accounted for. At control sites, C stock was based on soil 0–80 cm depth. At drained sites, it was calculated for the 0–(80–x) cm layer, where "x" represents the subsidence depth in centimetres.

GHG fluxes were estimated by calculating the linear regression slope of gas concentration changes with time in the chamber. Measurements were excluded if the regression coefficient of determination (R^2) was below 0.8 ($p < 0.01$). Only measurements that met the quality criteria were included in the flux calculation.

$$flux = \frac{M \times P \times V \times slope}{R \times T \times A \times 1000} \quad , \qquad (1)$$

where:
flux – the soil GHG flux (mg GHG m^{-2} h^{-1});
M – the molar mass of GHG (g mol^{-1});
R – a universal gas constant (m^3 Pa K^{-1} mol^{-1});
P – the air pressure inside the chamber (Pa);
T – air temperature (K);
V – chamber volume (0.0094 m^3);
Slope – linear regression slope coefficient of the GHG concentration changes inside the chamber;
A – collar area (0.0314 m^2).

A simplified approach applying the Shapiro-Wilk test was used to assess the normality of dependent variables (tree biomass, deadwood, soil, ground vegetation, litter, fine root C stock, and GHGs). Logarithmic transformation was performed to meet the normal distribution for non-parametric data. The t-test was used to compare two group means (drained vs undrained, pine vs spruce-dominated) for normally distributed variables, the Mann-Whitney U test for non-parametric variables. Tukey's HSD test was used for normally distributed variables to evaluate which groups differed significantly from one another. The Kruskal-Wallis test was used for data that did not meet normality assumptions to compare the mean values between groups.

Analysis of variance (ANOVA) was used to test the effect of dominant tree species, basal area, growing stock, and deadwood volume on the dependent variable – tree litter C stock.

Linear mixed effect models were used to test the stand, soil, and environmental parameter relationship with dependent variables (C stock of various pools, GHGs). Initially, all available parameters were included in the model as fixed effects, and the sample plot and stand ID were used as random effects. Subsequently, covarying variables were excluded based on the generalized variance inflation factor (GVIF) if the GVIF value was larger than 5. The best model was selected based on the smallest Akaike information criterion (AIC) value. Fixed and random effects of the models were evaluated with the ANOVA type III Wald χ^2 test. All data analyses were performed in the statistical software R (R Core Team 2025), using libraries lme4 (Bates et al. 2015) and emmeans (Lenth 2025).

3. RESULTS AND DISCUSSION

3.1. Tree biomass and deadwood carbon stock (Papers I, II, III)

Under increasing climate variability and the general increase in mean air temperature, has resulted in heated debates on the necessity of the drainage system and its role in climate change mitigation. Improved tree growth and consequently increased carbon stock in tree biomass following drainage have been reported in hemiboreal and boreal regions (Skaggs et al. 2016; Jansone et al. 2020). Similar results were also observed in this study – in old-growth forest stands on organic soils in Latvia, the long-term effect of drainage resulted in higher tree dimensions (DBH, tree height, and basal area) at the drained sites compared to undrained.

In old-growth forest stands, tree biomass C stock resulted in non-significant differences between pine and spruce-dominated stands on drained forests on organic soils ($p > 0.05$). Substantial spatial heterogeneity in tree biomass C stocks was evident across sample plots, ranging from 84 to 270 t C ha^{-1} in pine-dominated ecosystems and 103 to 237 t C ha^{-1} in spruce-dominated stands. The high variation indicates that the maximum C storage in tree biomass has been reached in old-growth forest stands. Tree biomass carbon stocks averaged 167.0 ± 24.6 t C ha^{-1} (mean ± 95% confidence interval) in pine-dominated old-growth stands, with comparable values (162.0 ± 25.0 t C ha^{-1}) observed in spruce-dominated stands (Paper I). Substantially lower tree biomass C stock was observed in pine-dominated old-growth forests on undrained organic soils, ranging from 61.1 to 81.3 t C ha^{-1}, averaging 74.0 ± 20.6 t C ha^{-1} (Paper IV). In old-growth spruce-dominated stands, the average tree biomass C stock reached 121.1 ± 7.6 t C ha^{-1}. The effect of long-term drainage on tree biomass C stocks resulted in significant differences ($p < 0.05$) across soil types, with drained sites exhibiting higher values compared to undrained sites. The differences in evaluated parameters can be explained by the water table level, which was higher at the undrained sites, reducing oxygen availability to tree roots and thereby constraining tree growth (Glenz et al. 2006; Sikström & Hökkä 2016). The obtained biomass C stock in drained organic soils is similar to that from old-growth Scots pine stands (171.0 ± 6.1 t C ha^{-1}) and Norway spruce stands (149.2 ± 18.9 t C ha^{-1}) on dry mineral soils in hemiboreal Latvia (Ķēniņa et al. 2018, 2019).

Soil type and growing stock exhibited a highly significant effect on tree biomass C stocks across both pine and spruce-dominated old-growth forest stands ($p < 0.01$). Conversely, stand age and dominant species composition showed no significant relationship with tree biomass C stock.

The amount of deadwood is a complex interplay between forest aging, competition between trees, past disturbance or management, which can store a large amount of C in a gradually fading C pool as a result of decomposition (Mäkinen et al. 2006). Mean deadwood carbon stocks ranged from 4.6 to 9.7 t C ha^{-1} across study sites (Fig. 3.1; Paper II). The lowest values were found in Norway spruce stands on undrained organic soils (4.6 ± 1.1 t C ha^{-1}), significantly lower ($p < 0.05$) than in Scots pine stands (7.9 ± 2.9 t C ha^{-1}) on the same soil type. For drained organic soils, Scots pine averaged 9.7 ± 1.9 t C ha^{-1}, which is by 9% more than in Norway spruce stands (9.0 ± 1.6 t C ha^{-1}); however, these differences between species on drained organic soils were not statistically significant ($p > 0.05$). Deadwood C stock was significantly ($p < 0.05$) influenced by mean stand DBH, stand basal area, and soil type, while mean stand age, tree species, height, and tree count per hectare were insignificant ($p > 0.05$).

The estimated deadwood C stock in old-growth coniferous forests in this study is comparable to that reported in other studies in old-growth deciduous forest stands on mineral soils (6.7–12.5 t C ha^{-1}; Šēnhofa et al. 2020, 2021) and for coniferous forest stands on organic soils (7.0–11.2 t C ha^{-1}; Jonsson et al. 2016). However, it is lower than the values reported for overmature Norway spruce stands in the Czech Republic (13.0 t C ha^{-1}; Seedre et al. 2015) and mature spruce forest in Estonia (14.5 to 20.6 t C ha^{-1}; Rosenvald et al. 2025). The observed high

variability of deadwood C stock between study sites, sample plots, and other studies indicates a strong influence of other factors (e.g., past disturbances) on deadwood C stock.

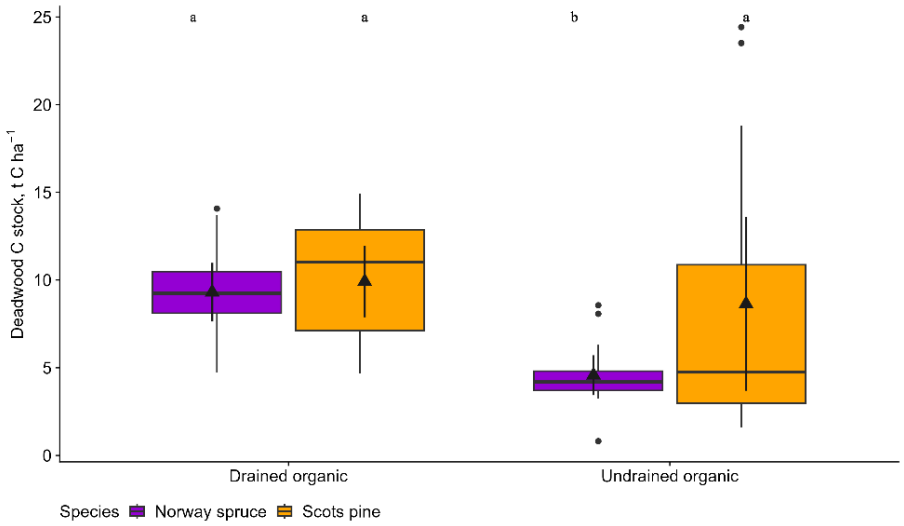


Fig. 3.1. **Mean deadwood carbon stock by soil type in spruce and pine stands. Triangles indicate mean values ± 95% confidence intervals; the box plots represent median values and the 25% and 75% percentiles, and the maximum and minimum values; different letters indicate significant ($p < 0.05$) differences**

3.2. Organic soil carbon stock and GHG emissions (Papers III, IV)

Soil subsidence is a common effect following drainage on organic soils (Lazdiņš et al. 2024). In the long-term, mean soil subsidence following drainage has been reported to be in the range from 22 to 25 cm in the boreal region of Finland (Minkkinen & Laine 1998). In the Kalsnava Forest District model territory, between 1974 and 2014, the observed total reduction in soil surface level was 25.7 ± 3.5 cm relative to the initial elevation. The most pronounced subsidence occurred within the first decade post-drainage, and declined over the subsequent decades (Paper III).

In the boreal region, organic forest soils hold more carbon than overstories (Gower et al. 1997), and such a trend was also observed in the hemiboreal region. Total soil C stock was 513.2 ± 49.7 t C ha^{-1} in drained sites, and 377.9 ± 126.5 t C ha^{-1} in undrained sites, and the differences were statistically significant ($p < 0.05$; Tab. 3.1). Carbon stocks within the evaluated upper (0–20 cm) soil layers exhibited significant ($p < 0.05$) differences between drained and undrained, however in deeper layers (20–80 cm) the differences are non-significant ($p > 0.05$; Fig. 3.2; Paper III). Increased carbon stocks in both soil and tree biomass after drainage have been reported in several studies conducted in hemiboreal and boreal regions (Minkkinen & Laine 1998; Lupikis & Lazdiņš. 2017; Lazdiņš et al. 2024), which highlights the effect of forest drainage on C stock.

Table 3.1. **Carbon stock in biomass and soil (mean ± 95% confidence intervals)**

Carbon stock, t C ha^{-1}	**Drained organic**	**Undrained organic**
O horizon	5.1 ± 2.1	0
Soil depth 0–10, cm	74.4 ± 7.7	41.8 ± 11.6
Soil depth 10–20, cm	67.5 ± 7.0	42.1 ± 14.3
Soil depth 20–40, cm	126.6 ± 13.3	85.9 ± 30.0
Soil depth 40–80, cm	239.7 ± 24.4	208.1 ± 73.5
Total in soil	513.2 ± 49.7	377.9 ± 126.5

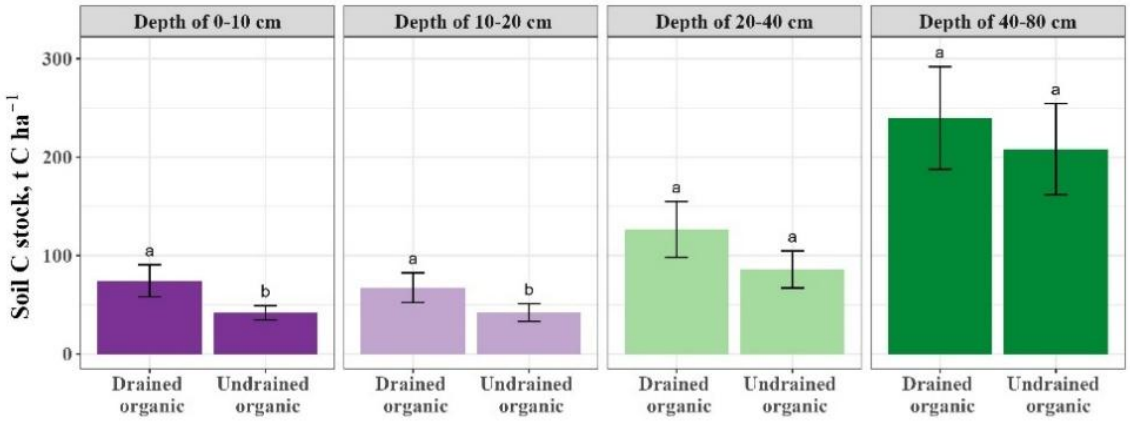


Fig. 3.2. **Soil carbon stock at different soil depths in drained and undrained organic soils. Different letters indicate significant differences ($p < 0.05$) between soil types in the evaluated soil layer**

Drainage systems can influence soil greenhouse gas (GHG) dynamics, with both positive and negative effects on emissions and removals (sinks) from soil (Strack & Waddington 2008; Butlers et al. 2025). In boreal forests, soils generally remain net carbon sinks following drainage (Minkkinen & Laine 1998; Lohila et al. 2011). However, climatic conditions and site-specific factors are key determinants of whether drained organic soils function as sources or sinks (Butlers et al. 2025). Therefore, it is essential to account for these factors and conduct site-specific studies to accurately assess carbon dynamics under varying environmental conditions.

Carbon dioxide flux followed a clear seasonal trend, with higher emissions during the summer season and lower during spring and autumn. The overall average $RtCO_2$ flux for the measurement season was 0.17 ± 0.01 mg m^{-2} s^{-1}. The average $RtCO_2$ flux was similar between drained (0.18 ± 0.018 mg m^{-2} s^{-1}) and undrained (0.17 ± 0.015 mg m^{-2} s^{-1}) sites, respectively. However, $RhCO_2$ flux values ranged from 0.007 to 0.33 mg m^{-2} s^{-1}, with a seasonal average of 0.07 ± 0.005 mg m^{-2} s^{-1}, and they were similar between drained (0.08 ± 0.007 mg m^{-2} s^{-1}) and undrained (0.07 ± 0.007 mg m^{-2} s^{-1}) sites, respectively. Soil $RhCO_2$ flux accounted for 37–49% of total forest floor ecosystem CO_2 respiration, averaging 41%. Comparable proportions of $RhCO_2$ (40–43%) have been observed in afforested peatlands in boreal regions (Berglund et al. 2011; Hermans et al. 2022).

A strong and statistically significant positive relationship ($p < 0.001$) was found between $RtCO_2$ flux and soil temperature (T_soil). The coefficient of determination (R^2) was 0.61 for $RtCO_2$ and 0.41 for $RhCO_2$ (Fig. 3.3), indicating a stronger relationship for total respiration compared to heterotrophic respiration. Although soil CO_2 fluxes are generally expected to decrease with rising groundwater levels (Von Arnold et al. 2005; Jungkunst et al. 2008), in our study the relationship was significant, yet weak ($R^2 = 0.06$–0.08), suggesting that other factors exerted a stronger influence on soil CO_2 fluxes (Paper IV).

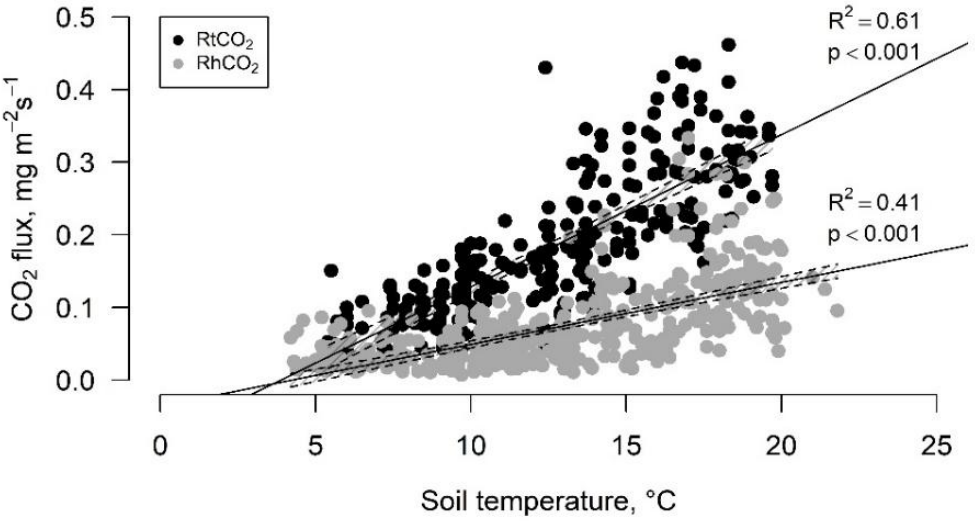


Fig. 3.3. **Relationship between the total forest floor ecosystem respiration ($RtCO_2$, mg m^{-2} s^{-1}) and heterotrophic respiration ($RhCO_2$, mg m^{-2} s^{-1}) and soil temperature at 10 cm depth (°C). The grey area denotes ± 95% confidence interval**

Soil CH_4 flux ranged from $-1.77 \cdot 10^{-6}$ to $2.90 \cdot 10^{-6}$ mg m^{-2} s^{-1}. The seasonal average CH_4 flux was $-3.67 \cdot 10^{-7} \pm 1.24 \cdot 10^{-6}$ mg m^{-2} s^{-1} at drained sites and $8.81 \cdot 10^{-9} \pm 2.97 \cdot 10^{-6}$ mg m^{-2} s^{-1} at undrained sites, and the difference was statistically significant ($p > 0.001$).

A significant negative relationship ($R^2 = 0.39$, $p < 0.001$; Fig. 3.4) was found between CH_4 flux and groundwater level. Higher groundwater levels were associated with increased CH_4 emissions, while lower groundwater levels resulted in CH_4 uptake (Paper IV).

Lowering the groundwater level promotes soil oxygenation, thereby enhancing the mineralization of organic matter, as aerobic decomposition is more rapid (Clymo 1984). Oxygen availability also regulates CH_4 production; thus, maintaining groundwater level (e.g., through stand drainage) 30–40 cm below the ground surface can reduce CH_4 efflux from soils (Elberling et al. 2011; Tong et al. 2022; Butlers et al. 2023) and, in the studied old-growth Scots pine forests, even resulted in net CH_4 uptake. In contrast, relatively high GWL (0–30 cm) and near-saturated (anaerobic) soil conditions may facilitate CH_4 production (Korkiakoski et al. 2019), and such coherence has also been observed in this study.

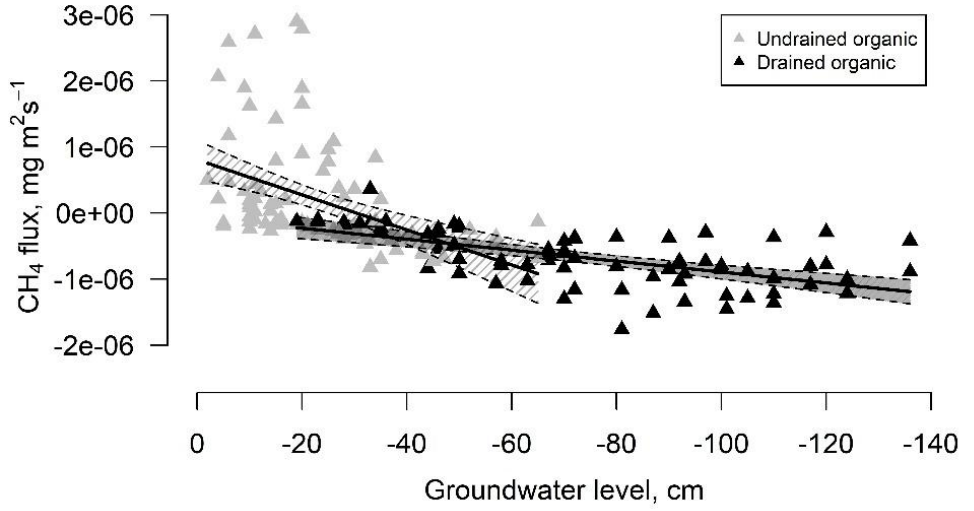


Fig. 3.4. **Relationship between the soil CH_4 flux (CH_4, mg m^{-2} s^{-1}) and groundwater level (cm) in drained and undrained organic soils. The grey area denotes ± 95% confidence interval**

3.3. Ground vegetation, litter, and fine-root C stocks (Papers V, VI, VII)

Tree litter is a significant source of carbon and nutrient input to the soil, forming soil organic layers (Feng et al. 2019; Uri et al. 2022). In spruce stands, the litter carbon stock was 2.5 ± 0.4 t C ha^{-1} yr^{-1} in drained sites, and 2.4 ± 0.3 t C ha^{-1} yr^{-1} in undrained sites. For pine, the litter carbon stock was higher in drained sites at 3.1 ± 0.5 t C ha^{-1} yr^{-1}, while in undrained sites it was 2.0 ± 0.3 t C ha^{-1} yr^{-1}. Total litter C stock in drained and undrained stands was similar (Tab. 3.2).

Estimates from northern European forests indicate an average carbon input via total tree aboveground litter of 1.7 ± 1.1 t C ha^{-1} yr^{-1} in conifer stands (Neumann et al. 2018). Reported annual litterfall dynamics in the Estonian hemiboreal region for main forestry tree species aged from 11 to 103 years were 0.06 to 3.4 t C ha^{-1} yr^{-1} (Uri et al. 2022), which is in line with the observed range in our study. By comparison, a local study reported carbon input of 1.8 ± 0.02 t C ha^{-1} yr^{-1} for young to middle-aged conifer stands on drained organic soils (Bārdule et al. 2021b). However, old-growth coniferous forests in our study exhibited higher annual litter production, and such a difference could be explained by the additional contribution to litter input by second-layer trees (Paper V).

Table 3.2. **Litter biomass and carbon stock in coniferous-dominated drained and undrained organic soils**

Species	Soil type	Litter biomass, t C ha^{-1} yr^{-1}	Litter carbon, t C ha^{-1} yr^{-1}
Spruce	Drained organic	5.1 ± 0.7	2.5 ± 0.4
	Undrained organic	4.7 ± 0.6	2.4 ± 0.3
Pine	Drained organic	6.2 ± 0.9	3.1 ± 0.5
	Undrained organic	4.0 ± 0.4	2.0 ± 0.3

The strongest predictor of annual litter C stock in old-growth coniferous forest stands was basal area, regardless of soil type ($p < 0.01$; Fig. 3.5). In spruce stands, the model showed a positive relationship between total basal area and litter carbon stock ($R^2 = 0.31$). In contrast, in pine stands, there was a strong positive relationship between total basal area and aboveground litter carbon stock ($R^2 = 0.9$; Paper V). Stand basal area has been considered as a typical independent variable for litter modelling as it correlates with canopy closure and foliage biomass (Starr et al. 2005).

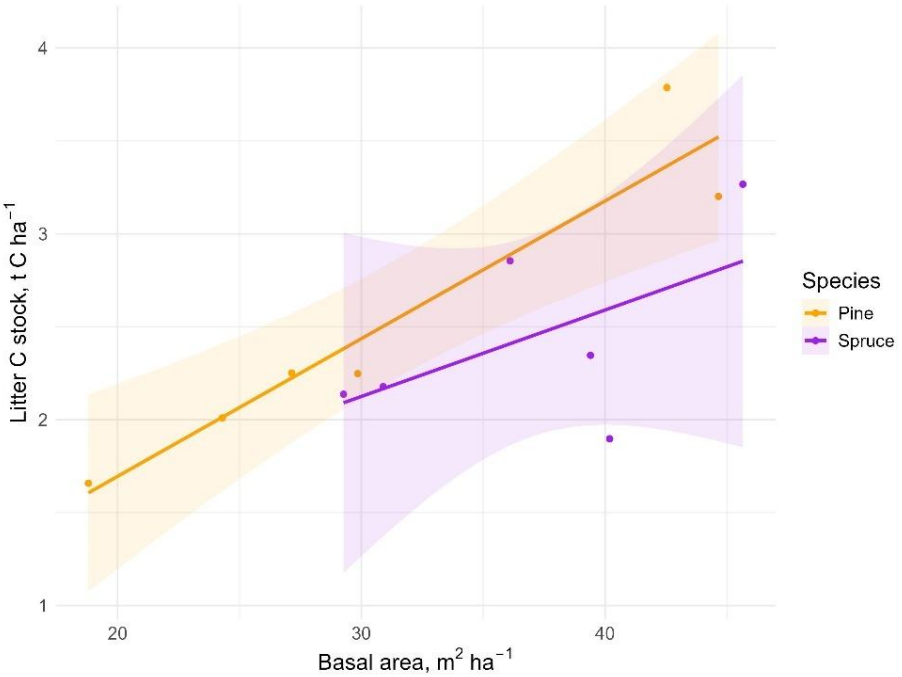


Fig. 3.5. **Annual carbon input by litter as a function of total basal area in pine and spruce-dominated old-growth forest stands**

The above-ground vegetation biomass depends on light availability below the canopy layer (Sigurdsson et al. 2005), and after the first two decades, it is not age-dependent (Peichl & Arain 2006).

In old-growth pine stands, above-ground biomass C stock of ground vegetation was 0.46 ± 0.32 t C ha^{-1} in drained organic soils and 0.48 ± 0.43 t C ha^{-1} in undrained organic soils. In old-growth spruce stands, above-ground biomass C stock of ground vegetation was 1.06 ± 0.74 t C ha^{-1} in drained organic soils and 0.96 ± 0.78 t C ha^{-1} in undrained organic soils (Fig. 3.6A). The differences between drained and undrained stands were non-significant ($p > 0.05$). Observed above-ground vegetation biomass C stock is in line with that observed in the boreal region (Ilvesniemi et al. 2009).

In old-growth pine stands, below-ground biomass C stock of ground vegetation was 3.19 ± 1.52 t C ha^{-1} in drained organic soils and 1.52 ± 0.88 t C ha^{-1} in undrained organic soils. In old-growth spruce stands, below-ground biomass C stock of ground vegetation was 3.27 ± 2.09 t C ha^{-1} in drained organic soils and 4.04 ± 1.47 t C ha^{-1} in undrained organic soils (Fig. 3.6B). A statistically significant difference ($p < 0.05$) was found only between the below-ground biomass C stocks of undrained pine stands and all other evaluated groups. Overall, tree roots (2–20 mm) consistently represented the largest proportion of below-ground biomass across all stands and soil types (drainage conditions; Paper VI).

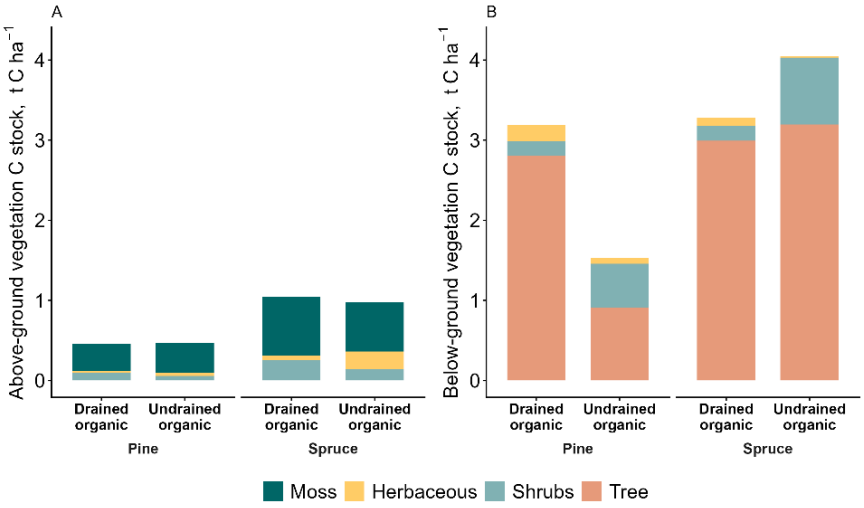


Fig. 3.6. **Ground vegetation above-ground (A) and below-ground (B) biomass carbon stock per forest type and dominant tree species**

Undrained old-growth stands had significantly higher total fine-root biomass (FRB) compared to drained stands (3.4 and 2.0 t C ha^{-1}, respectively). For Scots pine specifically, FRB was more than three times higher in undrained soils compared to drained, indicating an extensive foraging strategy under wetter, less aerated conditions. This pattern is consistent with previous findings in boreal peatlands, where undrained sites supported greater pine FRB (Lampela et al. 2023). In contrast, Norway spruce FRB in this study was higher in drained stands, largely due to species composition and higher spruce growing stock, which has also been observed in boreal forests where spruce tends to dominate drained peatlands (Finér & Laine 2000).

In both soil types, the majority of fine root biomass for Scots pine, Norway spruce, and dwarf shrubs was concentrated in the upper organic soil layer (0–10 cm). Herbaceous plants primarily contributed to FRB in the deeper organic layers (20–40 cm), with significantly higher values in certain forest stands (Fig. 3.7), which are determined primarily by the herbaceous vegetation composition, such as sedges and grasses, which are able to maintain their roots under anaerobic conditions to access nutrients in deeper soil layers (Lampela et al. 2023). Dwarf shrubs contributed the largest proportion of FRB in undrained soils (1.2 t C ha^{-1}) and remained an important component also in drained soils (0.6 t C ha^{-1}). This highlights that non-tree vegetation is a substantial contributor to belowground carbon storage, which has also been emphasized in boreal peatland studies (Bhuiyan et al. 2017).

The proportion of pine FRB in the topsoil layer (0–10 cm) in undrained and drained soils was 84% and 73%, respectively. The proportion of spruce FRB in this layer was similar in both soil types (~ 80%). Dwarf shrub FRB in the topsoil layer accounted for 54% and 51% in undrained and drained soils, while herbaceous plants accounted for 19% and 21%, respectively (Paper VII).

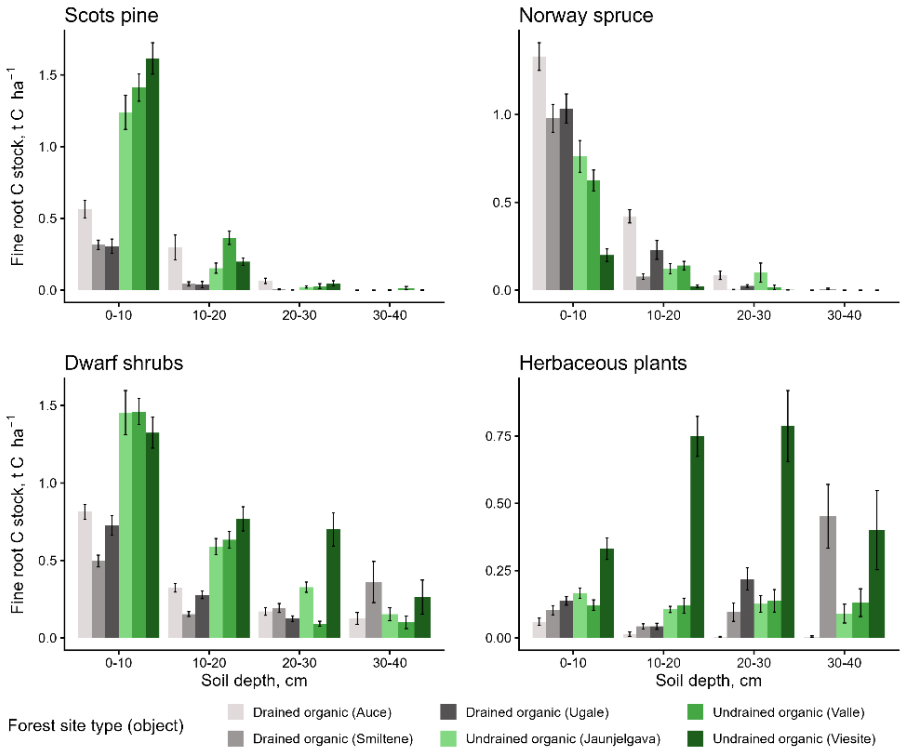


Fig. 3.7. **The vertical distribution of mean fine root biomass of Scots pine, Norway spruce, dwarf shrubs, and herbaceous plants in drained and undrained organic soils up to 40 cm depth**

Although FRB differed, fine-root production (FRP) was similar between drained and undrained stands (*ca.* 1 t C ha^{-1} yr^{-1}). This indicates that the annual carbon input through fine-root growth is not strictly controlled by drainage but rather by stand productivity and site-specific factors, which may also explain the observed variation among the study sites. Previous studies in boreal forests have also shown that FRP is tightly linked to stand age and soil fertility (Helmisaari et al. 2002; Yuan & Chen 2012).

Scots pine fine-root turnover (FRT) rates were approximately twice as high in drained soils 0.61 yr^{-1} compared to undrained soils (0.33 yr^{-1}). Norway spruce fine-root turnover rates remained similar between drained and undrained stands. This indicates that, while root biomass is lower, the roots are replaced more frequently, accelerating nutrient and carbon cycling. Faster turnover in drained stands is consistent with earlier observations that FRT is higher in more productive environments (Kriiska et al. 2019). The increased aeration after ditching likely shortens root lifespan, a trend reported for other species in improved site conditions (Förster et al. 2021).

CONCLUSIONS

In the long term (> 50 years), forest drainage significantly increased carbon stock in tree biomass in coniferous forests with mesotrophic organic soils, thereby contributing to climate change mitigation; it also significantly increased carbon storage in deadwood in old-growth spruce forests, though insignificantly in old-growth pine stands.

In hemiboreal forests, mesotrophic organic soil remained a stable carbon pool in the long-term, with changes in soil surface level due to compaction following drainage, but not in total carbon storage.

Forest drainage ensures a desirable climate change mitigation impact on soil greenhouse gas emissions in the long-term. Drained organic soils showed significant methane uptake, whereas undrained organic soils emitted methane. The dynamics of methane emissions are directly linked to groundwater level, with a depth of 30–40 cm serving as the emissions threshold. Drainage did not affect CO_2 emissions, which are dependent on soil temperature.

The carbon stock of ground vegetation and litter was lower than in other carbon pools and similar in both drained and undrained soils.

Forest drainage ensures faster fine-root turnover, leading to an overall higher input of organic carbon into the soil, but not a higher total carbon stock within the fine-root biomass component itself.

RECOMMENDATIONS

Maintain and, where possible, expand drainage systems in forests with mesotrophic organic soils, increasing the contribution of these areas to climate change mitigation.

In areas where groundwater level elevation is intended, use self-regulating systems and ensure that the groundwater level does not exceed 30–40 cm, thereby preventing additional long-term methane emissions. Conduct research in these areas to determine the factors affecting the critical groundwater level threshold.

Ensure groundwater level monitoring to determine the actual climate change mitigation effect in forests with organic soils.

Establish demonstration sites with open, real-time access to groundwater level and emission measurements, fostering a broader understanding of the long-term impact of forest drainage and incorporating these findings into legislation and carbon credit schemes.

