This item is the archived peer-reviewed author-version of:

Inter- and intra-annual variations in canopy fine litterfall and carbon and nitrogen inputs to the forest floor in two European coniferous forests

Reference:

Portillo-Estrada Miguel, Korhonen Janne F.J., Pihlatie Mari, Pumpanen Jukka, Frumau Arnoud K.F., Morillas Lourdes, Tosens Tiina, Niinemets Ülo.- *Inter- and intra-annual variations in canopy fine litterfall and carbon and nitrogen inputs to the forest floor in two European coniferous forests*

Annals of forest science - ISSN 1286-4560 - 70:4(2013), p. 367-379

DOI: <http://dx.doi.org/doi:10.1007/s13595-013-0273-0>

Inter- and intra-annual variations in canopy fine litterfall and carbon and nitrogen inputs to the forest floor in two European coniferous forests

Miguel Portillo-Estrada · Janne F. J. Korhonen ·
Mari Pihlatie · Jukka Pumpanen ·
Arnoud K. F. Frumau · Lourdes Morillas ·
Tiina Tosens · Ülo Niinemets

Received: 11 December 2012 / Accepted: 7 February 2013
© INRA and Springer-Verlag France 2013

Abstract

• **Context** The amount and chemistry of litterfall have been known to strongly vary among the years with important implications for ecosystem nutrient cycles, but there are few quantitative data describing such variations.

• **Aims** We studied the climatic implications on the variation in litterfall and its C and N input to soil in two distinct European coniferous forests.

Handling Editor: Erwin Dreyer

Contribution of the co-authors Miguel Portillo-Estrada: Original idea, design of the experiment, data analysis, writing the manuscript
Janne F. J. Korhonen: Running the experiment, data analysis, supervising the manuscript

Mari Pihlatie: Running the experiment, supervising the manuscript
Jukka Pumpanen: Running the experiment, supervising the manuscript
Arnoud K. F. Frumau: Running the experiment, supervising the manuscript

Lourdes Morillas: Data analysis, supervising the manuscript
Tiina Tosens: Design of the experiment, supervising the manuscript
Ülo Niinemets: Original idea, design of the experiment, supervising and writing the manuscript

M. Portillo-Estrada (✉) · T. Tosens · Ü. Niinemets
Institute of Agricultural and Environmental Sciences,
Estonian University of Life Sciences, Kreutzwaldi 1,
Tartu 51014, Estonia
e-mail: miguel.portillo@emu.ee

J. F. J. Korhonen · M. Pihlatie · J. Pumpanen
Department of Physical Sciences, University of Helsinki,
P.O. Box 64, 00014 Helsinki, Finland

A. K. F. Frumau
Energy Research Centre of The Netherlands,
P.O. Box 1, 1755 ZG Petten, The Netherlands

L. Morillas
Departamento de Sistemas Físicos, Químicos y Naturales,
Universidad Pablo de Olavide, Carretera de Utrera Km. 1,
41013 Sevilla, Spain

• **Methods** Year-to-year variations in canopy litterfall were measured in a Scots pine stand (Hyytiälä, Finland) over 13 years, and a Douglas fir stand (Speulderbos, The Netherlands) over 3 years.
• **Results** Important inter-annual variations in litterfall were observed in Scots pine. Litterfall was mainly driven by leaf senescence; however, premature needle fall was observed in high wind speed and early frost events. The seasonal variation in litterfall was characterized by a maximum in September in Scots pine, and by a biphasic variation pattern in Douglas fir, in May and November. Lower seasonal variations and lower annual average in litterfall N content were observed in Scots pine.
• **Conclusion** Significant inter- and intra-annual variations in litterfall and chemistry and between the sites were demonstrated; and it depended on year-to-year differences in climate and extreme weather events.

