



Interannual variability and seasonality of litterfall in three temperate and boreal forest ecosystems of eastern Canada: A synthesis of long-term monitoring

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ARTICLE INFO

Keywords:

Litterfall production
Seasonal pattern
Temperate and boreal forest
Forest floor stocks
Carbon cycle
Climate anomalies

ABSTRACT

Litterfall is a major pathway for transferring aboveground biomass to the forest floor and thus plays an important role in building forest soil carbon stocks. However, inter- and intra-annual variability of litterfall remains poorly documented, especially in North American temperate and boreal forests, due to the lack of recent long-term studies at high sampling frequencies. This potentially creates uncertainties in estimates of forest carbon budget models. The objectives of the present study were to 1) quantify the mean annual flux, interannual variability, and seasonality of litterfall in three sites (dominated respectively by sugar maple (*Acer saccharum* Marsh.), balsam fir (*Abies balsamea* (L.) Mill. 1768), and black spruce (*Picea mariana* (Mill.) B.S.P.)) in eastern Canada over a period of 22–32 years, 2) relate the litterfall amounts and temporal variations to the changes in the size of major organic matter pools in these ecosystems, and 3) compare our litterfall estimates with reference values used in national greenhouse gas inventories. Litterfall production decreased from the sugar maple to the balsam fir and black spruce sites, preponderantly due to species composition. Litterfall evolution was related to the aboveground biomass of live trees in both conifer sites; in contrast, in the broadleaf site, changes in forest composition and structure were apparently the main drivers. The litterfall seasonality varied between broadleaf and conifer sites and could be explained by a sigmoidal model. Substantial departures from the seasonality for some given years were likely due to important climatic anomalies. Forest floor biomass remained stable over time at all three sites despite the increase in litterfall at the balsam fir and sugar maple sites and rapid forest floor turnover at the latter site. Our analyses of litterfall suggest that reference values from the literature used for national greenhouse gas inventories underestimate annual litterfall and forest floor carbon stocks for temperate and boreal forests.

1. Introduction

Globally, forests play a major role in the global carbon (C) cycle. Since the end of the last century, they have accumulated more C than they have released, storing the equivalent of about one third of total anthropogenic C emissions (Friedlingstein et al., 2020). Given the vital role of forests, there is a need to reduce uncertainties about their influence on the global C budget and to assess the potential risks and opportunities of the forest sector for reducing atmospheric greenhouse gas concentrations and mitigating climate change (Friedlingstein et al., 2020; Parmesan et al., 2022).

Good practices in national greenhouse gas inventories consider the main C fluxes for forest ecosystems, specifically the change in C stocks in living biomass, dead organic matter (including forest floor or humus and dead wood or woody debris), and soils (Intergovernmental Panel on Climate Change (IPCC), 2003). Litterfall is the primary pathway for transferring C from aboveground biomass to the forest floor and thus plays an important role in the variability of dead organic matter C stocks (Binkley and Fisher, 2019; Osman, 2013). Litterfall is consequently an essential element to consider when assessing the contribution of forest ecosystems to the C cycle (Sitch et al., 2008).

Most terrestrial biogeochemical models assume that biotic factors

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<https://doi.org/10.1016/j.foreco.2024.122069>

Received 29 September 2023; Received in revised form 10 May 2024; Accepted 7 June 2024

Available online 23 July 2024

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such as stand structure, tree species composition and forest type, and abiotic factors such as soil fertility and climate control net primary productivity (NPP) and, thus, influence litterfall (Fisher et al., 2014; Wieder et al., 2015); this is at least partly supported by empirical data. For example, Jevon et al. (2022) using three separate data sources with different spatial and temporal extents, found that, in temperate forests, foliar litter production generally increased with aboveground woody production and this relation could be modified by plant functional group and climate. Another study showed that broadleaf forest stands produced more litterfall in boreal and temperate zones than mixed or softwood stands (Chen et al., 2017; Jevon et al., 2022). However, litterfall monitoring of five softwood or hardwood species in monospecific stands in Denmark revealed few differences between species compositions, but higher litter production at the richer loamy site compared to the two poorer sandy sites (Hansen et al., 2009). Bhatti & Jassal (2014) observed that the annual needle litter production in mature jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.) sites in western Canada was strongly influenced by cumulative growing degree-days (GDD). Similarly, based on a compilation of data from over 400 stands in Eurasia, where 43 % were coniferous and 57 % were broadleaf forests, Liu et al. (2004) reported that litterfall production at the continental scale was primarily influenced by the mean annual temperature, particularly for hardwood species stands. Shen et al. (2019) reported that, on a global scale, variability in litterfall was mainly explained by actual evapotranspiration. Beside forest characteristics and environmental variables, insect herbivores can also influence litterfall production, notably during epidemic periods (Gandhi and Herms, 2010; Risley and Crossley, 1993).

Litterfall varies spatially and temporally between years and within a given year. Generally, litterfall follows a different seasonality (i.e., regular and predictable changes recurring every year) depending on the forest type. For example, in temperate broadleaf forests, litterfall mainly occurs in the fall during leaf senescence. In contrast, in temperate and boreal coniferous forests, litterfall is more continuous throughout the year, with slight increases observed in the spring during the bud burst of new needles, and in the fall during the senescence of old needles

(Portillo-Estrada et al., 2013; Zhang et al., 2014). In addition to the interannual climate variability, extreme climatic events such as droughts, extreme cold events and windstorms can alter seasonality and annual litterfall (Bhatti and Jassal, 2014; Houle et al., 2016; Portillo-Estrada et al., 2013).

Many studies have quantified the amount of litterfall in various areas of the world (Holland et al., 2014; Shen et al., 2019). However, few provide long-term data at high sampling frequencies for North American temperate and boreal forests (Zhang et al., 2014). Furthermore, litterfall measurement studies are generally of short duration with varying sampling frequencies, which is not conducive to documenting seasonality and interannual variability. This potentially creates uncertainties in the forest C budget generated by models in which this process is often represented using default values from the literature (IPCC, 2003). The lack of knowledge of litterfall also generates uncertainties in Dynamic Global Vegetation Models (DGVMs) used to represent the contemporary and future global C cycle (Sitch et al., 2008). In addition, DGVMs rarely incorporate seasonality into their simulations, even though it is a crucial factor to consider when describing C dynamics in forest ecosystems (Portillo-Estrada et al., 2013; Zhang et al., 2014). Finally, few studies combine the estimation of litterfall production with the quantification of major organic matter pools (living biomass, dead organic matter, and soils) within forest ecosystems. Despite the different and complex dynamics observed within these pools and litterfall production, their interconnection directly influences C storage and cycling within forest ecosystems. For instance, changes in litterfall input could lead to cascading effects on biogeochemical processes by affecting decomposition rate and soil respiration and, thus, soil C content (Xu et al., 2013).

The first objective of this study was to quantify the mean annual flux, interannual variability, and seasonality of litterfall in three ecosystems representative of the major bioclimatic domains of the province of Quebec (eastern Canada), i.e., the sugar maple-yellow birch (*Acer saccharum* Marsh.-*Betula alleghaniensis* Britton), balsam fir-white birch (*Abies balsamea* (L.) Mill. 1768-*Betula papyrifera* Marsh.), and black spruce (*Picea mariana* (Mill.) B.S.P.)-feathermoss domains, over a period of 22–32 years. The second objective was to relate the litterfall amounts

Table 1
Climate, stand and soil characteristics of the sugar maple, balsam fir, and black spruce sites.

| | Sugar maple | Balsam fir | Black spruce |
|---|--|------------------------------------|-------------------------------------|
| Latitude | 46°57'N | 47°17'N | 49°13'N |
| Longitude | 71°40'W | 71°14'W | 73°39'W |
| Elevation (m) | 350 | 800 | 400 |
| Climate normal* | | | |
| Mean annual air temperature (°C) | 3.5 | 0.0 | 0.6 |
| Mean annual total precipitation (mm) | 1 408 | 1 429 | 971 |
| Mean annual growing degree-days (°C) | 1 500 | 935 | 1 233 |
| Stand** | | | |
| Forest cover type | <i>Deciduous</i> | <i>Coniferous</i> | <i>Coniferous</i> |
| Canopy composition (% basal area) | 47 % sugar maple 32 % American beech 21 % yellow birch | 87 % balsam fir 7 % white birch | 80 % black spruce 20 % jack pine |
| Mean age (years) | Uneven-aged | 80 | 80 |
| Stem density (stems ha ⁻¹) | 2 352 | 2 204 | 4 016 |
| Basal area (mean ± SE) (m ² ha ⁻¹) | 30.0 ± 2.1 | 49.4 ± 1.4 | 34.7 ± 1.3 |
| DBH (mean ± SE) (cm) | 8.9 ± 0.3 | 15.6 ± 0.5 | 9.7 ± 0.1 |
| Soil | | | |
| Humus type | Moder | Mor | Mor |
| Forest floor thickness (mean ± SE) (cm) | 5.0 ± 0.2 | 11.0 ± 0.4 | 14.0 ± 0.5 |
| Soil type*** | Ferro-Humic Podzol | Humo-Ferric Podzol | Humo-Ferric Podzol |
| Soil texture | Sandy loam | Sandy loam | Loamy sand |
| Drainage class | 2 | 3 | 2 |

* For the 1991–2020 period. Estimated according to the location of the sites with the weather generator of BioSIM software (Régnière, 1996).

** Stand characteristics for stems with a diameter at breast height (DBH) > 1.0 cm from the 2016 inventory for the sugar maple and black spruce sites and from the 2018 inventory for the balsam fir site.