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I Ķēniņa, L., Zute, D., Jaunslaviete, I., **Samariks, V.**, Jansons, Ā. (2022) Old-Growth Coniferous Stands on Fertile Drained Organic Soil: First Results of Tree Biomass and Deadwood Carbon Stocks in Hemiboreal Latvia. Forests, 13, 279. DOI: 10.3390/f13020279

II **Samariks, V.**, Jõgiste, K., Vodde, F., Bāders, E., Jansons, Ā. (2025) Deadwood carbon stock in overmature coniferous forests on different soil types in the hemiboreal region. Baltic Forestry, 31(2), 796. DOI: 10.46490/BF796

III Dubra, S., **Samariks, V**., Līcīte, I., Butlers, A., Purviņa, D., Lupiķis, A., Jansons, Ā. (2023) Effects of Drainage on Carbon Stock in Hemiboreal Forests: Insights from a 54-Year Study. Sustainability, 15, 16622. DOI: 10.3390/su152416622

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VI **Samariks, V.**, Jaunslaviete, I., Adamovičs, A., Dubašinska, S., Jansons, Ā. (2024) Ground vegetation biomass and carbon pool in hemiboreal coniferous stands on organic soils. Proceedings of 24th International Multidisciplinary Scientific GeoConference SGEM, 24(3.2), 285–293. DOI: 10.5593/sgem2024v/3.2/s13.36

VII **Samariks, V.**, Ķēniņa, L., Kitenberga, M., Aun, K., Varik, M., Liepiņa, A. A., Jansons, Ā. (2024) The effect of drainage on fine-root biomass, production, and turnover in hemiboreal old-growth forests on organic soils. Ecosphere, 15(4), e4849. DOI: 10.1002/ecs2.4849

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Communication

Old-Growth Coniferous Stands on Fertile Drained Organic Soil: First Results of Tree Biomass and Deadwood Carbon Stocks in Hemiboreal Latvia

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Abstract: Organic soils store a large amount of carbon stock, but they are also a large source of greenhouse gas emissions in a forest. Results of previous studies do not provide whole-country representative data of carbon stock in drained fertile organic soil forests in Europe, as the effects of stand age and dominant tree species are significant. Moreover, the growing role of old-growth stands has triggered interest in empirical data about drained organic soils. These data might serve as a reference of theoretical carbon carrying capacity that could be achieved in hemiboreal Latvia. We aimed to characterize tree biomass and deadwood carbon pools in coniferous old-growth stands on fertile, drained organic soils. Seven old-growth Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominated stands (131–174 years) were measured. Both groups of stands had similar carbon stocks, reaching 167 and 154 t C ha^{-1} in tree biomass and 11 and 10 t C ha^{-1} in deadwood, respectively. A large variation in deadwood carbon storage was found across sample plots, ranging from 0.6 to 26.6 t C ha^{-1}. Dead standing trees and downed logs store a great share of the total deadwood carbon, 5 and 4 t C ha^{-1}, respectively. Significantly less carbon was stored in dead standing trees with broken tops (1 t C ha^{-1}). Further assessment of soil carbon stock and fluxes is ongoing to reduce uncertainty in the soil carbon evaluation of old-growth stands in the context of climate change mitigation targets in a hemiboreal region.

Keywords: tree biomass; deadwood; carbon pools; peat soils; Scots pine; Norway spruce

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1. Introduction

Forests are expected to increase carbon removal from the atmosphere and decrease greenhouse gas emissions to achieve global climate change mitigation goals. Organic soils store a large amount of carbon stock [1], but drained areas are an especially large source of greenhouse gas emissions in the forest land of many European countries [2,3]. However, some authors have found that soil carbon stock can remain stable or even increase after drainage, especially in the boreal vegetation zone [4–6]. In hemiboreal Latvia, more than 20% of the total forest area is located on organic soils, and almost one-third of the total forest area (29.7%) has been drained, according to the National Forest Inventory (NFI). Few studies have dealt with carbon storage in drained hemiboreal organic soils, where tree biomass and soil carbon were assessed [1,6]. In an earlier study of forests with organic soils (both naturally wet and drained sites), it was concluded that forest age is an important factor affecting carbon stock in dynamics, demonstrating that carbon stocks subsequently decrease in decaying forests [3,6]. Under unmanaged conditions, stands on drained organic soils may also reach the old-growth stage as, in general, management intensity in European forests is decreasing [7]. Moreover, with increasing interest in promoting carbon sequestration in forests in a climate policy context, local reference data from old-growth stands on drained

organic soils is needed to use this information in decision support tools, particularly because old-growth stands have a great influence on biodiversity conservation [8].

The main carbon pools in forests include tree biomass, deadwood, soil, and litter. Old-growth forests are recognized as a major carbon store in the long term; however, natural disturbances can have a significant impact on depleting carbon stocks. Thus, carbon stocks of old-growth stands are highly variable due to large heterogeneity according to the site type, tree species, species structure, and the effects of past natural disturbances [9]. Tree biomass is a large, changing, and manageable forest carbon pool [7,9]. Compared to younger and managed stands, old-growth stands typically store a higher proportion of deadwood [9,10]. So far, a few studies of old-growth coniferous stands have accessed the carbon stocks of tree biomass and deadwood on dry, wet, and drained mineral soils in the hemiboreal region [11,12], but there are no data from old-growth stands on organic soils in this region. Old-growth stands influence biodiversity and species richness with an emphasis on deadwood availability, hosting many dependent species [13].

European hemiboreal forests are dominated by a mix of coniferous Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and deciduous species. According to the NFI, Scots pine and Norway spruce are the most widespread and economically important tree species in Latvia, comprising 28% and 19% of the total forest area. Moreover, in drained forests, Scots pine and Norway spruce take up to one-third of the most common forest type on drained organic soils—*Myrtillosa turf.mel*. Therefore, local carbon stock data are needed as the new data may serve as a reference of the carbon carrying capacity that theoretically can be achieved in the particular region. Thus, we aimed to characterize tree biomass and deadwood carbon pools in coniferous old-growth stands on fertile, drained organic soils. Based on the light requirements of the evaluated tree species and thus the potential of formation of a second layer in the stand with substantial contribution to biomass carbon pool, we hypothesized that in pine-dominated stands, carbon storage in tree biomass would be higher than in spruce-dominated old-growth stands.

2. Materials and Methods

Seven Scots pine (four stands) and Norway spruce (three stands) old-growth stands on drained peat soils were measured (Figure 1). Stand age on drained sites was 131 to 174 years. The forest type was *Myrtillosa turf.mel* (mesotrophic site type on drained soils) according to the Latvian forest type classification system [1,14]. The target species in *Myrtillosa turf.mel* forest types are Scots pine and Norway spruce, but also stands of deciduous trees, such as birch (*Betula pendula, Betula pubescens),* aspen *(Populus tremula*), and black alder (*Alnus glutinosa*) can be found. These forests typically have a ground cover of *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Pleurozium schreberi*, and *Hylocomium splendens*. Wet forests were drained intensively in the 1960s when open ditch systems were created [1,15]. Since then, no further maintenance or renovation has been completed. The peat layer in such sites does not exceed 20 cm in depth after drainage. The climate at the sampled stands can be characterized as temperate moist continental, yet with explicit coastal features of the Baltic Sea [16].

Stands were pre-selected and checked in the field for actual occurrence of a chosen forest type, age group (>130 years), dominance of target species (>50% from the basal area), and no signs of former logging. The cohort was only measured in stands where old trees are still dominant.

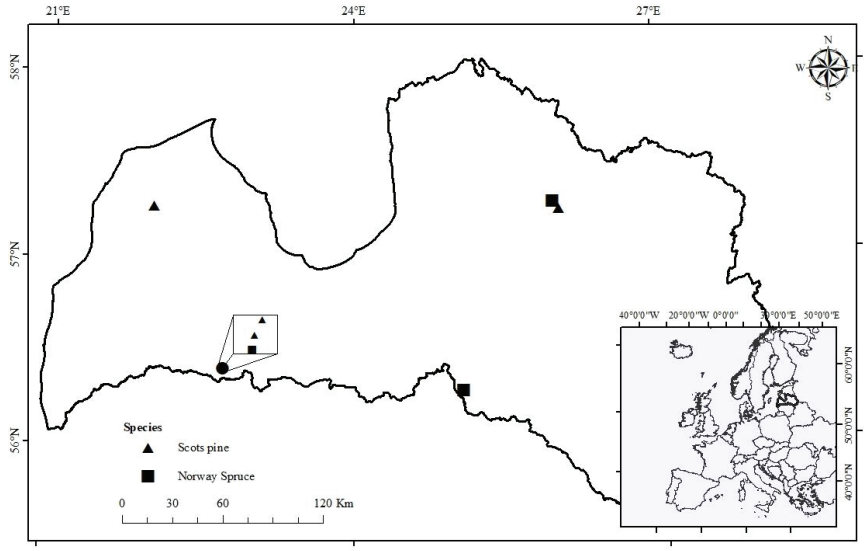

Figure 1. Distribution of sample stands with old-growth Scots pine (▲, *Pinus sylvestris*), and Norway spruce (■, *Picea abies*) in hemiboreal Latvia.

Fieldwork and the data analysis were performed as described in Ķēniņa et al. [11]. In total, 37 sample plots (500 m^2) (19 and 18 sample plots in pine-dominated and spruce-dominated stands, respectively) were systematically established. Six sample plots in each stand were established using previously generated coordinates at least 20 m from the edges. In each sample plot, tree species were recorded, and the diameter at the breast height of all live trees and standing dead trees (≥6.1 cm) was measured. The heights of five live trees in the I layer, three live trees in the II layer, and all dead trees (≥6.1 cm) were measured. Dead trees were classified as dead standing trees (trees with all primary branches and tops) and dead standing trees with broken tops (snags—standing dead tree with fallen primary branches and without top). The length and diameter of downed logs (≥14.1 cm at the thicker end) at both ends, decay stage in five classes (fresh to almost complete decay according to Sandström et al. [17]), and tree species (if possible) were recorded. In a smaller subplot (25 m^2) in the center of the sample plot, the diameters of live trees, standing dead trees (2.1 to 6.0 cm at breast height), and downed logs (6.1 to 14.0 cm at the thicker end) were recorded. In each sample plot, three dominant trees were cored using a Pressler increment corer to detect stand age. Only the sample plots where dominant tree species constituted more than 50% of the basal area were included in further analysis (Table 1).

Table 1. Characteristics of sampled old-growth Scots pine and Norway spruce stands.

No.	N	Dominant Species	I Layer	II Layer	Understory
1	5	Pine	7P3S	10S	4S2G1B1H1R
2	4	Pine	6P4S	10S	5A5R
3	5	Pine	7P3S	10S	3S4R1B1H1H
4	5	Pine	8P2S	10S	4S4B2R
5	6	Spruce	9S1P	10S	5S3R1H1A
6	6	Spruce	7S3P	7S3P	4S4R1H1A
7	6	Spruce	8S1P1B	10S	9S1B

N: number of sample plots; species composition is based on the proportion of the species' basal area in the respective stand layer (in understory based on the number of trees): 10 = 90–100%, 9 = 80–89%, 8 = 70–79%, etc. P: Scots pine (*Pinus sylvestris*), S: Norway spruce (*Picea abies*), B: birch (*Betula pendula* and *Betula pubescens*), R: rowan (*Sorbus aucuparia*), H: common hazel (*Corylus avellane*), A: alder buckhorn (*Frangula alnus*), and G: grey alder (*Alnus incana*).

Individual tree biomass (above- and below-ground) was estimated from diameter at breast height and calculated tree height according to local biomass models for the main tree species in Latvia [18]. The local carbon content values for the major tree species were used for tree biomass carbon stock estimation [19]. Deadwood carbon stock was estimated from volume and applying decay class-specific density to classes 1 through 5 to determine carbon content for the main hemiboreal tree species, according to Köster et al. [20].

A linear mixed-effect model (LMER) was used to test dominant tree species and age effect on forest inventory parameters. The LMER was used to test the effect of species, stand density, standing volume, and all two-way interactions with species (independent variables) on the dependent variable: carbon stocks of tree biomass, including separate models for above- and below-ground biomass and deadwood. Stand ID was used as a random factor in all models as sample plot data were used in the calculation. All data analysis was performed using R 4.1.0. software [21].

3. Results

All forest inventory parameters were similar in old-growth Norway spruce and Scots pine-dominated stands on drained peat soils ($p > 0.05$) (Table 2). There were no dominant tree species or age effects at the stand-level and I-layer forest inventory parameters ($p > 0.05$) in the old-growth stage. The mean old-growth stand age was 152 years. The mean I layer standing volume was similar in pine- and spruce-dominated stands, ranging from 204 to 855 m^3 ha^{-1}. The mean basal area in the I layer was 35.0 ± 4.37 m^2 ha^{-1}, of which 20 m^2 ha^{-1} was Scots pine in pine-dominated stands, and 13 m^2 comprised of Norway spruce. A similar mean I layer basal area was found in spruce-dominated stands (32.6 ± 4.49 m^2 ha^{-1}), of which 28 m^2 ha^{-1} was Norway spruce. The mean stand density of the upper tree layer was 374 ± 24 trees ha^{-1}. In the II layer, the mean standing volume was significantly different between pine- and spruce-dominated old-growth stands, 59.5 ± 12.24 m^3 ha^{-1} and 24.5 ± 10.54 m^3 ha^{-1}, respectively.

Table 2. Characteristics (mean ± 95% confidence interval) of old-growth Scots pine-dominated and Norway spruce-dominated stands in *Myrtillosa turf.mel*. forest type.

Characteristics	Pine Stands	Spruce Stands
Stand age, years	145 ± 8	162 ± 3
Diameter at breast height, cm	35.0 ± 1.27	34.1 ± 2.75
Tree height, m	28.2 ± 1.35	28.9 ± 2.00
I layer basal area, m^2 ha^{-1}	35.0 ± 4.37	32.6 ± 4.49
II layer basal area, m^2 ha^{-1}	7.1 ± 1.55	3.2 ± 1.28
I layer standing volume, m^3 ha^{-1}	459.3 ± 74.01	443.0 ± 82.24
II layer standing volume, m^3 ha^{-1}	59.5 ± 12.24	24.5 ± 10.54
I layer number of trees, ha^{-1}	380 ± 35	367 ± 37
II layer number of trees, ha^{-1}	545 ± 168	315 ± 151
Understory number of trees, ha^{-1}	1485 ± 434	2972 ± 660

Standing volume ($p < 0.01$) had a significant effect on tree biomass carbon stock in both pine- and spruce-dominated old-growth stands. Neither stand age, dominant tree species, nor other forest inventory parameters affected tree biomass carbon stock. The mean tree biomass carbon stock was 167 ± 24.6 t C ha^{-1} in pine-dominated old-growth stands. Similar tree biomass carbon stock (162 ± 25.0 t C ha^{-1}) was found in spruce-dominated stands. A large variation of tree biomass carbon stock was observed among sampling plots, varying from 84 to 270 t C ha^{-1} in pine-dominated stands and from 103 to 237 t C ha^{-1} in spruce-dominated stands. The mean carbon in above-ground biomass accounted for 79% of total tree biomass in both pine- and spruce-dominated old-growth stands (Figure 2).

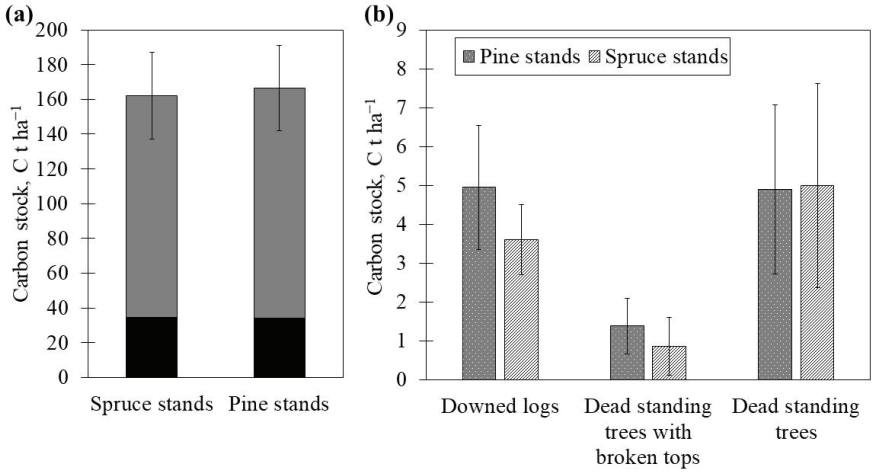

Figure 2. The mean (±95% confidence interval) carbon stock of live tree biomass: (**a**) above-ground biomass carbon stock (grey stacked bars) and below-ground biomass carbon stock (black stacked bars) in old-growth pine- and spruce-dominated stands; and (**b**) deadwood carbon stock by deadwood types in old-growth pine-dominated (dark grey dotted) and spruce-dominated (light grey diagonal stripes) old-growth stands.

Dominant tree species and other factors had no significant impact on deadwood carbon stock. The mean total deadwood carbon stock was 11 ± 3.0 and 10 ± 2.8 t C ha^{-1} in pine- and spruce-dominated stands. Deadwood carbon storage also was highly variable across sample plots, ranging from 0.6 to 20.4 t C ha^{-1} in pine stands and 1.2 to 22.0 t C ha^{-1} in spruce stands. Significant differences were observed between deadwood types ($p < 0.001$)—downed logs, dead standing trees, and dead standing trees with broken tops. Dead standing trees constituted the greatest share (pine-dominated stands, 5 ± 2.1 t C ha^{-1}, 44%; spruce-dominated stands, 5 ± 2.6 t C ha^{-1}, 53%) of the total deadwood carbon storage. A similar part of carbon was stored in downed logs (5 ± 1.6 t C ha^{-1}, 44% in pine-dominated stands; 4 ± 0.9 t C ha^{-1}, 38% in spruce-dominated stands). Significantly less ($p < 0.001$) carbon was stored in dead standing trees with broken tops in both pine- and spruce-dominated old-growth stands, only 1 ± 0.7 t C ha^{-1}. Only 10% of the total deadwood carbon was stored in recently dead deadwood (1 ± 0.77 C t ha^{-1}), but the largest share was weakly decayed deadwood (38%; 4 ± 2.12 C t ha^{-1}), followed by moderately decayed (29%; 3 ± 1.31 C t ha^{-1}) and very decayed wood (2 ± 1.30 C t ha^{-1}), and almost completely decomposed wood (0.3 ± 0.18 C t ha^{-1}) comprised the smallest share (2%) in pine-dominated stands. Most of the deadwood carbon came from Scots pine (58%) and Norway spruce (37%) trees in pine-dominated stands. In spruce-dominated stands, a similar distribution between decomposition stages was observed: 28% of the total deadwood carbon was stored in recently dead deadwood (3 ± 1.40 C t ha^{-1}), 32% in weakly decayed deadwood (3 ± 1.47 C t ha^{-1}), followed by moderately decayed (22%; 2 ± 0.86 C t ha^{-1}), very decayed (16%; 2 ± 0.64 C t ha^{-1}), and almost completely decomposed wood (2%; 0.2 ± 0.15 C t ha^{-1}). In spruce-dominated stands, Norway spruce trees comprised 57% of the deadwood carbon, followed by Scots pine (36%).

4. Discussion

Old-growth pine- and spruce-dominated stands had similar inventory parameters indicating equal growth between Scots pine and Norway spruce in similar growing conditions in the old-growth stage. However, growth rates for Scots pine and Norway spruce are more divergent in younger stands, especially in annual increments [22]. All examined stands were mixed according to species structure in old-growth pine- and spruce-dominated stands. Simi-

lar standing volume in pine-dominated and spruce-dominated stands indicated that a mixture of Scots pine and Norway spruce did not provide significantly higher standing volume [22]. Therefore, carbon storage was also similar for pine- and spruce-dominated stands. We found similar mean carbon stocks of tree biomass in pine-dominated and spruce-dominated old-growth stands in *Myrtillosa turf.mel*, 167 $\pm$ 22.3 t C ha^{-1} and 154 $\pm$ 23.7 t C ha^{-1}, respectively. The obtained results are similar to the results from old-growth Scots pine stands (171 $\pm$ 6.1 t C ha^{-1}) and Norway spruce stands (149.2 $\pm$ 18.9 t C ha^{-1}) on mineral soils in hemiboreal Latvia [11,12]. Carbon stock in tree biomass generally varies with stand age [23], but as selection age criteria of dominant tree species were the same in forests on mineral soils and drained organic soils, similar results can be obtained. Carbon storage in tree biomass increased significantly with increasing standing volume ($p < 0.001$). Although Norway spruce can produce the same or even more tree biomass in moderate and rich sites, the competition effect in mixed Scots pine and Norway spruce stands drives tree growth [22]. Therefore, we assume that the obtained tree biomass carbon pools were similar because Norway spruce had a higher proportion. Therefore, the effect on tree biomass in pine-dominated old-growth stands is an important part of the first and the second layer, as was also observed in hemiboreal old-growth stands on mineral soils [24].

Mean deadwood carbon stocks were similar between pine- and spruce-dominated stands on drained organic soils. The deadwood volume in the studied stands was high (mean 10 t C ha^{-1}), as it typically is at the old-growth stage. However, the large variation of deadwood carbon storage across sample plots (ranging from 0.6 to 26.6 t C ha^{-1}) might be the result of influence of various natural disturbances during the life span of these stands as well as tree age and species composition [13,25]. As stand age showed no relationship to deadwood carbon storage, we can assume that the large carbon storage in deadwood was because stand maturity was very high in these stands [13]. We did not have data about previous natural disturbance events; however, those events are likely due to the frequency of natural disturbances [26]. There was significant variation in carbon stocks between deadwood types, of which dead standing trees formed the greatest share. Previous studies reported downed logs as the main deadwood type in old-growth stands on mineral soils, revealing that different stand structures are impacted both by tree species and by site type [11,12,27]. Moreover, differences between deadwood types are in line with the species composition effect on the proportion of standing/downed deadwood; this is because dead Norway spruce falls down quickly, but Scots pine remains as standing deadwood [13]. Furthermore, the position of the deadwood of different tree species affects decomposition rates due to differences in wood properties [13]. Overall, deadwood carbon stock distribution according to decomposition stages indicates an increased dieback over recent years.

Recent estimations of carbon storage capacity in hemiboreal and boreal Europe have been biased toward above-ground forest-related components [28]. Moreover, in Latvia, country-specific weighted mean carbon values of above- and below-ground tree parts for the main tree species have been developed to improve the accuracy of National Greenhouse Gas Inventory estimates [19], but below-ground components—roots and soil carbon storage—remained neglected [28].

The results of our study provide an indication, that biomass and deadwood carbon storage might be similar for the same tree species in different site types [11,12], as well as conclude, that these carbon pools are similar in old-growth pine- and spruce-dominated stands on drained organic soils. These preliminary findings need to be further tested on larger variety of site and climatic conditions.

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Deadwood carbon stock in overmature coniferous forests on different soil types in the hemiboreal region

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Abstract

The amount of deadwood is a subject of heated debate regarding biodiversity conservation and carbon (C) storage as an instrument for climate change mitigation in north-eastern Europe. In the region, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) are among the principal forestry species providing a significant pool of stable deadwood, especially in overmature forests. Deadwood C stocks are highly variable, and regional deadwood estimates can be biased; thus, local data is vital, and accurately quantified deadwood C stocks, particularly in overmature stands on different soil types, are essential.

The study aims to characterise deadwood C stock, modes (standing or lying), and decay classes in hemiboreal overmature coniferous forest stands on dry mineral, drained, and wet organic soils. C stock in deadwood and forest inventory parameters were estimated in 95 overmature (aged 122 to 218 years) coniferous stands using the sample plot method, taking into account the form of deadwood standing, decomposition class and soil type.

Mean deadwood C stock (deadwood with a diameter ≥ 6.1 cm) in coniferous stands ranged from 4.59 C t ha^{-1} to 11.25 C t ha^{-1} in spruce stands on wet organic soil and pine stands on mineral soil, respectively. However, the amount of deadwood showed large spatial variability; at the same time, a statistically significant relationship between deadwood carbon stock and soil type, basal area, and the mean stand diameter at breast height, explaining a limited effect and maintaining high uncertainties. This suggests that the dynamics of deadwood were complex, driven by ageing, natural disturbances and any past management, perhaps carried out decades ago; for these reasons, the findings should be interpreted with caution due to the potential legacy effect of any disturbances in some stands. Nevertheless, the results highlight the crucial role of large-sized coniferous deadwood as a stable carbon store, contributing to both carbon storage and maintaining biodiversity, in the hemiboreal region.

Keywords: carbon stock; coarse woody debris; decay stage; organic soils; Norway spruce; Scots pine

Introduction

Forest ecosystems are some of the largest global biotic carbon (C) pools (Bonan 2008, Pan et al. 2011), playing an important role in the mitigation of climate change effects (Canadell and Raupach 2008). Estimates of C stock are essential for reporting the state of forest contribution to climate goals as defined by international legislation (Penman et al. 2003). The main C pools in forests are living tree biomass, soil, deadwood, and litter (Frouz et al. 2009, Ķēniņa et al. 2022). However, they show high regional and temporal variability; therefore, the uncertainty regarding individual components remains high (Müller and Bütler 2010), which needs clarification.

While C dynamics in young and middle-aged managed stands, as well as those for living trees, are relatively well understood (Uri et al. 2023, Kellomäki 2024), such dynamics in old, unmanaged stands are still poorly quantified due to scarcity and low economic interest. However, in the context of the European Union (EU) Nature Restoration Law, which aims at a significant increase in unmanaged forest areas, such areas will inevitably increase, leading to a greater extension of old-growth stands, associated natural mortality, and deadwood accumulation (EUR-Lex 2024). Although the primary ecological function of deadwood is to support biodiversity across spatial and temporal gradients (Felton et al. 2010), in doing so, deadwood serves as a temporary C stock, as it inevitably decomposes, releasing C back into the atmosphere (Humphrey et al. 2004, Mäkinen et al. 2006). Therefore, it is essential to estimate C stock in deadwood in overmature stands, which can already be done by a detailed survey of the existing forests falling under such a category.

The dynamics of deadwood C stock has regional and local characteristics, which are determined by natural

disturbance regime, forest management practices, stand age, successional stage, and climatic conditions, particularly soil microclimate and moisture conditions affecting decomposition rates (Köster et al. 2005, Garbarino et al. 2015, Jonsson et al. 2016, Vítková et al. 2018). Accordingly, regional extrapolations can be strongly biased, and local information is highly anticipated. In this regard, there is particular uncertainty regarding the impact of hydromelioration (drainage) of plantations on the dynamics of C stocks in deadwood, which is typical for the Eastern Baltic region (Ķēniņa et al. 2022).

The Eastern Baltic region, which is an important source of timber for the EU market (Jansson et al. 2017), is situated under a moist continental climate, where the excess of soil moisture is considered the main limiting factor for forest productivity (Zālītis 2012). Accordingly, since the 1960s, forest drainage, which has long-term effects on productivity, biodiversity, and C storage via altered growth, microclimate, and decomposition dynamics (Ranius and Fahrig 2006, Lõhmus et al. 2015, Tong et al. 2022), has been widely implemented (Zālītis 2012, Skaggs et al. 2016).

Due to their abundance, Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) are main species for commercial forestry in north-eastern Europe, especially in the Eastern Baltic region (Caudullo et al. 2016, Durrant et al. 2016), where they also have high ecological value (Tērauds et al. 2011, Fahlvik et al. 2015). Thanks to well-developed forest-related sectors, the ecological and economic services, including C credits, are under special attention in Latvia, making the country a good model for assessing the potential impact of the Nature Restoration Law on C stocks and their dynamics. Currently, C stocks in old-growth birch (*Betula* spp.) and European aspen (*Populus tremula* L.) stands are assessed on mineral soils (Šēnhofa et al. 2020, 2021). However, the information on over-mature coniferous forest deadwood C stocks, which have different dynamics (Lassauce et al. 2011), is still awaited. In addition, Latvia is in the hemiboreal zone, where the climate-related changes and forests are expected to be pronounced (Buras and Menzel 2019).

The study aims to characterise deadwood C stock, modes (standing or lying), and decomposition classes in hemiboreal overmature coniferous stands on dry mineral, drained, and wet organic soils to illustrate the amount of deadwood in different stages of decay under natural conditions and to show the effect of drainage on deadwood C stock. We hypothesised that: 1) deadwood carbon stock is lower in stands on wet soils, compared to dry mineral and drained organic soils, *and* 2) stand characteristics are significant predictors of deadwood C stock.

Materials and methods

Study area

Latvia is located in north-eastern Europe between 58°05'N–55°40'N and 28°14'E–20°58'E (Figure 1), corresponding to the hemiboreal zone, an intermediate belt that incorporates elements of both the boreal and nemoral zones. Latvia has a cool, moist climate with strong maritime influences. The average temperature in January is –6°C and in July is +16°C. The average annual precipitation is 685 mm (LEGMC 2020).

Forests cover 53% of Latvia's terrestrial area. Scots pine and Norway spruce are among the most common tree species, together accounting for 45% of the forested area. Specifically, Scots pine-dominated stands comprise 25%, while Norway spruce-dominated stands comprise 20% of the total forest area (LSFRI 'Silava' 2023).

Selected forest stands correspond to *Oxalidosa* (fertile dry mineral soils), *Aegopodiosa* (fertile dry carbonate soils), *Caricoso-sphagnosa* (poor wet peat soils), and *Oxalidosa turf. mel.* (drained fertile peat soils) forest types according to the local classification in Latvia (Bušs 1997). Soil conditions and forest type were confirmed in the field by visual and physical inspections (including peat layer depth measurements), and further selected forest types used in this study are referred to as mineral, wet organic, and drained organic soils. All measured stands were un-

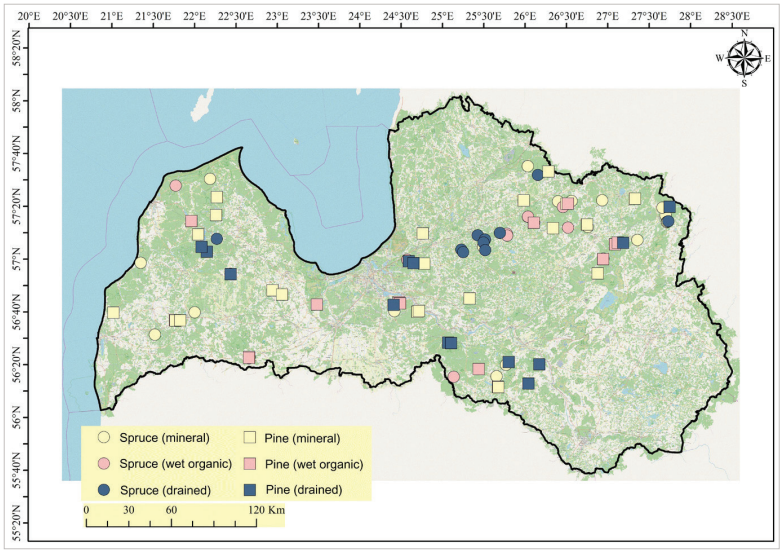

Figure 1. Locations of the study sites in Latvia

managed for at least 30 years (including no maintenance of forest drainage systems). Management history information and mean stand age were determined based on the State Forest Service database. The age of the study sites ranged from 122 to 218 years.

Data collection

In total, 600 sample plots were established and measured in 95 selected over-mature stands across Latvia, where old trees are the dominant forest elements. In each stand, six to eight 500-m^2 circular sample plots (radius = 12.62 m) were established randomly throughout the area of selected stands for measurements of main tree variables (tree species, DBH, tree height) to determine and calculate forest inventory parameters such as basal area, standing volume, and tree count per hectare (Table 1). For a more detailed sample description, see Ķēniņa et al. (2022).

Deadwood was characterised by using a concentric scheme with two distance steps: within a distance of 12.62 m, all deadwood with a diameter ≥ 14.1 cm, and within a distance of 5.64 m, deadwood with a diameter ≥ 6.1 cm was measured. The deadwood diameter threshold was based on the methodology of the National Forest Inventory (NFI). Modes of deadwood structures included lying deadwood and dead-standing trees. For lying deadwood, the diameter was measured at both ends of the log, and the length of the log was also measured. Standing deadwood was measured at breast height, and tree height was measured up to the top of the tree or the breakage point. The decay class of deadwood was observed visually and using the 'knife method', and decay was divided into five classes (Table 2; Stokland 2001, Köster et al. 2015).

Data analysis

Tree volume was calculated with locally developed equations (Liepa 1996). The volume of deadwood was calculated using Huber's formula (Eq. 1; for a more detailed methodology description, see Šēnhofa et al. 2021). Deadwood C stock was calculated by using the obtained deadwood volume and converting it to C stock by using decay class-specific wood density and C content for Norway spruce and Scots pine (Table 2; Köster et al. 2015).

Huber's formula takes the form as follows:

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

where

V – dead standing/lying dead tree volume,

L – length of the log or height of the snag/dead standing tree, *and*

d_m – mid-diameter of the log or the snag.

The Shapiro-Wilk test was used to check the normality of data distribution. Turkey's HSD was used for parametric variables to compare the means of different tree species in each soil type. The Mann-Whitney U test was used to observe significant differences in non-parametric variables. Linear mixed-effects models were developed to examine stand characteristics that influence deadwood C stocks. Initially, all available stand characteristic variables were included in the linear mixed-effects model. Subsequently, covarying variables were excluded. The dependent variable (deadwood C stock) was logarithmically transformed to meet normal distribution, and dominant tree species (2 levels: pine and spruce), soil type (3 levels: mineral, wet organic, drained organic), mean stand DBH (continuous variable), mean age (continuous variable), mean

Table 1. Main characteristics of studied forest stands and sample plots (mean values ± 95% confidence interval)

Tree species	Soil type	Number of study sites (n)	Number of sample plots (n)	Mean stand age, (years)	DBH (cm)	H (cm)	Total growing stock (m^3 ha^{-1})	Trees per ha (n)
Scots pine	Mineral	26	170	178 ± 15	47.1 ± 5.5	30.8 ± 2.3	568.3 ± 85.5	277 ± 69
Scots pine	Organic drained	13	78	150 ± 19	35.8 ± 2.0	27.9 ± 2.9	490.1 ± 133.5	370 ± 39
Scots pine	Organic wet	13	82	175 ± 15	27.6 ± 2.9	20.7 ± 2.4	293.2 ± 84.8	566 ± 172
Norway spruce	Mineral	17	114	177 ± 13	36.4 ± 6.2	28.5 ± 3.1	391.4 ± 100.0	239 ± 68
Norway spruce	Organic drained	13	78	151 ± 29	34.9 ± 3.9	29.4 ± 3.1	474.6 ± 126.8	349 ± 67
Norway spruce	Organic wet	13	78	159 ± 11	26.4 ± 2.6	24.3 ± 1.9	393.4 ± 96.6	554 ± 179

Table 2. Decay class description, dominant species carbon concentration and basic wood density (Köster et al. 2015)

Decay class	Decay class description	Scots pine		Norway spruce	
		basic density (kg m^{-3})	C concentration (%)	basic density (kg m^{-3})	C concentration (%)
1	The tree recently died, but the bark is intact and has retained colour	381.1	49.03	410.7	48.35
2	The bark has started to fall off, the stem is round, and the wood is still hard	337.2	49.26	354.2	48.31
3	Wood is becoming soft, bark covers < 50%, bark colour is intact	258.8	49.56	280.7	47.93
4	Wood is soft, no bark remains, and the wood structure has disintegrated	233.7	49.58	191.3	49.60
5	Parts of the stem are indistinguishable, wood is very soft and may be covered with plants or mosses	141.8	50.21	124.8	51.33

tree height (continuous variable), basal area (continuous variable), and trees per hectare (continuous variable) were used as fixed effects, but study site and sample plot as random effects. Significant variation ($p \leq 0.05$) in fixed effects was examined with the ANOVA type III Wald χ-square test. The pairwise comparison was used to compare the estimated marginal means of deadwood C stock. Data analysis was performed using the R statistical computing and graphics environment version 4.2.2 (R Core Team 2023), employing the packages "lme4" (Bates et al. 2015) and "emmeans" (Lenth 2025).