Keywords Litter production rate · Scots pine · Douglas fir · Temporal variability · Wind-influenced litterfall

1 Introduction

Litterfall is a key process in forest nutrient cycling, and it is the main above-ground contributor of carbon and nutrients to the forest floor (Vitousek et al. 1995). Total litter production and litter quality determine the soil microbial activity, and accordingly, the release of nutrients into the soil (Ganjugunte et al. 2004). Once the dead biomass is available for decomposition processes, leaching of nutrients by rainfall and biomass consumption by detritivores convert the biomass into a form that can be chemically used by bacteria and fungi (Aerts 1997). Thus, understanding the determinants of litter production and quality is of paramount significance for the understanding of nutrient turnover in forest soils (Melillo et al. 1989). Intra- and inter-annual variations in litter production and quality are also

importantly related to tree nutrient status. Alterations of such dynamic phenomena are pertinent to study and need consideration in modeling long-term nutrient cycles.

In mature coniferous temperate and boreal forests, above-ground litter is produced by the trees (needles, twigs and branches, cones and dead stems), and by the understory vegetation. Unlike from winter-deciduous forests, where the major litter production occurs during autumn leaf fall, litter is continuously produced in evergreen conifer stands, although more or less distinct peaks of litter production can be often identified during the year. As an example, it is well-known that the oldest needle class of Scots pine sheds needles during August–October in boreal forests (Ukonmaanaho et al. 2008), whereas Douglas fir presents two peaks of needle litterfall in Spring and Autumn.

The canopy tree litter production varies over the years and its components have different dynamics and turnover times. For example: (1) tree stems can live for decades to centuries, their litter production is measurable (Aerts and Berendse 1989), but reliable estimations can be done only after long-time studies. (2) Branches may last from years to decades, their litter production and input to the soil system are relatively unknown (Lehtonen et al. 2004). (3) Needles are renewed every few years in evergreen conifers, thus this litter fraction can be best assessed; however, the variation of annual needle litterfall can be very large (up to 40 % in a mature Scots pine forest (Kouki and Hokkanen 1992)). These premises suggest that short-term studies showing 1-year data of litter trap studies seem to be far from the actual average budget of biomass cycling, and that all types of litter must be taken into account in studies of the C and N cycle in forest ecosystems. But for short-term studies, litter trap method gives an overview of the canopy litter production, the speed of nutrient cycling, and the nutrient accumulation in the reservoirs.

Year-to-year variations in climate and extreme weather events such as storms can importantly alter the dynamics and total amount of litter production (Lodge et al. 1991). While all above-ground biomass ultimately ends up as litter, such environmental effects and extreme events can importantly alter the timing of peak litter events (Álvarez et al. 2009), thereby altering the soil microbial activity and the nutrient cycle (Sanford et al. 1991). Furthermore, these factors can even more strongly alter litter quality (Pérez-Suárez et al. 2009). As nutrient resorption is a time-consuming event, premature foliage and twig loss as the result of storm events or early frosts can result in litter with higher nutrient concentration (Killingbeck 1996). Thus, years with premature litter fall can importantly alter soil activity and affect plant growth in the subsequent season. There are evidences of enhanced soil nutrient availability after storm-induced litterfall (Pérez-Suárez et al. 2009; Sanford et al. 1991).

In this study, we investigated year-to-year variations in the canopy litter production, which is highly important for long-term prediction of ecosystem nutrient dynamics. The study was conducted in two coniferous forests with contrasting average

foliage longevity and climatic conditions to gain insight into the general and specific responses of litter production in two key conifer species. Scots pine, the dominant species in the northern site in Hyytiälä, Finland, has lower foliage retention time, on average 2 years (Wang et al. 2012), and supports lower leaf area index than Douglas fir, the dominant species in the Dutch site in Speulderbos that has an average foliar retention time of 2.6 years (Wang et al. 2012). We hypothesized that year-to-year variations in weather conditions importantly alter total litter production and litter quality. These effects could be more pronounced in the Douglas fir stand that supports larger number of foliage cohorts and overall more foliage area.

This study is based on a unique dataset of detailed leaf litterfall dynamics in two important conifer species in two European sites (13 years data in one and 3.5 years data in the other site). The results of such detailed long-term litterfall data demonstrate large year-to-year variations in litterfall dynamics and nutrient content that has potentially major significance for ecosystem performance.

