



The Contribution of Litterfall to Net Primary Production During Secondary Succession in the Boreal Forest

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ABSTRACT

Litterfall is a fundamental process in the nutrient cycle of forest ecosystems and a major component of annual net primary production (NPP). Despite its importance for understanding ecosystem energetics and carbon accounting, the dynamics of litterfall production following disturbance and throughout succession remain poorly understood in boreal forest ecosystems. Using a replicated chronosequence spanning 209 years following fire and 33 years following logging in Ontario, Canada, we examined the dynamics of litterfall production associated with stand development, overstory composition type (broadleaf, mixedwood, and conifer), and disturbance origin. We found that total annual litterfall production increased with stand age following fire and logging, plateauing in post-fire stands approximately 98 years after fire. Neither total annual litterfall production nor any of

its constituents differed between young fire- or logging-originated stands. Litterfall production was generally higher in broadleaf stands compared with mixedwood and conifer stands, but varied seasonally, with foliar litterfall highest in broadleaf stands in autumn, and epiphytic lichen litterfall highest in conifer stands in spring. Contrary to previous assumptions, we found that the contribution of litterfall production to net primary production increased with stand age, highlighting the need for modeling studies of net primary productivity to account for the effects of stand age on litterfall dynamics.

Key words: Boreal forest; Fire; Litterfall; Logging; Net primary productivity; Species composition; Stand age; succession.

INTRODUCTION

Litterfall is a fundamental process in the carbon and nutrient cycles of forest ecosystems and represents a major component of global forest productivity (Bray and Gorham 1964; Vitousek 1984; Clark and others 2001; Yuan and Chen 2009). The production of litterfall is considered to vary with climate, soil fertility, water availability, and

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species composition (Bray and Gorham 1964; Vitousek 1984; Hughes and Fahey 1994; Kaspari and others 2008; Yanai and others 2012) and is thought to be highly associated with annual net primary production (NPP) (Clark and others 2001) such that litterfall accounts for approximately 41% of NPP in old-growth tropical forests (Chave and others 2010; Malhi and others 2011; Malhi 2012). Across globally diverse forest types, ages, and resource conditions, carbon (C) partitioning to foliage production and respiration is estimated to account for approximately 26% of total annual gross primary production (Litton and others 2007), supporting the hypothesis of a constant contribution of litterfall to NPP and its ubiquitous application in modeling studies (Malhi and others 2011).

Forest biomass production is known to change in response to the time elapsed since the last stand-originating disturbance event, increasing rapidly following disturbance, peaking, then declining subsequent to canopy closure (Ryan and others 1997; Bond-Lamberty and others 2004; Yuan and Chen 2010; Goulden and others 2011; Yuan and Chen 2012; Seedre and others 2014; Tang and others 2014; Taylor and others 2014; Chen and Luo 2015). However, in boreal and cold-temperate forests, despite strong age-dependent trends in leaf area index (Coursolle and others 2012; He and others 2012), existing data on the production and contribution of litterfall to forest productivity are limited and currently inadequate to enable a comprehensive evaluation of age- and disturbance origin-related patterns of litterfall dynamics. For example, leaf litterfall production was found to have a weak negative correlation with stand age (35 to over 200 years) in *Pinus sylvestris* L. stands, whereas total litterfall did not change at all over time (Starr and others 2005). Annual litterfall production increased in regenerating hardwood stands (from 1 to 69 years) after logging (Hughes and Fahey 1994), but did not change over a chronosequence (from 13 to 135 years) of *Fagus sylvatica* L. stands following logging (Trap and others 2011). As both aboveground and belowground forest biomass production are known to peak at intermediate stand ages (Ryan and others 1997; Bond-Lamberty and others 2004; Yuan and Chen 2010; Goulden and others 2011; Yuan and Chen 2012; Tang and others 2014; Taylor and others 2014) and as litterfall production may represent a constant proportion of NPP (Litton and others 2007; Malhi and others 2011), we hypothesize that litterfall production also peaks at intermediate stand ages.

Net primary production tends to be higher in forests dominated by deciduous broadleaf tree species compared with coniferous species in boreal and cold-temperate biomes (Cleve and others 1983; Gower and others 1997; Reich and others 2001). Although some of this variation may be explained by differential species habitat affinity, for example, soil fertility (Pastor and others 1984; Zak and others 1989; Reich and others 1997), it is also considered to be caused by greater C allocation to leaf production in deciduous species, and by their generally higher light use efficiency (Reich and others 1995; Reich and others 1999). In the boreal forests, diverse species assemblages can be found on sites of similar environmental conditions following stand-replacing disturbance due to differences in pre-disturbance forest composition and post-disturbance availability of tree species propagules (Dovciak and others 2005; Chen and others 2009; Ilisson and Chen 2009). Consequently, multiple successional pathways are possible as stands age, further affected by secondary disturbances, such as insect outbreaks and windthrow, resulting in either broadleaf, conifers, or mixed-species dominance at any given stage of stand development (Chen and Popadiouk 2002; Taylor and Chen 2011). Although litterfall production is expected to change with stand age (as hypothesized above), how changes in species composition, as affected by succession, interact and influence temporal patterns in litterfall production remains unclear. Given the known effects of species composition on forest productivity and that deciduous species generally show higher rates of leaf turnover relative to conifer species, we hypothesize that independent of stand age, stands formed by deciduous broadleaf species through succession will have higher litterfall production compared with those formed by conifers, whereas mixed-species stands will display intermediate rates of litterfall production.

Similar to other forest biomes, clearcut logging has become an increasingly common stand-replacing disturbance in the North American boreal forest since the widespread application of mechanical harvesting in the 1970s (Natural Resources Canada 2014). Litterfall production has been found to not differ between post-fire and post-logged stands older than 25 years of age (Reich and others 2001). In young regenerating stands, although various differences in individual components of aboveground and belowground production and standing biomass have been found, no significant difference in total ecosystem carbon stocks and production between post-fire and post-logged stands have been observed (Yuan and Chen

2013a; Seedre and others 2014). Nonetheless, compared with fire, logging may directly influence post-disturbance litterfall dynamics in early succession forests by affecting plant community composition and diversity (Taylor and others 2013), which may influence the type and rate of litterfall. To date, there has yet to be any direct comparison of litterfall production between young (<25 years old) regenerating stands of fire and logging origin. As litterfall production may represent a constant proportion of total ecosystem production (Litton and others 2007; Malhi and others 2011), and because previous studies have found little to no difference in overall productivity in young stands following logging and fire (Reich and others 2001; Seedre and others 2014), we hypothesize that litterfall production does not differ between the two disturbance types during early succession, after accounting for the effects of stand age and overstory composition.