*** Orthic Ferro-Humic or Humo-Ferric Podzols according to the Canadian System of Soil Classification (Soil Classification Working Group, 1998) or Podzols according to the World Reference Base (IUSS Working Group WRB, 2015)

and temporal changes to variations in the size of major organic matter pools in these ecosystems. The third objective was to compare our litterfall estimates with reference values used in national greenhouse gas inventories. Based on current knowledge, we anticipated that 1) the mean annual litterfall and its seasonality vary by forest type (broadleaf vs. evergreen), 2) climatic anomalies alter annual litterfall production and seasonality, 3) annual litterfall increases with increased live tree aboveground biomass, and 4) our estimations of litterfall are different from reference values used for national greenhouse gas inventories (IPCC, 2003) and modelling of forest C dynamics in Canada (Kurz et al., 2009).

2. Materials and methods

2.1. Study sites

The three study sites are located within study watersheds that are part of the Québec Forest Ecosystem Research and Monitoring Network (Réseau d'Étude et de Surveillance des Écosystèmes forestiers; RESEF, Table 1). The first and southernmost site (hereafter referred to as the sugar maple site) is located in the Sugar Maple – Yellow Birch bioclimatic domain (Saucier et al., 1998). This site is affected by the contemporary decline in sugar maple regeneration and growth and the proliferation of American beech (*Fagus grandifolia* Ehrhart.).

The second site (balsam fir) is located further north and at a higher altitude, and is part of the Balsam Fir – White Birch bioclimatic domain (Saucier et al., 1998). This site is colder than the southernmost site but receives similar precipitation. The third and northernmost site (black spruce) is in the Black Spruce – moss bioclimatic domain (Saucier et al., 1998). The climate is drier than the southern sites and slightly warmer than the balsam fir site. The area of monitored plots is 50×100 m (0.5 ha) at the sugar maple site and 50×50 m (0.25 ha) at both coniferous sites. The sampling period was from 1986 to 2020 for the sugar maple site, from 1998 to 2020 for the balsam fir site and from 1996 to 2020 for the black spruce site.

2.2. Litterfall

Litterfall (including leaves and needles, twigs with diameter < 1 cm, flowers, fruits, bark, and other plant parts, insect and bird droppings and dead insects) was sampled at the three sites using litter traps inside the monitored plots. The litter traps were 20 cm-high open boxes with a nylon mesh bottom (0.3 mm), positioned horizontally 30 cm above the ground. The traps were 2 m² (1.41×1.41 m) in the maple site and 1 m² in the coniferous sites. The distance between any two litterfall traps was between 10 m and 70 m. In the maple site, a total of 10 litter traps, randomly distributed across the study plot (0.5 ha), were used to monitor litterfall in the maple site from 1988 to 1996; this number was reduced to 5 traps in 1997. No sampling took place in 1998 at this site. Five traps randomly distributed across the study plot (0.25 ha) were also used in the spruce and fir sites, for which sampling began in 1997 and 1999, respectively. The traps were placed on the ground during winter, so that winter litterfall could be captured at snowmelt. At the maple site, litterfall was collected once after snowmelt (April or May), once in late August, and biweekly from September through November. At the coniferous sites, litterfall was collected monthly during the snow-free period, roughly from May to November. Data were available until 2020 for the three sites.

The oven-dry weight (60 °C for 48 hours) of each sample was measured. Annual litterfall was calculated from June 1st to May 31st of the following year and identified by the first year. Given that it is estimated that about half of the dry mass of tree tissues, including litter, is composed of C (Kurz et al., 2009; Thomas and Martin, 2012), the organic C concentration of litterfall was not systematically analyzed throughout the study period. To establish reference values for our study, we measured organic C concentration for at least two harvests at each stand.

At the sugar maple site, it was assessed in November 2020 (n=19), as well as in May (n=5) and October (n=20) 2020. At the two coniferous sites, it was assessed in May (n=5) and June (n=5) 2022. Samples were oven-dried (105 °C) and grounded to 500 µm with an automated dry combustion instrument (model LECO CR-412) at 1350 °C under an oxygen atmosphere.

2.3. Tree

Forest stands were surveyed approximately every five years since monitoring began (1986, 1989, 1996, 2001, 2006, 2011 and 2016 at the sugar maple site, 1998, 2003, 2008, 2013 and 2018 at the balsam fir site and 1996, 2001, 2006, 2011 and 2016 at the black spruce site). The monitored plots were divided into subplots of 100 m². At each survey, all trees with a DBH greater than 1.0 cm were numbered, positioned, and measured for DBH and height within each subplot. Tree species and status (alive or dead) were also determined. We estimated the above-ground dry biomass of live and dead standing trees from these surveys using the Canadian national species-specific allometric aboveground biomass equations (based on DBH and height) developed by Lambert et al. (2005); these equations make it possible to estimate the biomass of compartments (foliage, branch, wood, and bark), which are constrained to equal the total biomass. The aboveground biomass of dead standing trees was estimated by excluding the tree foliage compartment but without considering the tree crown condition or trunk decay rates. We also compared foliage biomass estimates with our annual litterfall production measurements to calculate the foliage turnover rate.

2.4. Woody debris

Woody debris biomass was estimated in July (black spruce site), October (balsam fir site) and November (sugar maple site) 2003 (Tremblay et al., 2012) and July (sugar maple and balsam fir sites) and October (black spruce site) 2022 using the line intersect method described in Taylor (1997), adapted to measure woody debris with a diameter ≥ 1 cm. Six transects were delineated in the sugar maple site and three in the balsam fir and black spruce sites. At both coniferous sites, the first transect of 50–60 m was randomly delineated from the center of the plot and two others were set at 60° apart. At the sugar maple site, the plot was subdivided into two parts, in which three transects were delineated in the same way as for the coniferous sites. During the inventory, the diameter class (1–7.5 cm; 7.6–12 cm; 12.1–30 cm; > 30.0 cm) and decay class (intact (1) to totally decomposed (5)) of each woody debris intersecting the transect were noted. A wood slice of approximately 2 cm was also collected from debris representing each diameter-decay class inventoried on the transect (8–15 samples per site). The bulk density for each diameter-decay class was calculated from the volume (estimated using the Archimedes principle) and dry mass of the samples. Woody debris biomass for each transect was calculated using the Van Wagner (1968) formula:

$$W = \frac{\pi^2 S_{ij}}{8L} \sum d_{ij}^2$$

where W is weight per unit area (Mg ha⁻¹); S is density in units of weight per unit volume (g cm⁻³) for diameter class *i* and decay class *j*; *d* is diameter piece (cm) at the intersection for diameter class *i* and decay class *j*; and L is length (m) of a sample line.

2.5. Forest floor

Two types of soil sampling were carried out at the three sites: a soil pit survey and a spatiotemporal grid sampling. Soil surveys were performed approximately every ten years since monitoring began. Specifically, surveys were conducted between May and July 1993, 1998, 2008, and 2016 at the sugar maple site; between July and September 1998, 2007, and 2017 at the balsam fir site; and in October 1996, 2006, and

2016 at the black spruce site. At each survey, six pits of 1 m² were dug in the sugar maple site and four in each coniferous site on the periphery of the study plots. When present, the L, F and H horizons and mosses were sampled with a template for a known surface area, and their depth was recorded. The L, F and H samples were air-dried, weighted, and sieved to 2 mm to determine the bulk density, by dividing the dry mass by the sampled volume, and the organic matter content by the loss-on-ignition method (Gallardo et al., 1987). The organic C concentration of the forest floor was measured using the method described above to estimate organic C in litterfall.

In September 2002 and 2012, respectively, 60 and 10 forest floor samples were collected with a volumetric soil sampler (diameter = 4.8, 5.2 or 8.0 cm) within a 20 m² spatiotemporal sampling grid established on the periphery of the study plot to monitor temporal changes in soil properties. The depth and dry mass of each sample were determined, and the bulk density was calculated by dividing dry mass by volume.

Forest floor biomass was calculated for each soil pit by multiplying the organic matter concentration of LFH forest floor horizons from the soil pit survey by the average site-specific bulk density and forest floor thickness from the spatiotemporal grid samplings. A spatiotemporal sampling grid was more suitable than soil pits for quantifying forest floor biomass and detecting temporal trends due to lower variability. The forest floor was not sampled each time with a known surface area in the soil pits, thus restricting the use of these data to assess temporal changes in forest floor bulk density and organic matter pools. In addition, the number of observations was low in the soil pits, and the variability of layer depth observations was high for these samples.

2.6. Climate data

Annual climatic factors, including air temperature and precipitation, were obtained for the location of the sites with the weather generator of the BioSIM software from 1988 to 2020 in the sugar maple, from 2001 to 2020 in the balsam fir and from 1997 to 2020 in the black spruce (Régnière, 1996). Daily maximum wind speed (Met-One 013 A, Campbell Scientific, Logan, UT) was computed from meteorological stations at each of the study watersheds. Based on these data, we studied and documented the probability of occurrence of climatic anomalies associated with strong deviations from annual and seasonal patterns of litterfall.