2 Material and methods

2.1 Study sites

The study was conducted in two key sites of NitroEurope IP project (for detailed description of the project and sites see Owen et al. 2011). See Table 1 for more site description.

The Hyytiälä Forestry Field Station (Kolari et al. 2009) is situated in Southern Finland, 60 km northeast from Tampere. It supports a homogeneous Scots pine (*Pinus sylvestris* L.) stand. This species is dominant in more than half of the forest area in southern Finland. Stand management has been conducted according to the standard silvicultural guidelines for similar forest types in Finland, and by now, the stand is half-way through the rotation time. The site has a relatively flat topography.

The Speulderbos site (Su et al. 2009), operated by the National Institute for Public Health and the Environment (RIVM), is located in the central Netherlands. It is approximately 25 km northeast from the city of Amersfoort, within a large forested area in the Netherlands. The site supports a dense 2.5-ha Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand. The site topography is slightly undulating with height variations of 10 to 20 m within distances of 1 km.

2.2 Litter collection

The study was conducted for a period of 156 months (January 1999–December 2011) in Hyytiälä, and 43 months (June 2007–December 2010) in Speulderbos. Litter traps (mesh size <0.5 mm) were placed above the topsoil. Twenty circular litter traps of 0.2 m² in Hyytiälä

Table 1 Site description

Site description	Hyytiälä ^a	Speulderbos ^b
Coordinates	(61°50'51", 24°17'41") elevation 180 m.a.s.l.	(52°15'08", 05°41'26") elevation 52 m.a.s.l.
Tree species	Scots pine	Douglas fir
Year of plantation	1962	1962
Soil type and texture	Haplic podzol	Orthic podsol
Soil texture	Till material dominated by fine sand	Silty sand texture
Soil depth	From 0 to 200 cm	309 cm
Soil pH	3.3	3.7
Stand density	1,400 ha ⁻¹ (2006)	785 ha ⁻¹ (2006)
Stand height	16.3 m (2006)	32 m (2006)
Stand growth rate	8 m ³ ha ⁻¹ year ⁻¹	10.7 m ³ ha ⁻¹ year ⁻¹
Leaf area index	6.5 m ² m ⁻² (all sided)	7.8–10.5 m ² m ⁻² (projected) ^c
Annual mean air temperature	3.5 °C	9.6 °C
Annual mean soil temperature	4.6 °C	9.4 °C
Precipitation	713 mmyear ⁻¹ (1971–2000) ^d	889 mmyear ⁻¹ (1958–2002) ^e
Annual maximum snow cover	50 cm (1997–2012)	15 cm (1994–2012)

^a Kolari et al. (2009)

^b Su et al. (2009)

^c Van Wijk et al. (2000)

^d Drebs et al. (2002)

^e Reyer et al. (2010)

(Ilvesniemi et al. 2009) and 10 squared litter traps of 0.25 m² in Speulderbos were used. Distance between traps was 10 m. Tree litter was collected every ca. 30 days (every 3 months during 1999–2005 in Hyytiälä). Litter from each trap was enclosed in labeled plastic bags and transported to the lab. Samples were first air-dried at room temperature until constant mass. In Hyytiälä, during the monthly sampling in winter time, snow was carefully removed from the collectors so that snow did not flow over from the collectors. During winter, samples with snow cover were melted indoors. Litter was sorted manually with tweezers into four groups: needles, twigs (diameter<1 cm), bark, and cones; the sum of these groups is what we considered *canopy fine litter*. When litter fragments were difficult to identify due to their small size, they were considered the *rest* fraction. The rest fraction mainly consists of brittle twig bark and small needle pieces, including sometimes resin droplets. Twigs which diameter was >1 cm were not considered fine canopy litter, thus discarded in the total canopy litter values. After sorting, the mass of different litter fractions was determined after oven-drying at 60 °C to constant mass. Only the litter from the dominant conifer species was considered.

