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 ℃. February is the coldest month with an average air temperature of approximately -3.7 ℃, while July is the warmest month, recording an average air temperature of +17.4 ℃, 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).

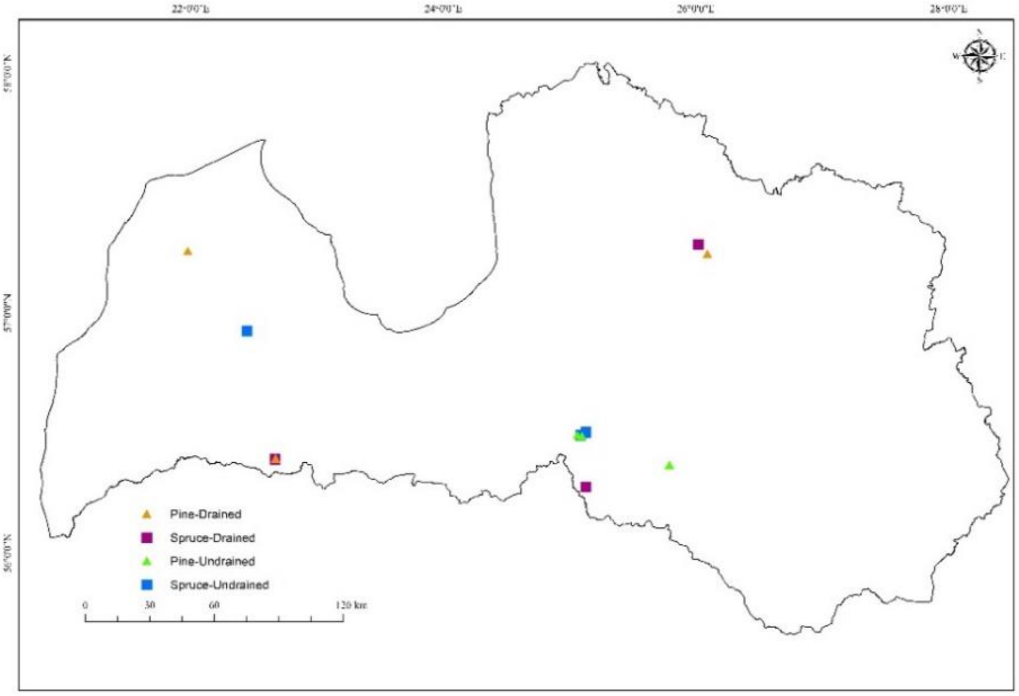

Figure 1. Research objects.

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.

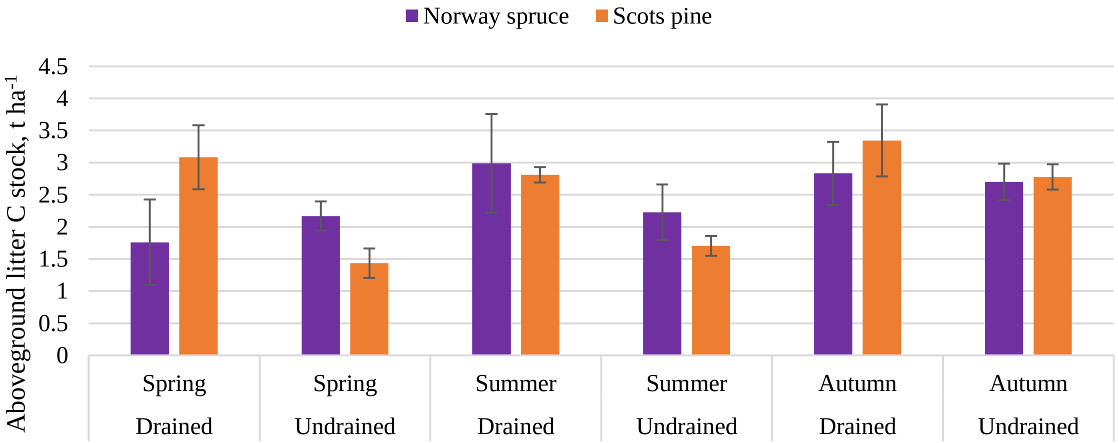

Figure 2. Seasonal aboveground litter C stock (Whiskers denote ± 95% confidence interval).

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.

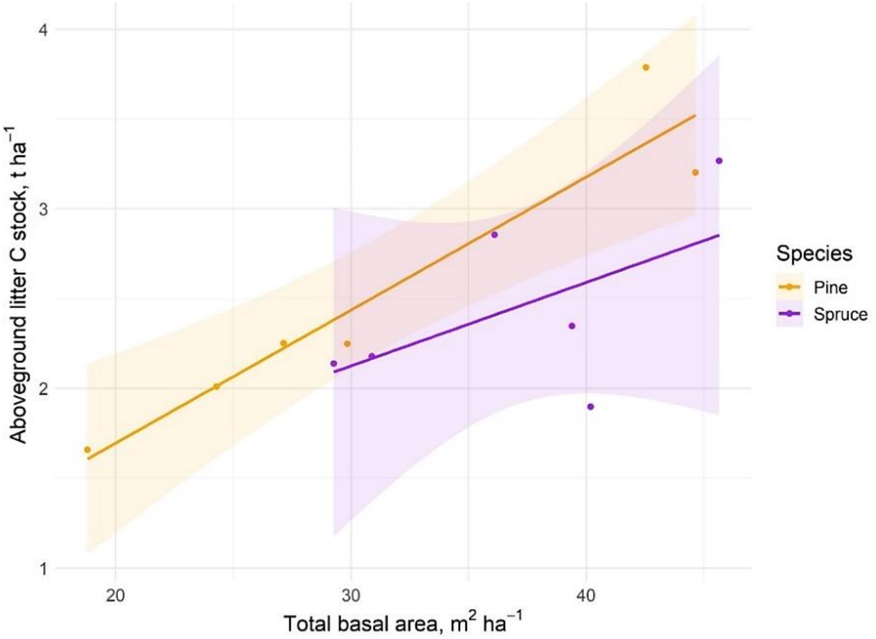

Figure 3. Annual C input by litter as a function of total basal area (± 95% confidence interval).

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 varialitity 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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