Results

Deadwood carbon stock, modes, and decay classes

Mean deadwood C stocks ranged from 4.59 C t ha^{-1} to 11.25 C t ha^{-1} and can be ranked in decreasing order based on soil type: mineral soil > drained organic soil > wet organic soil (Figure 2). Estimated ranges in C stocks exhibit relatively high variability, but, in general, in Scots pine stands, deadwood C stock tends to be higher compared to Norway spruce. The lowest deadwood C stock was observed in Norway spruce stands on wet organic soils (4.59 ± 1.10 t ha^{-1}), which was significantly ($p < 0.05$) lower compared to Scots pine-dominated stands (7.91 ± 2.87 t ha^{-1}). On mineral soils, the mean deadwood C stock for Scots pine was 11.25 ± 1.99 t ha^{-1} and larger by 19% compared to Norway spruce (9.47 ± 1.95 t ha^{-1}). Moreover, Scots pine deadwood C stock on drained organic soils was 9.74 ± 1.85 t ha^{-1} and larger by 9% compared to Norway spruce stands (8.96 ± 1.61 t ha^{-1}), yet, the differences between dominant tree species on mineral and drained organic soils were non-significant ($p > 0.05$). Estimated deadwood C stock are higher compared to that, observed in mature, managed spruce forests (2.6 t ha^{-1}) in Switzerland (Weggler et al. 2012), Sweden (ca 6.4 t ha^{-1}; Fridman and Walheim 2000), and old-growth birch forests (6.3–7.9 t ha^{-1}) on mineral soils in Latvia (Šēnhofa et al. 2020), but similar to old-growth, unmanaged aspen forests (8.2–12.5 t ha^{-1}) on mineral soils and coniferous forests (10–11 t ha^{-1}) on organic soils in Latvia (Šēnhofa et al. 2021, Ķēniņa et al. 2022), and overmature coniferous dominated forests in Scandinavia (ca. 7–11.2 t ha^{-1}; Jonsson et al. 2016).

However, estimated deadwood C stock in this study is lower than that observed in old-growth spruce forests (13 t ha^{-1} of which 7 t ha^{-1} for snags, and 6 t ha^{-1} for lying deadwood) in the Czech Republic (Seedre et al. 2015) and in Estonian mature spruce forests, where deadwood C ranges from 14.5 to 20.6 t ha^{-1} (Rosenvald et al. 2025) but in old-growth coniferous forests from ca. 8–53.5 t ha^{-1} for snags and 3.7–71.6 t ha^{-1} for logs (Lõhmus and Kraut 2010). In addition, the deadwood C observed in virgin forests dominated by European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.) in Romania ranges from 0.4 to 41.2 t ha^{-1} (Petritan et al. 2023). In general, the estimated and compared deadwood C stocks are highly variable. Lower deadwood C stocks in Norway spruce stands on wet organic soils could be explained by lower standing volume and tree dimensions due to harsher growing conditions (due to high soil moisture), where larger tree dimensions, biomass, and C stock can be reached more slowly compared to drained organic or dry mineral soils (Ranius and Fahrig 2006). This partly confirms our first hypothesis that deadwood C stocks are lower in forest stands on wet organic soils; however, this trend did not hold for Scots pine on wet organic soils, where the deadwood C stock was nearly identical to that found in drained organic soils. The highest deadwood values were observed for Scots pine-dominated stands on mineral and drained organic soils, as more productive forests tend to have higher amounts of deadwood due to higher biomass growth rates (Framstad et al. 2013). Estimated higher deadwood C stock in overmature coniferous forests than in old-growth deciduous forests, particularly in birch dominated stands, indicate that coniferous deadwood is more persistent and deciduous trees decompose more rapidly, due to differences in wood density and chemistry, leading to more rapid C loss (Mäkinen et al. 2006, Menichetti et al. 2021), thus coniferous deadwood provides more stable C stocks in the long term.

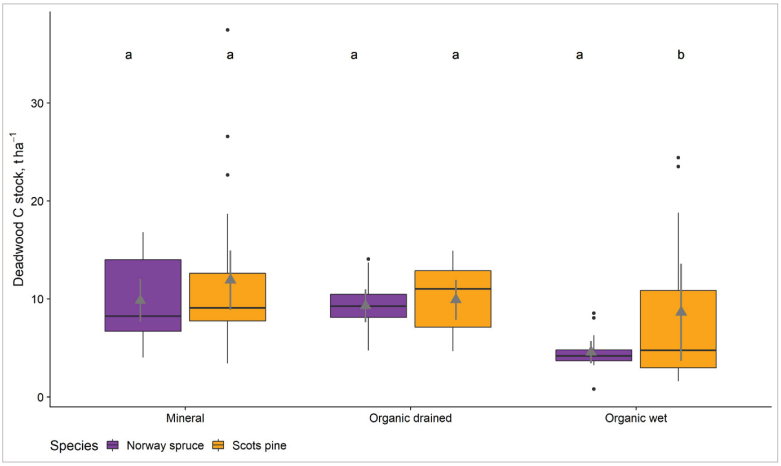

Figure 2. Mean deadwood C stock by soil type group for Scots pine and Norway spruce sample plots

Grey triangles indicate mean values ± 95% confidence intervals; the box plots represent median values and the 25% and 75% percentiles; the whiskers indicate the maximum and minimum values; different letters indicate significant differences.

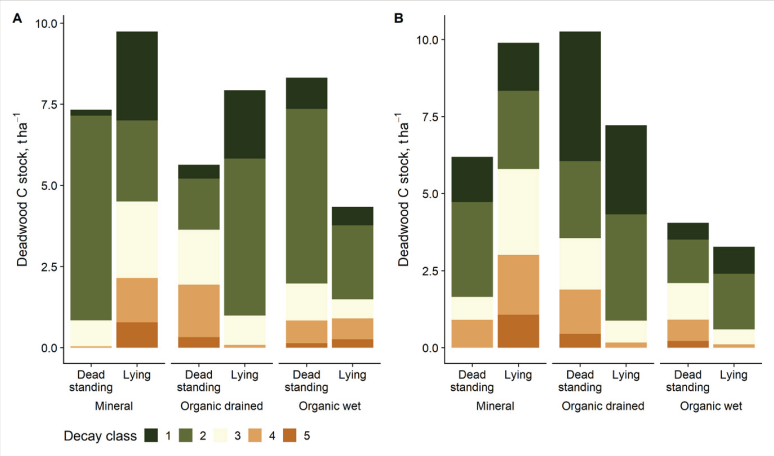

Figure 3. Distribution of deadwood modes (lying deadwood or dead standing tree) and decay classes (1–5) by deadwood C stock in Scots pine (A) and Norway spruce (B) stands on mineral, drained organic, and wet organic soils

The study results indicated variability in C stock across different deadwood modes (Figure 3). In Scots pine stands on mineral soils, dead standing trees and lying deadwood had similar mean C stocks (5.81 ± 0.88 t ha^{-1} and 5.44 ± 1.33 t ha^{-1}, respectively), indicating a relatively balanced distribution between deadwood modes (Figure 3A). On drained organic soils, lying deadwood held more C (5.88 ± 1.02 t ha^{-1}) than dead standing trees (3.86 ± 0.65 t ha^{-1}). In contrast, wet organic soils showed the opposite trend: dead standing trees deadwood C stock was more prominent (5.03 ± 2.04 t ha^{-1}) than lying deadwood (2.89 ± 0.53 t ha^{-1}). In Norway spruce stands on mineral soils, lying deadwood had the highest C stock (6.44 ± 1.34 t ha^{-1}), more than double that of dead standing trees (3.03 ± 1.0 t ha^{-1}). On drained organic soils, C stocks were more evenly distributed, with 4.65 ± 0.73 t ha^{-1} in standing trees and 4.31 ± 0.98 t ha^{-1} in lying deadwood (Figure 3B).

Wet organic soils exhibited low C stocks in both modes: 2.41 ± 0.43 t ha^{-1} in lying deadwood and 2.18 ± 0.49 t ha^{-1} in standing trees. Variability in deadwood C stocks between different soil types and dominant tree species suggests different causes of tree die-off: the natural disturbance, such as bark beetle (*Ips typographus*) infestation, leaves much of the deadwood standing, while windblow uproots dead trees. Moreover, after tree dieback, dead standing trees can remain standing for up to 40 years (Mäkinen et al. 2006) and decompose more slowly due to different microclimate conditions than lying dead wood (Peltola et al. 2000, Šēnhofa et al. 2020).

The degree of deadwood decomposition was classified into decomposition classes (Köster et al. 2015): deadwood with decomposition classes 1–3, due to its prevalence in most sample plots, accounted for the largest proportion of deadwood C stock among the analysed tree species, deadwood decomposition forms and soil type groups. Furthermore, the proportion of deadwood C stock in decay classes 1 to 3 varied by soil type and ranged from 64% to 100% of total deadwood C, while decay class 2 formed the largest proportion in most cases, and decay class 5 was not observed in all soil types and deadwood structures. However, in old-growth forests in Estonia, deadwood in decay class 5 has been observed in relatively higher proportion (Lõhmus and Kraut 2010), thus indicating possible past-management impact in our study sites even more than 30 years ago.

A relatively high proportion of decomposition class 2 indicates slow decomposition at the beginning of tree dieback, as this class represents deadwood, which is still hard. Moreover, the decomposition rates of coniferous trees are not constant, but highly variable and non-linear, with an initial slow decomposition phase after tree mortality, followed by a rapid decay period and a more moderate decomposition phase (Mäkinen et al. 2006). In addition, decomposition rates may vary depending on the mode of deadwood and site conditions (wet or dry), as dead standing trees and branches tend to decompose more slowly than lying deadwood, and C release occurs faster in moist soil (Mäkinen et al. 2006).

Factors affecting deadwood carbon stock in coniferous forests

Deadwood C stock was significantly influenced by soil type (p = 0.03), mean stand DBH (p = 0.03), and stand basal area (p = 0.004), while all other tested parameters were insignificant (Table 3). The model's conditional R^2 was high (0.88), while the marginal R^2 was low (0.11). Stand age and DBH are commonly used as predictors for coarse deadwood volumes (Pregitzer and Euskirchen 2004, Siipilehto et al. 2021). Forest C stocks are generally linked to stand age because higher stand age increases tree mortality caused by competition, self-thinning, senescence, and disturbances (Karjalainen and Kuuluvainen 2002, Kapusta et al. 2020), but our results indicate that stand age in overmature forests is a weak predictor of deadwood C stock.

Table 3. Stand characteristic variables affecting deadwood C stock

Variables	χ^2	*p*-value
(Intercept)	0.39	0.53
Species	2.48	0.12
Soil type	7.16	0.028 **
Stand age	0.01	0.92
Mean stand DBH	4.90	0.027 **
Mean tree height	0.66	0.42
Basal area	8.26	0.004 **
Trees per ha	0.82	0.36

Note: Significant variables ($p < 0.05$) marked with **.

An insignificant relationship between C stock and stand age in most cases may be attributed to the analysis being restricted to overmature stands. The assessed study stands had not been managed for at least the last 30 years; however, a full management history, allowing for the effects of neglecting past management practices and natural disturbances on deadwood abundance to be taken into account, was not available. Past management and natural disturbances can significantly alter stand age and DBH distribution; thus, the insignificance of stand age and deadwood C stock relationship in most cases is not surprising. Similar findings have been reported in local studies in the hemiboreal region (Ķēniņa et al. 2018, Ķēniņa et al. 2022). The results indicate significantly lower deadwood C stock in stands on wet organic soils, emphasising the differences in the tree dimensions and consequently deadwood dimensions in wet soils compared to mineral or drained soils. Overall, our second hypothesis was thus not confirmed, since the significant factors affecting deadwood C stock were soil types, mean stand DBH, and basal area; high uncertainty between study sites and sample plots was also observed, indicating strong other factors (e.g. past disturbances or past management) influence on deadwood C stock.

Past management, even that conducted decades ago, can have a lasting impact on deadwood C stock, as it can shift stand dynamics by promoting homogenization of forest structures and reducing natural mortality rates (Schulte et al. 2007). Moreover, historic thinnings or sanitary cuttings directly reduce the potential of deadwood accumulation and presence in the stand (Rosenvald et al. 2025). Consequently, even forests that appear unmanaged today may retain legacy effects of past management, and any assessment of their deadwood C stock must consider possible historical disturbances.

Tree senescence is also associated with declining growth rates and increased vulnerability of overmature stands (Siipilehto et al. 2021). In combination with senescence, exogenous and endogenous disturbances regulate the influx into the deadwood C pool in unmanaged forests. Natural disturbance sensitivity is often related to the presence of numerous trees nearing their maximum age, either in sparse stands with a few large-diameter trees or in denser stands with a high average diameter. High variability in small- and large-scale die-off and regeneration dynamics in overmature forests results in transitional states both in the C stock of deadwood and in the wider forest ecosystem (Frelich et al. 2020, Palm-Hellenurm et al. 2024).

Natural disturbances play a crucial role in deadwood dynamics (Krankina and Harmon 1995), and the disturbance cycle exhibits considerable variation, as indicated by maximum and minimum deadwood C stocks in sample plots. Tree mortality in forests is a complex process, and rare events, such as wind-throws and bark beetle infestation, are difficult to predict but can significantly impact the presence and size of the deadwood stock. Due to the lack of consistent data on natural disturbance types, gap dynamics were assumed to be the dominant disturbance process in hemiboreal coniferous stands (Angelstam and Kuuluvainen 2004). Surprisingly, the gap dynamics that could lead to a demographic transition appear to be delayed. This delayed transition, combined with the high mortality of large trees, can result in a sudden increase in deadwood C stock. Nevertheless, the deadwood C stock of conifers can have long-lasting storage, which contributes to both biodiversity and C storage goals (Menichetti et al. 2021). This is a very valuable aspect of the changing climate and expected shift in living forest composition (D'Amato et al. 2017).

Conclusions

The estimated moderate C stocks in deadwood showed explicit spatial variability, whilst stand characteristics exhibited limited effects, thus maintaining high uncertainties regarding underlying causes. The estimates were higher than those in conventionally managed commercial stands; however, reported deadwood C stocks in over-mature and old-growth forests in boreal and hemiboreal regions, implying that overmature stands were still in low senescence and deadwood C stocks can increase significantly in the future; however, much is dependent on any disturbances in the forest ecosystems. The high variability of deadwood mode C stocks and decomposition classes indicated inconsistent changes in deadwood C stocks and C release rates, highlighting that deadwood is a dynamic yet depleting C store; however, given the values of carbon storage and biodiversity, larger deadwood sizes are of particular importance, as hinted by relationships with mean diameter.

On the other hand, ageing and larger dimensions of trees increase the vulnerability of the overmature stands to natural disturbances, which would inevitably boost the transition of deadwood C stock as observed in some old-growth and virgin forests.

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Effects of Drainage on Carbon Stock in Hemiboreal Forests: Insights from a 54-Year Study

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Abstract: In the Northern Hemisphere, forests play an important role in carbon storage. During the past few decades in the eastern Baltic and Nordic regions, forest drainage has been a common occurrence, which also has an effect on carbon stock. Most of the studies on this issue were carried out in boreal zones and were focused on short-term effects. Thus, our aim was to evaluate the long-term (after 54 years) effect of drainage on carbon stock (CS) changes in organic soil (Fibric histosols) in hemiboreal forests. Three forest types were selected in drained (*Myrtillosa* turf. mel (Mmel)) and undrained (*Caricoso–phragmitosa* (CP) and *Sphagnosa* (Sph)) parts of the same area. Surface level changes, soil penetration resistance, and soil and tree biomass carbon stock were assessed to evaluate the drainage effect. Drainage caused an average surface level drop of 25 cm, but did not deplete the soil carbon pool, resulting in significantly and substantially higher (2 to 6 times) tree biomass carbon stock. The drainage of organic soils in managed wet forests leads to an increased long-term contribution to climate change mitigation, thus such areas should be established or maintained in conjunction with areas that maximize other ecosystem services to ensure the sustainability of forest landscapes.

Keywords: carbon storage; climate change mitigation; drained forest; organic soil

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1. Introduction

Boreal forests play an important role in global carbon stocks by providing approximately one-third of terrestrial carbon storage [1]. Many peat-forming ecosystems in the eastern Baltic and Nordic regions have been converted into forest land to increase tree biomass production, mostly by improving the growing conditions by reducing excess water using drainage systems consisting of ditches [2,3]. In vast areas of the boreal zone, a high water content in the soil hampers tree growth, especially at sites with mineral or peat soils [4,5]. This is because gas exchange occurs much faster in aerated soils than in water-saturated soils [6]. Furthermore, the subsequent limited oxygen availability due to high groundwater levels negatively affects the functioning of plant roots in terms of oxygen uptake. Therefore, a consistently high groundwater level results in shallow rooting, which leads to higher mortality and impairs tree growth [7].

In the boreal biome, forest soils hold more carbon than overstories [8–11]. Organic soils can be sources of both the emission and removal of greenhouse gases (GHGs; nitrogen (N) and carbon (C)) [12]. Organic soils are produced from partially decomposed plant material under anaerobic conditions through a gradual process of accumulation and compression in peat-forming ecosystems, and they are typically below the high water table [2]. It is known that in organic soils, drainage leads to enhanced aerobic decomposition [13,14], so the mobilization of C and N stores can occur. Previous studies have shown that drainage systems can have both positive and negative impacts on GHG emission and removal at

the landscape level [15–17]. Proper drainage can improve soil aeration, which is essential for the growth of vegetation, including trees [18]. This can lead to increased carbon sequestration, as trees absorb carbon dioxide from the atmosphere and store it in their biomass [12,19,20]. On the other hand, the establishment and maintenance of drainage systems can also cause soil disturbances, which can alter GHG emissions and removal. For example, the excavation of drainage ditches can release previously stored carbon in the soil, leading to increased emissions of carbon dioxide and other GHGs [21,22]. Additionally, the removal of vegetation and the altering of soil structure during the creation of drainage systems can reduce the overall carbon sequestration potential of the landscape and reduce soil carbon input in the first few years. However, in boreal zones, forestry practices based on ditching can be considered environmentally friendly for nutrient-poor boreal peatlands as the peat soil continues to be a CO_2 sink even after drainage [12]. This may be related to changes in litter quality and increased litter production [23,24].

Recently, in hemiboreal regions there have been studies evaluating different carbon pools of forests on dry, wet, and drained mineral and organic soils [25–27]. According to the National Forest Inventory (NFI), 29.7% of the total forest area in Latvia is located on drained soils. Therefore, it is important to consider the potential impact of drainage systems on soil carbon stock and GHG emissions and removal in order to make informed decisions about how to establish and maintain them. This can help to minimize the negative impact and maximize the positive impact on the environment. Recent studies have focused on assessing soil organic layer thickness and soil organic carbon stock [28], and the carbon budget of drained and undrained organic soils [29]. Moreover, there has been an additional focus on GHG emissions from organic soils and even drainage ditches [30,31]. However, knowledge about the long-term impact of drainage on soil subsidence and the influence of drainage ditches on changes in organic soil carbon stock is lacking; therefore, it is important to assess whether drainage (including the maintenance of amelioration systems) is suitable in terms of carbon storage and climate change mitigation measures. Thus, the aim of this study was to evaluate long-term C storage in organic soils and living tree biomass after drainage. The study hypotheses were as follows: (I) soil carbon stock will be higher at drained sites; (II) tree carbon stock will be higher at drained sites.

2. Materials and Methods

2.1. Location of Sample Plots

This study was conducted in hemiboreal forests in the central part of Latvia (N 56°; E 26°) in a catchment area of the Veseta River, which is dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.), with an average growing stock of 50 m^3 ha^{-1}. Stand age ranged from 40 to 110 years. The study area, which contains organic soils (Fibric histosols), originally existed as a transitional mire, corresponding to a hemiboreal vegetation zone. A drainage system was established in part of the study area in 1960, which led to changes in dominant forest types. In 1963, a forest research station was established, and three types of sites were established for our study: *Myrtillosa* turf. mel (Mmel, n = 20; representing poorly acidic peat soil formed by drainage of transitional bog), *Caricoso–phragmitosa* (CP, n = 4; representing moderate fertile, wet, and moderately decomposed peat soil), and *Sphagnosa* (Sph, n = 6; representing acidic peat soil, where groundwater is very shallow and peat is poorly aerated due to the high humidity) [32]. The peat depth in the studied sites was 4–4.5 m. The water table level varied among the considered sites (Figure 1).

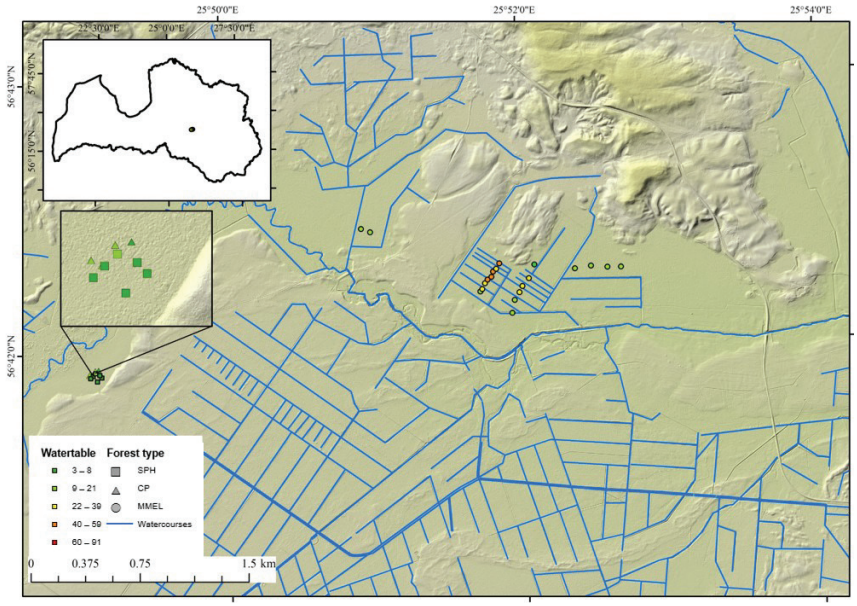

Figure 1. Location of sample plots and level of water table. Colors indicate water table depth; symbols indicate forest types, and the blue lines represent the Veseta River and drainage ditches.

2.2. Field Survey

We established circular sample plots 20 m from transects where the drainage ditches were located. The area of the sample plots was 500 m^2, with a radius of 12.62 m. In each sample plot, tree height and diameter at breast height (DBH) was measured during the last ground surface elevation measurement campaign for all trees > 14 cm to assess stand taxation indices and tree carbon stock. To determine morphometric stand characteristics, we established subplots with a radius of 6.64 m inside the circular sample plots, starting from the same center of the plots. The subplots were divided into quarters. In the quarters located between the north and east cardinal directions (0–90°), DBH was measured for all trees with a diameter of 2 to 6 cm. In the subplots, we determined the species, DBH, and height of the trees. In the 500 m^2 sample plots, we measured the stem diameter at both ends for all lying and standing deadwood trees > 6 cm.

Ground surface elevation was measured using an SEOP DS32 (Tianjin, China) optical nilevel instrument. Ground surface elevation was re-measured several times at the same measurement points in 1960, 1966, 1970, 1972, 1975, and 2014. All measurements in every data survey were carried out at the same drainage ditches. The number of sample plots was equal to the number of measurements of ground surface elevation. P.Zālītis, a scientist who participated in the installation of the drainage systems, took part in the field survey as a consultant.

Resistance to soil penetration was determined at three points in each sample plot: in the center of the plots, 7 m to the east from the center of the plots, and 7 m to the west from the center of the plots. A Royal Eijkelkamp penetrologger (Giesbeek, The Netherlands) was used to determine the resistance to penetration of the soil at depths up to 80 cm. Soil samples were collected in three replicates at each sample plot at four depths: 0–10 cm, 10–20 cm, 20–40 cm, and 40–80 cm. The volume of soil samples was 100 m^3. Sampling was performed using non-disturbing probes by digging soil pits and taking composite samples from a side of each pit at the top, middle, and bottom of each layer. Litter samples were collected in 10 × 10 × 10 cm boxes in three replicates (at the same location where the soil samples were collected).

2.3. Sample Preparation and Measurements

To determine the dry bulk density (kg m^{-3}) and carbon content (g C kg^{-1}) values of the soil samples, the soil and litter samples were dried at 105 °C until they reached constant mass (at least 48 h). A change in mass of less than 0.01% over 4 h was considered constant. The samples were cooled in a desiccator and weighed immediately after being removed. After drying, the soil samples were sieved and ground using an IKA A 11 basic analytical mill. Soil carbon content was determined using a LECO CR analyzer at a temperature higher than 900 °C. Peat subsidence was considered while calculating carbon stock (CS) changes. CS at the control sites was equal to soil CS at 0–80 cm depth, but at the drained sites, it was equal to soil CS at 0–(80–x), where x is subsidence (cm). Changes in CS were calculated as the difference between the CS profiles at the drained and control sites. All fine fallen deadwood samples were stored in a refrigerator using airtight packaging. The samples were dried at 105 °C until they reached constant mass for at least 3 days.

2.4. Calculations and Data Analyses

To assess the differences between stand parameters, we calculated the total biomass, total density, basal area, mean diameter, and height of the dominant species. The volume of living trees and of standing deadwood trees was calculated according to Liepa (Equation (1)) using DBH and tree height values with the respective coefficients for the species [33]:

$$v = \psi \times L^{\alpha} \times DBH^{\beta \lg L + \varphi}, \quad (1)$$

where v is stem volume (m^3); L is stem length (m); DBH is diameter at breast height (cm); ψ α β φ are species-specific coefficients, according to Liepa [33].

The volume of snags and of lying deadwood was calculated according to the formula for a cylinder multiplied by the basic density of a specific tree species in relation to its decay class [34]. The living tree biomass (above- and belowground) was estimated from the DBH and tree height for individual trees (coefficients for specific tree species are summarized in Table 1) based on the local biomass equation (Equation (2)) [35]:

$$lnY_{ki} = \ln(a) + b \times \ln(DBH) + u_k + \varepsilon_{ki}, \quad (2)$$

where Y is the predicted dry biomass of each component of tree i in stand k (kg); H is tree height (m); DBH is diameter at breast height (cm); a, b are regression coefficients (Table 1); u is the random effect for stand k; and ε is the random effect for tree i in stand k.

Table 1. Coefficients of biomass equations for Scots pine and Norway spruce according to Liepiņš [35].

Coefficient	Scots Pine		Norway Spruce	
	a	b	a	b
Stem	2.94	0.020	2.82	0.040
Living branches	1.576	0.201	1.639	0.336
Dead branches	2.102	0.006	3.289	0.000
Stump	2.442	0.007	2.698	0.004
Coarse roots	3.227	0.001	2.998	0.004
Fine roots	1.82	0.017	1.843	0.026

The CS in the living tree biomass was calculated based on the living tree biomass values multiplied by a carbon content of 50% [36,37]. The soil CS was calculated using the carbon content and sample density indicators.

To evaluate the relationship between penetration resistance, soil depth, and water table level, the linear mixed effect model was implemented using the lme4 package. To evaluate the relationship of soil carbon stock between the analyzed site and soil depth, the linear mixed effect model was used, where the significance of the tested fixed and random effects was evaluated by the maximum likelihood approach and the χ^2 criterion.

Tukey's HSD test was used to compare the significant levels of factors. All data analyses were carried out in the program R version 4.0.3 [38] using the lme4, dplR, and emmeans packages [39–41].

3. Results

3.1. Stand Parameters

The main forest inventory parameters (mean DBH, mean tree height, mean basal area, and mean volume) were determined during the study. The mean (mean ± SD) DBH was 20.75 ± 3.51 cm at the Mmel sites, 14.70 ± 3.06 cm at the CP sites, and 7.90 ± 2.33 cm at the Sph sites, and the differences between the sites were statistically significant in all cases ($p < 0.01$). The mean dominant tree height (mean ± SD) was 18.58 ± 2.01 m at the Mmel sites, 15.52 ± 2.07 m at the CP sites, and 9.48 ± 2.75 m at the Sph sites, and the differences between the sites were statistically significant in all cases ($p < 0.01$). The mean (mean ± SD) volume of dominant species was 197.47 ± 70.04 m^{-3} ha at the Mmel sites, 90.72 ± 42.07 m^{-3} ha at the CP sites, and 32.47 ± 35.04 m^{-3} ha in the Sph sites, indicating a positive impact of forest drainage on tree growth (height, DBH, basal area, and volume) because statistically significant differences ($p < 0.01$) were observed only between the drained sites (Mmel) and wet sites (CP and Sph). The mean (mean ± SD) basal area was 20.95 ± 6.84 m^2 ha^{-1} at the Mmel sites, 11.06 ± 4.48 m^2 ha^{-1} at the CP sites, and 4.78 ± 4.75 m^2 ha^{-1} at the Sph sites, and statistically significant differences ($p < 0.01$) were observed only between the drained and wet sites; thus, the wet sites did not differ significantly.

3.2. Soil Parameters

Based on the linear mixed effect model, forest site, soil depth, and water table level showed a complex effect on soil penetration resistance (Tables S1 and S2). At the Mmel sites, soil penetration resistance for all soil depths was similar ($p > 0.05$). At a soil depth of 0–10 cm, the mean (mean ± SD) penetration resistance was 0.47 ± 0.02 MPa. At 10–20 cm, it was 0.43 ± 0.02 MPa; at 20–40 cm, it was 0.43 ± 0.02 MPa, and at 40–80 cm, it was 0.45 ± 0.02 MPa.

3.3. Soil Characteristics

At the CP sites, soil penetration resistance was significantly lower ($p < 0.01$) at a soil depth of 40–80 cm compared to soil depths of 0–10 and 10–20 cm. At a soil depth of 0–10 cm, the mean (mean ± SD) penetration resistance was 0.76 ± 0.05 MPa. At 10–20 cm, it was 0.82 ± 0.05 MPa; at 20–40 cm, it was 0.64 ± 0.05 MPa, and at 40–80 cm, it was 0.49 ± 0.05 MPa.

At the Sph sites, the highest soil penetration resistance was found at a depth of 10–20 cm, which was significantly higher ($p < 0.01$) than at depths of 20–40 and 40–80 cm. At soil depths of 0–10 cm, the mean (mean ± SD) penetration resistance was 0.76 ± 0.04 MPa. At 10–20 cm, it was 0.89 ± 0.04 MPa; at 20–40 cm, it was 0.61 ± 0.04 MPa, and at 40–80 cm, it was 0.47 ± 0.04 MPa. At soil depths of 0–10 cm and 10–20 cm, soil penetration resistance was significantly higher ($p < 0.01$) at the Sph and CP sites than at the Mmel sites, but the values were similar between Sph and CP cm. All significant differences between the soil depths of the soil and the analyzed sites are shown in Figure 2.

Soil subsidence was elevated only at the Mmel sites. Our results show that soil subsidence occurred after drainage (Figure 3). The most intensive soil subsidence occurred during the first years after the amelioration system was established; 10 years after drainage, the top layer of the soil dropped by 12.3 ± 1.9 cm, and after 15 years, the top layer dropped by 15.8 ± 2.1 cm. Peat subsidence decreased over the next 40 years. From 1974 to 2014, the top layer of the soil dropped by 9.9 cm to 25.7 ± 3.5 cm from the initial level (Figure 3).

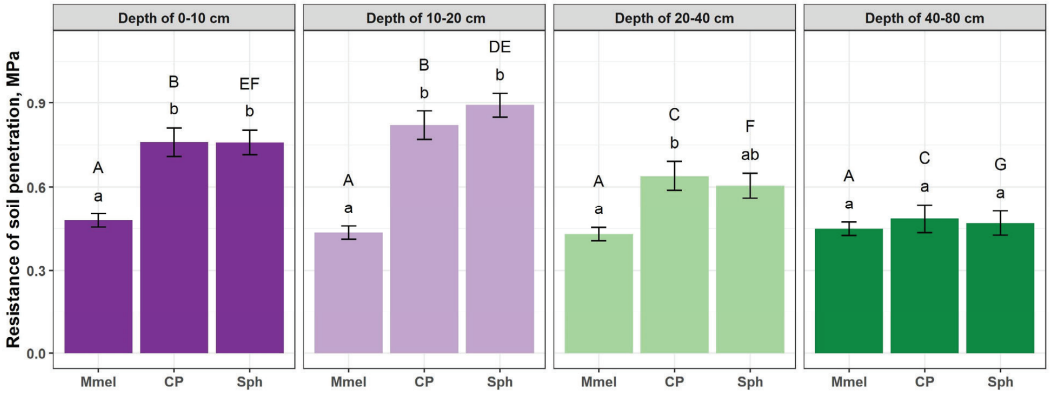

Figure 2. Resistance to soil penetration between certain depths of soil. Mmel, *Myrtillosa* turf. mel. sites; CP, *Caricoso–phragmitosa* sites; Sph, *Sphagnosa sites*. Different letters above bars represent significant differences ($p < 0.05$) in estimated means, as determined using Tukey's HSD test. Lowercase letters indicate significant differences between forest sites within each depth; uppercase letters indicate significant differences between soil depths within forest sites.

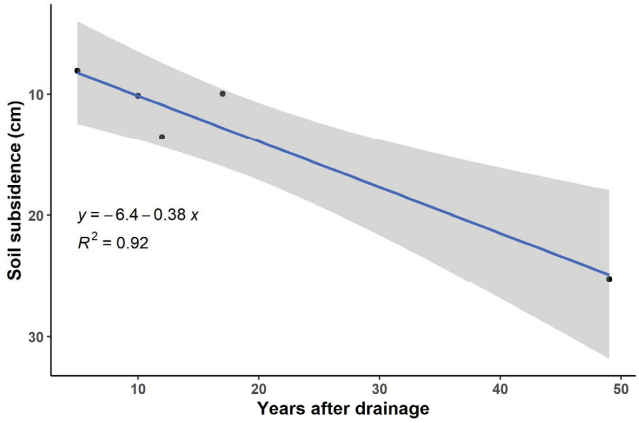

Figure 3. Differences in soil subsidence at various times after forest drainage at *Myrtillosa* turf. mel. (Mmel) sites.