2.3 Chemical analysis

The samples from different litter traps were pooled to one sample per collection day before the chemical analysis. Total nitrogen and carbon contents of oven-dried samples

were determined by dry combustion method separately for different litter fractions. Samples from Hyytiälä during 1999–2005 were analyzed by an elemental CN analyzer (LECO, Leco Corporation, St. Joseph, MI, USA). Samples from Hyytiälä during 2006–2010 and from Speulderbos were analyzed by a Vario MAX CNS elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany).

2.4 Meteorological data

The meteorological parameters measured and devices employed can be seen in Table 2.

Mean wind speed was calculated averaging 30 min data. Wind gusts were reported when the wind speed reached 8.2 m s⁻¹ and the variability of the wind from highest point to lowest was more than 4.6 ms⁻¹. Beaufort wind speed scale was used for qualitative identification of wind gusts: 8.0–10.7, 10.8–13.8; 13.9–17.1, 17.2–20.7; and 20.8–24.5 m s⁻¹.

2.5 Data analysis

Data of litterfall and meteorological parameters (2006–2011) were calculated by regular periods of one calendar month each: the dates of litter collection period did not correspond to calendar months, therefore, the value of daily litterfall rate measured at the end of each period was considered the same for every day of the collection period; an average daily value was then calculated for each calendar

Table 2 Meteorological devices used at the two study sites

Meteorological devices	Hyttiälä	Speulderbos
Air temperature	(16.8 m) ventilated and shielded Pt-100 sensor (platinum resistance thermometers)	(45 m) Vaisala WXT510 and Thermocouple E-type (Vaisala Oyj., Helsinki, Finland)
Wind speed	(23 m) sonic anemometer Solent 1012R2 (Gill Instruments, Lymington, UK)	(46 m) sonic anemometer 2D (Gill instruments Ltd., Lymington, UK)
Global radiation	(18 m) Reemann TP 3 pyranometer (Astrodata, Tõravere, Estonia)	(46 m) CNR-1 Net radiometer (Kipp & Zonen, Delft, The Netherlands)
Precipitation	(2 m) ARG-100 tipping bucket rain gauge (Institute of Hydrology, Wallingford, UK)	(47 m) Custom-made tipping bucket & Vaisala WXT510 (Vaisala Oyj, Helsinki, Finland)
Soil temperature	(−5 cm) five silicon temperature sensors KTY81-110 (Philips Semiconductors, Eindhoven, the Netherlands)	(−5 cm) NTC thermistors (Murata Machinery Ltd., Kyoto, Japan)
Soil water content (0–30 cm)	TDR-method with unbalanced steel probes 1502C (Tektronix Inc., Redmond, USA)	Water content reflectometer CS-616 (Campbell scientific Inc., Logan, USA)
Average snow cover	Daily measurements	Daily measurements

month as the arithmetic mean of all daily values for the month considered, thus 12 values per year. This transformation resulted in the standardization of number of data points along the year, and eliminated differences between both species in the litter collection dates. It permitted to compare statistically both datasets, to make year-to-year comparisons, and improved visual understanding of graphs. Outliers were defined using 1.5 times the difference between the third and first quartiles, as described in Morillas et al. (2012).

The leaf nitrogen resorption proficiency (NRP) was defined as the minimum N concentration per unit of leaf mass found in senescent leaves (Killingbeck 1996).

2.6 Numerical analysis

The spatial variability in the litterfall collected during the study period was assessed with the calculation of the coefficient of variation (CV) between litter traps: the cumulative mass collected over the whole study period (in gramme) was calculated for each litter trap. The standard deviation of the litter trap collection values was divided by their arithmetical mean.

C and N production rate in litterfall (gramme of C and milligramme of N per square metre per day) were calculated by multiplying the C or N content (gramme of C and milligramme of N per gramme of biomass) of each litter fraction for a given collection period by the respective litterfall rate (gramme per square metre per day). The values of C and N production rates for each collection period were subsequently transformed to calendar monthly values as explained in the chapter 2.5, thus obtaining one value per calendar month.