2.7. Statistical analyses

Linear mixed models (LMM) were used to investigate the site and time effects and their interactions on annual litterfall and aboveground (live and dead standing trees), woody debris and forest floor biomass. We considered respectively litter traps (n=5 and n=10 after and before 1997, n=5 and n=5 at the sugar maple, balsam fir and black spruce sites, respectively), 100 m² subplots (n=50, n=25 and n=25 at the sugar

maple, balsam fir and black spruce sites, respectively), transects (n=6, n=3 and n=3 at the sugar maple, balsam fir and black spruce sites, respectively) and soil pits (n=6, n=4 and n=4 at the sugar maple, balsam fir and black spruce sites, respectively) as random effects, and an autocorrelation structure of order 1 for the continuous time covariate. Differences among sites were tested for litterfall, foliage of live trees, wood of live and dead standing trees (aboveground biomass including wood, bark and branches), woody debris and forest floor. The homoscedasticity and normality of sample distributions were verified through residual plot analysis. We only transformed data that showed clear violations of key assumptions since LMM are robust to violations of distributional assumptions (Schielzeth et al., 2020). These transformations were limited to woody debris biomass (natural log). Adjusted means and standard errors (S.E.) were presented, except for woody debris, where mean and S.E. were at their original scale to facilitate interpretation. While our study does present a methodological limitation due to the absence of site replication caused by resource constraints, it still offers unique long-term data at high sampling frequencies.

Average intra-annual patterns in litterfall at each site were also modelled using a sigmoid equation considering all years of observation, except one specific year at each site due to their unusual seasonal trends (2009 in the sugar maple site, 2012 in the balsam fir site and 2001 in the black spruce site). For the balsam fir site, we also excluded the years 1999 and 2000 since the number of samplings for these years was only two (June and August) and three (June, July and October), respectively: this limited sampling size did not allow for an accurate characterization of seasonality.

Results from the study were then compared with default values related to litterfall proposed for the Tier 1 approach in the IPCC guidelines for national greenhouse gas inventories, and those used in the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3).

All analyses were performed in the R environment (R Core Team, 2023), using the package *dplyr* for data manipulation (Wickham et al., 2023), *ggplot2* for data visualization (Wickham, 2016), *nlme* for linear mixed models (Pinheiro et al., 2022; Pinheiro & Douglas, 2000), *emmeans* for adjusted means computation (Lenth et al., 2023), and *stats* for sigmoid models (R Core Team, 2022).

3. Results

3.1. Litterfall production

Comparisons among sites revealed that litterfall was highest in the sugar maple site ($3.8 \pm 0.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), intermediate in the balsam fir site ($3.0 \pm 0.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), and lowest in the black spruce site ($1.9 \pm 0.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$); the sugar maple site produced approximately twice as much litterfall as the black spruce site ($p < 0.001$, Table 2). The average organic C concentration of litterfall was $0.48 \pm 0.002 \text{ g C/g dry matter}$ for the sugar maple site and $0.50 \pm$

Table 2

Average dry mass of litterfall ($\text{Mg ha}^{-1} \text{ yr}^{-1}$, \pm S.E.) and organic matter pools (Mg ha^{-1} , \pm S.E.) in the sugar maple, balsam fir, and black spruce sites over the study period. Letters a, b and c indicate significant differences between sites ($p < 0.05$).

| | Sugar maple | Balsam fir | Black spruce |
|--|--------------------|-----------------------|--------------------|
| Litterfall ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) | 3.8 ± 0.1^a | 3.0 ± 0.2^b | 1.9 ± 0.2^c |
| Organic matter pools (Mg ha^{-1}) | | | |
| Foliage biomass of live trees | 5.0 ± 0.3^a | 14.8 ± 0.4^b | 13.3 ± 0.4^c |
| Aboveground biomass of live trees* | 200.0 ± 10.6^a | 154.0 ± 15.8^{ab} | 118.0 ± 15.6^b |
| Aboveground biomass of dead standing trees* | 27.7 ± 2.8^a | 9.07 ± 5.1^b | 11.1 ± 4.7^b |
| Woody debris biomass | 29.1 ± 6.6^a | 21.8 ± 4.3^a | 6.1 ± 0.7^b |
| Forest floor biomass | 53.0 ± 2.7^a | 127.4 ± 3.6^b | 98.0 ± 3.5^c |

* Including wood, bark and branches

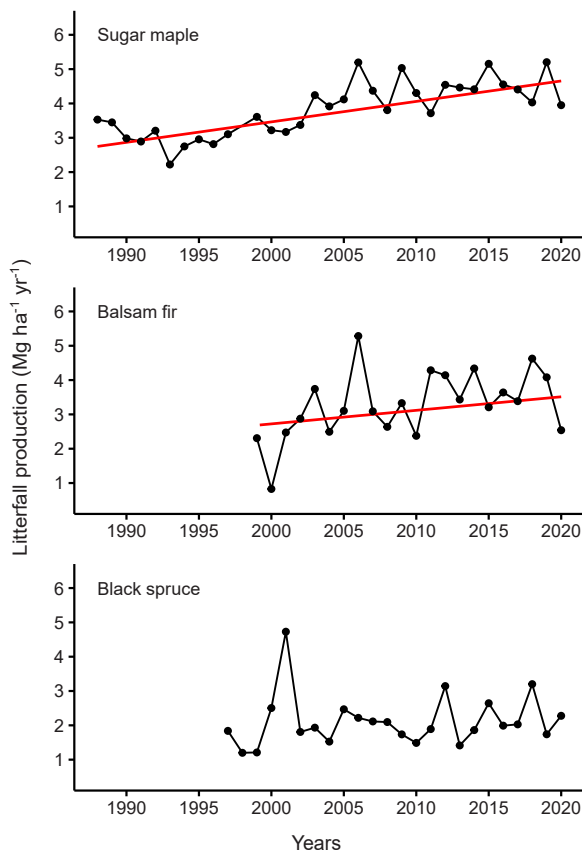


Fig. 1. Evolution of annual litterfall biomass ($\text{Mg ha}^{-1} \text{yr}^{-1}$) in the sugar maple, balsam fir, and black spruce sites. Statistically significant trends are expressed with a red line.

0.002 g C/g dry matter for the balsam fir and black spruce sites, corresponding to a litterfall production of 1.82, 1.50 and 0.95 $\text{Mg C ha}^{-1} \text{yr}^{-1}$, respectively.

Litterfall increased over time in the sugar maple ($p < 0.001$) and the balsam fir ($p = 0.010$) sites, but showed no change in the black spruce site ($p = 0.223$, Fig. 1). Over the study period, the increase was 59.6 $\text{Mg ha}^{-1} \text{yr}^{-1}$ for the sugar maple site and 39.5 $\text{Mg ha}^{-1} \text{yr}^{-1}$ for the balsam fir site, as estimated from the regression line. The analysis also revealed that the interannual variability of litterfall was higher in the balsam fir and black spruce sites (coefficient of variation (CV) = 29.7 % and 35.6 %, respectively) than in the sugar maple site (CV = 20.7 %, Fig. 1).

3.2. Litterfall seasonality

In the sugar maple site, litterfall generally followed a seasonality starting in August and ending in early November (Fig. 2). The majority of litterfall occurred in October, except for the year 2009, characterized by an early litterfall, mainly in September. Analysis of the climatic data revealed that the exceptionally early litterfall measured on September 16th, 2009, was possibly associated with severe drought in the preceding days. Precipitation was estimated at 29 mm over the 37 days prior to the 2009 September sampling, whereas the average for this period is 160 mm over the monitoring period (1988–2020); this value is less than the 0.001 quantile of the distribution. Moreover, the average daily mean minimum temperature was 5.7 °C over the same 37 days compared to the 8.3 °C average for the monitoring period; this value is less than the 0.05 quantile of the distribution.

In both coniferous sites, litterfall seasonality was less pronounced, particularly in the black spruce site (Fig. 2). In the balsam fir, the seasonal trends of litterfall were also similar among years except for years 2003, 2006, and 2011, which showed more intense litterfall in September and October, and 2012, which showed more intense litterfall in July to September. In July 2012, the total precipitation was estimated to be 20.1 mm compared to the 144 mm average for the monitoring period (2001–2020); this value is less than the 0.001 quantile of the distribution. For its part, the 2002 dry spell lasted from August 1st to September 9th, with 47 mm of precipitation over 41 days, whereas the average precipitation for the same period during the monitoring period was 153 mm; this value is less than the 0.001 quantile of the distribution. In 2010, the drier period extended from July 20th to September 2nd, with a total of 57 mm over 45 days. In comparison, the average precipitation over the 20 years of monitoring was 178 mm during this period; this value is less than the 0.001 quantile of the distribution. Following August 2002 and 2010, August 2006 was the third-driest month observed during the monitoring period. Between August 5th and August 26th, only 21 mm of rain was received, compared to the average of 79 mm over 20 years; this value is less than the 0.001 quantile of the distribution. Additionally, in 2006, September was the coldest among the 20 years of monitoring, with a daily mean temperature of 7.7 °C, compared to the average of 9.4 °C over 20 years; this value is less than the 0.001 quantile of the distribution.

In the black spruce site, only 2001 was characterized by a very intense litterfall occurring early in spring (June) and resulting in the highest annual litterfall over the study period. Moreover, on June 20th, 2001, 59.5 km/h winds were recorded, while the average daily maximum wind speed in June was 31.1 km/h between 1997 and 2020. Even though these winds were not the strongest throughout the entire study period, they represented the highest recorded daily wind among all the months of June between 2001 and 2020; the value is less than the 0.001 quantile of the distribution.

Excluding the most exceptional year at each site a sigmoid model explained 84–88 % of the variance associated with litterfall seasonality for the three sites (all years combined) (Fig. 3).