3.4. Carbon Stock

Carbon stock changes in the living tree biomass were evaluated based on the carbon stock in the stems, living branches, dead branches, coarse roots, fine roots, and stumps (Table 2). Soil carbon stock was calculated based on all analyzed soil depths (Table 2). Overall, carbon stock in living tree biomass at the Mmel sites was significantly higher (p value < 0.01) than at the CP and Sph sites (Figure 4).

Table 2. Carbon stock in biomass and soil (mean ± SD). Mmel, *Myrtillosa* turf. mel. sites; CP, *Caricoso–phragmitosa* sites; Sph, *Sphagnosa* sites. O horizon in soil refers to organic layer at soil surface.

Carbon Stock (Tons ha^{-1})	Mmel	CP	Sph
Stem	53.54 ± 15.14	20.94 ± 10.95	6.08 ± 6.94
Living branches	16.20 ± 8.11	7.93 ± 3.21	6.28 ± 5.10
Dead branches	1.38 ± 0.43	0.91 ± 0.34	0.37 ± 0.55
Coarse roots	11.86 ± 4.76	3.55 ± 1.32	1.40 ± 1.67
Fine roots	12.04 ± 4.83	3.61 ± 1.34	1.42 ± 1.70

Table 2. *Cont.*

Carbon Stock (Tons ha^{-1})	Mmel	CP	Sph
Stump	2.47 ± 1.04	1.31 ± 0.51	0.85 ± 0.78
Total in biomass	97.48 ± 27.41	38.27 ± 14.67	16.39 ± 16.12
O horizon	5.08 ± 2.06	0	0
Soil depth 0–10	74.40 ± 16.34	41.80 ± 7.30	37.95 ± 4.52
Soil depth 10–20	67.45 ± 15.01	42.12 ± 8.96	36.10 ± 5.29
Soil depth 20–40	126.55 ± 28.33	85.87 ± 18.83	75.97 ± 16.65
Soil depth 40–80	239.73 ± 52.12	208.12 ± 46.22	189.25 ± 40.31
Total in soil	513.21 ± 106.26	377.92 ± 79.51	339.28 ± 63.77

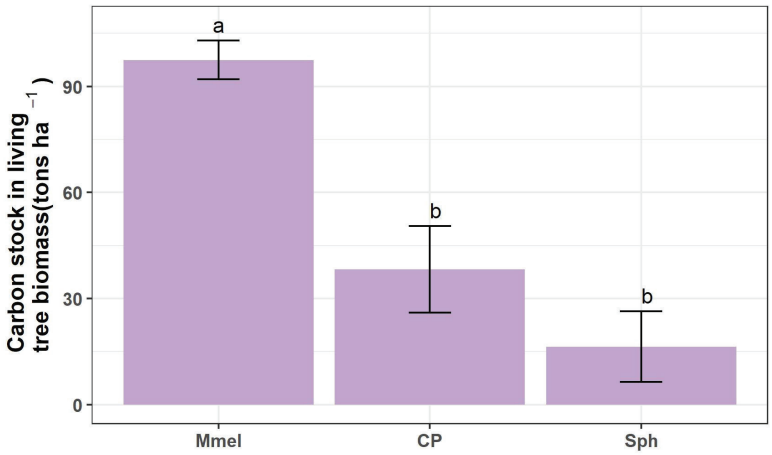

Figure 4. Carbon stock of living tree biomass. Mmel, *Myrtillosa* turf. mel. sites (n = 20); CP, *Caricoso–phragmitosa* sites (n = 4); Sph, *Sphagnosa* sites (n = 6). Different letters above bars represent significant differences ($p < 0.05$) in estimated means, as determined using Tukey's HSD test.

At the Mmel sites, the carbon stock in total living tree biomass was 97.48 ± 27.41 tons ha^{-1}. At the CP sites, it was 38.27 ± 14.67 tons ha^{-1}, and at the Sph sites, it was 16.39 ± 16.12 tons ha^{-1}. The highest carbon stock was found in the stems, and the lowest was found in the dead branches (Table 2). At the Mmel sites, the mean (mean ± SD) tree stem carbon stock was 53.54 ± 15.14 tons ha^{-1}; at the CP sites, it was 20.94 ± 10.95 tons ha^{-1}, and at the Sph sites, it was 6.08 ± 6.94 tons ha^{-1}.

Carbon accumulation in the soil was calculated using carbon content and soil density. Significant differences in estimated means were detected between the soil depths and sites (Figure 5). At soil depths of 0–10 and 10–20 cm, the carbon stock was similar between the forest sites (Table 2); however, significantly higher ($p < 0.01$) soil carbon stock was observed at the drained sites compared to the wet sites (CP, Sph). At greater depths (20–80 cm), the average carbon stock per 10 cm soil layer was lower compared to at 0–20 cm depth, but the differences were significant only between the Mmel and Sph sites. The linear mixed effect model for soil carbon stock determined that forest site type, soil depth, and their interaction were significant factors (Tables S3 and S4). The proportion of variance explaining the fixed effects was high (marginal R^2: 0.89).

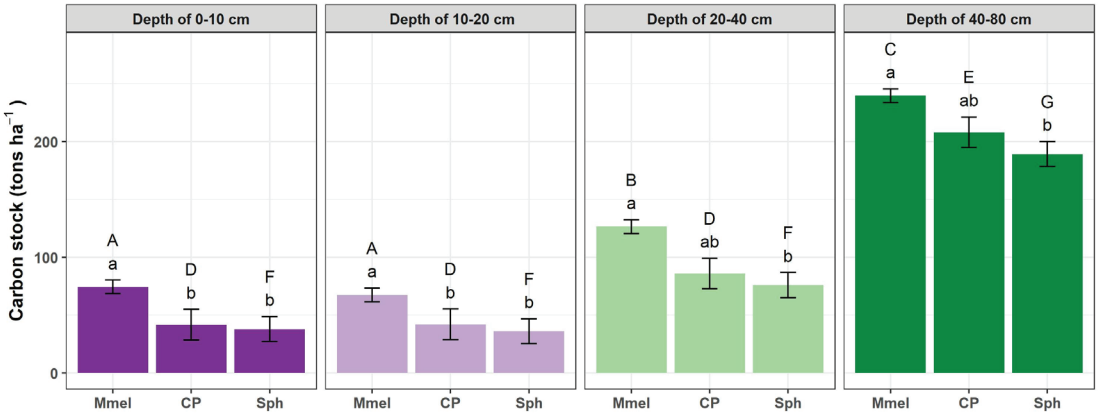

Figure 5. Soil carbon stock at different soil depths. Mmel, *Myrtillosa* turf. mel. sites; CP, *Caricoso–phragmitosa* sites; Sph, *Sphagnosa* sites. Different letters above bars represent significant differences ($p < 0.05$) in estimated mean carbon stock, as determined using Tukey's HSD test. Lowercase letters indicate significant differences between forest sites within each depth; uppercase letters indicate significant differences between soil depths within forest sites.

4. Discussion

Higher values of the forest inventory parameters (mean DBH, mean tree height, mean basal area, and mean volume) were found at the drained sites (Mmel) compared with the CP and Sph sites, resulting in higher tree biomass and tree CS (Table 2, Figure 4), thus validating our second hypothesis. This can be explained by the water table level (Figure 1). The water table level was higher at the Sph and CP sites, which limits oxygen availability for roots and impairs tree growth [7]. Enhanced tree growth and yield as a result of drainage has been reported in previous studies [42,43], but the results for these parameters vary between study sites [44]. In order to make generalized predictions and numerical estimates of additional growth induced by drainage in peatland forests, further studies with an expanded network of sample plots are needed due to various factors, such as ditch network design, site and environmental conditions, and stand history.

Soil penetration resistance was higher overall for the Sph and CP sites compared to the Mmel sites; however, the difference in penetration resistance was more distinct in the 0–20 cm layer than in deeper soil layers (Figure 2). Moreover, soil subsidence is a commonly reported finding in drained organic soils [18,45,46]. A study in Finland reported similar long-term soil subsidence values of 22 to 25 cm [45,46], which is in accordance with our observed soil subsidence results (Figure 3).

In the boreal biome, forest soils hold more carbon than overstories. Our results show that the soil carbon stock among the analyzed groups differed only between the Mmel and Sph sites ($p < 0.05$) when evaluated by the entire soil layer at a depth of 0–80 cm, thus validating our first hypothesis, as drained organic soil stores more carbon than undrained soil. Increased carbon stock in soil and trees has been reported in various studies of hemiboreal and boreal regions [26,46]. Previous studies have also shown that drainage systems can have both positive and negative impacts on greenhouse gas (GHG) emissions and removal at the landscape level [15–17], but the results may not be comparable due to the diverse stand factors. Climate conditions and variables are the main factors determining whether drained organic soil will be a source or a sink, and in boreal forests, drained organic soils mainly continue to act as sinks [19,46]. Therefore, it is important to consider these factors and conduct studies that are specific to the conditions of each individual site.

Our results show that the soil depth had a stronger effect on soil carbon stock than the analyzed site (Figure 5). Carbon stock increased with soil depth, which can be explained by the vertical movement of easily dissolvable organic compounds. After drainage,

the litter decomposition of organic matter on the soil surface accelerates, and C from litter decomposition penetrates into and is subsequently stored in the deeper layers of the soil [47,48]. Litter production (needles, small twigs) plays an important role in the enrichment of carbon storage, which may offset the increased decomposition of soil organic matter after drainage [26,49,50]. In our case, the control sites did not have litter production because of weak tree growth. At the sample sites, litter provided a small amount of carbon stock. However, changes in hydrology due to drainage (lower water table) have an impact on the depth of aerated peat as well as the activity of microorganisms and oxidative processes in the soil, and improved water quality in the form of water flow can increase the availability of cleaner water [12,19]. After drainage, the increased decomposition of organic matter increases plant biomass and primary production; thus, a somewhat higher inflow of C into the ecosystem occurs [23,45].

The long-term impacts of forest drainage depend on various factors, including the intensity of drainage, the properties of the peatland, and the management practices employed. We have shown that over a long period (54 years after drainage), stand biomass (aboveground and belowground) at the Mmel sites compensated for soil CO_2 emissions. Our results suggest that the drained sites did not become a source of CO_2 emissions because CO_2 emissions do not overrun CO_2 assimilation. Similar results were reported in studies in boreal zones in Finland, where the authors concluded that the assimilation of poor drained peat soil carbon exceeded the emissions [12,18,19]. Furthermore, some studies have shown that rich drained peat soils do not become a source of GHGs after drainage [51]. We did not include carbon stock from understory vegetation such as shrubs, herbaceous plants, and mosses in our analysis. However, most of the changes in understory vegetation occur after drainage, as the change from plants adapted to waterlogged conditions to plants that favor drier conditions mostly affects root biomass, according to a study by Murphy, and does not significantly affect the total carbon stock and changes after drainage [52].

In the eastern Baltic region, the drainage of peat-forming ecosystems via ditching is a common practice [2,3], but there is a lack of data about the long-term monitoring of amelioration systems. In order to evaluate CS changes in drained organic soils, ground surface height measurements and soil carbon accumulation analysis should be repeated in a sufficiently large number of forest stands to characterize the different growth conditions and the possible initial state of forest stands. Methodologically, this task could be addressed by selecting new research objects in forest stands in peat forest massifs with drainage systems built 40–50 years ago. Such findings, in combination with the current knowledge, would be valuable for forest management and policy recommendations and help to optimize the management practices for climate change mitigation with the aim of maximizing carbon sequestration as well as reaching and sustaining climate neutrality.

5. Conclusions

The long-term drainage of organic soils in forests resulted in significantly higher tree carbon stock, and drainage did not deplete the soil carbon stock over a 54-year period. However, the effect of drainage was soil subsidence by an average of 25 cm and lower soil penetration resistance in the upper soil layer (0–20 cm). The drainage of organic soils in wet forests can favor climate change mitigation via increased carbon sequestration in tree biomass without depleting soil carbon stock; however, such areas have to be established in conjunction with other ecosystem services to ensure sustainable and multifunctional management at the landscape level. Moreover, further studies are needed to evaluate forests with very poor organic soils to supplement the current knowledge and evaluate the impact of fertility on carbon stock and budget in relation to management practices. The results of this study would be useful for management plans and policy recommendations for spatial planning for the allocation of stands with various targets to ensure that society's needs are met, climate change mitigation efforts are effective, and carbon sequestration is maximized.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su152416622/s1, Table S1: Results of linear mixed effect model of soil penetration resistance; Table S2: Factors affecting soil penetration resistance based on analysis of variance (ANOVA) results; Table S3: Results of linear mixed effect model of soil carbon stock; Table S4: Factors affecting soil carbon stock based on analysis of variance (ANOVA) results.

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RESEARCH

Organic soil greenhouse gas flux rates in hemiboreal old-growth Scots pine forests at different groundwater levels

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Abstract
Tree biomass and soils (especially organic soils) are significant carbon pools in forest ecosystems, therefore forest management practices, in order to ensure carbon storage in these pools and to mitigate climate change, are essential in reaching climate neutrality goals set by the European Union. Overall studies have focused on diverse aspects of forest carbon storage and greenhouse gas (GHG) fluxes from mineral soils, and recently also from organic soils. However, the information about old-growth forests and the long-term effects of drainage on GHG fluxes of organic soils is missing. Additionally, a large proportion of Scots pine (*Pinus sylvestris* L.) forests on organic soils in the hemiboreal region are drained to regulate groundwater level and to improve above-ground carbon storage. The study aims to assess the intra-annual dynamics of soil carbon dioxide (CO_2) and methane (CH_4) fluxes in hemiboreal old-growth Scots pine stands on organic soils with diverse groundwater levels. Six old-growth stands (130–180 years old) were evaluated. In old-growth forests, the main source of soil CO_2 emissions is ground vegetation and tree roots (autotrophic respiration), while heterotrophic respiration contributes to almost half (41%) of the total forest floor ecosystem (soil) respiration. The total forest floor respiration and soil heterotrophic respiration are mainly affected by soil temperature, with minor but statistically significant contribution of groundwater level (model $R^2 = 0.78$ and $R^2 = 0.56$, respectively). The CO_2 fluxes have a significant, yet weak positive relationship with groundwater level ($RtCO_2$ $R^2 = 0.06$ $RhCO_2$ $R^2 = 0.08$). In contrast, total soil CH_4 uptake or release depends primarily on groundwater level fluctuations, with a minor but significant contribution of soil temperature (model $R^2 = 0.67$). CH_4 flux has high variability between stands.

Keywords Carbon dioxide · Groundwater level · Methane · Soil respiration · Sink · Source

Introduction

Greenhouse gas (GHG) emissions are playing a major role in the acceleration of climate change effects, and their concentration in the atmosphere has continued to rise rapidly since the pre-industrial era (IPCC 2014). To tackle the climate crisis European Union (EU) has set a target to reduce greenhouse gas emissions by 55% by 2030 and reach climate neutrality by 2050 (European Commission 2011, 2019). To reach climate neutrality, a balance in policy regulations between air and climate, nature, sustainability and well-being and economic sectors has to be found. Forests play an important role in the global carbon budget and in the climate change mitigation targets, as forestry is the only sector that can store and sequester large amounts of carbon into biomass or soil (Gundersen et al. 2021). It is crucial to understand and promote such forest management practices that contribute to long-term climate change mitigation.

In hemiboreal region, the most significant management measure (in terms of carbon storage and sequestration) is forest drainage, by which annual increment of trees can be improved several times (Sikström et al. 2020). The effect of drainage depends on climate and soil organic composition where the ditch system is established. Additionally, soil GHG emissions are dependent on time since the drainage system has been established (Conchedda and Tubiello

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2020), and on further land use of the drained soils (forestry or agriculture). The long-term effect of forest drainage can result in positive net ecosystem exchange (NEE) of carbon budget (Minkkinen and Laine 1998). However, tree and stand development plays an important role in the carbon balance of organic soils after drainage in boreal regions (Minkkinen and Laine 1998; Lohila et al. 2011), yet less is known about organic soils in the hemiboreal region. Change in soil hydrology due to drainage from anaerobic to aerobic conditions can trigger rapid peat decomposition and influence dissolved organic carbon (DOC) entering water systems (Freeman et al. 2004). However, the influence of soil organic matter composition on peat decomposition and C loss is not fully studied (Bader et al. 2018).

Old-growth forests are forests in late stages of stand development, characterized by old and large dimension trees, large dimension deadwood, various stand canopy layers, species composition and ecosystem functions (Buchwald 2005). Along with biodiversity strategy of EU, the role of old-growth forests has also been emphasized in the EU Climate policy. Therefore, with increasing interest to promote carbon sequestration and GHG balance through processes related to soil biogeochemistry in old-growth forests, it is necessary to acknowledge also long-term drainage ditching effect, which has been performed during past century in large parts of northern Europe (Tong et al. 2022). Scots pine (*Pinus sylvestris* L.) is economically one of the most important tree species in hemiboreal forest zone. Pine forests cover 26.3% of the total forest area in Latvia, but old Scots pine forests (age > 120 years) cover 10% of the total pine forest area in Latvia. Pine forests with organic soils cover ca. 29% of the total pine forest area, of which 14% are drained and 15% are periodically waterlogged (without drainage systems) (NFM 2018). Therefore, it is crucial to estimate GHG emissions from old-growth pine forests on organic soils with diverse groundwater levels. Such information is important in the evaluation of the effects of new drainage systems' establishment or maintenance, and the effect of drainage system dysfunctionality or wetland restoration, which also determines carbon dioxide (CO_2) and methane (CH_4) flux (Tong et al. 2022). Restoration of wetlands by closing the drainage systems has been practiced to favor biodiversity targets (Craft 2016; Minayeva et al. 2017) and ensure carbon storage in wetland soil organic matter (Temmink et al. 2022), as the majority of sequestrated carbon is stored in the soils rather than plants (Moomaw et al. 2018). Nevertheless, biodiversity is important and has to be balanced with carbon storage and climate change mitigation targets. Old-growth forests might positively contribute to both biodiversity and climate change mitigation; but there is still lack of empirical data on GHG balance in such stands.

In recent years, GHG monitoring and assessment of GHG flux trends have been widely studied in relation to improving knowledge on carbon storage, sequestration and substitution of fossil carbon for renewable carbon. The world's largest carbon sinks are oceans, atmosphere, soil (especially organic soils) and forests (Hamilton and Freiss 2018). Any changes in the carbon dioxide balance of the forest ecosystem can have a strong impact on the CO_2 emissions (Bradshaw and Warkentin 2015). The total forest floor ecosystem (soil) respiration (Rt) consists of autotrophic and heterotrophic respiration and comes from both, soil and forest floor. Autotrophic respiration (Ra) includes respiration from plants and originates from plant roots, mycorrhizae and other rhizospheric microorganisms (Bond-Lamberty et al. 2004). Heterotrophic respiration (Rh) is derived from the decomposition of soil organic matter (SOM) and plant residues (Ding et al. 2016). Even though methane is far more radiative forcing and responsive to environmental changes than CO_2, it has received less attention in terms of climate change (Hansen et al. 2013; Neubauer and Megonigal 2015). It is known that forested wetlands (under anaerobic conditions) are significant global source of CH_4 emissions from the soil (Matthews and Fung 1987), however upland forests on drained soils (under aerobic conditions) are functioning as CH_4 sinks (uptake) in the global CH_4 budget (Le Mer and Roger 2001). Recent studies have focused on the assessment of hemiboreal forest carbon pools in old-growth forests of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (Ķēniņa et al. 2018, 2019) relationship of carbon pools with stand age and elevation (Seedre et al. 2015), and chronosequence of carbon storage dynamics in Scots pine stands (Uri et al. 2022). Additionally, Krasnova et al. (2019) studied the net ecosystem carbon exchange in hemiboreal forest ecosystem in relation to tree species composition. Furthermore, studies of soil GHG fluxes from different management practices, e.g. partial and clear-cutting (Korkiakoski et al. 2019, 2023), soil fertilization (Håkansson et al. 2021), and drainage (Von Arnold et al. 2005), soil preparation, hydrology, fire and biodiversity management (Mäkipää et al. 2023) have been carried out. Also, studies have reported soil GHG fluxes after different natural disturbances, e.g. time since fire (Köster et al. 2016), experimental warming and drying after fire (Song et al. 2018), cleared and un-cleared windthrown stands (Köster et al. 2011), and experimental short-term flooding (Schindler et al. 2020). At the same time the information about soil GHG fluxes from old-growth forests with organic soils is missing.

The study aims to assess the seasonal dynamics of soil heterotrophic and total forest floor ecosystem respiration and CH_4 fluxes in old-growth Scots pine stands on organic soils along a moisture gradient. We hypothesize that in old-growth Scots pine stands on organic soils: (1) soil CO_2 efflux will increase with groundwater level decrease; (2) soil CH_4 efflux will increase with groundwater level rise.

Materials and methods

Study area

The study was carried out in the growing season of 2021. The study area is located in the hemiboreal vegetation zone in Latvia, where the climate is described as temperate, yet strongly affected by the Baltic Sea and the North Atlantic. The mean annual sum of precipitation in the study area is 692 mm, and the mean annual air temperature is 6.4 °C. The coldest month is February, with the average air temperature around − 3.7 °C, and the warmest month is July, when the average air temperature is 17.4 °C (LEGMC 2020). Information about the mean air temperature and precipitation during the measurement season of 2021 has been obtained from the Latvian Environment, Geology and Meteorology (Fig. 1a).

Study stands were selected based on soil type (organic soil) with different groundwater levels (with and without drainage systems). The old-growth forest stands selected for investigation within this study were checked in the

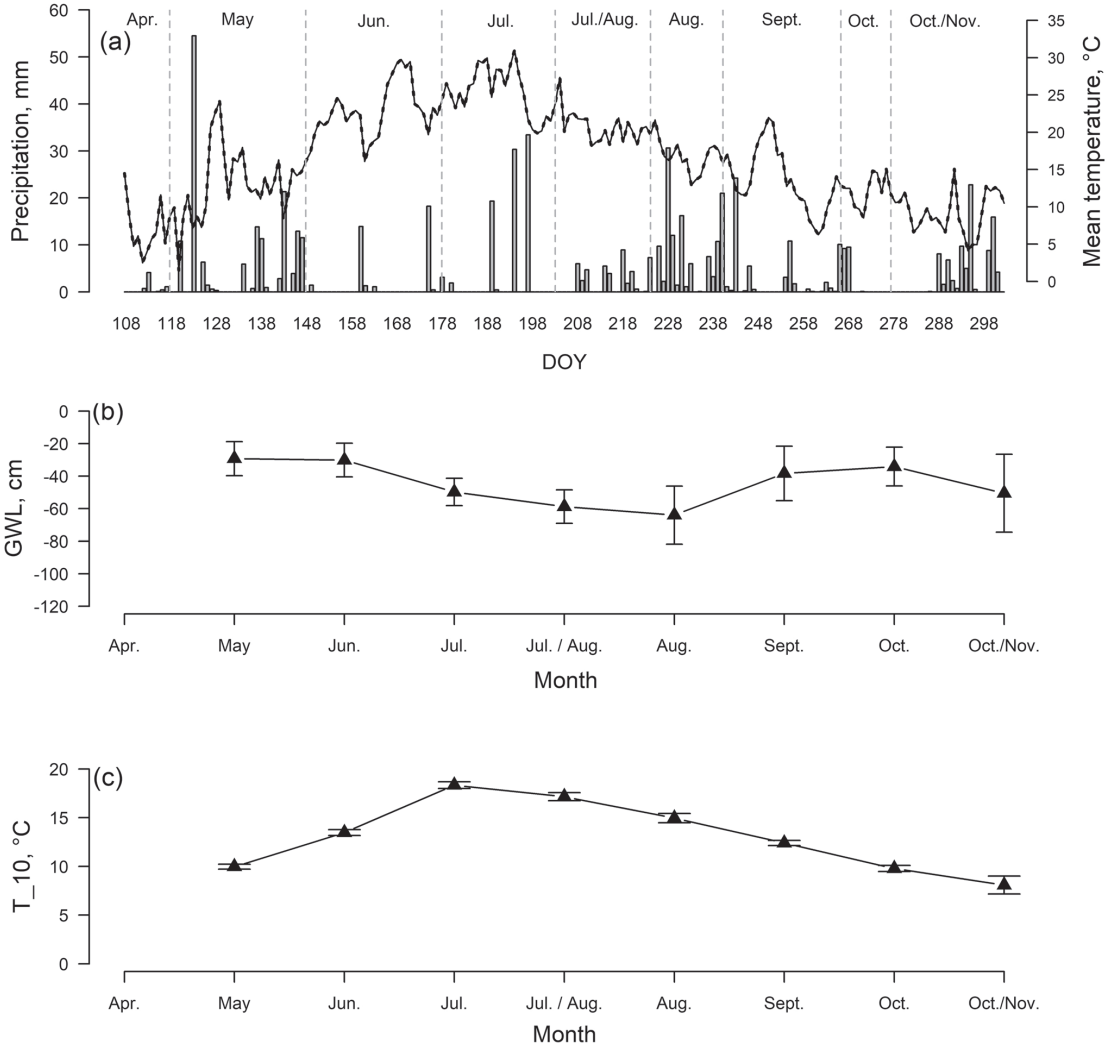

Fig. 1 Precipitation (mm) and the mean air temperature (°C); DOY—day of year; grey lines separate measurement cycles (**a**), the mean groundwater level (GWL) depth (**b**), and soil temperature (T_10) at 10 cm depth (**c**), during the measurement period in 2021 (data: LEGMC, 2020). Whiskers denote ± 95% confidence interval

field for the occurrence of target forest type, age group (> 130 years), the dominance of Scots Pine (> 60% from the basal area), old trees as dominant forest element and no signs of recent human intervention. Selected stands correspond to E. Buchwald (2005) old-growth forest definition's 'n6' category. Altogether six Scots pine dominated old-growth forest stands (130–180 years old) on deep peat soils with different soil moisture regimes and conditions were selected (Table 1). The selected study stands belong to two different forest site types—*Myrtillosa turf. mel*. and *Caricoso-phragmitosa.* The first forest site type –*Myrtillosa turf. mel*. described as fertile, very productive forests on mesotrophic drained peat soil. The organic layer is at least 20 cm thick, composed of cottongrass (*Eriophorum* spp.), tree biomass and small amounts of *Sphagnum* peat. Typically, the canopy is dominated by Scots pine, birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh..), Norway spruce (*Picea abies* (L.) Karst.) with an admixture of black alder (*Alnus glutinosa* (L.) Gaertn.). Ground vegetation is characterized by a dense and diverse herb, dwarf shrub and moss layer, dominated by European blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.), purple Moor-grass (*Molinia caerulea* (L.) Moench.), *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp. The shrub layer is dominated by alder buckthorn (*Frangula alnus*), willows (*Salix* spp.), common juniper (*Juniperus communis*) and rowan (*Sorbus aucuparia*). The second forest site type—*Caricoso-phragmitosa* described as forests of moderate productivity on mesotrophic peat soil. Soil consists of moderately decomposed acidic peat, at least 30 cm thick, composed mostly of sedge (*Carex* spp.), tree and sphagnum biomass. Typically, the canopy is dominated by Scots pine with an admixture of birch, black alder and Norway spruce. The ground vegetation is characterized by a dense herb and moss layer, dominated by sedges, reedgrass (*Calamagrostis* spp.), common reed (*Phragmites australis*), Sphagnum, *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp. The shrub layer is dominated by common juniper, alder buckthorn (*Frangula alnus*), and willows. Increased paludification in such sites causes the forest to change to a pine swamp (Bušs 1997, cited from Jansons et al. 2019). Stands at different forest types differ in soil moisture and groundwater levels due to drainage ditches established in *Myrtillosa turf. mel*. sites and no ditches in *Caricoso-phragmitosa* sites.

Sample plot design

The drainage system was established around the year 1960 (*ca.* 50–60 years ago)—therefore, the peat soil conditions have already changed/adapted as a result of drainage. In each of the selected stands six sample plots (R = 12.62 m, 500 m^2) were established to perform measurements and collection of the main tree variables (tree species, tree height, diameter at breast height, age) to determine the taxation indices (Table 1).

In each selected stand, on three of the six sample plots soil GHG measurements were carried out. Plots were prepared in the winter and early spring seasons (at least one month before measurements) to minimize the effect of root trenching and human intervention during plot establishment on GHG fluxes. The required time for trenched root decomposition is uncertain, however literature reports that decomposition of recently trenched roots occurs in the first two months (Chin et al. 2023). Plot establishment included installation of wooden pathway near the center of each sample plot, to reduce human movement factors on the GHG measurements (Fig. S1 in supplementary material). On one side of each pathway two collars (six collars per stand) for measurements of total forest floor ecosystem respiration were installed (D = 20.1 cm, H = 10 cm) and compacted with sand from the outside to prevent gas leakage. Vegetation inside the collars remained intact. On the other side of each pathway, a root trenching was performed to the depth of 45 cm, water permeable root isolation fabric material (geotextile) was placed and vegetation was removed (once before measurement season) to ensure that emissions were coming only from the organic matter of decomposition. In each prepared (trenched) plot, three heterotrophic soil respiration

Table 1 Taxation indices of old-growth Scots pine forests (average values ± 95% confidence interval)

Stand	Forest type	Age	Tree height, m	DBH, cm	Basal area, m^2 ha^{-1}	Trees per ha^{-1}	C, t ha^{-1}	Average GWL, cm
Auce	Mt	131	32.0 ± 0.6	36.3 ± 2.1	39 ± 12.5	397 ± 93	210.5 ± 64.2	− 87.3 ± 6.1
Ugale	Mt	174	26.2 ± 0.8	36.7 ± 2.2	31 ± 4.4	327 ± 69	159.4 ± 21.6	− 25.7 ± 1.9
Smiltene	Mt	144	24.8 ± 1.2	32.6 ± 2.3	25 ± 4.9	367 ± 81	112.3 ± 20.8	− 16.5 ± 1.7
Jaunjelgava	Cp	159	16.8 ± 0.3	25.6 ± 1.6	21 ± 7.9	600 ± 180	81.3 ± 26.1	− 17.7 ± 3.6
Valle	Cp	179	20.6 ± 0.2	25.9 ± 0.7	21 ± 2.9	393 ± 52	79.5 ± 11.1	− 39.0 ± 4.6
Viesite	Cp	177	20.1 ± 1.6	32.3 ± 5.4	15 ± 4.8	240 ± 102	61.1 ± 24.5	− 22.2 ± 4.0

Mt Myrtillosa turf. Mel, *Cp* caricoso-phragmitosa, *DBH* diameter at breast height, *C* carbon in tree biomass (aboveground and belowground), *GWL* groundwater level

collars (nine collars per stand) were installed in the soil ca. 8 cm deep. The size of trenched plot was 180 × 40 cm, and the distance between collar and root isolation fabric was ca, 10 cm from top and bottom, and ca. 30 cm distance between collars and sides of trenched plot. In each sample plot two groundwater pipes (six pipes per stand) were installed—one for manual water level monitoring and the other one for water sampling (Fig. 1b). To continuously monitor the changes in soil temperature and their influence on soil GHG fluxes, automatic temperature sensors with two depth measurement points (10 cm and 40 cm depth) were installed in the soil in the center of each plot (three sensors with two measurement depths per stand). Measurements were performed at least 1 month after sample plot establishment to minimize trenching artefact influence on GHG fluxes.

Soil GHG flux monitoring

Soil GHG (CO_2, CH_4) flux measurements on each stand was performed at a three-week interval starting from the beginning of the growing season in April 2021 and lasted till November 2021. Overall, the soil GHG measurements were performed in 9 measurement cycles, whereas in each cycle soil GHG fluxes were recorded at different times of the day (morning, noon, afternoon). Morning time corresponds to the time from 9:00 to 11:30, noon time from 11:30 to 13:00, and afternoon time from 13:00 to 17:00.

The total forest floor ecosystem respiration (total CO_2 flux, $RtCO_2$) and CH_4 fluxes ($RtCH_4$) were measured as a CO_2 and CH_4 concentration change in the chamber headspace and was registered for a 5 min chamber deployment time at 2 s interval between data loggings. We used a closed darkened cylindrical chamber (D = 20 cm, H = 30 cm) connected to a cavity ring-down spectroscopy gas concentration analyzer Picarro (Gas Scouter G4301, Picarro, Santa Clara, CA) (Korkiakoski et al. 2019; Villa et al. 2020). Next to the collars, soil temperature was measured (Fig. 1c) at four depths (10, 20, 30, 40 cm) with four temperature sensors connected to a data logger (Comet U0141, COMET SYSTEM s.r.o., Czech Republic).

The heterotrophic soil CO_2 flux ($RhCO_2$) of the trenched plots was measured with Vaisala non-dispersive infrared CO_2 probe (GMP-343, HMP76, MI70, Vaisala Oyj, Finland) using a closed chamber system consisting of a darkened cylindrical chamber (D = 20 cm, H = 40 cm) with inserted CO_2 analyzer, and relative humidity and temperature sensors connected to a data logger (Zhu et al. 2020). The time for each measurement was 5 min with a 5 s interval between data loggings. Additionally, soil moisture (%) and soil temperature (°C) were measured next to each collar inside the trenched plot with a digital thermometer at 5 cm depth (WET-2, HH2 moisture meter, Delta-T Devices Ltd., Cambridge, UK), connected to a data logger.

Additional sampling and measurements

Additional measurements were performed on the same sample plots as GHG measurements. Groundwater level and parameters (water temperature and pH) were measured in each cycle during the GHG measurements. Groundwater level was measured with a tape measure as a distance from the ground surface to the water level. Groundwater temperature and pH were measured with a YSI water quality meter (ProDss, YSI inc., Ohio, USA).

To perform soil chemical analysis, soil nutrient content and pH level, we collected soil samples using an auger (100 cm^3) with two replications per plot (Table 2). The soil samples were collected up to the depth of 40 cm and afterwards divided into 10 cm segments (0–10; 10–20; 20–30; 30–40 cm). Soil analysis was carried out in the certified laboratory of Latvian State Forest Research Institute 'Silava' using ISO standard methods.