For Hyttiälä site, the identification of two seasons in monthly C and N input to the forest floor (also called C and N production rate in litterfall) was found after a paired *t*

test: monthly values during the study period were grouped into two seasons (colder season vs. warmer season, covering the whole year period) throughout the possibilities (varying the season length and the starting month), the option which produced the highest significance (lowest *P* value) in a *t* tests was chosen as the most appropriate way to study the two seasons in each study site.

The inter-annual variations in Scots pine litterfall were assessed. The calculation of the average annual litter production in a given year is explained in Eq. 1, where: *P* is the litter collected (megagramme per hectare per year) in a given year *Y_i*, and *P_{av}* is the average annual litter production from *Y₀* until *Y_N*.

$$P_{av} = \frac{\sum_{i=0}^N P(Y_i)}{N + 1}$$

(1)

Normality tests (Shapiro–Wilk) were performed to yearly data prior to analysis (Morillas et al. 2012), which resulted in a reasonable number of rejected null hypotheses. Nevertheless, we used parametric tests to analyze the data. Statistical comparisons between stands and between years were performed by two-sample *t* tests and analysis of variance (ANOVA).

3 Results

3.1 Climatic differences

Maximum air and soil temperatures were similar at both sites (Fig. 1). Hyttiälä presented a wider range of air temperatures, usually below 0 °C from November to December, while the winters at Speulderbos were warmer (Fig. 1). Soil

Fig. 1 Daily averages of climatic data at Hyytiälä (Finland) and Speulderbos (the Netherlands) during the periods August 2007–December 2010 and June 2007–December 2010, respectively. Air temperature was measured at 16.8 (Hyytiälä) and 45 m (Speulderbos), volumetric soil water content at 0–30-cm depth and soil temperature at 5-cm depth. Gray area in air and soil temperature plots covers the range between daily maximum and minimum values

temperature was stable during winter time due to the snow cover at Hyytiälä; at Speulderbos, winter time was warmer (Fig. 1). Precipitation was fairly uniformly distributed along the year in both sites (Fig. 1). Relative air humidity during the growing season was lower at Hyytiälä (Fig. 1). Soil water content was relatively constant during the season in both sites, and was higher at Speulderbos (Fig. 1). Annual global radiation received was similar at both sites, being slightly higher at Speulderbos ($7.97 \text{ MJm}^{-2}\text{day}^{-1}$ in Hyytiälä vs. $9.60 \text{ MJm}^{-2}\text{day}^{-1}$ in Speulderbos).

3.2 Litter collection characteristics

The spatial variability in the litterfall collected returned as a result a CV of 21.5 % in the more open and shorter Scots pine stand in Hyytiälä, and 4.7 % in the more dense and taller Douglas fir stand in Speulderbos.

Inter-annual coefficient of variation of annual litter dry mass production during the study period was 26 % for Scots pine, and 13.3 % for Douglas fir.

The length of the study period importantly affects the assessment of the stand-level inter-annual average (Fig. 2). In Hyytiälä, the difference between the annual values and the long time period mean were great in some years (Fig. 2a). Two examples of that difference occurred in 2004 and in 2011, where the actual litterfall measurements were 35 % smaller than the full study period average of six and thirteen years, respectively (Fig. 2b). In contrast, in year 2002, the litterfall measured was 35 % greater than the average estimated for the last 4 years (Fig. 2b). Furthermore, this value was 72 % greater than the average from 1999 to 2011 period. If this value would be considered as an outlier, the new annual litterfall average for the site would change only by 6 %.

Fig. 2 Variations in annual litterfall in Hyttiälä in Scots pine-dominated conifer forest through years 1999–2011. In **a**, the grey bars represent the actual dry mass of litterfall collected by the litter traps during the entire year, whereas the line shows the averaged (average $\pm$ SE) annual litter production (P_{av}) from 1999 until the given year Y_i (Eq. 1). The dotted line shows the mean annual litterfall value for the whole study period ($2.86 \text{ Mg ha}^{-1} \text{ year}^{-1}$). In **b**, the solid line shows the difference in percentage between the actual collected litter and the annual litterfall average calculated since 1999 until the year Y_i . The dashed line represents the difference in percentage between the actual collected litter and the 13-year period litterfall average