In this study, we examined the factors influencing litterfall in boreal forest ecosystems. Specifically, we tested that (1) litterfall production peaks at intermediate stand ages following stand-replacing fire, (2) deciduous broadleaf stands have higher litterfall production than those dominated by conifers, whereas mixed stands have intermediate litterfall production, and (3) litterfall production does not differ during early succession following logging and fire disturbance. We sampled stands of different development stages, overstory composition types, and disturbance origins using replicated, well-studied conifer, mixedwood, and deciduous broadleaf-dominated chronosequences in the central boreal forest of Canada (Brassard and Chen 2008; Hart and Chen 2008; Bartels and Chen 2015). Furthermore, by compiling previously published data of net ecosystem productivity (that is, change in ecosystem carbon storage with time) and fine root production from stands of the mixedwood chronosequence (Yuan and Chen 2012; Yuan and Chen 2013a; Seedre and others 2014; Taylor and others 2014), we further tested the hypothesis that: (4) the contribution of litterfall to aboveground and total net primary production will be constant across a wide range of stand ages for stands established following the two dominant stand-replacing disturbances in the North American boreal forest. To fully appreciate the seasonal variation and diverse components of litterfall, we collected litterfall every 4 weeks over 14 months during snow-free periods, and stratified litterfall into foliage, epiphyte, and other materials that included cone scales and seeds, catkins, twigs, and branches smaller 1.0 cm in diameter.

MATERIALS AND METHODS

Study Area

The study was conducted in the mixedwood boreal forest north of Lake Superior and west of Lake Nipigon in the black spruce forest located approximately 100 km north of Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). The area falls within the Moist Mid-Boreal (MBX) ecoclimatic region (Ecoregions Working Group 1989) and is characterized by warm summers and cold, snowy winters. Mean annual temperature is 2.5°C, and mean annual precipitation is 712 mm at the closest meteorological station located in Thunder Bay, Ontario (Environment Canada 2016). Dominant overstory tree species include jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* [Mill.] B.S.P.), white spruce (*Picea glauca* [Moench] Voss), and balsam fir (*Abies balsamea* L. Mill.). Common understory shrub and herb species in the area, as studied by Hart and Chen (2008), include mountain maple (*Acer spicatum* Lam.), dwarf raspberry (*Rubus pubescens* Raf.), alder (*Alnus* spp.), beaked hazel (*Corylus cornuta* Marsh.), blue-joint reedgrass (*Calamagrostis canadensis* Michx.), Canada mayflower (*Maianthemum canadense* Desf.), violet (*Viola* spp.), and large-leaved aster (*Aster macrophyllus* L.). Soils of the upland sites belong to the Brunisolic order (Soil Classification Working Group 1998). Fire is the most common natural disturbance in the study area, oscillating between 40 and 820 years (Senici and others 2013), with an average fire-return interval of approximately 100 years for the past century (Senici and others 2010). Commercial logging, mainly clearcut harvesting, began in the area in the 1970s. Shortly after fire or logging, various tree species composition types occur, predominantly influenced by predisturbance tree species composition (Ilisson and Chen 2009).

Sampling Design

Although the use of the chronosequence method has been considered unreliable because it makes the assumption that sample stands along temporal sequences follow the same developmental history (Johnson and Miyanishi 2008), given careful site selection, replication, and demonstration of developmental links, the chronosequence method is well suited for studying successional processes over decadal to centennial time scales (Bond-Lamberty and others 2004; Walker and others 2010; Goulden and others 2011). Based on available fire-origin

stands that were not managed in the study area, we sampled six age classes: 7, 15, 33, 98, 146, and 209 years since fire (Table 1), representing stand initiation, early stem exclusion, late stem exclusion, early canopy transition, late canopy transition, and gap dynamic stages of stand development, respectively, modified from Chen and Popadiouk (2002). Stands of logging origin were sampled for 7, 15, and 33 years since logging as commercial harvesting of the study area did not begin until the early 1970s.

At any given stand development stage on mesic sites in the region, stands originating from fire or logging may be dominated by conifer or broadleaf trees, or a mixture of the two, in the overstory (Frelich and Reich 1995; Chen and Popadiouk 2002; Ilisson and Chen 2009; Taylor and Chen 2011). Thus, we made every effort to sample all three overstory composition types for each age class

originating from either disturbance origin. We attempted to have three replicates for each age class, overstory type, and disturbance origin. For the conifer overstory type, however, it was not possible to obtain three sample stands for the 98 ($n = 1$) and 146 ($n = 2$) year stand ages because the infrequency of fire in our study area narrowed our sampling possibilities. Furthermore, stands of conifer dominance, within the target age ranges, are primary candidates for logging in our region and were mostly harvested.

Clearcutting was the primary type of harvesting that occurred for all logging-origin stands, which were all mature before being harvested. The *Pinus banksiana* that dominated the conifer stands were largely planted, whereas the *Populus tremuloides* and *Betula papyrifera* that dominated the broadleaf stands established naturally via root suckering and

Table 1. Characteristics of the 78 Sampled Stands in Boreal Forests of Ontario, Canada

Origin	Age	Overstory	<i>n</i>	Standard density (stems ha ⁻¹) or basal area (m ² ha ⁻¹) ¹	Stand composition (%) ²					
					<i>Pinus banksiana</i>	<i>Populus tremuloides</i>	<i>Betula papyrifera</i>	<i>Picea</i> spp.	<i>Abies balsamea</i>	Others
Fire	7	B	3	5733 (1185)	8 (4)	33 (11)	24 (20)			34 (13)
		C	3	6867 (2978)	98 (2)	1 (1)	1 (1)			
		M	3	2333 (437)	48 (24)	30 (11)	15 (8)			6 (6)
	15	B	3	9867 (874)	10 (5)	60 (7)	6 (1)			23 (4)
		C	3	4200 (416)	68 (16)	15 (4)	2 (2)	8 (8)		7 (5)
		M	3	6067 (751)	25 (1)	41 (12)	9 (9)	6 (6)		19 (6)
	33	B	3	25.6 (0.7)	1 (1)	93 (4)	4 (4)			2 (1)
		C	3	21.5 (1.1)	96 (3)	3 (3)	1 (1)			
		M	3	16.8 (3.4)	49 (17)	45 (14)		6 (6)		
	98	B	3	49.2 (7.2)		94 (1)	2 (2)	2 (2)	1 (1)	1 (1)
		C	1	52.4	59		4	30	6	
		M	3	41.3 (5.2)	10 (6)	42 (12)	15 (13)	15 (8)	18 (3)	
	146	B	3	56.7 (7.0)		86 (4)	8 (4)	4 (2)	1 (1)	2 (2)
		C	2	61.5 (1.5)	77 (7)		2 (2)	11 (3)	3 (1)	6 (6)
		M	3	35.0 (2.1)		45 (9)	21 (10)	10 (4)	23 (6)	2 (2)
	209	B	3	39.4 (3.3)		56 (23)	24 (18)	10 (6)	10 (5)	
		C	3	39.2 (7.6)		5 (5)	7 (4)	37 (19)	50 (17)	
		M	3	46.0 (3.3)	5 (3)	11 (4)	39 (6)	38 (7)	7 (3)	
Logging	7	B	3	4067 (406)		69 (7)	7 (2)	2 (2)		22 (5)
		C	3	1533 (67)	67 (27)			4 (4)	12 (12)	17 (17)
		M	3	1600 (115)	8 (4)	9 (4)	20 (13)	20 (15)	17 (6)	25 (2)
	15	B	3	8400 (529)	2 (2)	52 (1)	13 (4)	6 (1)		27 (4)
		C	3	3867 (968)	63 (14)	1 (1)	2 (2)	23 (10)	2 (2)	8 (1)
		M	3	4333 (1157)	4 (2)	7 (4)	17 (6)	30 (6)	7 (7)	34 (8)
	33	B	3	17.1 (0.7)	1 (1)	90 (4)	8 (5)	2 (1)	0	0
		C	3	24.0 (1.6)	97 (1)	1 (1)	0	2 (1)	0	1 (1)
		M	3	27.1 (1.5)	51 (5)	42 (9)	1 (1)	3 (3)	0	2 (2)