Data analysis

Data processing and analysis were performed using the statistical software R 4.1.2. (R Core Team 2021). The linear regression between the measurement time and GHG concentration change within the chamber was used to calculate the flux rates of CO_2 (mg CO_2 m^{-2} s^{-1}) and CH_4 (mg

Table 2 Description of soil characteristics (average of 0–40 cm depth) of the studied stands (average values ± 95% confidence interval)

Stand	Forest type	Organic layer, cm	pH_{KCL}	C:N	Bulk density, kg m^{-3}	Total N, Kg m^{-2}	Total C, Kg m^{-2}
Auce	Mt	92.8	2.9 ± 0.1	43.1 ± 1.2	201.4 ± 7.2	1.06 ± 0.05	45.4 ± 1.8
Ugale	Mt	107.6	4.6 ± 0.2	18.2 ± 0.5	164.7 ± 16.2	1.40 ± 0.06	25.0 ± 0.8
Smiltene	Mt	98.6	4.1 ± 0.1	19.3 ± 0.4	103.7 ± 2.6	1.18 ± 0.03	22.4 ± 0.5
Jaunjelgava	Cp	178.3	4.8 ± 0.1	21.9 ± 1.5	96.5 ± 2.4c	0.98 ± 0.05	20.0 ± 0.5
Valle	Cp	79.3	2.6 ± 0.02	42.4 ± 1.0	88.8 ± 4.9	0.46 ± 0.02	19.2 ± 0.9
Viesite	Cp	71.3	3.0 ± 0.1	37.8 ± 1.5	–	0.58 ± 0.04	22.7 ± 1.9

Mt Myrtillosa turf. Mel, *Cp* Caricoso-phragmitosa. Total N and Total C values are the total sum of the entire 40 cm depth

CH_4 m^{-2} s^{-1}). Model estimates, chamber volume, ground area, air pressure and chamber temperature were used in the flux calculations for each measurement and compiled in a dataset. Model fit of each measurement was assessed with a linear regression model, if the coefficient of determination was lower than $R^2 = 0.80$ then the measurement was omitted and classified as an outlier. The gas flux rates of all measurements were expressed as mg m^{-2} s^{-1}. Seasonal variability was estimated for $RtCO_2$, $RhCO_2$, and $RtCH_4$ flux, the average flux and 95% confidence interval per measurement cycle in each stand were calculated. The average $RtCO_2$ and $RhCO_2$ fluxes of sample plots were subtracted from each other to assess the respiration from roots and ground vegetation ($RaCO_2$). Normal distribution of data was checked with the Shapiro–Wilk normality test. A T-test was used to assess differences in the mean values of parametric variables ($RtCO_2$ and $RhCO_2$). Mann–Whitney U test was used to assess significant differences between the non-parametric variables ($RtCH_4$).

Linear regression was used to assess single factor relationship with $RtCO_2$ and $RhCO_2$ fluxes. To examine the environmental factors affecting $RtCO_2$ and $RhCO_2$ fluxes, linear mixed effect models were developed using the R package "lmerTest" (Kuznetsova et al. 2017). Groundwater level (GWL), soil temperature (T_soil) were used as fixed effects, but stand, sample plot and measurement cycle were used as random effects. Model validation was performed by plotting model residuals versus fitted values, and using the Akaike information criterion (AIC) test. Models with normally distributed residuals and with the lowest AIC values were selected as the best. Significant variation ($p \leq 0.05$) in fixed effects was examined with ANOVA type III test (sum of squares).

Results

CO_2 respiration

The soil CO_2 flux rates were expressed as total forest floor ecosystem respiration ($RtCO_2$) and heterotrophic respiration ($RhCO_2$) from the soil (Fig. 2). In both cases, a clear seasonal trend was visible, as fluxes increased from spring to summer, with the highest values during the peak of the growing season (July and August) and decreased in the autumn. $RtCO_2$ flux ranged from 0.04 to 0.46 mg m^{-2} s^{-1}. The season's average $RtCO_2$ flux was 0.17 ± 0.01 mg m^{-2} s^{-1} (average ± 95% confidence interval). Average $RtCO_2$ flux in drained and undrained sites was 0.18 ± 0.018 mg m^{-2} s^{-1} and 0.17 ± 0.015 mg m^{-2} s^{-1}, respectively. $RhCO_2$ flux ranged from 0.007 to 0.33 mg m^{-2} s^{-1}. The season's average $RhCO_2$ flux was 0.07 ± 0.005 mg m^{-2} s^{-1}. Average $RhCO_2$ flux in drained and undrained sites was similar, 0.08 ± 0.007 mg m^{-2} s^{-1} and 0.07 ± 0.007 mg m^{-2} s^{-1},

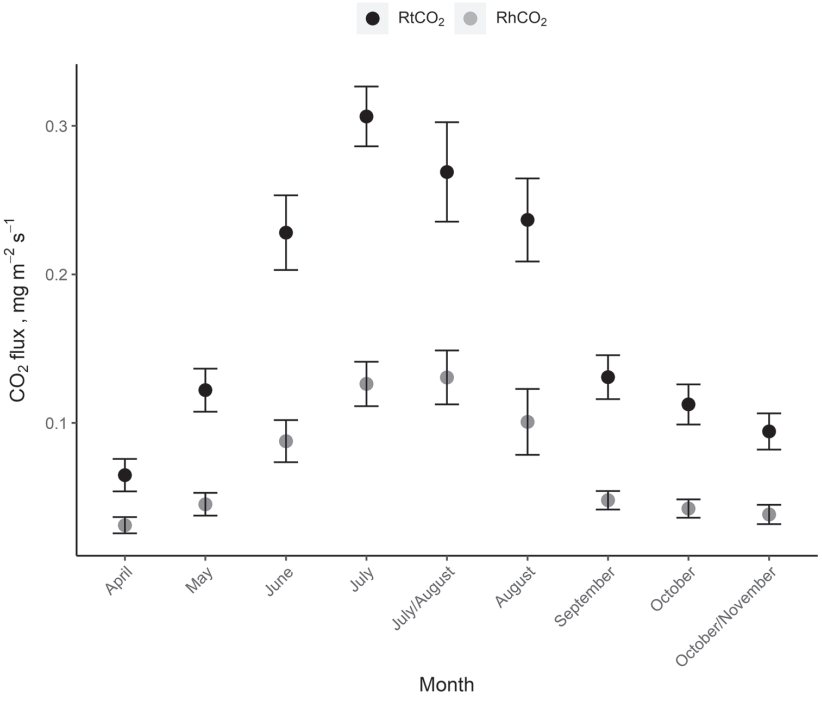

Fig. 2 The total forest floor ecosystem respiration ($RtCO_2$, mg m^{-2} s^{-1}) (**a**) and the heterotrophic respiration ($RhCO_2$, mg m^{-2} s^{-1}) (**b**) from the soil per measurement cycle. Whiskers denote a 95% confidence interval

respectively. The $RhCO_2$ flux in different measurement cycles ranged from 37 to 49%, and on average accounted for 41% of the total forest floor ecosystem CO_2 respiration. Furthermore, the soil autotrophic CO_2 ($RaCO_2$) flux ranged from 51 to 63%, and on average accounted for 59% of the total forest floor ecosystem respiration.

The linear relationship between CO_2 fluxes and groundwater level in analyzed stands was positive and significant ($p < 0.001$), but R^2 was very low for $RtCO_2$ and $RhCO_2$—0.06 and 0.08, respectively. Furthermore, a close significant positive relationship ($p < 0.001$) was observed between the $RtCO_2$ and T_soil, where the R^2 was 0.61 and 0.41, for $RtCO_2$ and $RhCO_2$, respectively (Fig. 3).

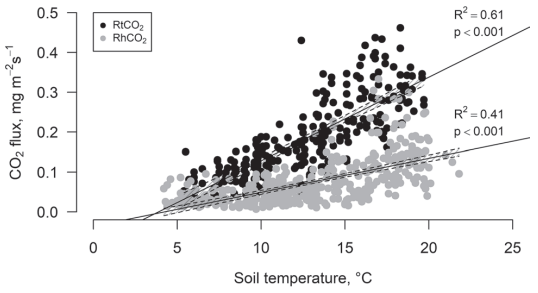

Fig. 3 Relationship between the total forest floor ecosystem respiration ($RtCO_2$, mg m^{-2} s^{-1}) and heterotrophic respiration ($RhCO_2$, mg m^{-2} s^{-1}) and soil temperature (°C). The grey area denotes a 95% confidence interval

Linear mixed effect model for the $RtCO_2$ flux from the soil indicated a significance of soil temperature (T_soil) at 10 cm depth ($p < 0.001$) and GWL ($p < 0.01$). Overall, the model's conditional R^2 was high—0.78 (Table 3 in supplementary material). Linear mixed effect model for the $RhCO_2$ flux from the soil also indicated a significance of soil temperature (T_soil) at 10 cm depth ($p < 0.001$) and GWL ($p < 0.01$). Overall, the model's conditional R^2 was moderate—0.56 (Table 4 in supplementary material).

CH_4 flux

The soil CH_4 flux had an opposite seasonal trend compared to the soil CO_2 flux. Highest CH_4 emissions from soil were observed at the beginning and at the end of the growing season, but CH_4 uptake by soil was observed in the summer (Fig. 4). The soil CH_4 flux ranged from − 1.77e-06 to 2.90e-06 mg m^{-2} s^{-1}. The annual (measurement season) average CH_4 flux was − 2.03e-08 ± 1.18e-07 mg m^{-2} s^{-1}. Moreover, in June, October and November high variability of CH_4 flux rates can be observed, as indicated by notably higher confidence intervals. Season average CH_4 flux rates in drained sites was 1.47e-06 ± 1.24e-06 mg m^{-2} s^{-1}, but in undrained sites 3.60e-06 ± 2.97e-06 mg m^{-2} s^{-1} ($p > 0.001$).

The relationship of $RtCH_4$ flux and groundwater level was negative ($R^2 = 0.39$, $p < 0.001$, Fig. 5) Higher groundwater level promotes CH_4 emissions from the soil, but lower groundwater levels result in CH_4 uptake by the soils.

Linear mixed effect model for the $RtCH_4$ emissions rates could not ensure a normally distributed residual linear

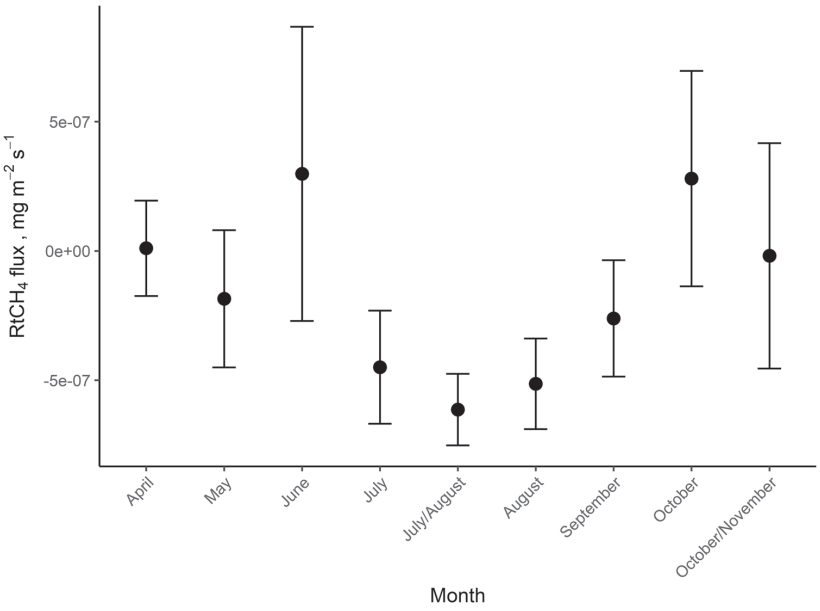

Fig. 4 The soil CH_4 flux ($RtCH_4$, mg m^{-2} s^{-1}) per measurement cycle. Whiskers denote a 95% confidence interval

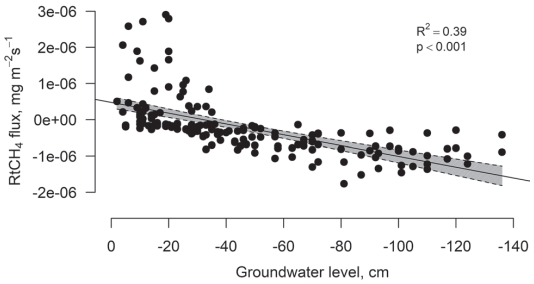

Fig. 5 Relationship between the soil CH_4 flux ($RtCH_4$, mg m^{-2} s^{-1}) and groundwater level (cm). The grey area denotes a 95% confidence interval

fitting, thus the influence of additional factors affecting $RtCH_4$ flux was strong and the model tended to underestimate high CH_4 flux. A good model fit could be obtained only for $RtCH_4$ uptake ($RtCH_4 < 0$; Table 5 in supplementary material), but not for $RtCH_4$ emission flux (Table 6 in supplementary material). The determined significant factor affecting the $RtCH_4$ uptake was groundwater level ($p < 0.001$) and T_soil ($p < 0.001$) with overall conditional $R^2 = 0.67$.

Discussion

In hemiboreal Latvia 14% of the total pine forests on organic soils are drained and 15% are periodically waterlogged (without drainage systems) (NFM 2018), and from climate's perspective it is important to adapt management practices to benefit climate change mitigation goals. The results from our study suggest that the existence of drainage systems alone is not sufficient to characterize the actual soil gas exchange from such areas as no differences between drained and not drained forest stands were observed, possibly due to overdue ditch maintenance at our selected stands. Moreover, the long-term impact of the ditch system has resulted in significantly higher tree carbon stock (Table 1), and significantly higher soil carbon and nitrogen stock over the upper 40 cm for drained (Mt) stands (Table 2). We are aware that our study excludes N_2O emissions and lacks flux data from winter periods (air temperature < 0 °C), which indicates a potential bias, however previous studies suggest low fluxes during winter periods, usually contributing less than 10% of the annual flux (Korkiakoski et al. 2017). Our study deals with one season measurements, thus the results are preliminary.

The studied old-growth Scots pine forests had a similar seasonal trend for $RtCO_2$ and $RhCO_2$ (Fig. 2), as the soil CO_2 flux is lower in spring, then increases during summer and decreases in autumn. The $RtCO_2$ follows similar seasonal trends at all analyzed stands with the main proportion (more than half: 59%) of soil CO_2 efflux is produced by the ground vegetation and tree roots ($RaCO_2$), and 41% originating from the $RhCO_2$ due to decomposition of soil organic matter. A similar proportion of $RhCO_2$ (40–43%) and $RaCO_2$ (57–60%) has been reported in studies of boreal region's afforested peatlands (Berglund et al. 2011; Hermans et al. 2022). Main components of $RaCO_2$ other than tree roots are dwarf shrubs and ground vegetation other than shrubs (e.g. grasses, mosses and herbs), and ericoid and ectomycorrhizal fungal hyphae which has been estimated as a proportion of $RtCO_2$ as 10%, 8%, and 4%, respectively (Ryhti et al. 2021). The required time for trenched root decomposition is uncertain, however literature reports that decomposition of recently trenched roots occurs in the first two months (Chin et al. 2023). Moreover, soil trenching and geotextile insertion might influence soil moisture conditions, which may affect decomposition of soil organic matter (Savage et al. 2018), therefore might result in $RhCO_2$ underestimation in these areas (Chin et al. 2023), as direct comparison of soil trenching influence on soil moisture between trenched and un-trenched plots is not possible due to experimental setup.

Moreover, the seasonal variability of the soil CO_2 fluxes (both $RtCO_2$ and $RhCO_2$) are driven by soil temperature (T_soil) and groundwater level. In our study the highest soil CO_2 flux was observed in July (Fig. 2), when the average air and soil temperatures were the highest (Fig. 1a, c). Overall, the peak of soil $RtCO_2$ flux during summer in old-growth stands was of similar magnitude compared to control plots of a study carried out in Finland (boreal region) in Scots pine stands on organic soil (Korkiakoski et al. 2019). In August, the air temperature was already decreasing, but soil temperature and consequently the total forest floor ecosystem respiration was still high. Such lack of clear link between air temperature and soil CO_2 flux can be explained by the lag effect, also mentioned in other studies, where soil CO_2 fluxes had delayed response to air temperature change (Kukumägi et al. 2017; Uri et al. 2022). The observed significant positive relationship between groundwater level and the soil CO_2 flux (both $RtCO_2$ and $RhCO_2$) indicates that soil CO_2 fluxes can be expected to decrease if the groundwater level increases. However, coefficient of determination was very low in our study, indicating stronger influence of other factors on soil CO_2 fluxes. Therefore, our proposed hypothesis that soil CO_2 flux decreases with a rise of groundwater level was partly confirmed, and similar relationship have been reported also in other studies (Von Arnold et al. 2005; Jungkunst et al. 2008). However, some studies have also reported a weak impact of groundwater level rise on soil CO_2 flux (Olefeldt et al. 2017; Minkkinen et al. 2018) which is also partly confirmed in our study by low values of coefficient of determination. Studies report that soil moisture content regulates CO_2 fluxes, at high soil moisture, aerobic respiration is limited by diffusive supply of oxygen, but at

low soil moisture CO_2 production is favored, yet limited by a diffusion of organic C substrate, thus at intermediate soil moisture CO_2 flux peaks (Movano et al. 2012; Fairbairn et al. 2023). Furthermore, some widely acknowledged models use soil temperature as a single predicting variable (Reichstein et al. 2005), however results of linear mixed effect models for $RtCO_2$ and $RhCO_2$ (Tables 3, 4 in supplementary material) highlights the significance and importance of soil temperature and groundwater level, thus soil CO_2 fluxes can be predicted with high certainty with T_soil and GWL as predictors.

The most important factor affecting the soil CH_4 flux ($RtCH_4$) is groundwater level—if it is close to ground surface, the soil emits CH_4, and if it is low, the organic soil can function as a CH_4 sink, however, our results indicate high variability of CH_4 fluxes (Fig. 4). The negative linear relationship between the $RtCH_4$ and groundwater level was significant (Fig. 5, $p < 0.001$). Previous studies have reported that the lowering of groundwater level promotes soil oxygenation, thus enhances the process of mineralization of organic matter as decomposition under aerobic conditions is faster (Clymo 1984). Oxygen pressure regulates the production of CH_4, therefore groundwater level change to lower (stand drainage) has the potential to reduce the CH_4 efflux from the soils (Elberling et al. 2011), and in the analyzed old-growth Scots pine forests even ensures CH_4 uptake. Studies from boreal and hemi-boreal regions have reported that maintenance of GWL 20–30 cm below ground surface results in CH_4 uptake (Butlers et al. 2023; Tong et al. 2022), however relatively high GWL (0–20 cm) and soil close to saturated conditions may facilitate CH_4 production (Korkiakoski et al. 2019), and such coherence has been observed also in our study. Thus, our second proposed hypothesis that soil CH_4 efflux increase with groundwater level rise was confirmed. Study results indicate that $RtCH_4$ uptake can be predicted with GWL and T_soil as variables with relatively high certainty (Table 5 in supplementary material); however mixed effect model of $RtCH_4$ emissions (release) did not show any significance of analyzed environmental parameters, indicating strong other factor influence on CH_4 release (Table 6 in supplementary material).

Old-growth forests on organic soils with naturally low GWL, or regulated with ditch systems to reduce excess water, has the potential to ensure CH_4 uptake and increase tree carbon stock (Fig. 5, Table 1), thus having a significant long-term contribution to climate targets. Observed insignificance of drainage system (forest type) indicates a ditch system malfunction and overdue ditch system maintenance, thus in the long-term increasing groundwater level and promoting soil moisture saturation. Ditch system maintenance is recommended 1 to 2 times during the stand rotation in order to keep favorable drainage conditions for tree growth, but due to additional costs, it can be avoided on stands where it contributes little to stand productivity (Sarkkola et al. 2013). However, the legacy effect of uncleaned ditches might result in CH_4 efflux from soil and create local hotspots for high CH_4 flux in the waterlogged areas in the forest or near the ditch (Tong et al. 2022).

From the carbon storage and climate change mitigation perspective fertile drained old-growth forests can store more C in tree biomass compared to not drained stands (Ķēniņa et al. 2022), and ensure CH_4 uptake (Le Mer and Roger 2001; Von Arnold et al. 2005), while CO_2 respiration can be elevated in stands with low groundwater levels (Freeman et al. 2004; Von Arnold et al. 2005), but possibly compensated with more C stored in biomass. Moreover, old-growth forests are commonly associated with structural complexity and species diversity at the latter stages of development (Buchwald 2005). Typically, a substantial quantity of woody debris is present in various decay stages of decomposition and this creates a habitat for multiple organisms (Herrmann et al. 2015). Old-growth forests on organic soils require further studies to assess other (especially broadleaved) dominant tree species, that may have different effects on ground vegetation and soil, thus also GHG fluxes. Moreover, forest management practices that contribute to long-term climate change mitigation may significantly impact the biodiversity measures in old-growth forests, which was not within the scope of this study.

Conclusions

The study reveals novel information about old-growth Scots pine forest organic soil GHG fluxes. The main source of total forest floor ecosystem respiration is autotrophic respiration (ground vegetation and roots) contributing more than half (59%) to the total respiration, while the heterotrophic respiration contributes slightly less (41%) to the total forest floor ecosystem respiration. The soil CO_2 fluxes demonstrate a clear seasonal trend and are closely linked to soil temperature indicating the potential increase of CO_2 efflux as the climate is warming, and significantly but weaker linked to groundwater level, indicating CO_2 flux decrease if groundwater level rises. The dynamics of CH_4 fluxes have high variability, however largely driven by groundwater level fluctuations: if the groundwater level is low, the organic soil functions as a CH_4 sink. A drainage system that reduces the excess groundwater level ensures a long-term positive (from a climate change mitigation perspective) effect on soil CH_4 uptake, however can result in elevated CO_2 efflux.

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Declarations

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TREE LITTER PRODUCTION IN CONIFEROUS OLD-GROWTH FORESTS ON ORGANIC SOILS

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Abstract
Canopy litterfall is a vital component of forest ecosystems, facilitating nutrient and organic carbon transfer to the soil. Understanding litterfall dynamics in forests is crucial for assessing carbon fluxes at the national level and refining carbon balance estimations. However, information about aboveground litterfall dynamics in old-growth forests remains scarce. The aim of the study was to characterize the annual litterfall carbon input in coniferous old-growth forests on drained and undrained organic soils. In total, 12 old-growth Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst) forests stands with the age range of 146 – 171 years were selected. Using cone-type litter traps, we obtained data on litterfall volumes over a one-year period. Our findings reveal that old-growth forest annual carbon input from litterfall exceeds estimates of mature forest stands aboveground litterfall. In drained sites, mean annual litter carbon input reached 2.80 ± 0.29 t ha^{-1} yr^{-1}, while in undrained sites, it amounted to 2.17 ± 0.17 t ha^{-1} yr. Basal area and deadwood showed a close positive correlation with annual litter carbon input, underscoring the peculiarities of late successional forest stand carbon dynamics. Total stand basal area as easily measurable forest inventory parameter was the best predictor of annual litter C input for practical application.
Key words: Canopy litterfall, carbon dynamics, drainage, overmatured forests, peat soil.

Introduction

Canopy litterfall of forest ecosystems is a significant component of net primary production that constitutes a fundamental pathway of carbon (C) and nutrient input to the forest floor. It has been estimated that litterfall of European forests transfer 351 Tg C, 8.2 Tg N, 0.6 Tg P and 1.9 Tg K annually (Neumann *et al*., 2018). In a forest ecosystem, litterfall is the main source of organic material that is forming humus and organic layers of soil. Furthermore, the chemical composition and quantities of litter are affecting soil microbial activity, litter decay rates and thus dynamics of soil organic matter (SOM) of forest soils. Litterfall storage and decomposition rates in turn has effect on C and nutrient cycling and thus affecting soil fertility. Site type has a strong effect on organic layer buildup and decomposition rates, where moisture regime is the main factor affecting these processes.

Canopy litterfall of forest ecosystem consists of diverse fractions of organic material. In general, three main fractions can be distinguished:

1. Fine litter – not always well-defined small size particles of organic matter, that includes buds, needles, leaves, barks. Needle and leaf litter production has a strong periodicity. In stands of younger age, there is a higher proportion of needle litter compared to older stands, relative to the total amount of litterfall. In a study conducted on Scots pine stands in Sweden, needle litter accounted for 83% of the total litterfall in stands aged 18-25 years. However, in older stands (120-126 years), this proportion decreased to 58%. Typically, mature stands that have reached a stable state show a decrease in annual litterfall production with minimal variation between years.
2. Branch and twig litter cannot be consistently attributed to specific periods but is rather influenced by particular weather events such as wind storms, heavy rain, or snowfall. A greater proportion of woody parts in litter is observed in middle to old stands due to increased branch mortality associated with older trees.
3. Cone litter is strongly reflecting periodicity and clear increase with increasing age of the stand.

Foliar litterfall exhibits distinct patterns among species in both boreal and temperate zones. For pines of boreal forest zone needles are shed regularly on average every 4 years with most of the litterfall (ca. 70%) occurring in the autumn. Spruce on the other hand, has completely different needle litterfall pattern, since needles can hold up to 10 years on shoots, and litterfall is continuous, meaning that needles that are located on a single shot can be of different years (Berg & Laskowski, 2006). Therefore, in contrary to pine, not all needles on a shot are shed on the same time. Spruce has no specific period at which most of needles fall, as it is for pine, so for spruce the needle shed is occurring all over the year with somewhat higher needle fall in the winter time. For both conifer species, dry periods can increase the needle litter fall. For deciduous trees, leaf litter fall is usually occurring in a short period in the autumn.

Annual litterfall production is influenced by various factors, including local and regional climate, soil nutrient status, and stand characteristics such as age, composition, and basal area. Management practices, such as fertilization (Jansone *et al*., 2020) and tree genetics (Matisons *et al*., 2019.), influence tree growth rates and consequently impact litter production variation between forest stands. Climate characteristics, including temperature and precipitation, strongly influence litter production. Litterfall in the boreal zone tends to be relatively low compared to temperate continental zones, while regions with a Mediterranean climate exhibit different litterfall patterns and quantities altogether. In a study conducted in Sweden within the boreal zone, Scots pine mean annual litterfall ranged from 530 kg ha^{-1} $year^{-1}$ near the Arctic Circle to 3700 kg ha^{-1} $year^{-1}$ at latitudes of 57° N (in southern Scandinavia). Under relatively similar growing conditions regarding soil fertility, needle litter fall tends to be lower in drier and

cooler climates. The lowest amount of litter fall is predominantly observed in nutrient-poor sites, where the basal area is generally low. Basal area serves as a widely utilized forest stand index, successfully employed in modeling annual litterfall within forest stands of various species and potentially at the genus level. Litterfall models are valuable tools for forecasting annual litterfall and contribute to the development of soil organic carbon models (Viskari *et al*., 2022). A study in Sweden effectively integrated litterfall measurements from various species, including Scots pine and Norway spruce, into the same regression model (Berg & Meentemeyer, 2011). The findings revealed that Scots pine generally produces a greater overall quantity of litter compared to Norway spruce, as measured by total litter. However, it was observed that Norway spruce tends to produce more needle litter compared to Scots pine.

Reliable data on litterfall, obtained from litter traps across different species and site types, is crucial for a wide audience, including soil scientists involved in modeling soil organic carbon and policymakers responsible for estimating greenhouse gas emissions at the national level. Recent regional studies have provided insights into litterfall dynamics on drained and undrained organic soils for various tree species highlighting notable variations in carbon input across different stand ages, particularly between young and middle-aged stands. Yet there remains a gap in understanding litter production in old-growth forests. The structure of old-growth forests, including dominant and secondary canopy layers, as well as increased deadwood formation, significantly influences overall canopy litterfall. Nutrients released from decaying deadwood influence soil nutrient status (Khan *et al*., 2021), which can subsequently impact canopy litterfall production (Berg & Laskowski, 2006). This study aims to address this gap by characterizing the annual litterfall in coniferous old-growth forests on drained and undrained organic soils.

Materials and Methods

The research was conducted within the hemiboreal zone located in Latvia. Temperate climate is influenced by the Baltic Sea and the North Atlantic. Average annual precipitation is 692 mm and maintains a mean annual air temperature of +6.4 °C. February is the coldest month with an average air temperature of approximately -3.7 °C, while July is the warmest month, recording an average air temperature of +17.4 °C, according to data from the Latvian Environment Geology and Meteorology Centre.

In total, 3 objects were selected for each tree species and site type 'Figure 1'. Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst) as dominant species of the forest stand were selected, where proportion of dominant species ensures at least 50% of stand composition (standing stock). Two site types with organic soils, characterized by different moisture regime, were selected for the study: an undrained site classified as *Caricoso-phragmitosa* and a drained site classified as *Myrtillosa turf. mel*. according to local forest typology (Bušs, 1997). Stand measurements and calculations of stand parameters were conducted following the local old-growth conifer stand characterization methodology outlined by Ķeniņa *et al*. (2018). Stand characteristics of mean diameter at breast height (D, cm), tree height (H, m), basal area (G, m^2 ha^{-1}), standing stock (M, m^3 ha^{-1}) and stand density (N, trees per ha^{-1}) for dominant and secondary canopy layer (Table 1).

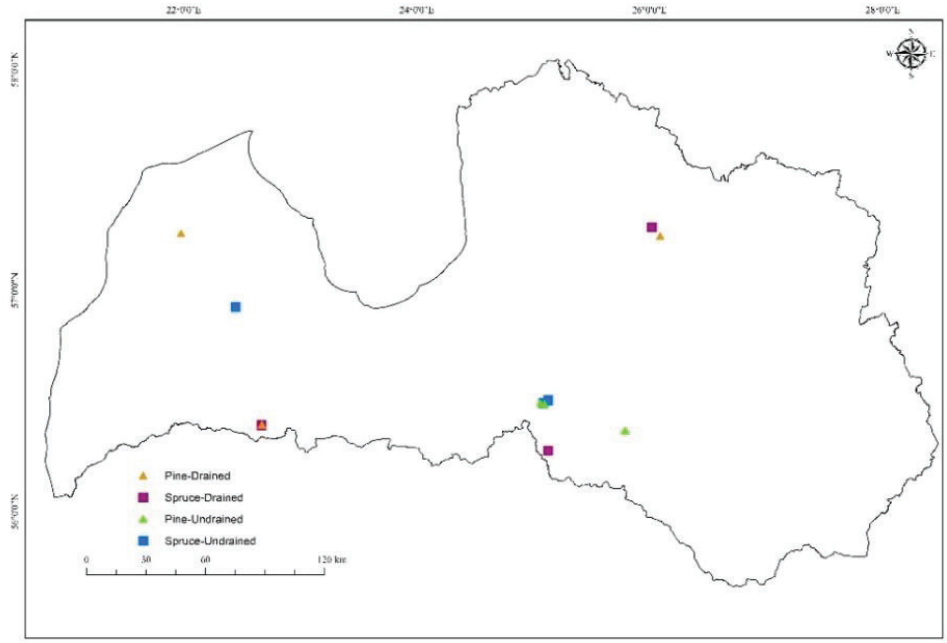

Figure 1. Research objects.

Table 1

Forest stand mean values of stand parameters

Species	Site type	Age	Dominant canopy layer					Secondary canopy layer				
			D1	H1	G1	M1	N1	D2	H2	G2	M2	N2
Spruce	Drained	162	34.0	28.9	33	443.0	367	14.8	14.9	3	21.9	157
	Undrained	153	25.7	24.1	36	428.7	664	12.5	13.7	3	24.8	266
Pine	Drained	150	35.2	27.7	32	404.7	363	16.1	16.1	7	59.5	423
	Undrained	172	27.9	19.2	19	168.1	411	9.7	9.3	5	27.1	644

Note: D1; D2 – mean diameter at breast height (cm); H1; H2 – mean tree height (m); G1;G2 – mean basal area (m^2 ha^{-1}); M1; M2 – mean growing stock (m^3); N1;N2 – mean tree count (trees per ha^{-1}).

Six conus shaped litter collectors, each with a diameter of 110 cm and an area of 0.95 m², were positioned at a height of 1.3 m above the ground along a transect in each stand. At the base of each litter collector, a litter bag was attached to accumulate all aboveground litter. Litter bag samples were collected over full calendar year with intervals of 2 weeks during the spring, summer, and autumn seasons. Winter litter was collected once in early spring and combined with spring litter. Samples were dried at a temperature of 70°C until reaching constant mass and then weighed. Carbon content of total aboveground litter was assumed as 50% of the litter dry weight mass.

Results and Discussion

Both conifer species in drained sites demonstrated generally higher litter quantities, with a concurrently higher variability in data compared to undrained sites. However, the difference between site types did not reach statistical significance (Table 2). In drained sites, pine stands exhibited higher carbon input via litter, while in undrained sites, higher litter carbon inputs were observed in spruce stands.

The estimates from northern European forests suggest an average carbon input through total tree aboveground litter of 1.7 ± 1.1 t C ha^{-1} yr^{-1} for conifer stands (Neumann *et al*., 2018). In contrast, local study estimated the carbon input for young to middle-aged conifer stands growing on drained organic soils to be slightly higher at 1.82 ± 0.02 t C ha^{-1} yr^{-1} (Bārdule *et al*., 2021). Our results indicate that old-growth forests can achieve even higher annual carbon input through aboveground litter, with mean values of 2.80 ± 0.29 t ha^{-1} yr^{-1} and 2.17 ± 0.17 t ha^{-1} yr^{-1} in drained and undrained sites, respectively.

Table 2

Mean annual litter fall biomass and C input

Species	Site type	Litter biomass t ha^{-1} $year^{-1}$	SE	Litter C t ha^{-1} $year^{-1}$	SE
Spruce	Drained	5.05	0.74	2.53	0.37
	Undrained	4.73	0.55	2.37	0.28
Pine	Drained	6.16	0.89	3.08	0.45
	Undrained	3.95	0.35	1.98	0.28

Such difference in annual litter production compared to other studies could be explained with additional litter input by second layer trees (Table 1). Although it is considered that stands exceeding age of 120-130 years are rather stable in terms of annual litter production, Berg & Laskowski (2006) documented an increase in annual litter production within overmatured (>120 years) Scots pine stands over an 8-year survey period. Seasonal litterfall does not exhibit any distinct patterns 'Figure 2', unlike what was reported by Berg and Laskowski (2006), who found that 70% of Scots pine needles were shed in the autumn unless a dry summer occurred. Although in both site types, Scots pine litterfall shows the highest rates in autumn, the differences are not as pronounced. Therefore, it is possible that our study's dry summer may have influenced these results, or other factors may be affecting seasonal litterfall altogether. To better understand seasonal variation, further research spanning multiple seasons should be conducted. For spruce, it has been reported that no clear litterfall season is registered, but needles are shed throughout the year with somewhat higher rates in autumn and winter (Berg & Laskowski, 2006). Our results show that the highest seasonal rates differ between site types: for spruce in drained sites, the highest rates are observable in summer, while in undrained sites, they occur in autumn.

Local study by Butlers (2023) shows that the age has the closest relationship (R=0.8) with the total biomass of tree crown litter; however, our results do not align with this statement, showing weak negative association (R= -0.006). This suggests that old-growth forests in late successional development (age > 150 years) may exhibit distinct pattern in the relationship between stand age and litter production.