3.3. Ecosystem pools

Litterfall represented 76.0 %, 20.3 % and 14.3 % of the foliage biomass in the sugar maple, balsam fir and black spruce sites, respectively. Aboveground biomass of live trees (excluding foliage) was higher in the sugar maple site than in the black spruce site ($p < 0.001$, Table 2) while the balsam fir site was not significantly different from the other two sites ($p \geq 0.053$, Table 2). The aboveground biomass of dead standing trees in the sugar maple site was three times higher than in the two coniferous sites ($p < 0.001$). The analysis revealed a linear increase in aboveground biomass of live trees (including foliage) over the study period in the balsam fir site ($p < 0.001$, slope = 2.5 $\text{Mg ha}^{-1} \text{yr}^{-1}$), but no significant trend was noted at the two other sites (Table 3). Aboveground biomass of dead standing trees in the sugar maple, balsam fir and black spruce sites respectively increased by 1.0, 1.3 and 1.1 $\text{Mg ha}^{-1} \text{yr}^{-1}$ ($p \leq 0.040$, Table 3).

Woody debris biomass was lower in the black spruce site than in the two other sites ($p < 0.001$, Table 2). No statistically significant temporal variation was detected in woody debris biomass between 2003 and 2022, although the mean amount almost decreased by half at the maple site ($p = 0.084$, Table 4).

Forest floor biomass in coniferous sites was two-fold that measured in the maple site ($p < 0.001$, Table 2). The forest floor average C concentration was 0.39 ± 0.02 , 0.49 ± 0.01 , and $0.50 \pm 0.01 \text{ g g}^{-1}$ for the maple, balsam fir and black spruce sites, respectively. The mean bulk density (\pm S.E.) of the forest floor in the sugar maple, balsam fir, and black spruce sites was 0.15 ± 0.01 , 0.14 ± 0.01 and $0.08 \pm 0.001 \text{ g cm}^{-3}$, and mean depth was 5.04 ± 0.17 , 11.01 ± 0.39 and $14.03 \pm 0.48 \text{ cm}$, respectively. The evolution of forest floor depth and organic matter concentration from the soil pits samples was tested, and no trend over

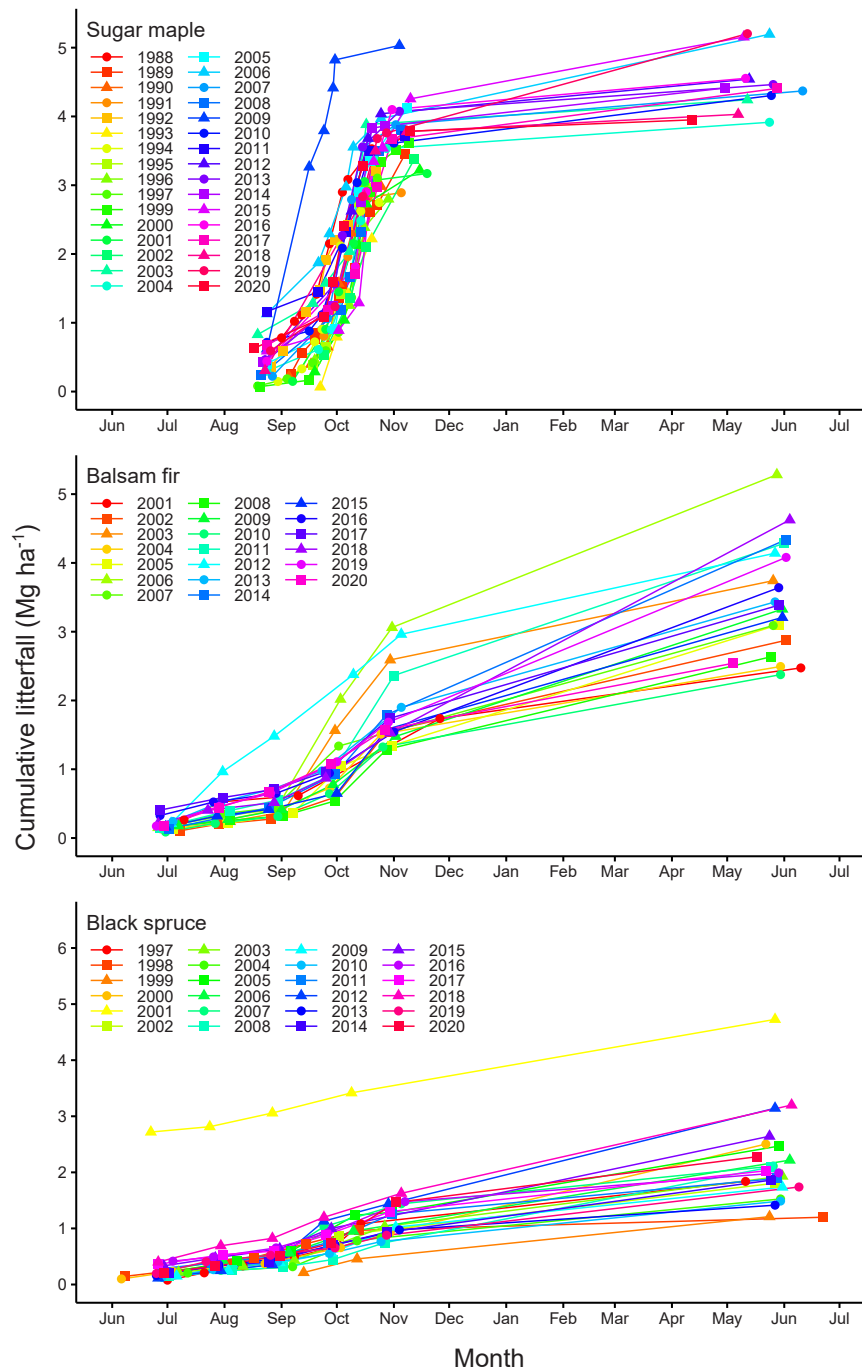


Fig. 2. Seasonality of litterfall biomass (Mg ha⁻¹) at the sugar maple, balsam fir, and black spruce sites.

time was detected ($p \geq 0.223$), except for the forest floor depth in the black spruce site, for which an increase of 0.29 cm yr^{-1} was observed ($p = 0.006$). No significant temporal trend in the forest floor biomass was detected at the three study sites ($p \geq 0.088$, Table 5). Annually, litterfall represented approximately 7.2 % (sugar maple), 2.4 % (balsam fir) and 1.9 % (black spruce) of forest floor biomass (Table 2). Assuming the steady state of the forest floor, the average residence time of litter biomass in the forest floor could be estimated by dividing the total organic matter pool by the annual litterfall (Malhi et al., 1999; Olson, 1963), which corresponded to a residence time of approximately 14, 43 and 52 years in the sugar maple, balsam fir and black spruce sites, respectively.

4. Discussion

4.1. Litterfall production

Based on our estimations, temperate deciduous forests produce twice as much litter as boreal softwood forests and stand composition could explain most of the differences. Our litterfall quantification is consistent with values from previous studies on temperate and boreal forests of the world (Table 6); earlier studies revealed that temperate forests produce approximately 4.0 Mg ha^{-1} of litterfall annually compared to 2.6 Mg ha^{-1} for boreal forests. Broadleaf tree species, for which annual litterfall usually represents the entire foliage stock, produce more litterfall than coniferous

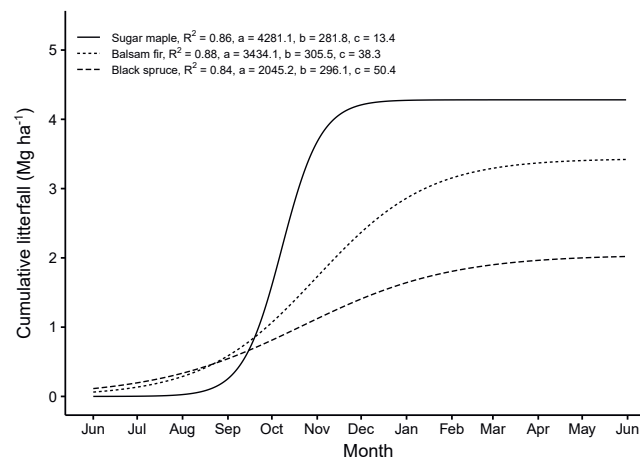


Fig. 3. Sigmoid models of the seasonality of litterfall biomass (Mg ha^{-1}) in the sugar maple (solid line), balsam fir (dotted line), and black spruce (dashed line) sites. The sigmoid function is $Y = a / (1 + \exp((b-x)/c))$, where x corresponds to the number of days of the year (DOY) from June 1st (day 152) to May 31st of the following year (day 516).

Table 3

Estimates of aboveground biomass of live (including foliage) and dead standing trees (Mg ha^{-1} , \pm S.E.) at the sugar maple, balsam fir, and black spruce sites. The p-values relate to significance of the linear trends over time.

| Site | Year | Aboveground biomass of trees (Mg ha^{-1}) | |
|--------------|---------|--|-----------------|
| | | Live | Dead |
| Sugar maple | 1986 | 207.4 \pm 16.3 | 7.4 \pm 3.0 |
| | 1989 | 213.1 \pm 17.5 | 6.8 \pm 3.0 |
| | 1996 | 210.3 \pm 15.2 | 23.8 \pm 10.9 |
| | 2001 | 197.3 \pm 16.3 | 34.7 \pm 8.9 |
| | 2006 | 191.2 \pm 15.2 | 31.9 \pm 7.0 |
| | 2011 | 197.7 \pm 15.4 | 35.0 \pm 6.4 |
| | 2016 | 203.9 \pm 16.5 | 36.9 \pm 6.9 |
| | p-value | 0.729 | < 0.001 |
| Balsam fir | 1998 | 155.3 \pm 5.8 | 2.4 \pm 0.8 |
| | 2003 | 169.9 \pm 6.0 | 7.5 \pm 1.0 |
| | 2008 | 182.4 \pm 5.8 | 15.4 \pm 1.8 |
| | 2013 | 193.9 \pm 6.0 | 22.5 \pm 2.8 |
| | 2018 | 203.3 \pm 6.3 | 28.1 \pm 3.0 |
| p-value | < 0.001 | 0.014 | |
| Black spruce | 1996 | 129.3 \pm 4.9 | 3.0 \pm 0.7 |
| | 2001 | 135.9 \pm 5.0 | 9.4 \pm 1.0 |
| | 2006 | 136.9 \pm 5.2 | 13.4 \pm 1.3 |
| | 2011 | 137.3 \pm 5.3 | 18.7 \pm 1.4 |
| | 2016 | 131.0 \pm 5.2 | 25.9 \pm 1.8 |
| | p-value | 0.902 | 0.040 |

species that lose only a part of their total foliage throughout the year.