B, broadleaf; C, conifer; M, mixedwood.

¹Values are means with 1 SEM in parentheses. Stand density (stems ha⁻¹) was determined for the younger (7- and 15-year-old) stands and basal area (m² ha⁻¹) for older stands.

²The 'Others' category includes *Salix* sp., *Acer spicatum*, *Populus balsamifera*, *Alnus viridis*, *Sorbus decora*, *Corylus cornuta*, *Amelanchier*, *Pinus resinosa*, and *Larix laricina*.

stem sprouting, respectively. Mixedwood stands were also planted with *Pinus banksiana* and *Picea glauca*, but also contained a large component of naturally established *Populus tremuloides* and *Betula papyrifera*. Each logged stand also contained legacy trees from the predisturbance stand.

Every effort was made to avoid sampling stands of the same age in close proximity to one another to minimize the impact of spatial autocorrelation, resulting in distances between stands in the range of 0.5–10 km. Interspersion was achieved by selecting stands of the same age class from different road access routes. A true spatially interspersed sample of different stand ages was, however, impossible due to fire history and fire size in the study area. For example, there was only one 33-year-old fire of 120,000 ha and one 209-year-old fire of 2000 ha.

To minimize site variability, all selected stands were located on mesic sites on flat, mid-slope positions, with no slope exceeding 5%. All stands were located on well-drained (sandy or silty loams) glacial moraines (>50 cm depth), which is the prevailing soil type in our study area. To ensure that each sample stand met the selection criteria, soil pits were excavated at each candidate stand to verify whether the site was indeed mesic, following the procedures described by Taylor and others (2000). Moreover, similarity of sites was validated by soil textures of the mineral layer at a depth of 30–50 cm (Hume and others 2016). All selected stands were at least 1 ha in area, and visually homogeneous in stem density and composition, as assessed from aerial photos and ground surveys.

Time since last stand-replacing fire (TSF) for sample stands no older than 70 years old was determined from detailed fire records (Senici and others 2010). For stands that were more than 70 years old, tree ages were used to estimate TSF following the procedures described by Senici and others (2010). For all the sampled stands more than 70 years old, we were able to select either *Pinus banksiana* or *Populus tremuloides* trees to determine minimum TSF. No fewer than three canopy stems were sampled for each stand with the exception of the 209-year-old stands, where only one live *Pinus banksiana* tree and several standing snags were used to determine stand age (Brassard and Chen 2008; Hart and Chen 2008). For each selected tree, a core or disk at breast height (1.3 m above root collar) was obtained and transported to the laboratory, where the cores were mounted on constructed core strips, and disks were cut transversely and sanded to highlight the rings. The rings were then counted using a hand-held magnifier until identical sums

were obtained three successive times. Based on a locally derived age correction model, developed by Vasiliauskas and Chen (2002), we added 7 years to the ring counts to determine minimum TSF. Harvesting records were obtained to assist with plot selection and determination of the number of years since logging.

Field Measurements

For each selected stand, we established a 400 m² circular plot within which all measurements were obtained. Plots were randomly located in the selected stands, but were at least 50 m from the forest edge to avoid edge effects. We identified all tree species and measured the diameter at breast height (DBH; 1.3 m above the root collar) of all trees in each sample plot for stands at least 33 years old. For younger (7- and 15-year-old) stands, tree stems were counted by species. Stand density and basal area by species were summed to the plot level and then scaled-up to a per hectare level (Table 1). Overstory types were assigned based on the relative density or basal area of broadleaf and conifer tree species in a plot. Broadleaf and conifer stands were defined as having greater than 65% broadleaf or conifer tree species composition by stand basal area or stem density. Mixedwood stands were defined as those where neither broadleaf nor conifer tree species comprised more than 65% of composition by stand basal area or stem density (Table 1).

Within each of the 78 plots, four 0.322 m² litterfall traps were randomly located to collect litterfall. Total area of litterfall trap coverage for each stand in this study was greater than the recommended size for sampling litterfall in forest ecosystems (Mcshane and others 1983; Finotti and others 2003). All traps were placed in late August 2012 and collected every 4 weeks during the snow-free period, until late October 2013. Because multi-year data of litterfall production improves estimation accuracy (Yanai and others 2012), our litterfall collection covered one full calendar year plus an additional peak litterfall season. Samples collected from each trap were transferred to paper bags and then sorted into the following constituents: leaves with petioles attached, needles, arboreal epiphytic lichens (hereafter referred to as epiphytes), and other materials, which consisted of: cone scales and seeds, catkins, twigs, and branches less than 1.0 cm in diameter, following the recommendations by Clark and others (2001). Epiphyte lichens were sorted as their own category when they could be detached from other litter. The samples were dried

at 65°C in a convection oven until a constant mass was achieved, which was generally less than 48 hours.

Litterfall Production and NPP

Total oven-dry biomass of annual litterfall production was calculated as $\text{Mg ha}^{-1} \text{y}^{-1}$ by summing all litterfall collections from the entire calendar year. Litterfall values for September and October were the average of the 2-year collections. To examine seasonal variations, daily litterfall production ($\text{kg ha}^{-1} \text{day}^{-1}$) was calculated from each collection by dividing the total litterfall collected during each collection period by the number of days elapsed between collection periods.