Fig. 3 Monthly average litter production rate in Hyttiälä (**a**) for 2006–2010 and Speulderbos (**b**) for July 2007 to December 2010. The trendlines correspond to third-order (**a**) and fifth-order (**b**) polynomial regressions with r^2 values of 0.46 (**a**) and 0.47 (**b**) ($P < 0.001$ for both). The data point of high litterfall in February 2010 (**a**) corresponded to snow damage in Scots pine trees, the two observations of high litterfall in October 2009 and 2010 (**b**) corresponded to storms with exceptionally high wind speed episodes

3.3 Overall patterns in litter production

The average ($\pm$ SE) annual fine litter dry mass production for the study period was $2.86 \pm 0.22 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in the Scots pine stand in Hyttiälä (1999–2011) and $4.34 \pm 0.33 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in the Douglas fir stand in Speulderbos (2008–2010). Fine litter production rates in Scots pine showed an unimodal distribution with a maximum in autumn ($2.82 \text{ gm}^{-2} \text{ day}^{-1}$ in August 2006, $1.43 \text{ gm}^{-2} \text{ day}^{-1}$ in September 2007, $3.27 \text{ gm}^{-2} \text{ day}^{-1}$ in October 2008, $2.84 \text{ gm}^{-2} \text{ day}^{-1}$ in September 2009, and $1.99 \text{ gm}^{-2} \text{ day}^{-1}$ in September 2010) (Fig. 3a). During snow cover period (November–March) a small amount of litter was produced. Minimum Scots pine litterfall rates were reached in months between December to February, and ranged from 0.078 to $0.127 \text{ gm}^{-2} \text{ day}^{-1}$. Douglas fir (Fig. 3b) showed a more likely bimodal distribution. Litterfall was more evenly distributed during the year, and maximum peaks were less pronounced than as for Scots pine because of the less severe winter period in Speulderbos; nevertheless, litter was mainly produced from April to May and from October to November. Annual maximum values of litter production were 1.93 and $1.61 \text{ gm}^{-2} \text{ day}^{-1}$ in May and October 2008, 2.24 and $2.54 \text{ gm}^{-2} \text{ day}^{-1}$ in May and October 2009, 1.71 and $2.62 \text{ gm}^{-2} \text{ day}^{-1}$ in April and October 2010 for these two peaks (Fig. 3b). Annual minimum values were reached in December and January, with values from 0.21 to $0.33 \text{ gm}^{-2} \text{ day}^{-1}$.

3.4 Fractional composition of litter

Fractional litterfall compositions resulted in significantly different dynamics between the litter fractions (needle cones, twigs, bark, rest, and cones and seeds) in both species (paired-samples t tests, $P < 0.001$); using monthly time series of litterfall (2006–2010 for Scots pine and July 2007–December 2010 for Douglas fir). Douglas fir produced a greater relative amount of needle litter (inter-annual average $\pm$ SE = $78.929 \pm 0.011 \%$) than Scots pine ($60.952 \pm 0.035 \%$).

There was a strong relationship between the leaf litterfall fraction and the total litterfall (Table 3).

Scots pine litter production rates by fraction followed typical unimodal distributions with absolute maxima in September (needle, Fig. 4a), May (twigs, Fig. 4b), June and July (cones and seeds, Fig. 4c; bark and rest, Fig. 4d); while the maximum total litterfall during the 2006 to 2010 period was reached in September (Fig. 3a). In spring, Scots pine bark was an important component of the total amount produced. In late summer and early autumn, needle fraction predominated. In May 2006 and February 2010, there were peaks of twig litter, and in June and July 2007, peaks of cones and seeds.

Douglas fir needle litterfall (Fig. 4e) peaked in May and October, twig fraction (Fig. 4f) in March and October, and cones and seeds (Fig. 4g) in June. Bark (Fig. 4h) litterfall rates were more distributed along the year, not showing a specific pattern.