Due to the absence of site replications, relationships between litterfall production and any gradient between sites could not be tested. Yet, based on the general characteristics of each stand, litterfall production does not seem to be directly related to the temperature and precipitation gradients among our study sites, nor to the foliage of live trees or stand basal area. We suppose that litterfall production at these sites is thus predominantly governed by stand composition. However, for forests with similar species compositions, climate can be an important factor that influences the amount of litterfall, given its direct influence on forest productivity (Bhatti and Jassal, 2014; Jevon et al., 2022; Liu et al., 2004), a factor not tested here.

Litterfall evolution is related to the aboveground biomass of live trees in both conifer sites. In contrast, in the broadleaf site, changes in forest composition and structure are apparently the main drivers, partially invalidating our second hypothesis. Indeed, our results revealed that litterfall increased over the study period by 69.4 % in the

Table 4

Estimates of woody debris biomass (Mg ha^{-1} , \pm S.E.) in the sugar maple, balsam fir, and black spruce sites. The p-values relate to significance of the linear trends over time.

| Site | Year | Woody debris biomass (Mg ha^{-1}) |
|--------------|---------|--|
| Sugar maple | 2003 | 38.4 \pm 11.5 |
| | 2022 | 19.9 \pm 5.1 |
| | p-value | 0.084 |
| Balsam fir | 2003 | 19.4 \pm 2.1 |
| | 2022 | 24.2 \pm 9.1 |
| | p-value | 0.841 |
| Black spruce | 2003 | 4.9 \pm 1.0 |
| | 2022 | 7.3 \pm 0.6 |
| | p-value | 0.412 |

Table 5

Estimates of forest floor biomass (Mg ha^{-1} , \pm S.E.) in the sugar maple, balsam fir, and black spruce sites. The p-values relate to significance of the linear trends over time.

| Site | Year | Forest floor biomass (Mg ha^{-1}) |
|--------------|---------|--|
| Sugar maple | 1993 | 49.6 \pm 3.5 |
| | 1998 | 54.5 \pm 3.0 |
| | 2008 | 57.4 \pm 3.7 |
| | 2016 | 52.5 \pm 2.8 |
| | p-value | 0.588 |
| Balsam fir | 1998 | 122.2 \pm 9.5 |
| | 2007 | 132.2 \pm 4.2 |
| | 2017 | 133.0 \pm 4.6 |
| | p-value | 0.088 |
| Black spruce | 1996 | 94.5 \pm 4.4 |
| | 2006 | 100.8 \pm 1.2 |
| | 2016 | 100.4 \pm 4.1 |
| | p-value | 0.353 |

sugar maple site and 30.9 % in the balsam fir site. The increase in the fir site appeared to be linked to the increased aboveground biomass of live trees (19.0 % over the same period), whereas the increase in the maple site occurred despite stable live tree biomass over the same period. In this case, the increase in litter production over time (particularly from 1993 to 2006) was apparently linked to the rise in foliage production and crown density associated with compositional and structural changes

Table 6Average litterfall biomass estimations ($\text{Mg ha}^{-1} \text{yr}^{-1}$) reported for temperate and boreal forest ecosystems, from this study and from the literature.

| Climatic zone | Cover type | Region | Litterfall ($\text{Mg ha}^{-1} \text{yr}^{-1}$) | Reference |
|------------------|-------------------|---------------|--|------------------------|
| Temperate | Coniferous | United States | 5.9 | Abee & Lavender, 1972 |
| Temperate | Deciduous | Belgium | 5.5 | Staelens et al., 2011 |
| Temperate | Deciduous | Eurasia | 4.4 | Liu et al., 2004 |
| Temperate | Coniferous | United States | 4.3 | Grier & Logan, 1977 |
| Temperate | Deciduous | Global | 4.0 | Zhang et al., 2014 |
| Temperate | Deciduous | Canada | 3.8 | This study |
| Temperate | Deciduous | France | 3.7 | Lebret et al., 2001 |
| Temperate | Coniferous | Canada | 3.6 | Keenan et al., 1995 |
| Temperate | Coniferous | United States | 3.6 | Edmonds & Murray, 2002 |
| Temperate | Deciduous | United States | 3.5 | Newman et al., 2006 |
| Temperate | Coniferous | Eurasia | 3.2 | Liu et al., 2004 |
| Temperate | Coniferous | Canada | 3.0 | Turner & Singer, 1976 |
| Temperate | Deciduous | United States | 2.9 | Yanai et al., 2012 |
| Mean | | | 4.0 | |
| Boreal | Coniferous | Global | 3.4 | Zhang et al., 2014 |
| Boreal | Deciduous | Canada | 2.8 | Chen et al., 2017* |
| Boreal | Coniferous | Canada | 2.8 | Chen et al., 2017* |
| Boreal | Mixed | Canada | 2.7 | Chen et al., 2017* |
| Boreal | Coniferous | Eurasia | 2.7 | Liu et al., 2004 |
| Boreal | Coniferous | Canada | 2.5 | This study** |
| Boreal | Deciduous | Eurasia | 2.3 | Liu et al., 2004 |
| Boreal | Coniferous | Canada | 1.2 | Bhatti & Jassal, 2014 |
| Mean | | | 2.6 | |
| Overall mean | | | 3.4 | |

* Excluding young stands of 7- and 15-year-old.

** Mean of the balsam fir and black spruce sites.

following the historical sugar maple decline in this ecosystem; the American beech population responded to sugar maple decline by doubling its pole cohort density over 10 years (Duchesne et al., 2005, 2010).

Our results revealed a high interannual variability in litterfall production. Several studies have identified climate as a significant factor influencing litterfall dynamics (Neumann et al., 2018; Portillo-Estrada et al., 2013; Wang et al., 2021; Zhang et al., 2014). Climate influences the production of foliage by affecting productivity and, thus, litterfall production. The interannual variability in litterfall was higher in the balsam fir and black spruce sites than in the sugar maple site; this suggests that litter production in coniferous sites may be more sensitive to climate fluctuations. Reich et al. (2014) showed a more substantial effect of climate on biomass allocation on gymnosperms than angiosperms. Identifying climatic factors influencing the interannual variability of litterfall production and possible links with annual tree growth are beyond the scope of the present study but merit examination in future analyses. Nevertheless, the high interannual variability observed in our estimation of litterfall underlines the importance of long-term studies on litterfall production to obtain a representative understanding of litterfall dynamics and its driving factors. The interannual variation of litterfall can introduce biases in annual estimates, mainly when the study period is relatively short.

4.2. Anomalous years

Our results support the hypothesis that climatic anomalies alter the seasonality and amount of annual litterfall. Indeed, some years strongly deviated from the generally consistent seasonality. Between August 2nd and September 16th, 2009, litterfall was particularly high in the sugar maple site, while meteorological data revealed abnormally dry and cold weather conditions. Therefore, these weather conditions could have been the underlying factor contributing to the early litterfall in 2009 in the sugar maple site. Wang et al. (2021) showed that temperature is an important factor in controlling the litterfall seasonality. Some studies also showed that drought stress, particularly in summer, increases

litterfall (Andivia et al., 2018; Estiarte and Peñuelas, 2015). This leaf loss is seen as a conservation strategy of trees to prevent transpiration losses (Limousin et al., 2009).

Our results suggest that the early litterfall in 2012 in the balsam fir site could be attributed to a known drought event: indeed, July 2012 was documented as the driest summer month (July-August-September) observed in this area in four decades, and it was reported that this drought caused damage to balsam fir needles and their premature shedding (Houle et al., 2016). We also suspect that the 2002 and 2010 droughts, occurring after the growing season, may be the leading cause of the early and more pronounced litterfall during subsequent growing seasons, specifically in 2003 and 2011. However, further analyses are necessary to confirm the underlying processes. Accordingly, previous investigations demonstrated that the climate in a given year has an impact on litter production the following year, especially in coniferous forests (Jevon et al., 2022; Martínez-Alonso et al., 2007; Starr et al., 2005). Lastly, we hypothesize that the early litterfall observed in 2006 was associated with the dry and cold weather observed during this year. Other studies in coniferous forests also observed peaks of litterfall related to cold temperatures and droughts in coniferous sites (Bhatti and Jassal, 2014; Houle et al., 2016; Portillo-Estrada et al., 2013).

Finally, our results suggest that strong winds in June 2001 in the black spruce site generated a higher and earlier litterfall. It is plausible that trees were more susceptible to these strong winds in spring when leaves are younger and possibly more fragile. Portillo-Estrada et al. (2013) also noted premature needle litterfall in coniferous trees due to strong wind events.