Of the 78 stands with litterfall production measurements, 27 mixedwood stands (18 and 9 fire- and logging-origin stands, respectively) were previously studied for age-dependent dynamics of aboveground vegetation (Seedre and Chen 2010), coarse woody debris (Brassard and Chen 2008), fine root production (Yuan and Chen 2012; Yuan and Chen 2013a), and net ecosystem productivity (Seedre and others 2014; Taylor and others 2014). Following the method described by Clark and others (2001), we calculated aboveground NPP (ANPP) and total NPP (NPP_T) as:

ANPP

$$= \frac{(\sum \text{AGB Increment}) + \sum (\text{AGB loss via mortality})}{t_2 - t_1} + \text{Annual litterfall production} \quad (1)$$

NPP_T

$$= \frac{(\sum \text{TB Increment}) + \sum (\text{TB loss via mortality})}{t_2 - t_1} + \text{Annual litterfall production} + \text{Annual fine root production}, \quad (2)$$

where $\Sigma \text{AGB Increment}$, $\Sigma \text{TB Increment}$, $\Sigma \text{AGB loss via mortality}$, and $\Sigma \text{TB loss via mortality}$ are the increments and mortality losses of aboveground (AGB) and total (TB) biomass of all live vegetation (trees, shrubs, herbs, and bryophytes) between t_2 and t_1 (t_2 and t_1 are stand ages in years). The estimates for biomass increment and biomass loss via mortality were derived from measured live and dead biomass pools (Seedre and others 2014; Taylor and others 2014). However, these stands were not repeatedly measured. Accordingly, we used space-for-time substitution to estimate ΣAGB

Increment (and $\Sigma \text{TB Increment}$) and $\Sigma \text{AGB loss via mortality}$ (and $\Sigma \text{TB loss via mortality}$) from two successive age classes, using the decision matrix method that accounts for increment via growth and loss via mortality described by Yuan and Chen (2013b). Because this method requires successive biomass measurements to estimate rates of biomass increment and biomass loss via mortality, we derived estimates for each of the 7-, 15-, 33-, 98-, and 146-year-old post-fire stands and the 7- and 15-year-old post-logged stands. We assumed that losses to heterotrophs, volatile and leached organics, and carbohydrates exported to symbionts were negligible. Annual fine root production for our sample stands has been previously reported (Yuan and Chen 2012; Yuan and Chen 2013a). Because year of measurement differed between litterfall production, fine root production, and biomass measurements, we calculated annual fine root production and annual biomass change in relation to litterfall production by linear interpolation between two successive stand ages. We obtained the proportions of total annual litterfall production to ANPP and NPP_T by dividing measured total annual litterfall production by estimated ANPP and NPP_T from equations (1) and (2).

Statistical Analyses

As the number of levels for the independent variable of stand age is unbalanced for stands that originated by wildfire (six levels) and those that originated via logging (three levels), we conducted two separate analyses of variance (ANOVA). To determine the effects of overstory composition type and stand age on total annual litterfall production and its constituents, the following linear model was used:

$$Y_{ijk} = \mu + A_i + C_j + A \times C_{ij} + \epsilon_{(k)ij}, \quad (3)$$

where Y_{ijk} is total annual litterfall production or a constituent ($\text{Mg ha}^{-1} \text{y}^{-1}$), μ is overall mean, A_i ($i = 1, 2, 3 \dots 6$) is stand age class, C_j ($j = 1, 2, 3$) is overstory composition type, $\epsilon_{(k)ij}$ ($k = 1, 2, 3$) is sampling error among replicates within stand age and overstory composition type.

To test the effects of disturbance origin (logged versus wildfire), overstory composition type, and stand age on total annual litterfall production and its constituents, the following linear model was used:

$$Y_{ijkl} = \mu + A_i + C_j + D_k + A \times C_{ij} + A \times D_{ik} + C \times D_{jk} + A \times C \times D_{ijk} + \epsilon_{(l)ijk}, \quad (4)$$

where Y_{ijkl} , μ , A_i , and C_j , are the same as in equation (3), D_k is disturbance origin ($k = 1, 2$), and $\epsilon_{(l)ijk}$ ($l = 1, 2, 3$) is sampling error among replicates within stand age, overstory composition type, and disturbance origin. The assumption of normality was examined with Q–Q plots, histograms, and the Shapiro–Wilk test; that of homogeneity was examined using Bartlett's test. Data of total litterfall production and foliage production met these assumptions without transformation, but square root transformations and rank-transformation were required to meet these assumptions for data on the production of litter classified as 'other,' and annual epiphytic litterfall, respectively.

To investigate seasonal effects on litterfall production, we used the following linear model with all stand age classes combined:

$$Y_{ijk} = \mu + C_i + M_j + C \times M_{ij} + \epsilon_{(k)ij}, \quad (5)$$

where Y_{ijk} is mean daily litterfall production ($\text{kg ha}^{-1} \text{ day}^{-1}$) during a given month, M_j ($j = 1, 2, \dots, 5$) is collection date (June, July, August, September, October), and $\epsilon_{(k)ij}$ ($k = 1, 2, \dots, 18$) is error within overstory composition type and collection date.

To examine whether litterfall contributions to ANPP and NPP_T changed with stand age and disturbance origin for the replicated mixedwood chronosequence, we used:

$$P_{ijk} = \mu + A_i + D_j + A \times D_{ij} + \epsilon_{(k)ij}, \quad (6)$$

where P_{ijk} is the proportion of total annual litterfall production to ANPP or NPP_T , and other terms are the same as in equation (2).

Statistical significance for ANOVA was based on $\alpha = 0.05$. Tukey-HSD multiple comparisons were performed using the *glht* function in the *multcomp* package when significant primary effects or interaction effects emerged following ANOVA. All statistical analyses were conducted using R version 3.2.2.

RESULTS

From pooling all stand ages and overstory composition types for post-fire stands, the average total annual litterfall production was $2.1 \pm 0.2 \text{ Mg ha}^{-1} \text{ y}^{-1}$. Total annual litterfall consisted of $78.6 \pm 1.6\%$ foliage (leaves and needles combined), $20.6 \pm 1.6\%$ other materials (woody debris and reproductive parts), and $0.7 \pm 0.2\%$ shed epiphytes.

In the post-fire stands, total annual litterfall production, annual foliar litterfall, and the annual litterfall of other materials differed significantly with stand age (Table 2). Total, foliar, and other litterfall were significantly higher for stands at least 33 years old than for 7- and 15-year-old stands (Figure 1). Total and foliar litterfall also differed significantly among overstory composition types (Table 2), with broadleaf stands on average producing more total and foliar litterfall than conifer

Table 2. Effects of Time Since Fire ($A = 7, 15, 33, 98, 146, 209$ years) and Overstory Composition Type ($O = \text{broadleaf, conifer, vs. mixedwood}$) on Total Annual Litterfall Production ($\text{Mg ha}^{-1} \text{ year}^{-1}$) and Its Constituents

Annual production	Source	df	SS	F	P
Total	A	5	46.78	69.3	<0.001
	O	2	1.18	4.4	0.021
	A \times O	10	1.72	1.3	0.284
	Error	33	4.46		
Foliage	A	5	26.42	66.4	<0.001
	O	2	1.95	12.2	<0.001
	A \times O	10	1.09	1.4	0.235
	Error	33	2.63		
Epiphyte	A	5	0.35	38.7	<0.001
	O	2	0.05	14.3	<0.001
	A \times O	10	0.06	3.2	0.006
	Error	33	0.06		
Other	A	5	2.52	12.7	<0.001
	O	2	0.06	0.8	0.462
	A \times O	10	0.38	0.9	0.500
	Error	33	1.31		

Values in bold are significant at $\alpha = 0.05$. Source is explained in equation (3).