However, in our study, this assertion cannot be confirmed due to insufficient evidence, primarily stemming from the low number of stands available for such analysis.

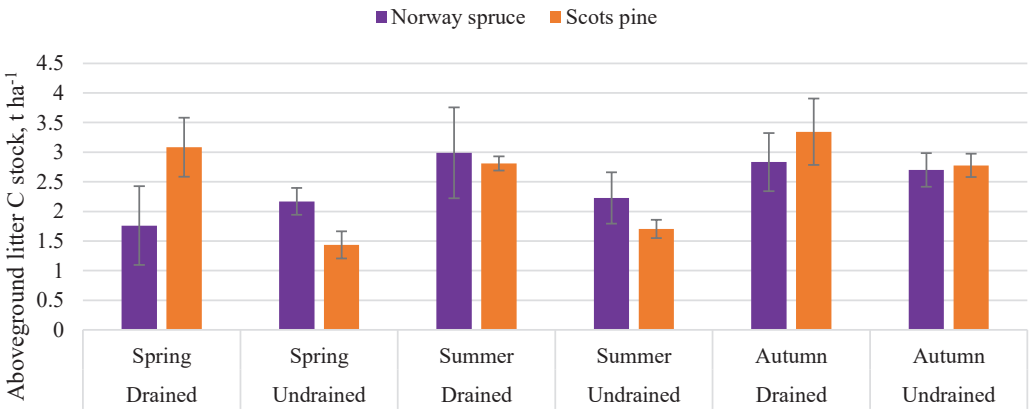

Figure 2. Seasonal aboveground litter C stock (Whiskers denote ± 95% confidence interval).

Our results show positive moderate correlation between annual litter C input and stand characteristics such as mean tree diameter and height of dominant canopy layer (Table 3). Our results reveal a stronger correlation when the secondary canopy layer is included, as observed in the correlation with total basal area (G_{total}) and total standing stock (M_{total}). The strong positive correlation (R = 0.77) between total deadwood volume and litter production is noteworthy. However, establishing causation in our study is challenging due to the lack of experimental design. A simpler explanation could stem from the observation that dead standing trees, with remaining yet collapsing crowns, continue to produce litter, primarily comprising of needles, bark, and small branches. However, it is important to note that such an assertion remains theoretical. Nonetheless, deadwood could serve as an indicator of changes in site conditions that may have affected litter production. Factors such as bark beetle (*Ips typographus*) infestation or strong wind disturbances could lead to both - increased litterfall and deadwood formation simultaneously (Kosunen *et al*., 2020). Pronounced litterfall due to changes in environmental conditions could also be explained by changes in stand structure – as more deadwood is produced, the competition for light and nutrients is reduced for remaining trees. This, in turn, could affect crown development for the secondary canopy layer and thus, litter production. Other potential relationships should not be overlooked and merit further investigation. For instance, it is plausible that lying deadwood, as it decomposes and releases nutrients, may enhance soil nutrient status, thereby influencing litter production in the secondary canopy layer (Kulka *et al*., 2024).

Table 3

Correlations matrix of stand characteristics and litter input

	Age, yr	Diameter, cm	Height, m	G_{total}, m^2 ha^{-1}	M_{total}, m^3 ha^{-1}	Total deadwood, m^3 ha^{-1}	Litter C, t ha^{-1} yr^{-1}
Age, yrs	1	0.03	-0.32	-0.37	-0.38	-0.18	-0.06
Diameter, cm	0.03	1	0.74	0.38	0.5	0.61	0.64
Height, m	-0.32	0.74	1	0.73	0.88	0.58	0.6
G_{total}, m^2 ha^{-1}	-0.37	0.38	0.73	1	0.95	0.49	0.76
M_{total}, m^3 ha^{-1}	-0.38	0.5	0.88	0.95	1	0.47	0.68
Total deadwood, m^3 ha^{-1}	-0.18	0.61	0.58	0.49	0.47	1	0.77
Litter C, t ha^{-1} yr^{-1}	-0.06	0.64	0.6	0.76	0.68	0.77	1

Our results align with other studies (Starr *et al*., 2005; Berg & Laskowski, 2006; Bārdule *et al*., 2021; Butlers, 2023), that basal area is the best predictor for annual litter production. Study results suggest that in old growth forest stands basal area of dominant and secondary canopy layer are significant predictors ($p<0.01$) (Table 4). When deadwood was included in the model, the predictive power increased, indicating its influence. The highest predictive power was observed in the model (Basal_Dw) that included basal area of both canopy layers and total deadwood amount explaining 79% of the data variance.

Developing models with many variables can result in very accurate model predictions (Viskari *et al*., 2022). However for practical application, a simpler model with fewer, easily measurable variables is more useful, yet with reduced precision.

Table 4

Linear regression models for predicting annual litterfall in old-growth stands

Model name	Predictors	Estimate	P value	R^2	R^2_{adj}	P
Stock	M_{total}, m^3 ha^{-1}	0.003	0.016	0.46	0.40	0.016
Basal	G_{total}, m^2 ha^{-1}	0.06	0.004	0.58	0.54	0.004
Dw	Total deadwood, m^3 ha^{-1}	0.02	0.003	0.6	0.56	0.003
Basal_Dw	G_{total}, m^2 ha^{-1}	0.04	0.017	0.79	0.75	0.0009
	Total deadwood, m^3 ha^{-1}	0.01	0.015			

Therefore, we constructed a linear regression model using total basal area, which explained 58% of the data variance. Two separate linear regression models were constructed to assess the relationship between total basal area and litter carbon stock for spruce and pine dominated stands 'Figure 3'. For Spruce, the model revealed a non-significant positive relationship between total basal area and litter carbon stock (R^2=0.31, p = 0.252). Conversely, for pine, the model indicated a significant positive association between total basal area and aboveground litter carbon stock (R^2=0.9, p = 0.00373). These results suggest differing relationships between species, considering species-specific factors in understanding litter carbon dynamics in old growth forests.

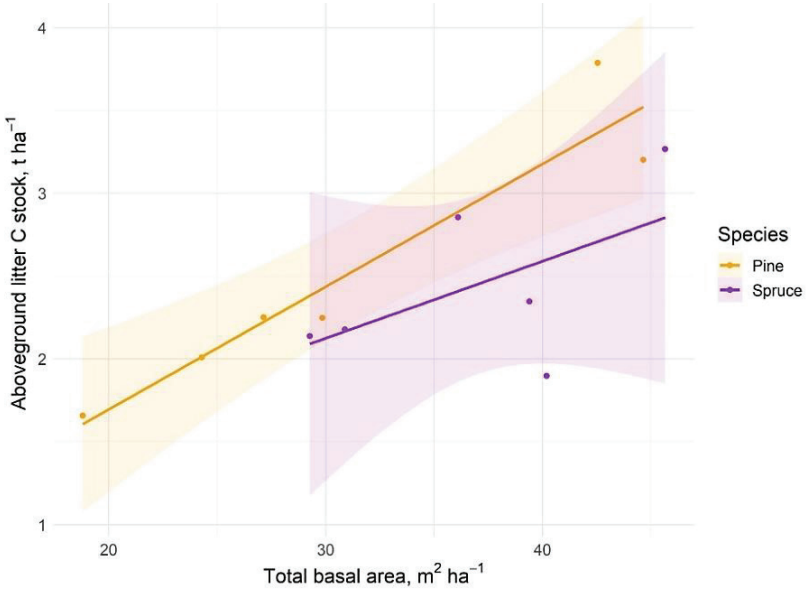

Figure 3. Annual C input by litter as a function of total basal area (± 95% confidence interval).

Conclusions

1. Drained sites exhibited higher annual litterfall C input compared to undrained sites, but differences were not statistically significant.
2. Seasonal litterfall did not exhibit any distinct patterns, indicating of high variality in late succession forest stands.
3. Total basal area (m^2 ha^{-1}) and total deadwood volume (m^3 ha^{-1}) showed a strong positive correlation with litterfall C input.
4. Stand basal area is the best individual predictor of annual litter C input, and provides reliable estimates for practical application using easily measurable stand parameter.
5. Further studies should focus on long-term litter dynamics and sorting of litterfall by categories (needles, bark, branches, etc.) to develop more precise estimates.

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GROUND VEGETATION BIOMASS AND CARBON POOL IN HEMIBOREAL OLD-GROWTH CONIFEROUS STANDS ON ORGANIC SOILS

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ABSTRACT

Forest ground vegetation biomass plays a significant role in carbon (C) storage and contributes to the overall carbon pool of forest ecosystems. Ground vegetation, including understory plants, shrubs, and grasses, not only affects carbon sequestration through photosynthesis but also contributes to the carbon cycle as it decomposes and release carbon into atmosphere and soil. This process adds to soil organic matter and affects it carbon dynamics. Understanding the above and below-ground biomass of forest ground vegetation and its associated carbon pool is essential for improving local and global estimates of carbon storage and cycling, especially in forests on organic soils where the information is scarce.

A total of 12 study sites were selected, with six stands dominated by Norway spruce (*Picea abies* (L.) H. Karst.) and six stands dominated by Scots pine (*Pinus sylvestris* L.). Of the selected stands, six were on drained organic soils and six on undrained organic soils. In each study site, four samples of ground vegetation biomass (both above- and below-ground) were collected in tree replicates. Each sample (above- and below-ground) was sorted into three groups (herbs, shrubs, trees), air-dried until reaching a constant weight, and then weighed to determine dry weight and carbon content.

Our study provides novel information on ground vegetation biomass and C pool estimates in old-growth stands dominated by different coniferous tree species in the hemiboreal region. Ground vegetation biomass and carbon pools were similar between drained and undrained stands.

Keywords: climate change mitigation, overmature stands, peat soil, forest amelioration

INTRODUCTION

Forests play a crucial role in carbon storage and sequestration, making them increasingly important in climate change mitigation strategies and research. As a result, there is a pressing need to assess biomass and carbon stocks at regional and national levels to guide forest-related policies and strategies for climate change mitigation and

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adaptation. However, the research and policy initiatives has traditionally focused on tree aboveground biomass, while the role of ground vegetation has often been overlooked.

Ground vegetation—comprising grasses, dwarf shrubs, mosses, ferns, and other understory plants—plays an important role in forest ecosystems carbon (C) cycling. Ground vegetation biomass, though smaller in quantity compared to trees, is vital for nutrient and carbon cycling, and biodiversity [1]. Carbon stock in this layer consists of live plant material above-ground, plant roots below-ground, and decomposing organic matter, making it an essential part of the forest carbon pool each playing distinct roles in carbon storage and ecosystem function. The ground vegetation is relatively small compared to trees and it contributes to short-term carbon storage by capturing carbon dioxide through photosynthesis. As ground vegetation dies and decomposes, it releases carbon into the atmosphere or transfers it to the soil, contributing to the nutrient cycle [2]. Below-ground carbon pool consists of roots, soil organic matter, and decomposed material that has been incorporated into the soil. The carbon stored below ground is typically more stable and longer-lasting than above-ground biomass, as it is less vulnerable to disturbances. Together, the above- and below-ground carbon pools form a dynamic system that not only influences the carbon cycle but also plays a key role in mitigating climate change by acting as a carbon sink.

The carbon sequestration potential of ground vegetation has not been extensively quantified, particularly at regional and national levels. This gap in knowledge presents a challenge for climate change mitigation, which are increasingly reliant on accurate estimates of forest carbon pools. Commonly used method for ground vegetation biomass estimation is destructive sampling, and is time consuming, compared to non destructive methods such as remote-sensing [3]. Moreover, accurate empirical estimates of ground vegetation biomass are necessary and can help in further remote sensing research to simplify biomass and C stock estimation at larger scale [4]. It is crucial to understand both the above- and below-ground biomass of forest ground vegetation and this is particularly important in forests with organic soils, where such data is limited, and especially in old-growth stands. The aim of the study is to assess ground vegetation biomass and carbon stock in old-growth stands on drained and undrained organic soils. We hypothesize that ground vegetation carbon stock will be similar between drained and undrained sites.

MATERIALS AND METHODS

The study was carried out in the hemiboreal vegetation zone [5]. The climate in this region is temperate, significantly influenced by the Baltic Sea and the North Atlantic. The average annual precipitation sum is 692 mm, and the mean annual air temperature is +6.4°C. According to data from the Latvian Environment, Geology, and Meteorology Centre, February is the coldest month with an average temperature of -3.7°C, but July is the warmest, with an average temperature of +17.4°C.

Study object is Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) old-growth stands on organic soils. In total 12 study sites were selected, of which 6 were drained and 6 undrained. Drained sites are representing fertile drained organic soils - the *Myrtillosa turf. mel* forest type, but undrained sites - *Caricoso-phragmitosa* forest type according to the Latvian forest type classification [6].

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Following forest drainage, the *Caricoso-phragmitosa* forest type is transformed into the *Myrtillosa turf. mel* forest type.

Table 1. Description of study sites

Site type	Dominant species	Mean age	DBH, cm	H, m	Basal area, m^2 ha^{-1}	M, m^3 ha^{-1}
Drained	Scots pine	150	34.9±1.5	27.5±5.0	32.0±6.0	404.7±82.4
Undrained	Scots pine	179	27.9±2.2	19.2±1.0	18.7±2.9	168.1±26.5
Drained	Norway spruce	162	34.1±2.7	28.9±2.0	32.6±4.4	443.0±81.9
Undrained	Norway spruce	153	26.9±1.6	24.6±0.7	35.6±2.7	428.7±35.3

The soil in drained forest type contains tree (70%), sedge (30%), and small amount of *Spghagnum* peat. The ground vegetation in drained forest type was characterized by a diverse dwarf shrub layer, dominated by European blueberry (*Vaccinium myrtillus* L.) and lingonberry (*Vaccinium vitis-idaea* L.), a herb layer (up to 87 species recorded in this forest type) dominated by purple moor-grass (*Molinia caerulea* [L.] Moench.), and a moss layer (up to 60 species recorded in this forest type) dominated by *Pleurozium schreberi*, *Hylocomium splendens*, and *Dicranum* spp. [6].

The soil in undrained forest type contains moderately decomposed acidic *Carex* and tree peat, and might be mixed with *Spagnum* peat. The ground vegetation in undrained forest type was characterized by a dense herb and moss layer (up to 150 species recorded in this forest type), dominated by sedges (*Carex* spp.), reedgrass (*Calamagrostis* spp.), and common reed (*Phragmites australis*). The moss layer was dominated by *Sphagnum*, *P. schreberi*, *H. splendens*, and *Dicranum* spp. [6].

In each stand three 1x1 m large sampling plots were selected, and in each plot four 25x25x25cm large ground vegetation biomass samples were collected. In field, samples were divided in two parts: above-ground and below-ground part. Samples were delivered to Latvian State Forest Research Institute "Silava" laboratory, where all samples were sorted into smaller fractions and air-dried at 70°C until reaching constant weight, weighted to determine dry mass. Above-ground samples were sorted in three fractions: herbaceous plants, dwarf shrubs and mosses, but below-ground samples were sorted in herbaceous plant roots, dwarf shrub roots, and tree root fractions. Below-ground root group classification was based on root diameter, where we analysed only small roots (diameter 2–20 mm) based on ICP Forest classification [7] [Cools et al., 2010]. All sorted roots were larger than 2mm in dimeter, to exclude fine-roots from the study, but smaller than 20mm in diameter to exclude coarse tree roots.

Statistical analysis

From each analysed sample plot average ground vegetation values were calculated as tons per hectare. Obtained biomass dry weight was expressed as C tons per hectare. Mean C content of ground vegetation above-ground, below-ground parts and moss was used from local study conducted in Latvia [8]. Normal distribution of data was checked

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with the Shapiro–Wilk normality test. Mann–Whitney U test was used to assess significant differences between the non-parametric variables. All tests were performed with the statistical software R 4.1.2. [9].

RESULTS

Ground vegetation biomass is similar between study sites in all cases ($p>0.05$). Ground vegetation above-ground biomass dry weight in drained and undrained pine stands was 0.85±0.64 t ha^{-1} and 0.93±0.97 t ha^{-1}, respectively, but in spruce stands it was 2.14±1.50 t ha^{-1} and 1.95±1.57 t ha^{-1}, respectively. Ground vegetation above-ground biomass carbon stock in drained and undrained pine stands was 0.42±0.32 t ha^{-1} and 0.41±0.43 t ha^{-1}, respectively, but in spruce stands it was 1.06±0.74 t ha^{-1} and 0.96±0.78 t ha^{-1}, respectively (Fig. 1A).

Ground vegetation below-ground biomass dry weight in drained and undrained pine stands was 5.66±3.0 t ha^{-1} and 2.85±1.73 t ha^{-1}, respectively, but in spruce stands it was 5.98±4.09 t ha^{-1} and 7.06±2.88 t ha^{-1}, respectively. Ground vegetation below-ground biomass carbon stock in drained and undrained pine stands was 2.88±1.52 t ha^{-1} and 1.45±0.88 t ha^{-1}, respectively, but in spruce stands it was 3.05±2.09 t ha^{-1} and 3.60±1.47 t ha^{-1}, respectively (Fig. 1B). Significant differences have been observed only between drained pine and spruce stand below-ground biomass dry weight and carbon stock ($p<0.05$).

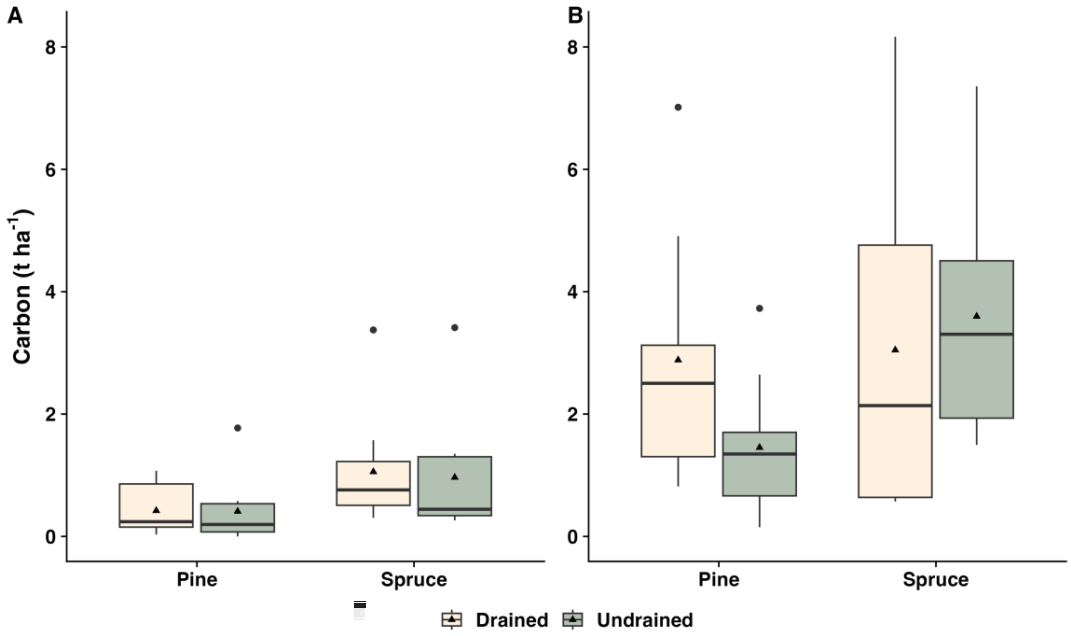

Figure 1. Ground vegetation above-ground (A) and below-ground (B) biomass carbon stock per forest type and dominant tree species. The box plots represent median values and the 25% and 75% percentiles; the whiskers indicate the maximum and minimum values; and the black dots represent outliers. Black triangles indicate mean values.

Above-ground part of ground vegetation biomass was sorted in three fractions: moss, herbaceous plants and dwarf shrubs (Fig. 2A). The largest fraction in all sites was moss

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biomass. In pine dominated stands the biomass distribution was similar between drained and undrained sites. In drained sites carbon stock of moss, herbaceous plant and dwarf shrub biomass was 0.34±0.25 C t ha^{-1}, 0.03±0.03 C t ha^{-1}, and 0.09±0.11 C t ha^{-1}, respectively. In undrained sites carbon stock of moss, herbaceous plant and dwarf shrub biomass was 0.38±0.42 C t ha^{-1}, 0.04±0.04 C t ha^{-1}, and 0.06±0.07 C t ha^{-1}, respectively. In spruce dominated stands the herbaceous plant and dwarf shrub biomass distribution differed between drained and undrained sites. In drained sites carbon stock of moss, herbaceous plant and dwarf shrub biomass was 0.73±0.67 C t ha^{-1}, 0.06±0.06 C t ha^{-1}, and 0.26±0.25 C t ha^{-1}, respectively. In undrained sites carbon stock of moss, herbaceous plant and dwarf shrub biomass was 0.61±0.57 C t ha^{-1}, 0.22±0.25 C t ha^{-1}, and 0.14±0.08 C t ha^{-1}, respectively.

Below-ground part of ground vegetation biomass was sorted in three fractions: tree roots, herbaceous plant roots and dwarf shrub roots (Fig. 2B). The largest fraction in all sites was tree root biomass. In pine dominated drained sites carbon stock of tree root, dwarf shrub root, and herbaceous plant root biomass was 2.81±1.56 C t ha^{-1}, 0.18±0.11 C t ha^{-1}, and 0.20±0.53 C t ha^{-1}, respectively. In pine dominated undrained sites carbon stock of tree root, dwarf shrub root, and herbaceous plant root biomass was 0.91±0.53 C t ha^{-1}, 0.54±0.58 C t ha^{-1}, and 0.07±0.10 C t ha^{-1}, respectively. In spruce dominated drained sites carbon stock of tree root, dwarf shrub root, and herbaceous plant root biomass was 2.99±2.15 C t ha^{-1}, 0.18±0.12 C t ha^{-1}, and 0.10±0.10 C t ha^{-1}, respectively. In spruce dominated undrained sites carbon stock of tree root, dwarf shrub root, and herbaceous plant root biomass was 3.20±1.65 C t ha^{-1}, 0.83±1.64 C t ha^{-1}, and 0.01±0.10 C t ha^{-1}, respectively.

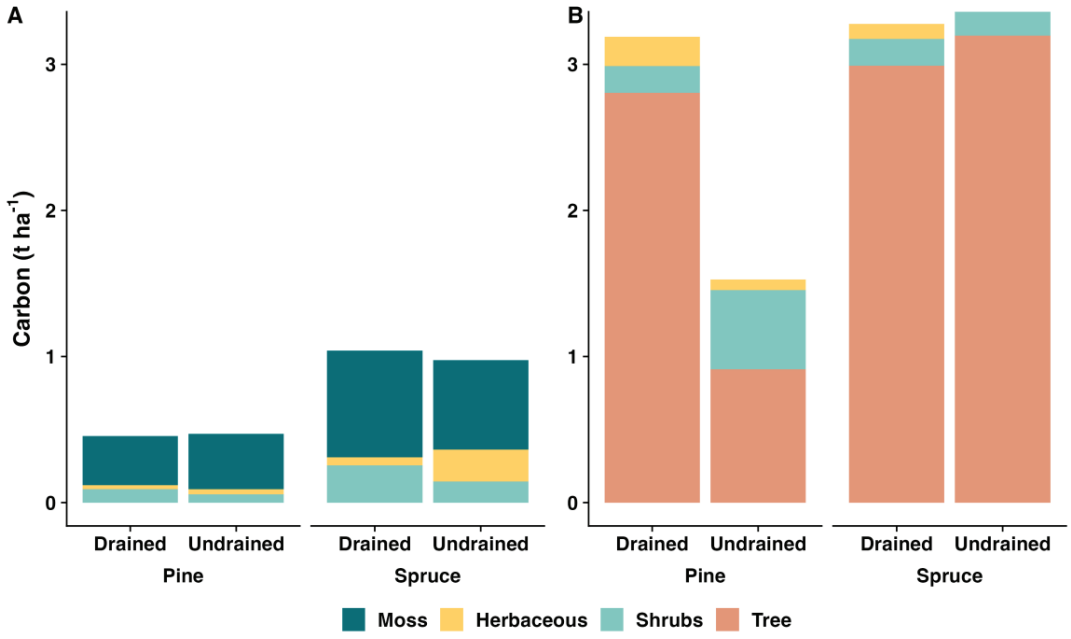

Figure 2. Ground vegetation above-ground (A) and below-ground (B) biomass carbon stock per forest type, dominant tree species and functional group

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Correlation matrix shows tree height as the single variable correlating with above-ground vegetation biomass, however the correlation is weak r=0.34. Below-ground vegetation biomass positively correlates with stand growing stock, tree height and basal area, r=0.48, r=0.49, and r=0.39, respectively, but negatively (r=-0.39) with stand age.

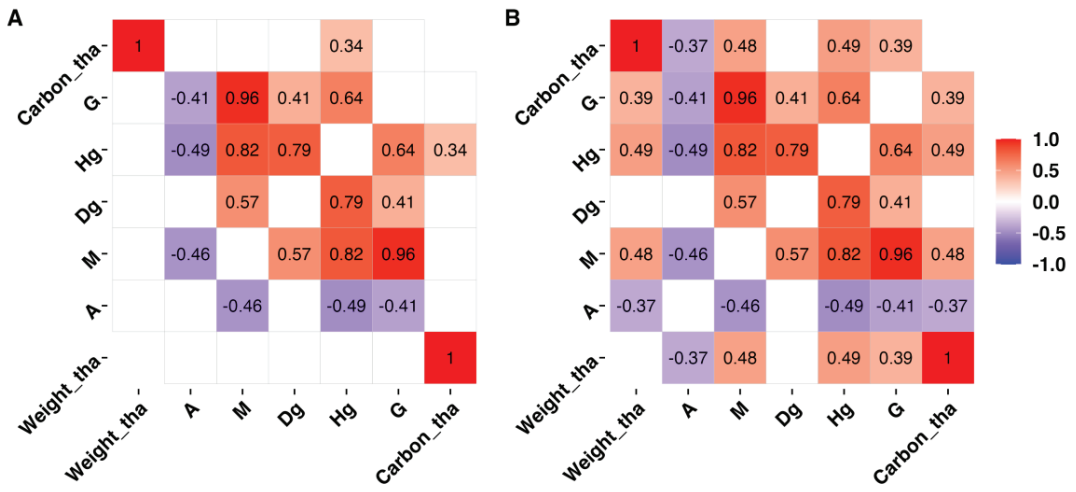

Figure 3. Correlation matrix of significant variables of ground vegetation above ground (A) and below-ground (B) root biomass weight (t ha^{-1}), carbon stock (t ha^{-1}) and stand parameters. A – mean stand age, years; M – mean stand growing stock, m^3 ha^{-1}; Dg – mean diameter at breast height, cm; Hg – mean stand tree height, m; G – stand basal area, m^2.

DISCUSSION

Ground vegetation biomass carbon stock is small, but significant carbon pool in forest ecosystems. Study results indicate that ground vegetation biomass is similar between drained and undrained stands, however biomass might differ between different functional groups making up this carbon pool. The proportion of above-ground biomass C stock from total ground vegetation C stock is 13%, 26%, 22%, and 21% in drained pine, spruce, and undrained pine and spruce stands, respectively. However, the proportion of below-ground biomass C stock from total ground vegetation C stock is 87%, 74%, 78%, and 79% in drained pine, spruce, and undrained pine and spruce stands, respectively. Obtained biomass values have high confidence intervals, indicating large variability within sites.

Above-ground biomass C stock differed between functional groups, but moss biomass was the largest part in all forest types. Moss as the largest part could be explained with soil and growing conditions of forests on peat soils, as some part of peat is formed from *Sphagnum*. Overall, proportion of moss biomass C stock from total above-ground C stock ranged from 63% to 81%, but herbaceous plant biomass C stock ranged from 5% to 22%, and dwarf shrub biomass C stock ranged from 12% to 25%. All functional

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group biomass of above-ground part was similar between forest types and tree species ($p>0.05$). The above-ground vegetation biomass C stock in our study is slightly larger than those reported in young to mature pine stands on mineral soil of boreal region of Canada, and it has been reported not to be age-dependent after first two decades [10]. However, compared to study in Sweden our study results of above-ground biomass are in line with their findings [11]. Moreover, ground vegetation biomass has been reported to be dependent on light availability in lower levels to promote vegetation growth and diversity [12], thus affected by genetically determined differences in adaptation of genotypes [13-14].

Blow-ground biomass C stock differed between functional groups, and tree small root biomass was the largest part in all forest types. Typically, tree roots could be expected as the largest C stock of below-ground biomass in forest ecosystems. Overall, proportion of tree root biomass C stock from total above-ground C stock ranged from 58% to 91%, but herbaceous plant biomass C stock ranged from 0% to 7%, and dwarf shrub biomass C stock ranged from 6% to 37%. All functional group biomass of below-ground part was similar between forest types and tree species ($p>0.05$), except for tree root biomass C stock of undrained pine dominated stands which was noticeably lower compared to other analysed stands. Lower values for below-ground tree root C stock can be explained with notably lower stand parameter values (tree height, diameter at breast height, basal area and growing stock).

CONCLUSION

The study provides novel information on ground vegetation biomass and C pool estimates in old-growth stands on drained and undrained organic soils dominated by different coniferous tree species in the hemiboreal region. Overall, the above- and below-ground biomass C stock does not differ between drained and undrained stands, however are linked to stand parameters (especially tree height), and indicates light availability as important factor. Dominant tree species alone does not affect vegetation biomass C stock; however, tree size plays a role in below-ground biomass amount of small tree roots. The largest part of ground vegetation biomass C pool is below-ground part and tree root biomass which makes up 87%, 74%, 78%, and 79% of total ground vegetation biomass samples in drained pine, spruce, and undrained pine and spruce stands, respectively

Further studies should focus on assessing ground vegetation biomass of different aged forest, forest types and ground vegetation biomass influencing factors to develop accurate models for this C pool, because ground vegetation biomass is often omitted from ecosystem C models. Moreover, accurate empirical estimates of ground vegetation biomass can help in further remote sensing research to simplify biomass and C stock estimation at larger scales.

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ARTICLE
Climate Ecology

The effect of drainage on fine-root biomass, production, and turnover in hemiboreal old-growth forests on organic soils

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Abstract

Information on the capacity of organic soils to capture and store carbon in old-growth forests in the hemiboreal forest zone is scarce and fragmented. However, fine-root data can provide valuable insights into soil carbon fluxes. Thus, the aim of the current study was to provide estimates of the fine-root biomass (FRB), fine-root production (FRP), and fine-root turnover (FRT) rate by tree species and other functional groups in old-growth (stand age 131–179 years) forests on mesotrophic organic soils dominated by Scots pine (*Pinus sylvestris* L.), with and without the effects of forest drainage. The sequential soil coring method was used to estimate the FRB and FRP. The total FRB was significantly higher in the undrained sites (6.8 ± 0.3 t ha^{-1}) than in the drained sites (3.97 ± 0.1 t ha^{-1}). The FRB of Scots pine in the undrained forest was significantly higher (1.7 ± 0.1 t ha^{-1}) than in the drained forest (0.5 ± 0.1 t ha^{-1}), supporting an extensive foraging strategy. The significantly higher mean FRB of Norway spruce (*Picea abies* [L.] Karst.) (1.4 ± 0.1 t ha^{-1}) in the drained sites than the undrained sites (0.7 ± 0.2 t ha^{-1}) can be explained by there being a higher proportion of spruce in the stand compositions, thus a higher standing volume of this species and an increased FRB. The FRB of dwarf shrubs (2.43 ± 0.2 t ha^{-1}) formed the largest part of the total FRB in the undrained sites and the second largest (1.16 ± 0.1 t ha^{-1}), following Norway spruce, in the drained sites. The total FRP was similar between the undrained (2.05 ± 0.31 t ha^{-1} year^{-1}) and drained (1.82 ± 0.26 t ha^{-1} year^{-1}) stands. However, considerable variability in the FRP was observed between different sites of the same forest site type. The FRT rate of Scots pine was twice as high in the drained sites than the undrained sites, suggesting faster nutrient and carbon input into the drained soil compared with the undrained soil. Estimates of FRB, FRP, and FRT rates for different functional groups can be used in carbon-cycle modeling and in further calculations to estimate the carbon budget (balance) in forests on organic soils.

KEYWORDS
fine-root production, fine-root turnover, forest drainage, hemiboreal, peat

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INTRODUCTION

The unprecedented rapid increase in carbon dioxide (CO_2) in the atmosphere is driving the interest of researchers and society in carbon (C) sequestration and the accumulation capacity of forest ecosystems. The adaptation of forestry practices to enhance C capture and storage in forest ecosystems has become part of global environmental policies to mitigate the negative effects of climate change. The C sequestration capacity of forest soils is altered by forestry activities and shaped by the biotic and abiotic characteristics of forest ecosystems (Mäkipää et al., 2023). Reliable estimates of belowground C stocks and fluxes are crucial for global C cycling models and for developing comprehensive recommendations for climate-smart forest management practices (Brunner et al., 2013; Finér et al., 2011).

Fine-roots (FRs) (diameter <2 mm) are the most dynamic parts of root systems and play a significant role in C and nitrogen (N) accumulation in forest soils (Kriiska et al., 2021). Fine-root production (FRP) is one of the most significant annual inputs into the soil C pool (Aun, Kukumägi, Varik, Becker, Aosaar, Uri, Buht, et al., 2021; Kriiska et al., 2019). Fine-root growth has shown great plasticity, with the response to edaphic, climatic, and environmental conditions being species-specific (Förster et al., 2021; Helmisaari et al., 2002; Ostonen et al., 2017). The fine-root biomass (FRB) and FRP are shaped by local conditions, such as stand age, aboveground primary productivity (Förster et al., 2021; Makkonen & Helmisaari, 2001; Yuan & Chen, 2012), and forest management (Aun, Kukumägi, Varik, Becker, Aosaar, Uri, Morozov, et al., 2021).

Forests on organic soils are common ecosystems in boreal and hemiboreal forest zones. The development of organic soils is linked to the natural paludification process, which determines the accumulation of the organic layer (peat). Hemiboreal forests on organic soils are dominated by trees, which can form a closed-canopy forest (>5 m high) that can produce a layer of organic soil more than 30 cm thick (Zoltai & Martikainen, 1996). In comparison with boreal forests, hemiboreal forests on organic soils have, on average, higher standing volumes, especially following drainage by ditching (Gustavsen et al., 1998; Macdonald & Yin, 1999). In the 20th century, in Northern Europe and the Baltic countries, forest drainage was a widespread forest management activity for improving tree growth (Barthelmes et al., 2015; Pärn et al., 2018; Vasander et al., 2003). As a result, in Northern Europe, 44% of the total organic soils have been drained, while in Latvia, 77% have been drained (Barthelmes et al., 2015). Some small areas of drained forests on organic soils have been left untouched since the establishment of open-ditch systems in the middle of the previous century. Now, these areas exhibit features of "old-growth forests" (Buchwald, 2005), for example, stand age (130–170 years), amount of deadwood (~10 t C ha^{-1}), and no human interventions for the last 60–80 years (Ķēniņa et al., 2022). Such stands provide valuable insights into long-term forest dynamics in a human-altered environment.