4.3. Modelling litterfall seasonality

We found that litterfall seasonality varies according to forest type (deciduous, mixed, and coniferous), which is consistent with our hypothesis. The rise in litterfall in autumn was higher in the balsam fir site than the black spruce site, probably due to the presence of paper birch (7%), which sheds all its leaves during this period. Litterfall seasonality in this study is consistent with those found in other studies in temperate

and boreal forests (Portillo-Estrada et al., 2013; Zhang et al., 2014). Many studies associate litterfall peaks in autumn with temperature, photoperiod and water stress (Delpierre et al., 2016; Kramer et al., 2000; Piao et al., 2019). The litterfall seasonality in coniferous forests can be explained by the characteristics of evergreen forests, where leaf shedding occurs more evenly throughout the year, with a small peak of litterfall in autumn (Zhang et al., 2014).

Understanding the litterfall seasonality provides valuable insights into nutrient cycling, C dynamics and, therefore, C budget (Craig et al., 2022; DeForest et al., 2009; Krishna and Mohan, 2017; Li et al., 2010). These results also highlight the importance of collecting litter throughout the year. Indeed, collecting litter for only part of the year could underestimate or overestimate the amount of annual litterfall; collection during autumn only captures on average 72 % of the total litterfall in a given year (Jevon et al., 2022). To our knowledge, our study is the first to provide an explicit mathematical model of litterfall seasonality for temperate and boreal forests in eastern North America. This seasonality could be incorporated into C budget models and Dynamic Global Vegetation Models (DGVMs), as seasonality is a crucial factor to consider when describing C dynamics in forest ecosystems (Portillo-Estrada et al., 2013; Zhang et al., 2014).

4.4. Comparisons with ecosystem pools

Our results in the sugar maple and balsam fir sites suggest that an increase in litterfall does not lead to an increase in forest floor biomass. For the balsam fir site, the apparent stability of the forest floor biomass was somehow expected given the long residence time of litter (43 years) relative to the time span between our two soil samplings (22 years). However, considering the high litterfall increase (69.4 %) at the maple site as well as its shorter litter residence time in the forest floor (14 years), the forest floor biomass should have increased substantially, assuming no changes in litter quality and constant decomposition rates. It suggests that the decomposition process of litterfall had accelerated concurrently with the litterfall increase, but further investigations should be conducted to confirm the underlying processes. An increase in the decomposition rate could limit the net accumulation of organic matter in the forest floor. The decomposition of organic matter is controlled by climate (mainly temperature and humidity), litter quality and soil organisms (Augusto et al., 2015; Craig et al., 2022; Krishna and Mohan, 2017). Coniferous sites have a litter that generally decomposes more slowly than deciduous sites due to the chemical properties of their tissues, soil moisture, and unfavorable soil conditions for certain effective decomposers (Augusto et al., 2015; Bélanger et al., 2019; Krishna and Mohan, 2017). On a global scale, the average residence time for litter is around 5 years (Matthews, 1997), varying from a few months in tropical forests with very high decomposition rates to over 6 decades in boreal evergreen forests with very slow decomposition rates (Olson, 1963). Thus, forest soils in coniferous sites generally have a thicker layer of organic matter, less efficient nutrient recycling and, consequently, soils characterized by marginal fertility (Augusto et al., 2015).

The aboveground biomass of dead standing trees was higher in the sugar maple site than in both coniferous sites, possibly linked to the historical decline of sugar maple in this ecosystem. Yet, this difference was not reflected in the biomass of downed woody debris: indeed, this pool was similar between the sugar maple and the balsam fir sites. From 2003–2022, the biomass of woody debris remained stable in the three sites despite a significant increase in the aboveground biomass of dead standing trees over the study period. This is contrary to the expected proportionality of these two pools. In the future, the increase in the aboveground biomass of dead standing trees should result in an increase in the biomass of woody debris in the three sites studied because dead snags will eventually fall to the ground. However, our results reveal a high variability associated with the measurement of woody debris biomass, limiting the detection of a statistically significant difference. Consequently, quantifying and assessing the temporal evolution of

woody debris remains challenging and should likely involve a larger number of transects per plot.

4.5. Comparisons of litterfall estimations with reference values

The IPCC (2003) proposes a value of 0.37 g of C per gram of dry biomass for the forest floor (L, F and H horizons, based on Smith and Heath (2002)) as default value for Tier 1 methodology. In contrast, the average of our three study sites gives a value of 0.46 ± 0.01 g of C per gram of dry litter in the forest floor, suggesting that local data is preferable over using default values. An underestimation could lead to an inaccurate estimation of C stocks in forest ecosystems, compromising the accuracy of C balance assessments.

Conversely, our estimates of the organic C concentration of litterfall were close to the assumption used in the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3), used for the international reporting of the C dynamics of Canadian managed forests. The CBM-CFS3 model uses a default conversion factor of 0.50 g C/g dry matter for all live and dead organic matter pools, including the litterfall and forest floor (Kurz et al., 2009). In our study, the organic C concentration of litterfall was 0.48 ± 0.002 g C/g dry matter for the sugar maple site, and 0.50 ± 0.002 g C/g dry matter for both coniferous sites.

On the other hand, our results suggest that CBM-CFS3 underestimates annual litter production. Kurz et al. (2009) ran the CBM-CFS3 model on a dataset of 427 plots dominated by softwood species and 125 plots dominated by broadleaf species. The data for the softwood plots were obtained from a forest ecosystem C database (Shaw et al., 2005), encompassing a variety of species from different regions across Canada. The broadleaf plots were primarily characterized by trembling aspen (*Populus tremuloides* Michx.) and were sourced from the Ontario Terrestrial Assessment Program. Estimates of litter production from the CBM-CFS3 model estimated that annual litter production was 1.17 ± 0.59 – 1.86 ± 0.58 Mg C ha⁻¹ in deciduous forests, and 0.30 ± 0.21 – 0.55 ± 0.21 Mg C ha⁻¹ in coniferous forests (Kurz et al., 2009). Based on our estimation of litterfall in our three study sites and the conversion factor of CBM-CFS3 (0.50 g C/g dry matter), the annual litter production would be estimated at 1.90 Mg C ha⁻¹ in the sugar maple, 1.50 Mg C ha⁻¹ in the balsam fir, and 0.95 Mg C ha⁻¹ in the black spruce site.

Nevertheless, our leaf turnover estimates are coherent with default values of CBM-CFS3, considering the phenomenon of leaf resorption and the errors associated with the estimations of aboveground biomass by allometric equations. CBM-CFS3 considers that the annual leaf renewal rate for broadleaf forests is 95 %, while for coniferous forests, this rate varies from 5 % to 15 %, depending on the ecozone (Kurz et al., 2009). In addition, the model assumes that 100 % of dead foliage transfers to the soil dead organic matter pool (Kurz et al., 2009). We calculated a foliage turnover rate of 76.0 % for the broadleaf site and 14.3–20.3 % for the coniferous sites. Van Heerwaarden et al. (2003) estimated that autumnal foliage mass losses can be as high as 40 %. Their study estimates an average literature value of changes in leaf mass of 21 %, based on the first global dataset of leaf mass loss (126 records).

5. Conclusion

Based on our estimations, temperate deciduous forests produce twice as much litter as boreal softwood forests; stand composition could explain most of the differences. Litterfall evolution was related to the aboveground biomass of live trees in both conifer sites. In contrast, in the broadleaf site, changes in forest composition and structure were apparently the main drivers. Moreover, we found that litterfall seasonality varied by forest type, and we speculate that climatic anomalies altered the annual and seasonal patterns of litterfall. In addition to these climatic extremes, the high interannual variability of litterfall suggests that climate is the main influencing factor. Further analyses should,

therefore, be carried out to more specifically identify the climatic factors responsible for these variations and the possible links with annual tree growth. While our results indicate no impact of increasing litterfall on forest floor biomass, further investigations should be conducted to enhance our understanding of the relation between litterfall and forest floor biomass in forest ecosystems, considering litter quality and potential changes in decomposition rates.

Finally, we suggest that reference values from the literature used for national greenhouse gas inventories underestimate annual litterfall production and forest floor C stock in temperate and boreal forests. Incorporating our estimations in those models can increase the accuracy of predictions. Although our study is limited to three forest sites, it is one of the few that provides long-term data at high sampling frequencies, enabling us to obtain precise estimates of litterfall and thus improve our understanding of C dynamics in temperate and boreal forest ecosystems.

Funding

This work was funded jointly by the Ministère des Ressources naturelles et des Forêts (Quebec, Canada, project number 112332064 and 112332065 conducted at the Direction de la recherche forestière and led by Louis Duchesne and Rock Ouimet, respectively), and by the Projet de recherche orienté en partenariat / Contribution du secteur forestier à l'atténuation des effets des changements climatiques (funding reference number 2022-0FC-309053, granted to Evelyne Thiffault from Laval University).

CRedit authorship contribution statement

Rosalie Frisko: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, review & editing. **Louis Duchesne:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing, Funding acquisition. **Evelyne Thiffault:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing. **Daniel Houle:** Conceptualization, Validation, Writing – review & editing. **Rock Ouimet:** Conceptualization, Data curation, Funding acquisition, Investigation, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

We would like to thank the field technicians who participated in the maintenance of the monitoring sites and carried out sampling over the years. We also acknowledge the personnel of the organic and inorganic chemistry laboratory of the *Direction de la recherche forestière* for performing numerous analyses and Marie-Claude Lambert, also of the *Direction de la recherche forestière*, for her statistical advice.