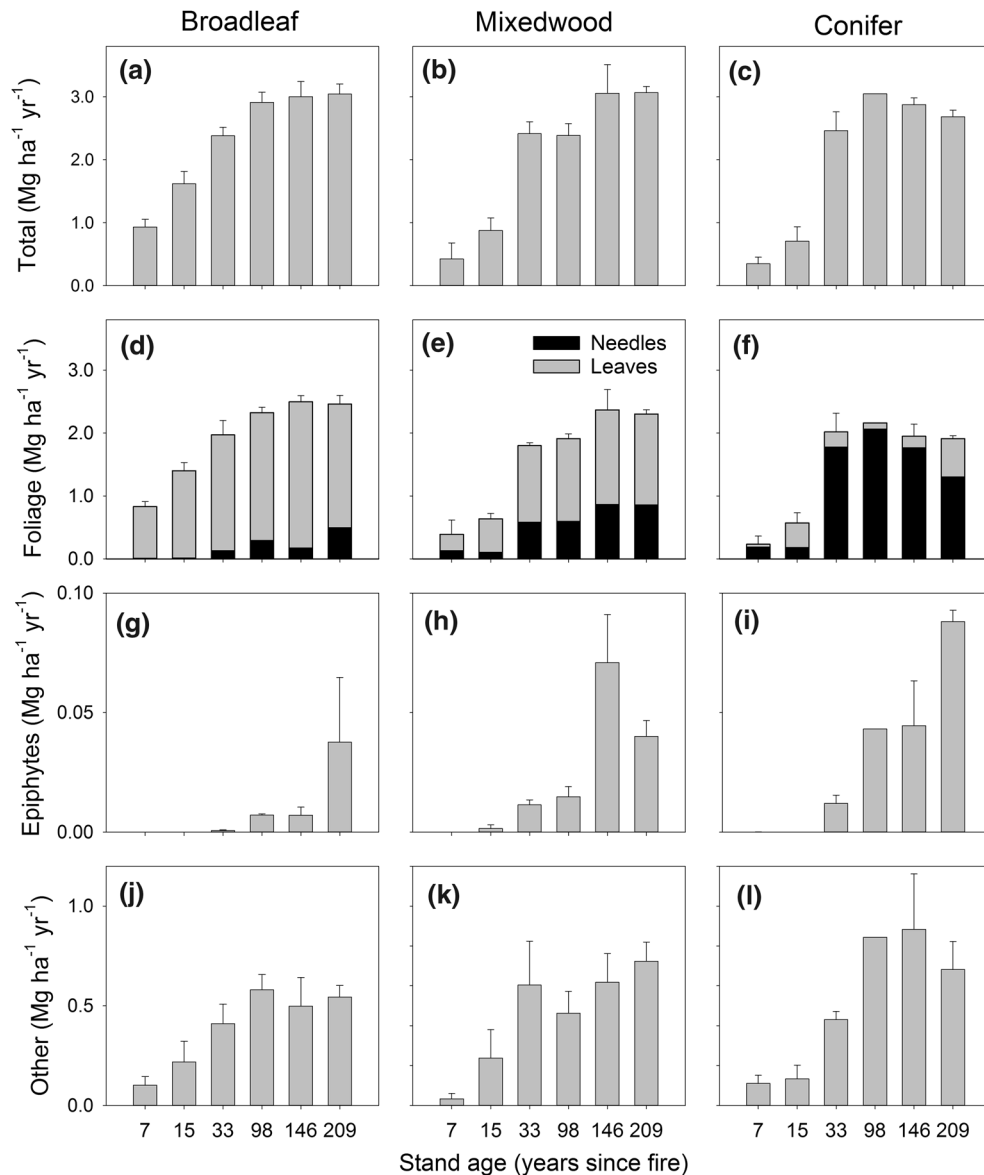


Figure 1. Total annual litterfall production and its constituents ($\text{Mg ha}^{-1} \text{yr}^{-1}$) in post-fire stands in relation to stand age and overstory composition type. Values are mean + 1 SEM.

and mixedwood stands (Figure 1). Annual epiphyte litterfall differed with stand age and overstory composition type (Table 2). Epiphyte litterfall increased continuously with stand age in broadleaf and conifer stands. Among mixedwood stands, 146-year-old stands exhibited higher epiphytic litterfall than all younger stands. Epiphytic litterfall was only significantly higher in conifer stands than broadleaf stands at 209 years old. Other litterfall increased with stand age but did not differ among overstory composition types.

Total annual litterfall production, and each of its constituents, did not significantly vary with dis-

turbance type (Table 3; Figure 2). Similar to post-fire stands, total litterfall, foliar litterfall, epiphytic litterfall, and the litterfall of other materials increased for post-logged stands from 7 to 33 years after disturbance (Figure 2).

There was a significant interaction between overstory composition type and month of collection for total litterfall production, foliar litterfall production, and other litterfall production (Table 4). Total and foliar litterfall productions were significantly higher in September and October than in spring and summer months for all overstory composition types (Figure 3). Total litterfall pro-

Table 3. Effects (*P* values) of Time Since Disturbance (*A* = 7, 15, 33 years), Overstory Composition Type (*O* = broadleaf, conifer, mixedwood), and Disturbance Type (*D* = fire vs. logging) on Total Annual Litterfall Production ($\text{Mg ha}^{-1} \text{yr}^{-1}$) and Its Constituents

Source	Total	Foliage	Epiphyte	Other
<i>A</i>	<0.001	<0.001	<0.001	<0.001
<i>O</i>	<0.001	<0.001	<0.001	0.065
<i>D</i>	0.748	0.553	0.268	0.640
<i>A</i> × <i>O</i>	0.004	0.003	<0.001	0.059
<i>A</i> × <i>D</i>	0.153	0.213	0.854	0.356
<i>O</i> × <i>D</i>	0.248	0.413	0.863	0.123
<i>A</i> × <i>O</i> × <i>D</i>	0.254	0.481	0.347	0.486

Values in bold are significant at $\alpha = 0.05$. Source is explained in equation (4).