Forest management activities shape the growth and decomposition rates of FRs by altering the stand characteristics (stand density, canopy openness, species composition) and the physiochemical properties of the soil and microbial communities (Philpott et al., 2018). The retention trees in post-harvest areas have decreased the decomposition rate of FRs in coastal Douglas fir (*Pseudotsuga menziesii*) forests in British Columbia (Philpott et al., 2018). In addition, the results of a short-term study have indicated that, following thinning, the retained trees have slightly higher FRB per tree compared with unthinned stands, suggesting a positive feedback favoring better growing conditions in thinned pole and middle-aged Scots pine (*Pinus sylvestris* L.) stands (Aun, Kukumägi, Varik, Becker, Aosaar, Uri, Buht, et al., 2021). However, no significant differences in FR systems (morphology, biomass, necromass) have been found between old-growth beech (*Fagus sylvatica*) and mature production stands in temperate forests (Klingenberg & Leuschner, 2018). In Northern Europe, only a relatively small number of studies have investigated the long- and short-term effects of management on FR systems and their morphology.

Stand age is a variable widely used for characterizing the developmental stage of forest stands, their productivity, and C sequestration. Studies have shown that the FRB and FRP are closely linked to the stand age (Makkonen & Helmisaari, 2001; Yuan & Chen, 2012). In boreal Scots pine forests, it has been found that FRP estimates gradually increase between the sapling stage and the mature stand (100 years) (Helmisaari et al., 2002; Makkonen & Helmisaari, 2001). Contrastingly, the highest estimates of FRB have been reported from the pole stage when canopy closure has been reached (Helmisaari et al., 2002). In older stands, there is a higher proportion of FR necromass (Makkonen & Helmisaari, 2001). In boreal and hemiboreal forests, less is known about FR system characteristics when the mean stand age reaches 130 years, and more when trees have lower growth efficiency than in previous developmental stages (Martínez-Vilalta et al., 2006).

In Northern Europe, the majority of studies on organic soils with and without tree cover have been carried out in the boreal forest zone. Two drained boreal forested peatlands (bog vs. fen), with a mean stand basal area of 17 m^2 ha^{-1}, have been compared in Finland

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(Bhuiyan et al., 2017). The ingrowth bag method has been tested in drained and wet mires in the boreal forest zone, where the stand mean volume ranged from 35 to 150 m^3 ha^{-1} (Finér & Laine, 2000). In the hemiboreal forest zone, the effects on the morphological characteristics of absorptive roots of distance from the ditch have been investigated in drained organic soils dominated by birch (*Betula pubescens* Ehrh.) and Norway spruce [*Picea abies* (L.) Karst.], with stand basal areas ranging from 14 to 20 m^2 ha^{-1} (Rezapour et al., 2022). Due to the laborious sampling procedure, previous studies have often used only a small number of sites per study, but because forests on organic soils vary greatly in terms of fertility gradient, more studies are required for a better understanding of FRP and C fluxes in these ecosystems (Bhuiyan et al., 2017), especially in the hemiboreal forest zone, where the available information on forests on organic soils is fragmented and scarce. Some novel aspects of the short-term effects of drainage (2 years) on FR characteristics in boreal peatlands have been recently published (Bhuiyan et al., 2023; Lampela et al., 2023) that highlight the multilevel influence of abiotic and biotic factors.

In this study, we aimed to provide a comparison between the FRB and FRP in old-growth, fertile, drained, and undrained forests on organic soils dominated by Scots pine in the hemiboreal forest zone. Because it was known that the FRB can be higher in undrained Scots-pine-dominated peatland sites in the boreal region (Lampela et al., 2023), we hypothesized that we would find higher Scots pine FRB and FRP in the undrained sites than in the drained sites in the hemiboreal forest zone. We also hypothesized that Scots pine, as the dominant tree species, would have higher estimates of FRB and FRP than the other functional groups. Studies have shown that the FR turnover (FRT) is faster in the more productive sites (Kriiska et al., 2019). Therefore, we hypothesized that the FRs of Scots pine would have a higher turnover rate in the drained sites than in the undrained sites. To the best of our knowledge, this work provides novel insights into the characteristics of the FR system in old-growth forests on organic soils dominated by Scots pine in the hemiboreal forest zone.

MATERIALS AND METHODS

Study sites

The characteristics of FRs were studied in six Scots-pine-dominated stands in two forest site types (drained vs. undrained deep organic soils) in the hemiboreal forest zone (Ahti et al., 1968) (55°–58° N, 21°–28° E). In Latvia, the climatic conditions are strongly influenced by the moist maritime air masses that originate over the Baltic Sea and Atlantic Ocean. These air masses are brought by prevailing westerlies (Avotniece et al., 2017; Dravniece, 2003). The long-term (1991–2020) mean annual temperature is +6.8°C, the warmest month is July (+17.8°C), and the coldest month is February (−3.1°C). The mean annual precipitation is 685.6 mm, with the wettest months being August (76.8 mm) and July (75.7 mm), and the driest being April (35.8 mm), based on data from the Latvian Environment, Geology and Meteorology Centre.

Our selection of old-growth forests was based on stand age (dominant tree cohort >130 years old) and disturbance (no recorded or visible signs of former management activities) criteria (Buchwald, 2005). We aimed to sample stands in their later stages of development, with large, old trees and large-sized standing or fallen deadwood. The only known human intervention had been the creation of an open-ditch network in the 1960s, meant to improve the growing conditions for the trees. A similar methodology of selecting old-growth forest stands has been used in earlier studies to investigate C pools (Ķēniņa et al., 2018, 2019, 2022).

Three of the studied stands were growing on drained mesotrophic organic soils—the *Myrtillosa turf. mel* forest site type, according to the Latvian forest site type classification (Bušs, 1976). The drained forest sites are referred to here as Ugale, Auce, and Smiltene. The organic layer was at least 20 cm thick and was composed of cottongrass (*Eriophorum* spp.) and tree biomass. Typically, the canopy was dominated by Scots pine, birch (*Betula pendula* Ehrh.), and Norway spruce, with an admixture of black alder [*Alnus glutinosa* (L.) Gaertn.]. The ground vegetation was characterized by a dense and diverse dwarf shrub layer, dominated by European blueberry (*Vaccinium myrtillus* L.) and lingonberry (*Vaccinium vitis-idaea* L.), a herb layer dominated by purple moor-grass (*Molinia caerulea* [L.] Moench.), and a moss layer dominated by *Pleurozium schreberi*, *Hylocomium splendens*, and *Dicranum* spp. The shrub layer was dominated by alder buckthorn (*Frangula alnus*), willows (*Salix* spp.), common juniper (*Juniperus communis*), and rowan (*Sorbus aucuparia*).

The other three old-growth stands studied were growing on mesotrophic organic soils—the forest site type *Caricoso-phragmitosa*, based on the Latvian forest site type classification. These undrained forest sites are referred to here as Viesite, Valle, and Jaunjelgava. The organic layer was at least 30 cm thick and was composed mostly of sedge (*Carex* spp.), tree, and sphagnum biomass. Typically, the canopy was dominated by Scots pine, with an admixture of birch, black alder, and Norway

spruce. The ground vegetation was characterized by a dense herb layer, dominated by sedges (*Carex* spp.), reedgrass (*Calamagrostis* spp.), and common reed (*Phragmites australis*). The moss layer was dominated by sphagnum, *P. schreberi*, *H. splendens*, and *Dicranum* spp. The shrub layer was dominated by common juniper (*J. communis*), alder buckthorn (*F. alnus*), and willows (*Salix* spp.). Following forest drainage, the *Caricoso-phragmitosa* forest site type is transformed into the drained mesotrophic organic soil *Myrtillosa turf. mel* forest site type, according to the Latvian forest site type classification (Bušs, 1997).

Estimation of stand characteristics

At each site, six circular sampling plots (each 500 m^2) were established, in which all live trees with dbh of >6.1 cm were identified and measured. In the same plots, all the standing deadwood with dbh > 6.1 cm and laying deadwood with dbh ≥ 14.1 cm at the thicker end were measured. The heights of five trees from the first layer were measured, along with three trees from the second layer. In a circular subplot of 25 m^2 (located within the large sample plots), all live trees with dbh of 2.1–6.0 cm and deadwood with dbh of 6.1–14.0 cm at the thicker end were identified and measured. Based on the collected data, the stand density (in trees per hectare), stand basal area (in square meters per hectare), standing volume (in cubic meters per hectare), and amount of deadwood were calculated. Detailed descriptions of the study sites and the calculations are available in Ķēniņa et al. (2018).

The ground vegetation sample plots were located within the large sampling plots. Three sampling plots (1 × 1 m), at 1-m regular intervals, were set up from the center of the large sampling plot in four cardinal directions (east, west, north, and south). Accordingly, there were 12 vegetation sample plots per large sample plot and 36 vegetation sample plots per study site. In each sample plot, the percentage projection cover of the understory plants, lichen, and bryophyte species was estimated.

Soil analysis

For the soil chemical analysis, soil nutrient content, and pH level, we collected soil samples (100 cm^3) using an auger, making two replications per plot during the period from March to November 2021. The soil samples were taken down to a depth of 50 cm and then were cut into 10-cm segments (0–10, 10–20, 20–30, 30–40, 40–50 cm). The top of the organic layer was regarded as the 0-cm reference. In the laboratory, the soil samples were air-dried, crushed, and sieved to obtain the soil fractions (diameter >2 mm) for chemical analysis. The total C (in grams per kilogram) was assessed using the dry combustion method according to LVS ISO 10694:2006. The Kjeldahl method was used to calculate the total N content (in grams per kilogram) according to LVS ISO 11261:2002. The suspension ratio of the pH (in potassium chloride [KCl]) was 1:5 mL. The gravimetric method was used to assess the bulk density (in kilograms per cubic meter) according to LVS ISO 11272:2017. The soil analysis was carried out in the laboratory of the Latvian State Forest Research Institute "Silava."

We measured the soil temperature (in degrees Celsius) at depths of 10, 20, 30, and 40 cm using four temperature sensors connected to a data logger (Comet U0141, COMET SYSTEM s.r.o., Czech Republic). In each sampling plot, we installed one piezometer pipe (2 m deep) to measure groundwater fluctuations manually with a ruler (in centimeters). We visited each sampling plot approximately once a month during the vegetation season to record these measurements. We measured the thickness of the organic layer manually using a ruler (in centimeters).

FR sampling

We used the sequential soil coring method (Ostonen et al., 2005) to estimate the biomass and production of the FRs (Brunner et al., 2013). The sampling was carried out in May, August, and October 2021, and in March 2022. In each stand (six in total), FR samples were collected from three circular sampling plots. From each sample plot, we randomly collected 10 soil cores (monolith) using a cylindrical soil corer (inner diameter 50 mm) to a soil depth of 40 cm. We sectioned each soil core into 10-cm segments (0–10, 10–20, 20–30, and 30–40 cm), which resulted in a total of 2880 FR samples. Each soil section was then placed in a plastic box, transported to the laboratory, and kept frozen (−5°C) until needed for further processing. In the laboratory, the soil samples were defrosted at room temperature and carefully washed with tap water. While washing, a stack of three laboratory test sieves with descending aperture sizes were used to collect all the FRs. Based on appearance, color, and fragility (Bhuiyan et al., 2017), and with the help of forceps, we sorted all the FRs into living or dead for the Scots pine, Norway spruce, and other functional groups (dwarf shrubs and herbaceous plants). The Scots pine FRs were identified, primarily, by the dichotomously branched mycorrhizae and their color. The Norway spruce FRs were identified by their straight and short mycorrhizae and darker color (compared to the

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Scots pine). In contrast to the trees, the FRs of the herbaceous plants (graminoids, forbs, ferns) and dwarf shrubs had no visible ectomycorrhizal tips. The herbaceous plants had a lighter (white, yellowish) and curlier FR structure than the dwarf shrubs. The dead FRs were distinguished by their color, stiffness, and elasticity (being typically darker than living roots and easily broken) (Bhuiyan et al., 2017). The FRs not associated with any of the functional groups (e.g., tree species <10% of the stand species composition) or fragmented into tiny pieces (<1 mm) were not included in the analysis. The FR samples were dried to a constant mass at 60°C, and then were weighed using an analytical balance (Kern & SOHN GmbH, model ALJ 250-4AM) to estimate the biomass.

Calculation of FRB, FRP, and FRT

The mean FRB from all four samplings was calculated to minimize the effects of seasonal variation (Brunner et al., 2013). The FRB and necromass of each sampling were used in the decision matrix to calculate the FRP proposed by Fairley and Alexander (1985). The annual FRP was divided by the mean FRB to calculate the FRT (per year) (Gill & Jackson, 2000; McClaugherty et al., 1982). To calculate the FRP of the dwarf shrubs, we used an average turnover of 0.20 year^{-1} (Uri et al., 2019).

Statistical analysis

To test the normality of the analyzed variables, we used the Shapiro–Wilk test. We used the ANOVA to test whether the mean values of the groups (diameter, stand density, volume) differed significantly between the drained and undrained forest types and sites. Tukey's honestly significant difference multiple pairwise comparison test was used for the normally distributed data to evaluate which groups (forest types, sites) were statistically different from one another. For the variables that did not meet normality assumptions, we used the Kruskal–Wallis rank sum test to compare the mean values. All the tests were performed with $\alpha = 0.05$, and significance was proved if $p < 0.05$.

To assess the effects of the stand and soil parameters on the FRB of the different functional groups, we employed a linear mixed-effects model. The variable FRB was log-transformed to meet data normality requirements. The fixed effects in the model were the stand properties (number of trees, mean diameter, basal area, standing volume) and the soil variables (pH, bulk density, C and N contents, C:N ratio). The FRB per stand basal area was used to assess the effect of stand characteristics on the FRB of the Norway spruce and Scots pine (Helmisaari et al., 2007; Ostonen et al., 2017; Rezapour et al., 2022). Both the sampling plot ID and sampling time were used as random effects in the model to account for the possible correlation effects of the same sampling unit. A generalized variance inflation factor (GVIF) was used to assess the multicollinearity between the explanatory variables, with GVIF > 5 set as the threshold of multicollinearity. The final (best) model was selected based on the smallest Akaike information criterion estimate (McGullagh & Nelder, 1989). An ANOVA was used to assess the significant factors affecting the dependent variables (FRB and FRP of multiple functional groups) of the linear mixed-effects model.

We used principal components analysis (PCA) to reveal the relationships between the FRB, FRP, stand characteristics, soil analysis, and ground cover vegetation. In the PCA, only quantitative variables were used, all of which were scaled. All calculations were performed using R.4.1.3 software (R Core Team, 2022), using the "lme4" library (Bates et al., 2015).

RESULTS

The standing volume (in cubic meters per hectare) of the Scots pine and the mean stand density were similar between both forest site types ($p > 0.05$, $df_1 = 1$, $df_2 = 16$), while the mean diameter, basal area, and standing volume of the Norway spruce were significantly ($p < 0.05$, $df_1 = 1$, $df_2 = 16$) higher in the drained forest than in the undrained forest (Table 1).

The mean soil pH was significantly ($p < 0.05$, $df_1 = 1$, $df_2 = 142$, $F = 7.63$) higher in the drained forest (3.9 ± 0.1) than in the undrained forest (3.5 ± 0.1) type (Table 2). Also, the mean C:N ratio was significantly ($p < 0.001$, $df_1 = 1$, $df_2 = 142$, $F = 13.76$) higher in the undrained forest (34.3 ± 1.5) than in the drained forest (26.9 ± 1.4). The mean bulk density was significantly ($p < 0.001$, $df_1 = 1$, $df_2 = 142$, $F = 2.55$) higher in the drained forest (156.6 ± 7.6 kg m^3) than in the undrained forest (100.1 ± 3.2 kg m^3). The total C content was similar ($p > 0.05$, $df_1 = 1$, $df_2 = 142$, $F = 3.66$) in both types, at 532.4 ± 4.17 g kg^{-1} (undrained forest) and 514.0 ± 11.2 g kg^{-1} (drained forest). The total N content was significantly ($p < 0.001$, $df_1 = 1$, $df_2 = 142$, $F = 21.75$) higher in the drained forest (21.9 ± 0.9 g kg^{-1}) than in the undrained forest (17.7 ± 0.8 g kg^{-1}).

The mean soil temperature was similar in both forest site types at 10-, 20-, 30-, and 40-cm depth ($p > 0.05$, $df_1 = 1$, $df_2 = 52$, $F = 0.15$) in March through November, ranging from +3.8°C in March to +17.9°C in July at 10-cm depth (Figure 1a). The groundwater level (GWL) was

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TABLE 1 Description of the studied stand characteristics (mean ± SE): drained forest, *Myrtillosa turf. mel*; undrained forest, *Caricoso-phragmitosa*.

Forest site by type	Species composition (%)	Stand age (year)	Pine standing volume (m^3 ha^{-1})	Spruce standing volume (m^3 ha^{-1})	Stand density, first layer (ha^{-1})	dbh (cm)	Basal area (m^2 ha^{-1})
Drained							
Ugale	70SP30NS+BA +SB	174	230.8 ± 51.6^{a}	160.7 ± 42.7^{a}	293.3 ± 40.6^{a}	35.2 ± 1.4^{a}	30.2 ± 3.7^{a}
Auce	70SP30NS	131	280.1 ± 69.4^{a}	244 ± 12.6^{b}	353.3 ± 46.7^{a}	35.6 ± 1^{a}	33.2 ± 4.5^{a}
Smiltene	90SP10NS	144	195.9 ± 10.1^{a}	76 ± 19.1^{c}	300 ± 30.6^{a}	32.6 ± 0.4^{a}	21.3 ± 1.9^{b}
Undrained							
Viesite	100SP	177	123.4 ± 22.5^{b}	5.6 ± 1.4^{d}	200 ± 30.6^{b}	29.9 ± 4.4^{a}	13.1 ± 1.7^{c}
Valle	100SP	179	196.8 ± 18.7^{a}	21.3 ± 6.6^{e}	380 ± 41.6^{a}	26 ± 0.3^{b}	20.2 ± 2^{b}
Jaunjelgava	70SP30NS+SB	159	143.4 ± 21.9^{b}	$100.3 \pm 28.2^{a,c}$	760 ± 61.1^{c}	25 ± 0.5^{ab}	27.9 ± 2^{a}

Note: The plus sign indicates additional individual trees in the stand (<10% of the species composition). Lowercase letters in superscript indicate statistically significant ($p < 0.05$) differences between sites. dbh was measured at 1.3 m above the ground surface.
Abbreviations: BA, black alder; NS, Norway spruce; SB, silver birch; SP, Scots pine.

TABLE 2 Description of the soil characteristics (mean ± SE, based on the 0–40 cm peat layer) of the studied stands: drained forest, *Myrtillosa turf. mel*; undrained forest, *Caricoso-phragmitosa*.

Forest site by type	Organic layer (cm)	pH_{KCL}	C:N	Bulk density (kg m^3)	Total N (g kg^{-1})	Total C (g kg^{-1})
Drained						
Ugale	107.6	4.6 ± 0.2^{a}	18.2 ± 0.5^{a}	164.7 ± 16.2^{a}	24.2 ± 1.5^{a}	440.1 ± 28.0^{a}
Auce	92.8	2.9 ± 0.1^{b}	43.1 ± 1.2^{b}	201.4 ± 7.2^{b}	13.2 ± 0.3^{b}	560.7 ± 4.4^{b}
Smiltene	98.6	4.1 ± 0.1^{c}	19.3 ± 0.4^{a}	103.7 ± 2.6^{c}	28.3 ± 0.6^{a}	541.2 ± 2.5^{c}
Undrained						
Viesite	71.3	3.0 ± 0.1^{b}	37.8 ± 1.5^{b}	...	9.0 ± 1.3^{b}	362.2 ± 53.0^{abc}
Valle	79.3	2.6 ± 0.02^{e}	42.4 ± 1.0^{b}	88.8 ± 4.9^{c}	12.7 ± 0.3^{b}	531.9 ± 6.7^{ac}
Jaunjelgava	178.3	4.8 ± 0.1^{a}	21.9 ± 1.5^{a}	96.5 ± 2.4^{c}	25.1 ± 1.0^{a}	517.1 ± 3.3^{a}

Note: Lowercase letters in superscript indicate statistically significant ($p < 0.05$) differences between sites.

significantly ($p < 0.05$, $df_1 = 5$, $df_2 = 48$, $F = 18.31$) lower at the Auce site (drained forest) than all the other sites in March through November, based on the Wilcoxon test (Figure 1b). At Auce (drained forest), the GWL fluctuated from 31.9 cm in March to 123.3 cm in August, while at the other sites, on average, it differed from 4.6 cm in October (at Jaunjelgava) to 70.6 cm in August (at Valle).

The mean projection cover of the lichens and bryophytes in the understory was 84% in the undrained forest and 56% in the drained forest sites. The projection cover of the dwarf shrubs was 12% and 38% in the drained and the undrained forests, respectively. The projection cover of the understory plants constituted 36% and 18% in the drained and undrained forests, respectively. Forbs were considerably more common in the drained forest (35% mean projection cover) than in the undrained forest (6%) (Appendix S1: Table S1), whereas the graminoids were more common in the undrained forest (8.2%) than in the drained forest (1.2%). Graminoids were especially abundant in the undrained Viesite site (17.6%). Forbs were only present in the undrained Jaunjelgava site (12.2%). The most common dwarf shrubs in the undrained forest were *V. myrtillus* (observed in 80 of 108 sample plots), *V. vitis-idaea* (60 plots), *Ledum palustre* (40 plots), and *Vaccinium ulignosum* (18 plots). In the drained forest, we detected *V. myrtillus* in 49 plots and *V. vitis-idaea* in two plots.

Mean FRB, FRP, and FRT

The total FRB was significantly higher ($p < 0.05$, $df_1 = 1$, $df_2 = 4$, $F = 17.08$) in the undrained forest type

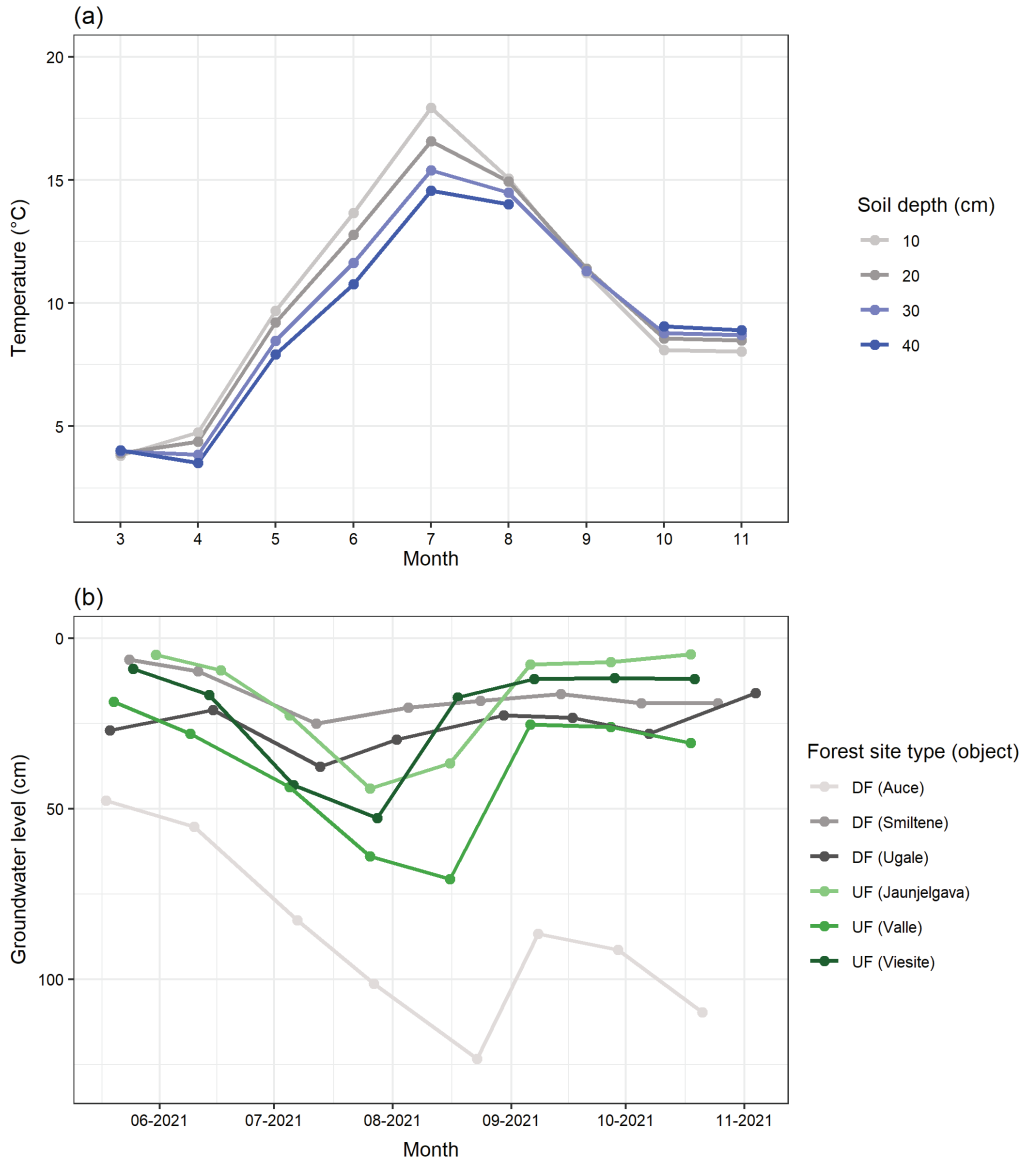

FIGURE 1 (a) Mean soil temperature for all sample sites at four different depths (10–40 cm) from March to November; (b) groundwater level dynamics from May to November. DF, drained forest (*Myrtillosa turf. mel*); UF, undrained forest (*Caricoso-phragmitosa*).

(Jaunjelgava, Valle, Viesite) than in the drained forest type (Auce, Smiltene, Ugale), ranging from 6.04 ± 0.2 to 7.35 ± 0.4 t ha^{-1} and from 3.37 ± 0.01 to 4.95 ± 0.2 t ha^{-1}, respectively (Figure 2). The FRB of the Scots pine was significantly ($p < 0.001$, $df_1 = 1$, $df_2 = 70$, $F = 54.37$) higher in the undrained forest (1.69 ± 0.1 t ha^{-1}) than in the drained forest (0.54 ± 0.1 t ha^{-1}) (Table 3). Also, the FRB of the herbaceous plants was significantly higher ($p < 0.05$, $df_1 = 1$, $df_2 = 70$, $F = 9.74$) in the undrained forest (0.92 ± 0.3 t ha^{-1}) than in the drained forest (0.29 ± 0.1 t ha^{-1}). In the undrained Viesite site, the FRB of the herbaceous plants (1.9 ± 0.47 t ha^{-1}) was four times greater than in other undrained sites (Figure 2, Table 3). Similarly, the FRB of the dwarf shrubs was significantly

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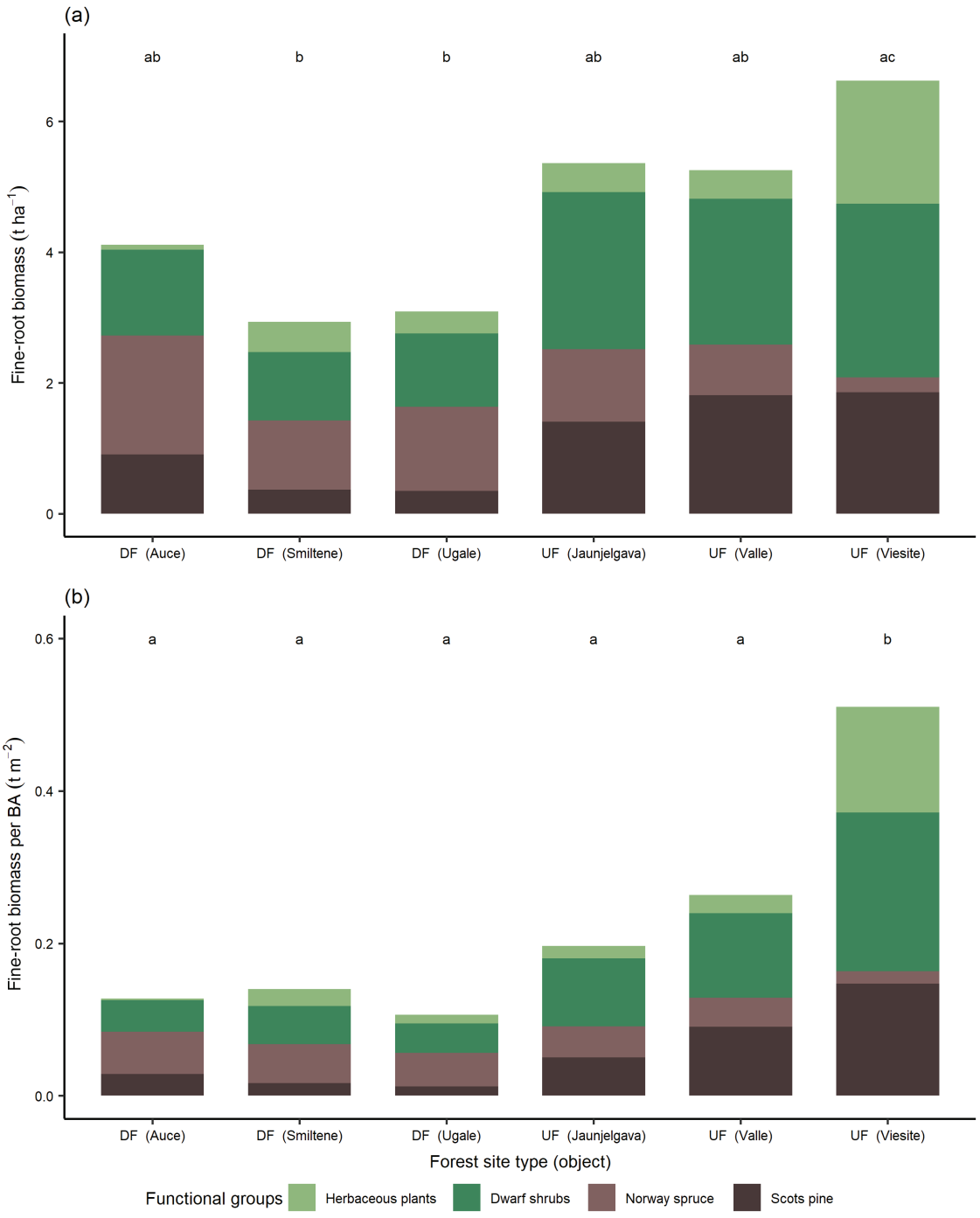

FIGURE 2 (a) Total fine-root biomass by functional group and forest site type; (b) fine-root biomass per stand basal area (BA) by functional group and forest site type. DF, drained forest (*Myrtillosa turf. mel*); UF, undrained forest (*Caricoso-phragmitosa*). Lowercase letters in superscript indicate statistically significant ($p < 0.05$) differences between sites.

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($p < 0.001$, $df_1 = 1$, $df_2 = 70$, $F = 36.39$) higher in the undrained forest (2.43 ± 0.2 t ha^{-1}) than in the drained forest (1.16 ± 0.1 t ha^{-1}). Only the FRB of Norway spruce was significantly ($p < 0.001$, $df_1 = 1$, $df_2 = 70$, $F = 25.84$) higher in the drained forest sites (1.39 ± 0.1 t ha^{-1}) than in the undrained forest sites (0.71 ± 0.2 t ha^{-1}). Similarly, the necromass of the Norway spruce was significantly higher ($p < 0.001$, $df_1 = 1$, $df_2 = 70$, $F = 11.85$) in the drained forest sites (0.39 ± 0.04 t ha^{-1}) than in the undrained forest sites (0.24 ± 0.04 t ha^{-1}). The necromass of the Scots pine was significantly ($p < 0.001$, $df_1 = 1$, $df_2 = 70$, $F = 50.03$) higher in the undrained forest sites (0.59 ± 0.06 t ha^{-1}) than in the drained forest sites (0.20 ± 0.03 t ha^{-1}). In the undrained forest, the largest proportion of the total FRB was constituted by dwarf shrubs, followed by Scots pine and herbaceous plants (Figure 2). In the drained forest, the largest proportion of the total FRB was constituted by Norway spruce, followed by dwarf shrubs and live Scots pine.

The total FRP (sum of the FRP of the trees and shrubs) between the forest types was similar ($p > 0.05$, $df_1 = 1$, $df_2 = 16$, $F = 0.31$), with the undrained forest producing 2.05 ± 0.31 t ha^{-1} year^{-1} and the drained forest producing 1.82 ± 0.26 t ha^{-1} year^{-1}. The FRP of the Scots pine showed no statistically significant differences ($p > 0.05$, $df_1 = 1$, $df_2 = 16$, $F = 3.11$) between the drained and undrained forest sites, at 0.39 ± 0.12 and 0.93 ± 0.27 t ha^{-1} year^{-1}, respectively (Table 4). Similarly, the FRP of the Norway spruce was similar ($p > 0.05$, $df_1 = 1$, $df_2 = 16$, $F = 1.82$) between both forest site types, at 1.11 ± 0.22 t ha^{-1} year^{-1} (drained forest) and 0.72 ± 0.17 t ha^{-1} year^{-1} (undrained forest). Likewise, the FRP of the dwarf shrubs was similar ($p > 0.05$, $df_1 = 1$, $df_2 = 16$, $F = 1.47$) between both forest types, at 0.40 ± 0.1 t ha^{-1} year^{-1} (undrained forest) and 0.31 ± 0.1 t ha^{-1} year^{-1} (drained forest). The undrained Jaunjelgava site had a considerably higher Scots pine FRP (1.97 ± 0.1 t ha^{-1} year^{-1}) than all the other drained and undrained sites, whereas the FRP of the Norway spruce (1.05 ± 0.2 t ha^{-1} year^{-1}) at Jaunjelgava was similar to that at Valle (1 ± 0.23 t ha^{-1} year^{-1}). The FRP of the dwarf shrubs was similar among all undrained sites.

TABLE 3 Fine-root biomass (FRB) and necromass (in tons per hectare; mean ± SE) of different functional groups: drained forest, *Myrtillosa turf. mel*; undrained forest, *Caricoso-phragmitosa*.