References

Abee, A., Lavender, D., 1972. Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands 133–144.
 Andúvia, E., Bou, J., Fernández, M., Caritat, A., Alejano, R., Vilar, L., Vázquez-Piqué, J., 2018. Assessing the relative role of climate on litterfall in Mediterranean cork oak forests. *iForest* 11, 786–793. <https://doi.org/10.3832/ifer2825-011>.

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., Ranger, J., 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests: Spermatophytes and forest functioning. *Biol. Rev.* 90, 444–466. <https://doi.org/10.1111/brv.12119>.
 Bélanger, N., Collin, A., Ricard-Piché, J., Kembel, S.W., Rivest, D., 2019. Microsite conditions influence leaf litter decomposition in sugar maple bioclimatic domain of Quebec. *Biogeochemistry* 145, 107–126.
 Bhatti, J.S., Jassal, R.S., 2014. Long term aboveground litterfall production in boreal jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) stands along the Boreal Forest Transect Case Study in western central Canada. *Écoscience* 21, 301–314. [https://doi.org/10.2980/21-\(3-4\)-3699](https://doi.org/10.2980/21-(3-4)-3699).
 Binkley, D., Fisher, R.F., 2019. Ecology and management of forest soils, Fifth edition. ed. Wiley-Blackwell, Hoboken, NJ, USA.
 Chen, H.Y.H., Brant, A.N., Seedre, M., Brassard, B.W., Taylor, A.R., 2017. The contribution of litterfall to net primary production during secondary succession in the boreal forest. *Ecosystems* 20, 830–844. <https://doi.org/10.1007/s10021-016-0063-2>.
 Craig, M.E., Geyer, K.M., Beidler, K.V., Brzostek, E.R., Frey, S.D., Stuart Grandy, A., Liang, C., Phillips, R.P., 2022. Fast-decaying plant litter enhances soil carbon in temperate forests but not through microbial physiological traits. *Nat. Commun.* 13, 1229. <https://doi.org/10.1038/s41467-022-28715-9>.
 DeForest, J.L., Chen, J., McNulty, S.G., 2009. Leaf litter is an important mediator of soil respiration in an oak-dominated forest. *Int J. Biometeorol.* 53, 127–134. <https://doi.org/10.1007/s00484-008-0195-y>.
 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T., Rathgeber, C.B.K., 2016. Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. *Ann. For. Sci.* 73, 5–25. <https://doi.org/10.1007/s13595-015-0477-6>.
 Duchesne, L., Ouimet, R., Houle, D., 2010. Nutrient transfer by leaf litterfall during a sugar maple decline episode at Lake Clair watershed, Québec, Canada. *Plant Ecol.* 208, 213–221. <https://doi.org/10.1007/s11258-009-9699-8>.
 Duchesne, L., Ouimet, R., Moore, J.-D., Paquin, R., 2005. Changes in structure and composition of maple-beech stands following sugar maple decline in Québec, Canada. *For. Ecol. Manag.* 208, 223–236. <https://doi.org/10.1016/j.foreco.2004.12.003>.
 Edmonds, R.L., Murray, G.L., 2002. Overstory litter inputs and nutrient returns in an old-growth temperate forest ecosystem, Olympic National Park, Washington. *Can. J. Res.* 32, 742–750. <https://doi.org/10.1139/x01-227>.
 Estiarte, M., Peñuelas, J., 2015. Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. *Glob. Change Biol.* 21, 1005–1017. <https://doi.org/10.1111/gcb.12804>.
 Fisher, J.B., Huntzinger, D.N., Schwalm, C.R., Sitch, S., 2014. Modeling the Terrestrial Biosphere. *Annu. Rev. Environ. Resour.* 39, 91–123. <https://doi.org/10.1146/annurev-environ-012913-093456>.
 Friedlingstein, P., O'Sullivan, M., Jones, M.W., Andrew, R.M., Hauck, J., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Canadell, J.G., Ciais, P., Jackson, R.B., Alin, S., Aragão, L.E.O.C., Arneeth, A., Arora, V., Bates, N.R., Becker, M., Benoit-Cattin, A., Bittig, H.C., Bopp, L., Bultan, S., Chandra, N., Chevallier, F., Chini, L.P., Evans, W., Florentie, L., Forster, P.M., Gasser, T., Gehlen, M., Gilfillan, D., Gkritzalis, T., Gregor, L., Gruber, N., Harris, I., Hartung, K., Havard, V., Houghton, R.A., Ilyina, T., Jain, A.K., Joetzjer, E., Kadono, K., Kato, E., Kitidis, V., Korsbakken, J.L., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Liu, Z., Lombardo, D., Marland, G., Metzl, N., Munro, D.R., Nabel, J.E.M.S., Nakaoka, S.-I., Niwa, Y., O'Brien, K., Ono, T., Palmer, P.I., Pierrot, D., Poulter, B., Resplandy, L., Robertson, E., Rödenbeck, C., Schwinger, J., Séférian, R., Skjelvan, I., Smith, A.J.P., Sutton, A.J., Tanhua, T., Tans, P.P., Tian, H., Tilbrook, B., van der Werf, G., Vuichard, N., Walker, A.P., Wanninkhof, R., Watson, A.J., Willis, D., Wiltshire, A.J., Yuan, W., Yue, X., Zaehle, S., 2020. Global Carbon Budget 2020. *Earth Syst. Sci. Data* 12, 3269–3340. <https://doi.org/10.5194/essd-12-3269-2020>.
 Gallardo, J.F., Saavedra, J., Martin-Patino, T., Millan, A., 1987. Soil organic matter determination. *Commun. Soil Sci. Plant Anal.* 18, 699–707. <https://doi.org/10.1080/00103628709367852>.
 Gandhi, K.J.K., Herms, D.A., 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol. Invasions* 12, 389–405. <https://doi.org/10.1007/s10530-009-9627-9>.
 Grier, C.C., Logan, R.S., 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* 47, 373–400. <https://doi.org/10.2307/1942174>.
 Hansen, K., Vesterdal, L., Schmidt, I.K., Gundersen, P., Sevel, L., Bastrup-Birk, A., Pedersen, L.B., Bille-Hansen, J., 2009. Litterfall and nutrient return in five tree species in a common garden experiment. *For. Ecol. Manag.* 257, 2133–2144. <https://doi.org/10.1016/j.foreco.2009.02.021>.
 Holland, E.A., Post, W.M., Matthews, E.G., Sulzman, J.M., Staufer, R., Krankina, O.N., 2014. A Glob. Database Litterfall Mass Litter Pool. *Carbon Nutr.* <https://doi.org/10.3334/ORNLDAAAC/1244>.
 Houle, D., Lajoie, G., Duchesne, L., 2016. Major losses of nutrients following a severe drought in a boreal forest. *Nat. Plants* 2, 16187. <https://doi.org/10.1038/nplants.2016.187>.
 Intergovernmental Panel on Climate Change, 2003. Good practice guidance for land use, land-use change and forestry. Institute for Global Environmental Strategies (IGES), Hayama, Kanagawa.
 IUSS Working Group WRB, 2015. World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps, [3. ed.]. ed. FAO, Rome.
 Jevon, F.V., Polussa, A., Lang, A.K., William Munger, J., Wood, S.A., Wieder, W.R., Bradford, MarkA., 2022. Patterns and controls of aboveground litter inputs to