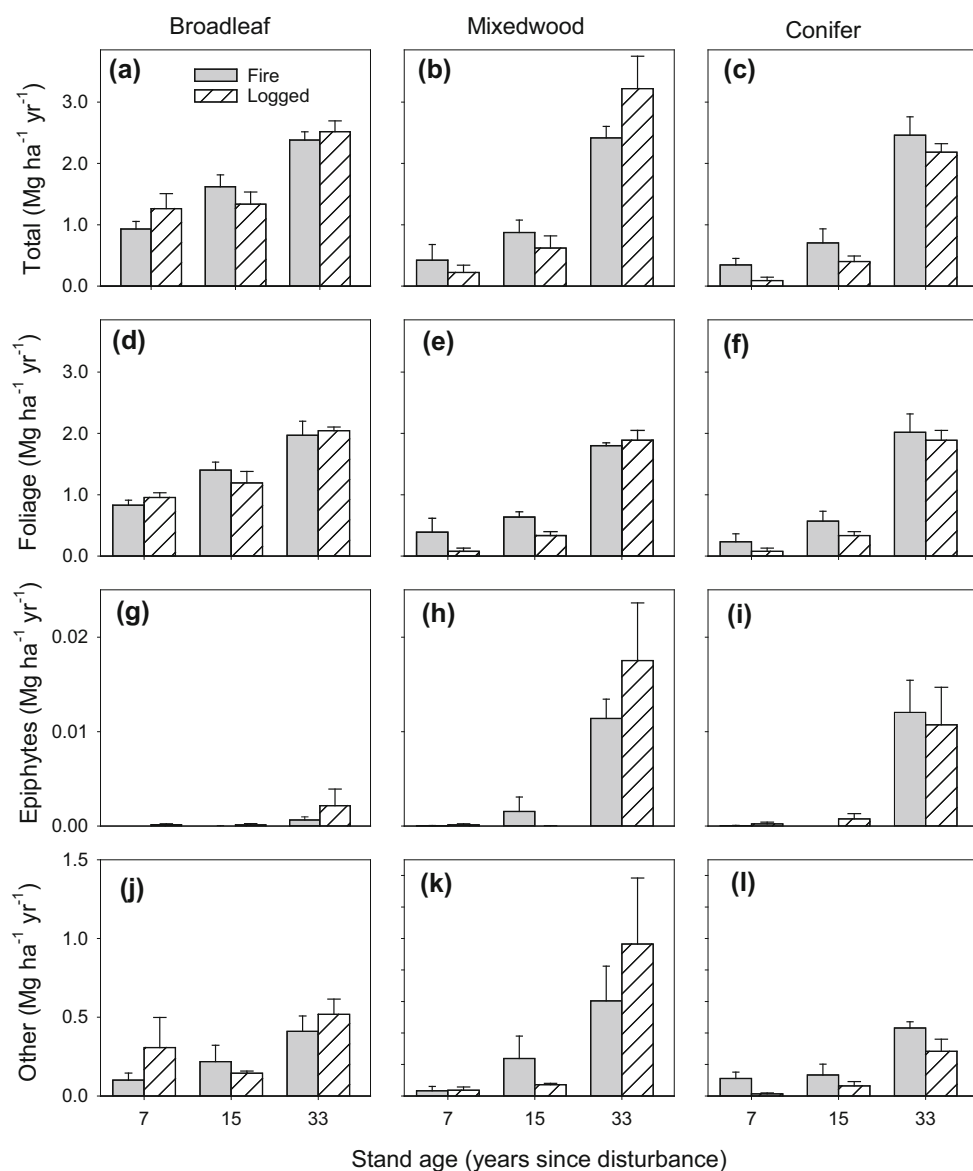
**Figure 2.** Total annual litterfall production and its constituents ($\text{Mg ha}^{-1} \text{yr}^{-1}$) in relation to stand age, overstory composition type, and disturbance type. Values are mean + 1 SEM.

Table 4. Effects of Overstory Composition Type (O = broadleaf, conifer, vs. mixedwood) and Month (M) on Mean Daily Litterfall Production ($\text{kg ha}^{-1} \text{ day}^{-1}$) and Its Constituents

Daily production	Source	df	MS	F	P
Total	O	2	6.06	4.6	<0.001
	M	4	168.8	129.1	<0.001
	O \times M	8	7.2	5.5	<0.001
	Error	237	1.3		
Foliage	O	2	0.4	1.4	0.259
	M	4	64.1	204.3	<0.001
	O \times M	8	1.9	6.0	<0.001
	Error	237	0.3		
Epiphytes	O	2	0.2	7.3	<0.001
	M	4	0.1	3.9	0.004
	O \times M	8	0.01	0.5	0.855
	Error	237	0.03		
Other	O	2	1.0	0.4	0.373
	M	4	3.0	9.2	<0.001
	O \times M	8	0.8	2.4	0.019
	Error	237	0.3		

Values in bold are significant at $\alpha = 0.05$. Source is explained in equation (5).

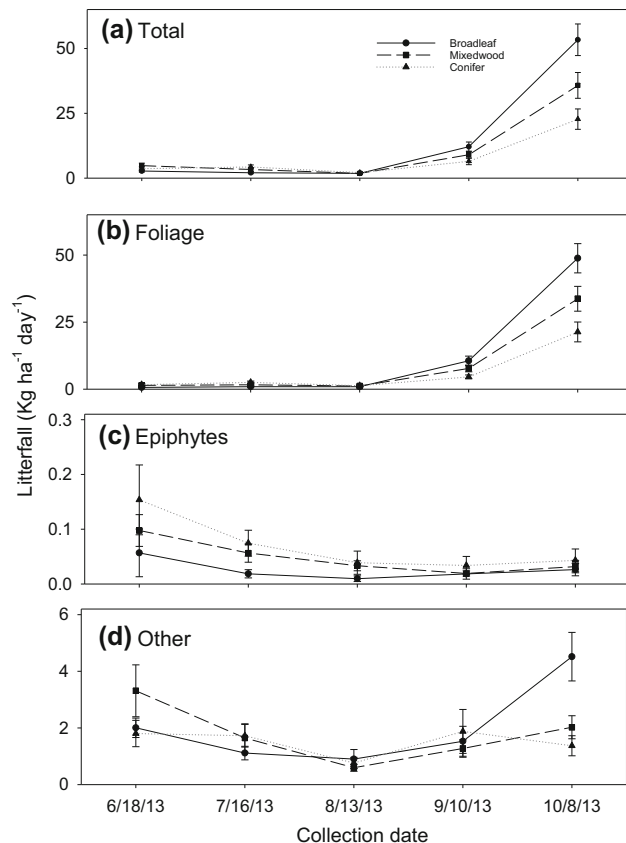


Figure 3. Monthly production of litterfall and its constituents ($\text{kg ha}^{-1} \text{ day}^{-1}$) in 2013 of fire-origin stands with all ages pooled. Months of September and October averaged for 2012–2013. Values are mean + 1 SEM.

duction was higher for broadleaf stands in October than mixedwood and conifer stands, and foliar litterfall production was higher in broadleaf stands in