	FRB of trees		Necromass		Understory	
Forest site by type	**Scots pine**	**Norway spruce**	**Scots pine**	**Norway spruce**	**FRB of dwarf shrubs**	**FRB of herbaceous plants**
Drained						
Ugale	0.35 ± 0.12	1.29 ± 0.02	0.1 ± 0.02	0.4 ± 0.06	1.1 ± 0.1	0.3 ± 0.07
Auce	0.9 ± 0.16	1.82 ± 0.16	0.3 ± 0.05	0.5 ± 0.06	1.3 ± 0.13	0.07 ± 0.02
Smiltene	0.36 ± 0.07	1.06 ± 0.07	0.2 ± 0.03	0.3 ± 0.04	1 ± 0.1	0.5 ± 0.12
Undrained						
Viesite	1.85 ± 0.15	0.23 ± 0.1	0.6 ± 0.09	0.1 ± 0.02	2.7 ± 0.51	1.9 ± 0.47
Valle	1.81 ± 0.22	0.78 ± 0.16	0.8 ± 0.07	0.3 ± 0.03	2.2 ± 0.15	0.4 ± 0.1
Jaunjelgava	1.41 ± 0.24	1.11 ± 0.17	0.4 ± 0.05	0.3 ± 0.05	2.4 ± 0.31	0.4 ± 0.04

TABLE 4 Fine-root production (FRP) of Scots pine, Norway spruce, and dwarf shrubs and fine-root turnover (FRT) of Scots pine and Norway spruce of the studied stands: drained forest, *Myrtillosa turf. mel*; undrained forest, *Caricoso-phragmitosa*.

	FRP (t ha^{-1} year^{-1})			FRT (year^{-1})	
Forest site by type	**Scots pine**	**Norway spruce**	**Dwarf shrubs**	**Scots pine**	**Norway spruce**
Drained					
Ugale	0.70 ± 0.27	1.58 ± 0.3	0.22	2.42 ± 0.75	1.23 ± 0.25
Auce	0.18 ± 0.1	1.15 ± 0.19	0.26	0.18 ± 0.09	0.62 ± 0.05
Smiltene	0.31 ± 0.18	0.59 ± 0.48	0.2	1.04 ± 0.58	0.52 ± 0.41
Undrained					
Viesite	0.64 ± 0.19	0.11 ± 0.07	0.54	0.36 ± 0.12	0.86 ± 0.56
Valle	0.19 ± 0.07	1 ± 0.23	0.44	0.1 ± 0.03	1.44 ± 0.55
Jaunjelgava	1.97 ± 0.1	1.05 ± 0.2	0.48	1.49 ± 0.26	0.95 ± 0.07

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The turnover in Scots pine was higher in the drained forest sites, at 1.21 ± 0.42 year^{-1}, although not statistically different ($p > 0.05$, $df_1 = 1$, $df_2 = 16$, $F = 1.35$) from that of the undrained forest sites, at 0.65 ± 0.23 year^{-1}. The turnover in Norway spruce was similar ($p > 0.05$, $df_1 = 1$, $df_2 = 16$, $F = 0.91$) between both forest site types, at 1.08 ± 0.25 year^{-1} (undrained forest) and 0.79 ± 0.18 year^{-1} (drained forest).

In both forest types, most of the FRB of the Scots pine, Norway spruce, and dwarf shrubs was obtained from the upper organic soil layer (0–10 cm), while for herbaceous plants, it was from the lower organic soil layers (20–40 cm) (Figure 3). In the upper organic layer (0–10 cm), 83.7% and 72.5% of the FRB originated from the Scots pine in the undrained and drained forests, respectively. In the same soil layer, the Norway spruce contributed a similar proportion of FRB in both forest types (~79.7%). The dwarf shrubs in the same soil layer contributed 50.8% and 53.9% in the drained and the undrained forest, respectively. The herbaceous plants in the uppermost organic soil layer (0–10 cm) contributed 19% and 21.4% to the FRB in the undrained and the drained forest, respectively, and in the lower organic soil layers (20–40 cm), they contributed 71.5% and 51.2% of the FRB in the drained and the undrained forest, respectively.

The seasonal dynamics of the FRB of the Scots pine and Norway spruce differed between forest types (Figure 4). In both forest types, the seasonal highest and lowest estimates of Scots pine FRB coincided in May and October 2021, respectively. For the Norway spruce, in the drained forest, the seasonal maximum was estimated in August 2021 (1.47 ± 0.19 t ha^{-1}), but in the undrained forest, it was in May 2021 (1.01 ± 0.23 t ha^{-1}). The lowest Norway spruce FRB estimates coincided in both forest types (October 2021), at 1.28 ± 0.23 t ha^{-1}

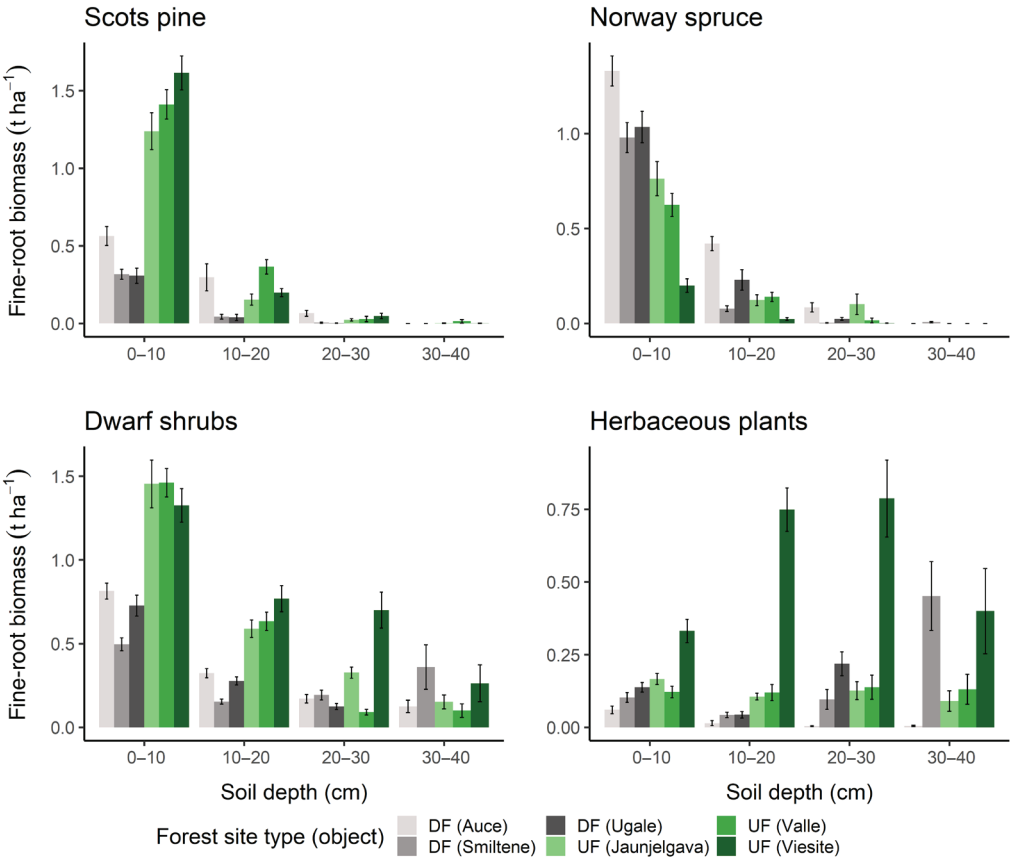

FIGURE 3 Vertical distribution of the mean fine-root biomass (mean ± SE) of Scots pine, Norway spruce, dwarf shrubs, and herbaceous plants in organic soil down to 40-cm depth. DF, drained forest (*Myrtillosa turf. mel*); UF, undrained forest (*Caricoso-phragmitosa*).

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(drained forest) and 0.53 ± 0.21 t ha^{-1} (undrained forest). In all seasonal maxima and minima, the differences between tree species and forest type were statistically significant ($p < 0.05$, $df_1 = 1$, $df_2 = 16$).

The variation in the FRB of the Scots pine per basal area was best explained by the pine standing volume and the mean cover of the shrub layer, according to the linear mixed-effects model (Table 5, Figure 5a). The variation in the FRB of the Norway spruce per basal area was best explained by the spruce standing volume (Figure 5c). The FRB of the dwarf shrubs was best explained by the forest site type (Figure 5b). The variation in the herbaceous plants was best explained by the stand basal area (Figure 5d).

From the PCA, PC1 and PC2 explained 37.6% and 22.2% of the variation, respectively. The PCA indicated the differences between the two forest site types (drained, undrained), with some overlapping also being captured. The variables that correlated negatively with PC1 were the FRB of the Scots pine, the FRB of the herbaceous

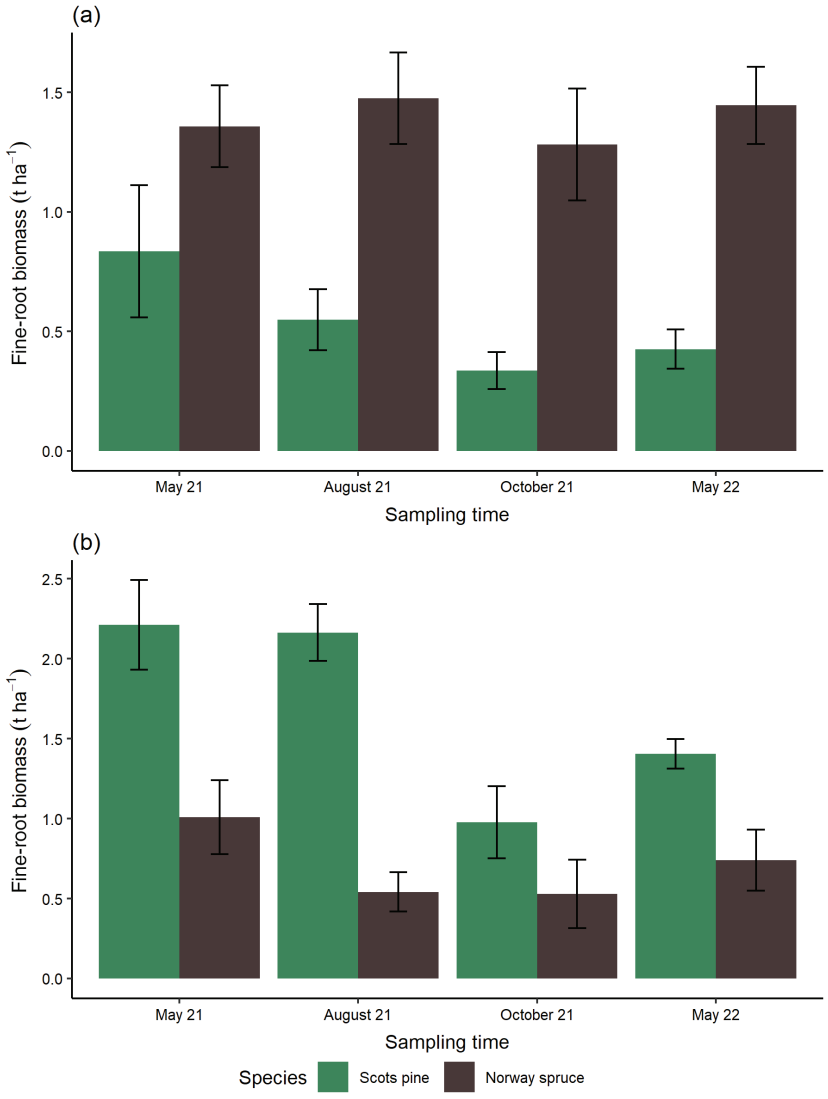

FIGURE 4 Seasonal dynamics of the mean fine-root biomass (mean ± SE) of Scots pine and Norway spruce in (a) drained forest (*Myrtillosa turf. mel*) and (b) undrained forest (*Caricoso-phragmitosa*).

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TABLE 5 Main effects of explanatory variables on the mean fine-root biomass (FRB) of different functional groups (linear mixed-effects models).

Functional group	Explanatory variable	Likelihood ratio chi-squared	df	*p*
FRB of Scots pine per basal area	Pine standing volume (m^3 ha^{-1})	24.6	1, 430	<0.001
	Shrub percentage (%)	65.1	1, 430	<0.001
FRB of Norway spruce per basal area	Spruce standing volume (m^3 ha^{-1})	10.5	1, 70	<0.01
FRB of dwarf shrubs	Forest site type	57.1	1, 70	<0.001
FRB of herbaceous plants	Basal area (m^2 ha^{-1})	13.8	1, 70	<0.005

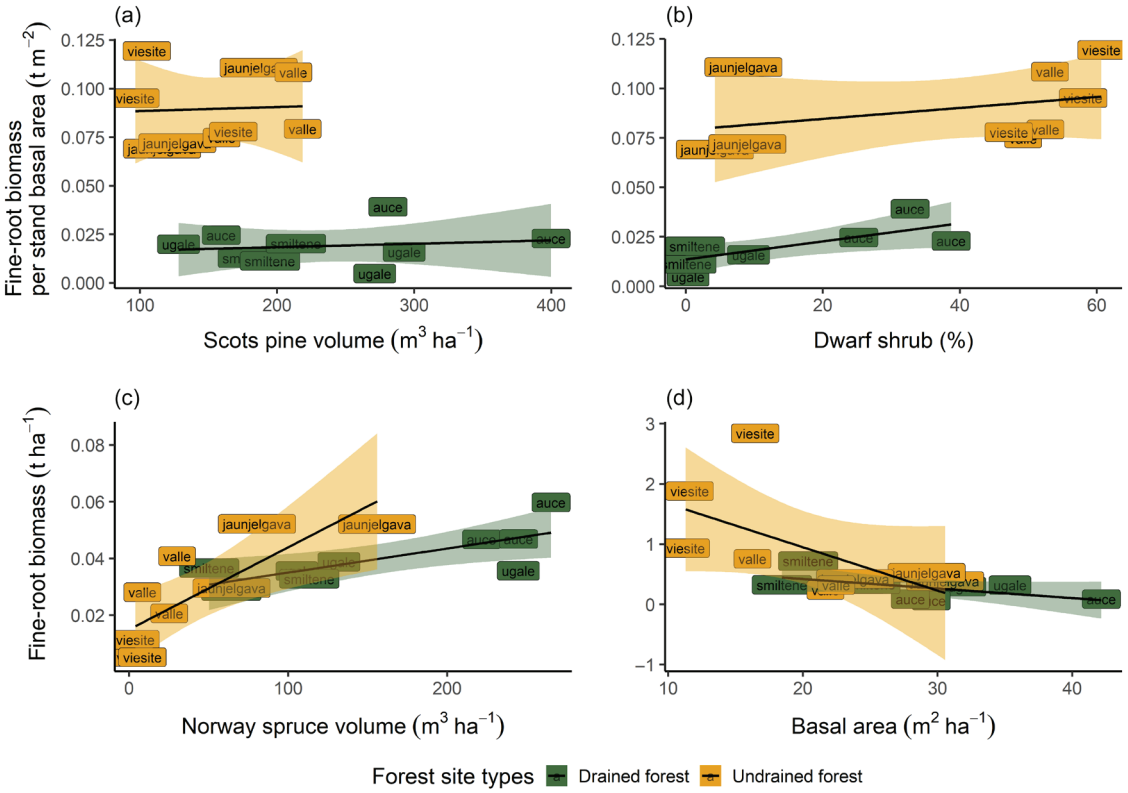

FIGURE 5 (a) Significant effects on fine-root biomass (FRB) based on the linear mixed-effects models, the relationship between the FRB of Scots pine per basal area, and the standing volume of Scots pine by forest site type; (b) relationship between the FRB of Scots pine per basal area and projected cover of dwarf shrubs by forest site type; (c) relationship between the FRB of Norway spruce and standing volume of Norway spruce; and (d) relationship between the FRB of herbaceous plants and stand basal area. Drained forest, *Myrtillosa turf. mel*; undrained forest, *Caricoso-phragmitosa*.

plants, and the FRB of the dwarf shrubs, the dwarf shrub cover, and the C:N ratio. For the Norway-spruce-related variables (FRB, FRP), the standing volume of Norway spruce, soil pH, basal area, mean height, and diameter correlated positively with PC1 (Figure 6b). From the PCA, we captured that the undrained Jaunjelgava site overlapped with the ellipsoid of the drained forest sites. The ellipsoid of the undrained sites also overlapped with the Smiltene drained forest site and partially with the Ugale site (Figure 6a).

DISCUSSION

Forest drainage can fundamentally alter the developmental trajectory of a forest stand. At our study sites, the

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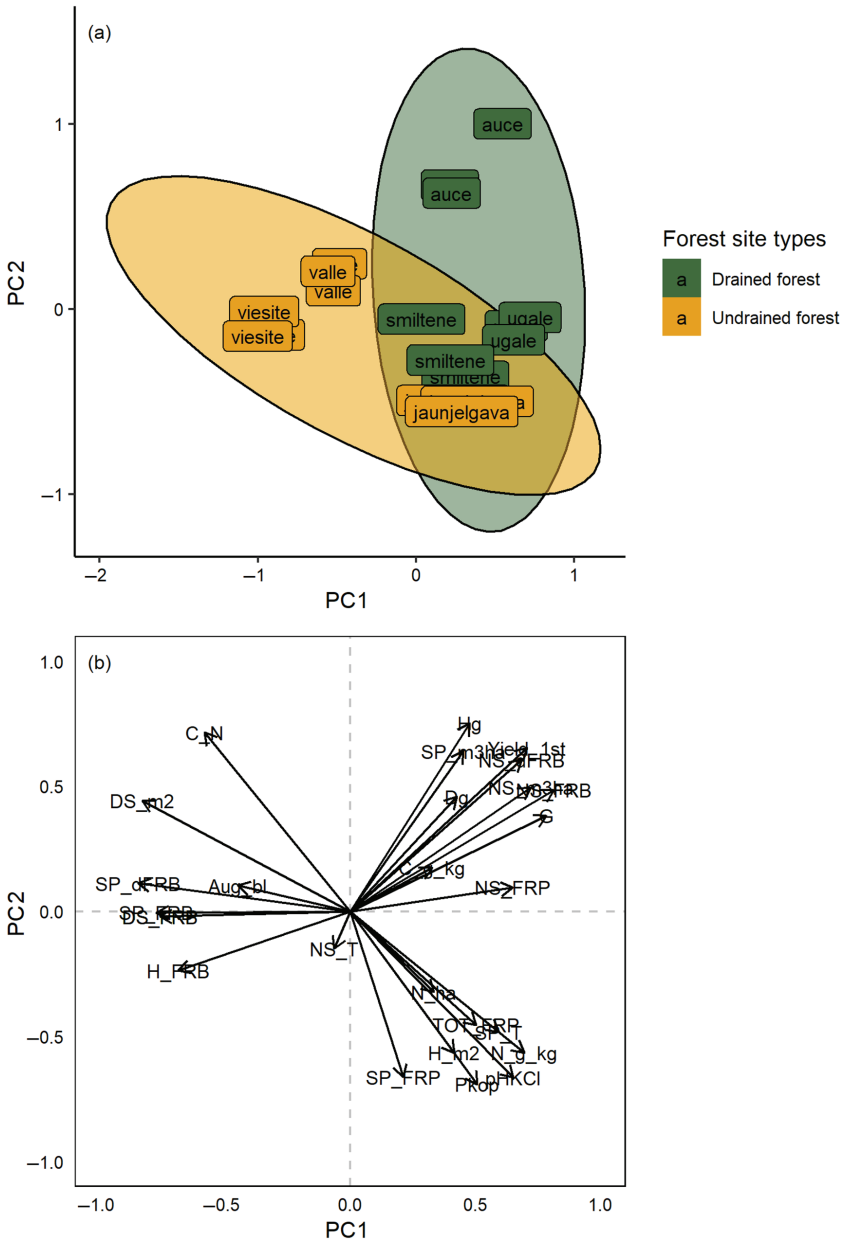

FIGURE 6 Results of the principal components (PC) analysis of the forest site types. PC1 and PC2 are displayed, together explaining 59.8% of the overall variation in the data. Drained forest, *Myrtillosa turf. mel*; undrained forest, *Caricoso-phragmitosa*.

effect of the old drainage system (established 60–80 years ago) was indicated by differences in ecosystem features (Tables 1 and 2). However, the observed high variability (stand and soil characteristics) among the drained sites suggests that the drainage effect was likely confused with other biotic and abiotic factors. It is highly likely that, besides the differences related to the ditch systems (Finér & Laine, 1998; Rezapour et al., 2022), the fundamental soil heterogeneity (Janssens et al., 2002) and tree-species-specific effects (Lampela et al., 2023) played

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significant roles in shaping the differences in the FRB and FRP between and within the sites, as has been reported in other studies (e.g., Laiho & Finér, 1996). Hence, it is difficult to extract a pure long-term drainage effect on the FR characteristics. The GWL was similar among the drained and undrained sites, except for the drained site Auce, which had a significantly lower GWL (Figure 1b). Although the ditches are still visible, the lack of GWL differences is most likely due to the poorly or practically nonfunctioning ditch system (Paavilainen & Päivänen, 1995; Sikström & Hökkä, 2016). In our case, the absence of proper ditch maintenance has likely led to a rise in the GWL at the drained sites. However, we have no information on how long the ditch systems have been nonfunctional at Smiltene and Ugale. In forestry, ditch network maintenance is carried out approximately once or twice during a stand rotation (~100 years) (Hökkä et al., 2000), which suggests that the ditch systems at our sites might have gradually degraded over the last 20–30 years. The difficulty in precisely evaluating the GWL effect on the FR characteristics in different boreal peatlands has also been reported in a short-term (2-year) study by Lampela et al. (2023), the effects overlapping with other biotic and abiotic factors, and also being shaped by tree-species-specific effects. In our study, the long-term effect of drainage on the ecosystem was suggested by the significantly higher mean diameter, basal area, and standing volume of Norway spruce at the drained Ugale and Auce sites (Table 1). Minkkinen and Laine (1998) found that the long-term drainage effect included a higher mean peat bulk density at the drained sites; we also observed higher values at the drained sites (Ugale, Auce). The drained site Smiltene shared some similarities with the undrained sites in terms of soil and stand characteristics, which was also picked up visually by the PCA (Figure 6a). The PCA supported the distinction between the drained and undrained sites by providing a logical association of Norway-spruce-linked variables with the drained forest, and Scots-pine- and dwarf-shrub-linked variables with the undrained forest (Figure 6).

Fine-root biomass

The total FRB was significantly greater in the undrained forest (6.8 ± 0.3 t ha^{-1}) than in the drained forest (3.97 ± 0.1 t ha^{-1}). This larger FRB suggests a greater addition of root litter to the soil organic matter (Hansson et al., 2013). The lower FRB estimates from the drained forest are likely to be linked to better soil nutrient availability than in the undrained forest type. Studies have shown that, in undrained soils, in order to obtain enough mineral nutrition, trees predominantly modify their FR growth to achieve an extensive foraging strategy, characterized by a higher FRB and morphological adaptations (Kalliokoski et al., 2010; Kriiska et al., 2019; Ostonen et al., 2007). In our study, in the undrained forests, Scots pine had a higher FRB (1.7 ± 0.1 t ha^{-1}) than in the drained forest (0.5 ± 0.1 t ha^{-1}), thus supporting an extensive foraging strategy. However, the FRB of Norway spruce being twice that in the drained forest (1.4 ± 0.1 t ha^{-1}) than in the undrained forest (0.7 ± 0.2 t ha^{-1}) suggests a considerably higher proportion of spruce in the stand composition (Table 1). The stepwise regression analysis also showed that the Norway spruce FRB was best explained by the spruce standing volume in the forest stand (Table 5, Figure 5c). Similar positive associations between the FRB of spruce and increasing stand basal area have been found in other studies (Ostonen et al., 2011; Rezapour et al., 2022). However, based on the stepwise regression, the FRB of Scots pine also had a significant positive link with the increasing standing volume of Scots pine, the regression slope being near zero, which suggests a rather small effect on the FRB increase (Figure 5a). Similar estimates of the total FRB to that in our study have been obtained from a drained bog forest (4.80–6.24 t ha^{-1}), although the value was approximately twice as high (11.03–14.73 t ha^{-1}) in a drained fen forest in Finland (Bhuiyan et al., 2017). The higher FRB estimates from the drained forested peatland in Finland might reflect differences in soil fertility, climatic conditions, and/or geographical location, with trees at higher latitudes (in the boreal zone) investing proportionally more in their belowground FRB and in the root elongation rate than their more southerly located counterparts (Helmisaari et al., 2007; Leppälammi-Kujansuu et al., 2014; Ostonen et al., 2017). Also, previous studies have highlighted that the associations between soil fertility and FRB are species- and region-specific (Finér et al., 2007; Leppälammi-Kujansuu et al., 2014).

In mesotrophic boreal and hemiboreal forests, dwarf shrubs form a significant part of the ground vegetation biomass and have a significant impact on C and nutrient cycling (Nestby et al., 2011). Our second hypothesis was not proved—the Scots pine FRB was not the highest out of all the functional groups. In our study, in both forest site types, dwarf shrubs constituted a significant part of the total FRB. In the undrained forest, it contributed the largest part of the total FRB (2.43 ± 0.2 t ha^{-1}), and in the drained forest, it was the second largest (1.16 ± 0.1 t ha^{-1}) (Figure 2a). Similar estimates for the dwarf shrub FRB (1.3–1.7 t ha^{-1}) have been obtained from a drained bog forest, although considerably lower estimates (0.22–0.53 t ha^{-1}) have been determined from a drained fen forest (Bhuiyan et al., 2017). The stepwise regression

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model showed that the FRB of the dwarf shrubs was best predicted by forest site type (Table 5). The significantly higher FRB of dwarf shrubs in the undrained forest was likely because there was an overall higher (38%) mean aboveground projection cover of dwarf shrubs there than in the drained forest (12%). Similar observations have been reported from forests on organic and mineral soils in Finland (Bhuiyan et al., 2017; Helmisaari et al., 2007). In the undrained forest type, the Scots-pine-dominated canopy was open, allowing sunlight to easily reach the understory and enhance the growth of the understory flora (Helmisaari et al., 2007; Kriiska et al., 2019); the proportion of Norway spruce in the stand composition was considerably lower than in the drained forest (Table 1). The mean FRB of the herbaceous plants was higher in the undrained forest than in the drained forest (Table 3). An exceptionally high mean FRB, compared with the other sites, was observed at the undrained Viesite site (1.9 ± 0.47 t ha^{-1}). A likely cause of the higher herbaceous plant FRB at this site is the high abundance of graminoids (17.6%) (Appendix S1: Table S1), which have rather large and vigorous root systems (Wang et al., 2016). Sedges were more common in the undrained forests, with the graminoids most likely having been replaced by forbs in the drained forests. A similar observation was reported by Laiho and Finér (1996).

Fine-root production

FRP can provide valuable insights into soil biochemical cycles and is a key component used to characterize annual soil C fluxes (Finér et al., 2011). In our study, the total FRP was similar in both forest types, at 2.05 ± 0.31 and 1.82 ± 0.26 t ha^{-1} year^{-1} in the undrained and drained forests, respectively. Slightly higher values than those from our study have been reported from a drained bog forest (2.24–2.44 t ha^{-1} year^{-1}) and twice as high values have been reported from a drained fen forest (5.52–5.61 t ha^{-1} year^{-1}), both in Finland (Bhuiyan et al., 2017). The FRP estimates in Bhuiyan et al. (2017) were proportionally comparable with their reported FRB estimates, which indicates overall higher FRB and FRP values from drained forests in Finland compared with those from our study. Unfortunately, Bhuiyan et al. (2017) did not provide any information on the stand age, and so we cannot assess their possible effects on their FRB and FRP estimates.

In our study, the mean FRP of the Scots pine in the drained forests was lower (0.39 t ha^{-1} year^{-1}) than in the undrained forest sites (0.93 t ha^{-1} year^{-1}). Hence, our first hypothesis was partially proved—the Scots pine FRB was higher in the undrained forest, although the FRP estimates were not statistically significant between the forest site types (Tables 3 and 4). Similar estimates have been obtained from drained fen and bog forests in Finland, with values of 0.83 and 1.34 t ha^{-1} year^{-1}, respectively (Bhuiyan et al., 2017). Rather similar values have also been obtained from drained sites on organic soils (0.42–0.71 t ha^{-1} year^{-1}) using the ingrowth method (Finér & Laine, 1998, 2000). For comparison, higher values of Scots pine FRP have been obtained from mineral soils in pole (2.28–3.93 t ha^{-1} year^{-1}) and middle-aged (1.69–2.52 t ha^{-1} year^{-1}) stands (Aun, Kukumägi, Varik, Becker, Aosaar, Uri, Morozov, et al., 2021), and 8.60 t ha^{-1} year^{-1} in a 100-year-old Scots pine stand on mineral soil (Makkonen & Helmisaari, 2001). In drained peatland sites in Southern Finland, the FRP of Scots pine has been found to be higher in sites with lower nutrient availability. However, similarities to our sites are likely due to high variability among the sites and the differences not being statistically significant (Finér & Laine, 1998). In the drained forest, the Norway spruce FRP (1.11 t ha^{-1} year^{-1}) was higher than in the undrained forest (0.72 t ha^{-1} year^{-1}), but this was not statistically significant. Similar results have been obtained in Finland (Bhuiyan et al., 2017), where, as in our sites, the higher Norway spruce FRP was linked to a higher proportion of Norway spruce in the stand composition. In our study, a higher dwarf shrub FRP was observed in the undrained forest (0.48 t ha^{-1} year^{-1}) than in the drained forest (0.22 t ha^{-1} year^{-1}), which is similar to the FRB estimates and most likely linked to the aboveground cover projection. The same magnitude of estimates for dwarf shrubs were obtained from the drained bog and fen forests in Finland, at 0.68 and 0.27 t ha^{-1} year^{-1}, respectively (Bhuiyan et al., 2017). By comparison, considerably lower values of dwarf shrub FRP have been obtained from middle-aged Scots pine stands on mineral soils (0.05–0.11 t ha^{-1} year^{-1}) (Aun, Kukumägi, Varik, Becker, Aosaar, Uri, Morozov, et al., 2021). The undrained Jaunjelgava site had an exceptionally high mean Scots pine FRP, which was at least three times greater than that in the other undrained sites (Table 4). The mean Scots pine FRB was similar to that obtained from other undrained sites (Table 3). The summer (June–August) of 2021 was the warmest since 1924, according to the Latvian Environment, Geology and Meteorology Centre. Such conditions likely triggered a growth response in Scots pine. However, as only one site had an exceptionally high Scots pine FRP, this was likely caused by site-specific effects coupled with the meteorological conditions. In the study published by Lampela et al. (2023), the possible reasons for the extremely low/high FRP and FRB estimates are likely linked to nutrient availability and the sampling method.

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Fine-root turnover

FRT is used in biogeochemical and C-cycle modeling (Brunner et al., 2013). Consequently, it is important to provide reliable estimates from different ecosystems. In our study, we found no statistically significant differences between the forest site types, which might be because of the high variability between the study sites within the same forest site type (Table 4). Among the drained sites, the lowest Scots pine FRT obtained was 0.18 $year^{-1}$ at Auce, and the highest was 2.42 $year^{-1}$ at Ugale. The large variability between the sites was also visible in the FRB and FRP values (Tables 3 and 4). Other studies have found that tree FRT is faster in more fertile soils (e.g., Kriiska et al., 2019). In our study, we found that the Scots pine turnover was almost twice as high in the drained forest sites (1.21 $year^{-1}$) than in the undrained forest sites (0.65 $year^{-1}$), which supports our third hypothesis. For the Norway spruce, we found a slightly higher turnover in the undrained forest (1.08 $year^{-1}$) than in the drained forest (0.79 $year^{-1}$), although this was not statistically significantly different.

Vertical distribution of FRs

In our study, we obtained similar results to those reported in earlier studies (Hansson et al., 2013; Ostonen et al., 2005), with the majority of the tree (Scots pine, Norway spruce) FRs located in the uppermost 10 cm of the soil profile (Figure 3). On mineral soils, the majority of Scots pine and Norway spruce FRs have been located in the humus or the uppermost soil layer, depending on the soil type (Hansson et al., 2013; Makkonen & Helmisaari, 2001; Ostonen et al., 2005, 2007). The depth distribution of FRs is affected by the stage of stand development (Makkonen & Helmisaari, 2001), soil characteristics (Kirfel et al., 2019), and tree species (Yuan & Chen, 2010). The majority of herbaceous plant FRs were located in the lower organic soil layers (20–40 cm) (Figure 3). Similar observations have been reported by Bhuiyan et al. (2017) from drained boreal bog and fen peatland forests. Studies have shown that the FRs of sedge species can form aerenchyma tissues, which allow them to transport gases/oxygen from the hypoxic zone (Wang et al., 2016), thus allowing the development of deeper root systems. Also, the highest proportion of herbaceous FRB in the deeper soil layers might be linked to the competitive displacement of FRs (Schmid, 2002). In our study, root competition might have been the highest in the uppermost 10 cm, where the majority of the tree FRs were located. Hence, in order to obtain water and soil nutrients, the herbaceous plants developed root systems extensively distributed in the deeper soil layers.

Seasonal variation in FRs

There is a considerable seasonal and yearly variation in the growth of the FRB (Ostonen et al., 2005). In Northern Europe, the FRB is rather evenly distributed throughout the vegetation season, with the seasonal maxima falling in June and August, and the lowest at the end of vegetation season in November (Ostonen et al., 2005). In our study, the sampled FRB was rather evenly distributed over the sampling months. However, large fluctuations were observed in the Scots pine FRB (Figure 4), with the seasonal maximum in May. One of the main factors shaping FR growth responses is the weather conditions, especially severe drought, which can cause a reduction in the FRB (Brunner et al., 2015; Zang et al., 2014). The lower FRB estimates in the summer months could be explained by the extreme heat conditions that occurred in Latvia, which started at the end of June and lasted until the end of July, according to information from the Latvian Environment, Geology and Meteorology Centre.

CONCLUSIONS

Our work has revealed novel aspects of FR characteristics in drained and undrained forests in the hemiboreal forest zone. To incorporate the natural variability of forests on organic soils, we sampled several stands to represent two forest site types in order to provide mean estimates of the FRB, FRP, and FRT of different functional groups, as well as to illustrate the great variability in FR data between different stands. The effect of old forest drainage systems that are no longer managed has altered the developmental trajectory of the stands, which can be detected in the differences in stand composition, soil chemistry, and FR characteristics. Changes in the FR characteristics in the drained forest sites were also revealed by the twofold higher FRB of Norway spruce there than in the undrained forest sites, suggesting a rapid development of this tree species. Similarly to the FRB of Norway spruce, the dwarf shrub FRB had close positive associations with increasing vegetation cover. For Scots pine, which was the dominant tree species in the studied stands, the differences in the FRs between the two forest site types suggested adaptation to an extensive foraging strategy.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Samariks, 2024a) are available from Dryad: https://doi.org/10.5061/dryad.b8gtht7kg. Code (Samariks, 2024b) is available from Zenodo: https://doi.org/10.5281/zenodo.10209650.

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