- temperate forests. *Biogeochemistry* 161, 335–352. <https://doi.org/10.1007/s10533-022-00988-8>.
- Keenan, R.J., Prescott, C.E., (Hamish) Kimmins, J.P., 1995. Litter production and nutrient resorption in western red cedar and western hemlock forests on northern Vancouver Island, British Columbia. *Can. J. Res.* 25, 1850–1857. <https://doi.org/10.1139/x95-199>.
- Kramer, K., Leinonen, I., Loustau, D., 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *Int. J. Biometeorol.* 44, 67–75. <https://doi.org/10.1007/s004840000066>.
- Krishna, M.P., Mohan, M., 2017. Litter decomposition in forest ecosystems: a review. *Energ. Ecol. Environ.* 2, 236–249. <https://doi.org/10.1007/s40974-017-0064-9>.
- Kurz, W.A., Dymond, C.C., White, T.M., Stinson, G., Shaw, C.H., Rampley, G.J., Smyth, C., Simpson, B.N., Neilson, E.T., Trofymow, J.A., Metsaranta, J., Apps, M.J., 2009. CBM-CFS3: a model of carbon-dynamics in forestry and land-use change implementing IPCC standards. *Ecol. Model.* 220, 480–504. <https://doi.org/10.1016/j.ecolmodel.2008.10.018>.
- Lambert, M.C., Ung, C.H., Raulier, F., 2005. Canadian national tree aboveground biomass equations. *Can. J. For. Res.* 35, 1996–2018. <https://doi.org/10.1139/X05-112>.
- Lebreton, M., Nys, C., Forgeard, F., 2001. Litter production in an Atlantic beech (*Fagus sylvatica* L.) time sequence. *Ann. Sci.* 58, 755–768. <https://doi.org/10.1051/forest:20011.161>.
- Lenth, R.V., Bolker, B., Buurkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., Singmann, H., 2020. emmeans: estimated marginal means, aka least-squares means.
- Li, X., Hu, Y., Han, S., Liu, Y., Zhang, Y., 2013. Litterfall and litter chemistry change over time in an old-growth temperate forest, northeastern China, 206–206. *Ann. Sci.* 67. <https://doi.org/10.1051/forest/2009099>.
- Limousin, J.M., Rambal, S., Ourcival, J.M., Rocheteau, A., Joffre, R., Rodriguez-Cortina, R., 2009. Long-term transpiration change with rainfall decline in a Mediterranean *Quercus ilex* forest. *Glob. Change Biol.* 15, 2163–2175. <https://doi.org/10.1111/j.1365-2486.2009.01852.x>.
- Liu, C., Westman, C.J., Berg, B., Kutsch, W., Wang, G.Z., Man, R., Ilvesniemi, H., 2004. Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia. *Glob. Ecol. Biogeogr.* 13, 105–114. <https://doi.org/10.1111/j.1466-882X.2004.00072.x>.
- Malhi, Y., Baldocchi, D.D., Jarvis, P.G., 1999. The carbon balance of tropical, temperate and boreal forests. *Plant, Cell Environ.* 22, 715–740. <https://doi.org/10.1046/j.1365-3040.1999.00453.x>.
- Martínez-Alonso, C., Valladares, F., Camarero, J.J., Arias, M.L., Serrano, M., Rodríguez, Y.J.A., 2007. The uncoupling of secondary growth, cone and litter production by intradecadal climatic variability in a mediterranean scots pine forest. *For. Ecol. Manag.* 253, 19–29. <https://doi.org/10.1016/j.foreco.2007.06.043>.
- Matthews, E., 1997. Global litter production, pools, and turnover times: Estimates from measurement data and regression models. *J. Geophys. Res.: Atmospheres* 102, 18771–18800. <https://doi.org/10.1029/97JD02956>.
- Neumann, M., Ukonmaanaho, L., Johnson, J., Benham, S., Vesterdal, L., Novotný, R., Verstraeten, A., Lundin, L., Thimonier, A., Michopoulos, P., Hasenauer, H., 2018. Quantifying carbon and nutrient input from litterfall in European forests using field observations and modeling. *Glob. Biogeochem. Cycles* 32, 784–798. <https://doi.org/10.1029/2017GB005825>.
- Newman, G.S., Arthur, M.A., Muller, R.N., 2006. Above- and belowground net primary production in a temperate mixed deciduous forest. *Ecosystems* 9, 317–329. <https://doi.org/10.1007/s10021-006-0015-3>.
- Olson, J.S., 1963. Energy Storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331. <https://doi.org/10.2307/1932179>.
- Osman, K.T., 2013. *Forest Soils*. Springer International Publishing, Cham. <https://doi.org/10.1007/978-3-319-02541-4>.
- Parmesan, C., Morecroft, M.D., Trisurat, Y., Adrian, R., Anshar, G.Z., Arneth, A., Gao, Q., Gonzalez, P., Harris, R., Price, J., Stevens, N., Talukdar, G.H., 2022. 2022: Terrestrial and Freshwater Ecosystems and Their Services. In: Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), in: *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 197–377.
- Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., Zhu, X., 2019. Plant phenology and global climate change: current progresses and challenges. *Glob. Change Biol.* 25, 1922–1940. <https://doi.org/10.1111/gcb.14619>.
- Pinheiro, J.C., Douglas, B.M., 2000. Mixed-effects models in S and S-PLUS, Statistics and Computing. Springer-Verlag, New York. <https://doi.org/10.1007/b98882>.
- Pinheiro, J.C., Douglas, B.M., R. Core Team, 2022. nlme: linear and nonlinear mixed effects models.
- Portillo-Estrada, M., Korhonen, J.F.J., Pihlatie, M., Pumpanen, J., Frumau, A.K.F., Morillas, L., Tosens, T., Niinemets, Ü., 2013. Inter- and intra-annual variations in canopy fine litterfall and carbon and nitrogen inputs to the forest floor in two European coniferous forests. *Ann. For. Sci.* 70, 367–379. <https://doi.org/10.1007/s13595-013-0273-0>.
- R Core Team, 2023. AD scientific index 2023 [WWW Document]. URL <https://www.adscientificindex.com/scientist/r-core-team/641937> (accessed 6.13.23).
- R Core Team, 2022. R: the R project for statistical computing [WWW Document]. URL <https://www.r-project.org/> (accessed 7.6.23).
- Régnière, J., 1996. Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. *Environ. Entomol.* 25, 869–881. <https://doi.org/10.1093/ee/25.5.869>.
- Reich, P.B., Luo, Y., Bradford, J.B., Poorter, H., Perry, C.H., Oleksyn, J., 2014. Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proc. Natl. Acad. Sci. U. S. A.* 111, 13721–13726. <https://doi.org/10.1073/pnas.1216053111>.
- Risley, L.S., Crossley, D.A., 1993. Contribution of herbivore-caused Greenfall to litterfall nitrogen flux in several southern Appalachian forested watersheds. *Am. Midl. Nat.* 129, 67–74. <https://doi.org/10.2307/2426436>.
- Saucier, J.-P., Bergeron, J.-F., Grondin, P., Robitaille, A., 1998. Les régions écologiques du Québec méridional: un des éléments du système hiérarchique de classification écologique du territoire mis au point par le Ministère des Ressources Naturelles. Supplément 1–12.
- Schielzeth, H., Dingemanse, N.J., Nakagawa, S., Westneat, D.F., Allogue, H., Teplitsky, C., Réale, D., Dochtermann, N.A., Garamszegi, L.Z., Araya-Ajoy, Y.G., 2020. Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods Ecol. Evol.* 11, 1141–1152. <https://doi.org/10.1111/2041-210X.13434>.
- Shaw, C., Bhatti, J., Sabourin, K.J., 2005. An Ecosystem Carbon Database for Canadian Forests. Natural Resources Canada, Canadian Forest Service 403.
- Shen, G., Chen, D., Wu, Y., Liu, L., Liu, C., 2019. Spatial patterns and estimates of global forest litterfall. *Ecosphere* 10. <https://doi.org/10.1002/ecs2.2587>.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I., 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Glob. Change Biol.* 14, 2015–2039. <https://doi.org/10.1111/j.1365-2486.2008.01626.x>.
- Smith, J.E., Heath, L.S., 2002. A model of forest floor carbon mass for United States forest types. U.S. Department of Agriculture, Forest Service, Northeastern Research Station. *Soil Classification Working Group, 1998. The Canadian system of soil classification, 3rd ed. ed. Publication. Agriculture and Agri-Food Canada, Ottawa, ON.*
- Staelens, J., Nachtergale, L., De Schrijver, A., Vanhellefont, M., Wuyts, K., Verheyen, K., 2011. Spatio-temporal litterfall dynamics in a 60-year-old mixed deciduous forest. *Ann. For. Sci.* 68, 89–98. <https://doi.org/10.1007/s13595-011-0010-5>.
- Starr, M., Saarsalmi, A., Hokkanen, T., Merilä, P., Helmsaari, H.-S., 2005. Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. *For. Ecol. Manag.* 205, 215–225. <https://doi.org/10.1016/j.foreco.2004.10.047>.
- Taylor, S.W., 1997. A field estimation procedure for downed coarse woody debris.
- Thomas, S.C., Martin, A.R., 2012. Carbon Content of Tree Tissues: A Synthesis. *Forests* 3, 332–352. <https://doi.org/10.3390/f3020332>.
- Tremblay, S., Ouimet, R., Houle, D., Duchesne, L., 2012. Base cation distribution and requirement of three common forest ecosystems in eastern Canada based on site-specific and general allometric equations. *Can. J. Res.* 42, 1796–1809. <https://doi.org/10.1139/x2012-125>.
- Turner, J., Singer, M.J., 1976. Nutrient distribution and cycling in a sub-alpine coniferous forest ecosystem. *J. Appl. Ecol.* 13, 295–301. <https://doi.org/10.2307/2401949>.
- Van Heerwaarden, L.M., Toet, S., Aerts, R., 2003. Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. *Oikos* 101, 664–669. <https://doi.org/10.1034/j.1600-0706.2003.12351.x>.
- Van Wagner, C.E., 1968. The line intersect method in forest fuel sampling. *For. Sci.* 14, 20–26.
- Wang, C.G., Zheng, X.B., Wang, A.Z., Dai, G.H., Zhu, B.K., Zhao, Y.M., Dong, S.J., Zu, W. Z., Wang, W., Zheng, Y.G., Li, J.G., Li, M.-H., 2021. Temperature and precipitation diversely control seasonal and annual dynamics of litterfall in a temperate mixed mature forest, revealed by long-term data analysis. *J. Geophys. Res. Biogeosci.* 126. <https://doi.org/10.1029/2020JG006204>.
- Wickham, H., 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag New York, pp. 241–253. https://doi.org/10.1007/978-3-319-24277-4_12.
- Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D., Software, P., PBC, 2023. dplyr: a grammar of data manipulation.
- Wieder, W.R., Grandy, A.S., Kallenbach, C.M., Taylor, P.G., Bonan, G.B., 2015. Representing life in the Earth system with soil microbial functional traits in the MIMICS model. *Geosci. Model Dev.* 8, 1789–1808. <https://doi.org/10.5194/gmd-8-1789-2015>.
- Xu, S., Litu, L.L., Sayer, E.J., 2013. Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments. *Biogeosciences* 10, 7423–7433. <https://doi.org/10.5194/bg-10-7423-2013>.
- Yanai, R.D., Arthur, M.A., Acker, M., Levine, C.R., Park, B.B., 2012. Variation in mass and nutrient concentration of leaf litter across years and sites in a northern hardwood forest. *Can. J. Res.* 42, 1597–1610. <https://doi.org/10.1139/x2012-084>.
- Zhang, H., Yuan, W., Dong, W., Liu, S., 2014. Seasonal patterns of litterfall in forest ecosystem worldwide. *Ecol. Complex.* 20, 240–247. <https://doi.org/10.1016/j.ecocom.2014.01.003>.