September and October than conifer and mixedwood stands (Figure 3). Epiphytic litterfall was significantly higher in conifer stands than broadleaf

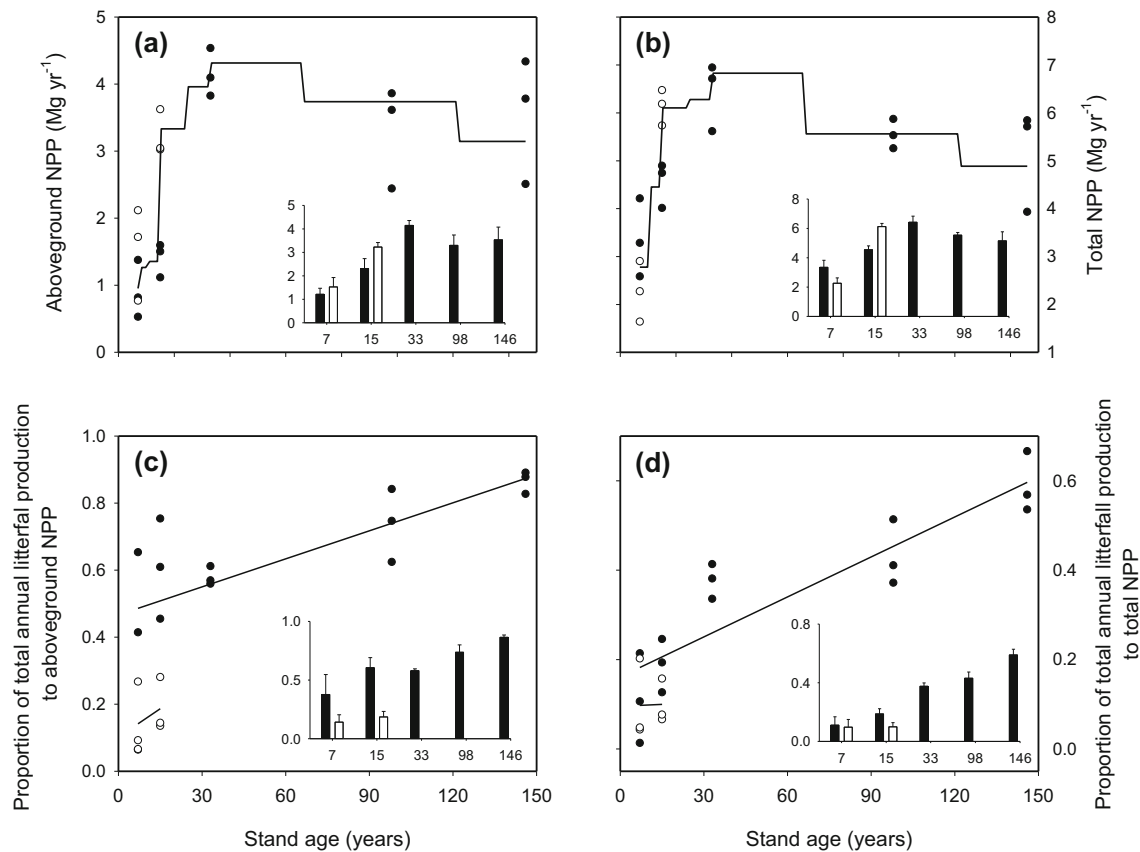


Figure 4. Aboveground and total annual net primary production (ANPP and NPP_T) and litterfall proportions. **A, B** ANPP and NPP_T in relation to stand age. Curves are running medians of neighboring points. **C** Litterfall proportion to ANPP (fitted regression for post-fire stands: $y = 0.47 + 0.028x$, $R^2 = 0.52$, $P < 0.001$; for post-logged stands: $y = 0.10 + 0.006x$, $R^2 = 0.08$, $P = 0.599$). **D** Litterfall proportion to NPP_T (fitted regression for post-fire stands: $y = 0.16 + 0.030x$, $R^2 = 0.78$, $P < 0.001$; for post-logged stands: $y = 0.096 + 0.0003x$, $R^2 < 0.001$, $P = 0.972$). Inserts are bar plots with mean + 1 SEM. Filled symbols and bars are stands of fire origin, and unfilled are stands of logging origin.

and mixedwood stands in June, but similar among overstory composition types from August to October (Table 4; Figure 3). Other litterfall was most prolific in October for broadleaf stands among all sampling dates, whereas mixedwood stands peaked in June. There were no significant differences across months for conifer stands (Table 4; Figure 3).

As expected, ANPP and NPP_T increased rapidly with stand age early in stand development and then declined thereafter (Figure 4A, B). Litterfall contributions to ANPP and NPP_T increased with stand age and differed with disturbance origin (Table 5). Litterfall contribution to ANPP increased from approximately 50% to over 80% from 7 to 146 years after fire and was significantly lower in young post-harvest compared with young post-fire stands (Figure 4C). Similarly, litterfall contribution to NPP_T increased from about 20–60% with age in post-fire stands and was marginally lower in young

post-harvest than young post-fire stands (Figure 4D).

DISCUSSION

We found that total annual litterfall and annual foliar litterfall production increased with stand age, plateauing as stands approached 98 years after fire for all overstory types. This finding contrasts with our hypothesis that litterfall production peaks at intermediate stand ages, declining thereafter, based on the understanding that NPP peaks at intermediate stand ages and that litterfall accounts for a constant proportion of NPP through stand development. However, our results do support the collective findings of previous litterfall studies, which relied on shorter-aged chronosequences (Hughes and Fahey 1994; Starr and others 2005; Trap and others 2011) that annual foliar litterfall increases initially during early stand development, then re-

Table 5. Effects of Time Since Disturbance (A, stand age in years) and Disturbance Type (D, fire vs. logging) on the Proportion of Total Annual Litterfall Production to Aboveground Annual Net Primary Production (ANPP) and That to Total Annual Net Primary Production (NPP_T)

Proportion to	Source	df	MS	F	P
ANPP	A	1	0.897	43.43	<0.001
	D	1	0.384	18.59	<0.001
	A × D	1	0.001	0.04	0.849
	Error	17	0.021		
NPP _T	A	1	0.601	78.29	<0.001
	D	1	0.032	4.13	0.058
	A × D	1	0.001	0.09	0.766
	Error	17	0.008		

Values in bold are significant at $\alpha = 0.05$. Source is explained in equation (6).

mains relatively static in mature and old stands. We also observed considerable age-related increases in annual epiphytic lichen litterfall and other litterfall that included cone scales and seeds, catkins, twigs and branches less than 1.0 cm in diameter. Higher annual epiphytic litterfall in older stands is consistent with the higher diversity and abundance of epiphytic lichen communities found in old growth, conifer-dominated boreal forests (Lie and others 2009; Bartels and Chen 2015). Similarly, age-related increases in other litterfall constituents, relative to foliar litter, support previous reports from long-term chronosequences in boreal forest that show a reduction in net litter quality as stands age (Dearden and others 2006), potentially contributing to reductions in NPP in old forests (Bonan and Shugart 1989; Prescott and others 2000).

Our results show litterfall production was highest in deciduous broadleaf-dominated stands compared with conifer or mixedwood stands, corroborating previous reports for boreal forests (Gower and others 1997; Reich and others 2001). Higher litterfall production in the deciduous broadleaf stands was primarily caused by higher rates of foliar litterfall production. Furthermore, although we did not explicitly differentiate foliar litter by species in our samples, deciduous broadleaf stands in our area generally support higher diversity of understory herbs and shrubs (Hart and Chen 2008), which may have also contributed to higher litterfall production. Indeed, non-tree vegetation growing in the understory invests a higher proportion of biomass production to foliage and has a higher turnover rate than overstorey trees (Grime 1977; Bloom and others 1985; Cavard and others 2011). Although there was little difference in other litterfall constituents among stand types, conifer stands had higher annual epiphytic lichen

litterfall than the other stand types. The higher epiphytic lichen litterfall in conifer stands is attributable to the higher abundance of macro-lichens in these stands compared with broadleaf and mixedwood stands (Cleavitt and others 2009; Bartels and Chen 2015).

We found no significant difference in total annual litterfall production, or any of its constituents, between stands originating from wildfire or logging disturbance, supporting and building upon those findings reported by Reich and others (2001). In logged stands, annual litterfall production followed the same age-dependent pattern as observed for stands originating from fire, that is, a steady increase from 7 to 33 years of age. Although previous studies conducted in our area have shown significant differences in post-disturbance plant community structure (Taylor and others 2013; Seedre and others 2014), including higher tree density, height, and relative abundance of late-succession conifers (for example, black spruce and balsam fir) following harvesting and greater abundance of standing dead trees following fire, these differences in structure were not enough to cause significant departures in litterfall dynamics between young post-fire and post-harvest stands.

As expected, total and foliar litterfall productions peaked in autumn, triggered by seasonal changes in solar radiation (Zhang and others 2014). However, the seasonality of non-foliar litterfall differed from foliar litterfall, suggesting that the shedding of non-foliar material is governed more by other factors. For epiphytic lichens, seasonal growth depends on availability of precipitation (Muir and others 1997), and epiphytic litterfall appears to increase with precipitation as well (Esseen 1985). For the present study, the peak shedding of epiphytic lichens in late May to early June is attributable to the onset of

spring thawing, rainfall, and wind. Similarly, the shedding of woody materials is heavily influenced by wind patterns (Cragg and others 1977), rainfall (Fyles and others 1986), and small mammal (that is, red squirrel) activity (Steele and others 2005). The peak shedding of other materials in spring and autumn is attributed to catkin and cone litterfall in the spring, due to snowmelt and rainfall, and woody litterfall in the fall months due to wildlife activity (Cragg and others 1977; Fyles and others 1986; Steele and others 2005).

Age-related patterns of litterfall production differed from aboveground and total NPP, both of which peaked in the 33-year-old stands, and then declined thereafter. In contrast to previous evidence for a constant proportion of litterfall to NPP in old-growth tropical forests (Chave and others 2010; Malhi and others 2011; Malhi 2012) and litterfall-to-total annual gross primary production (Litton and others 2007), our results show that litterfall contribution to aboveground and total NPP increased with age in our mixedwood, post-fire stands. This increase in contribution is mainly caused by a lack of age-related decrease in litterfall production after stands reach maturity, which has been similarly noted in other studies (Hughes and Fahey 1994; Starr and others 2005; Trap and others 2011), contrasted with strong age-associated declines in non-litterfall components of aboveground NPP with strong reduced growth and increased tree mortality (Figure 5), similar to the patterns observed in the western boreal forest of Canada (Chen and Luo 2015). We also found lower contributions of litterfall to NPP in post-logged stands compared with post-fire stands. However, this may be related to the fact that our post-logged, mixedwood stands were treated with herbicide (Paul Poschmann, *personal communications*) that promoted commercial trees at the expense of non-tree vegetation in comparison with post-fire stands, resulting in higher net woody biomass production, particularly for *Picea* spp. (Seedre and others 2014), which has a lower litterfall-to-NPP proportion than *Pinus* spp. and *Populus* spp. (Reich and others 2001).

In summary, this study represents the first comprehensive investigation of litterfall production dynamics associated with forest stand development, succession, and disturbance origin in the boreal forest. The use of a post-fire chronosequence, with stands ranging in age from 7 to 209 years old, revealed that litterfall production continually increased up until approximately 98 years after fire and then remained relatively stable thereafter at approximately $2.5 \text{ Mg ha}^{-1} \text{ y}^{-1}$.

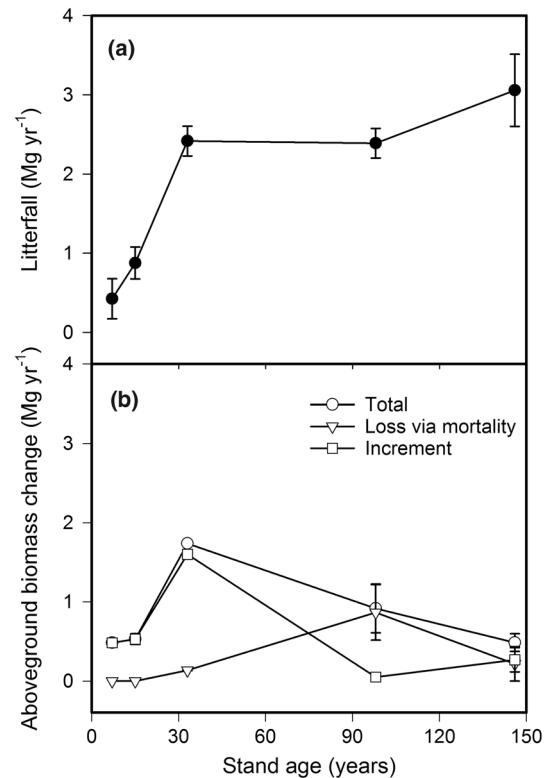


Figure 5. Components of aboveground annual net primary production in relation to age in post-fire stands. **A** Litterfall production, **B** Aboveground increment, loss via mortality, and the sum. Values are mean + 1 SEM ($n = 3$).

Litterfall production was generally higher in deciduous broadleaf stands compared with mixedwood or conifer stands, and fluctuated seasonally, with foliar litterfall production peaking in October, epiphytic lichen litterfall peaking in June, and all other materials being highest in both June and October. Furthermore, contrary to previous assumptions, we found that the contribution of litterfall production to net primary production increased with stand age, highlighting the need for modeling studies of forest ecosystem productivity to account for stand age effects on litterfall production and contribution to forest dynamics.

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