The minimum annual litterfall rates were mainly constituted of needle litterfall in Douglas fir (82 ± 10 % in average). However, in Scots pine, at the litterfall minima, the needles represented only the 40 ± 17 % (twigs 25 ± 8 % and bark 21 ± 10 %).

3.5 Inter-annual and seasonal differences in litter production in relation to climatic drivers and extreme weather events

Monthly data of climatic variables (global radiation, air temperature, soil temperature, and soil water content) did not significantly correlate ($P > 0.05$) with the total litterfall, needle litterfall, and C and N production rate in both sites.

In Hyytiälä, horizontal wind speed recorded from 1999 to 2011 was rarely higher than 8 ms^{-1} , and maximum wind gusts over the period were lower than 21 ms^{-1} . No significant relationships were found between wind speed and litterfall production ($P > 0.5$). The number of hours per month of 30-min averaged high wind speed data (wind speed 8.0 – 10.7 and 10.8 – 13.8 ms^{-1}) did not show correlation to monthly amount of litterfall ($P > 0.05$).

In Speulderbos, wind gusts recorded from July to March had an average speed of $18.8 \pm 3.6 \text{ ms}^{-1}$ with a maximum of 30.3 m s^{-1} . The maximum wind gust speed data correlated positively to total litterfall ($r^2 = 0.40^{***}$), and with needle ($r^2 = 0.32^{***}$) and twig ($r^2 = 0.38^{***}$) production rates. The high values 2.544 ± 0.041 and $2.6 \pm 1.0 \text{ g litter m}^{-2} \text{ day}^{-1}$ in October for 2009 and 2010, respectively (Fig. 4b), could have been caused by storm episodes at Speulderbos. We identified half-hour averaged wind speed of 8.0 – 9.1 ms^{-1} during several hours with maximum wind gusts of 20 ms^{-1} . The needle litterfall in those episodes was 44 % higher than in the same period of year 2008. The litterfall for those months contained higher non-needle fractions (bark 1.0 %, twigs 13.2 %, and cones and seeds 2.7 %) compared with the same periods in years 2007 and 2008 (bark 0.2, twigs 6.0 %, and cones and seeds 1.3 %). Finally, the litter produced during storm episodes increased the annual litterfall by 6.7 % in 2009 and 6.8 % in 2010, compared to October 2008.

At Hyytiälä site, early frost events and unusual low temperatures were identified in September 1999, October 2000, October 2008 and September 2009, and these events were possibly related to high litter production rates. Also, severe snow damage to the trees was recorded during winters 2009–2010 and 2010–2011. In 2009–2010, about 7 % of the basal area was lost, increasing the litterfall (Fig. 3a). This point was considered an outlier and not taken in account for the trend line in Fig. 3a.

In Hyytiälä, extremely low precipitation values were associated with extreme litter production rates. The year 2002 was exceptionally dry (535 mm), specially in summer time, and annual litterfall was extraordinarily high (4.90 Mg

$\text{ha}^{-1} \text{ year}^{-1}$; Fig. 2). These values of precipitation and litterfall were distribution outliers (atypical points) in the 13-years distribution from 1999 to 2011. Scots pine annual needle litterfall peak in year 2006 occurred in August, earlier than in the subsequent years, probably related to drought effect observed during the year 2006. A peak of $1.938 \text{ g litter m}^{-2} \text{ day}^{-1}$ constituted mainly by twigs and needles was observed in February 2010 (Fig. 3a), possibly related to the combined effect of the snow load on the branches and high 24-h averaged wind speed of 5.72 ms^{-1} with associated wind gusts and maximum 30-min average wind speed of 7.94 m s^{-1} .

3.6 Carbon and nitrogen inputs to the forest floor

Annual C and N inputs to soil were mainly driven by needle litterfall (Table 4). The N annual input through litterfall to Hyytiälä stand soil ($15.9 \pm 1.5 \text{ kg N ha}^{-1} \text{ year}^{-1}$) was much lower than in Speulderbos stand ($75 \pm 8 \text{ kg N ha}^{-1} \text{ year}^{-1}$), if compared with the C annual input ($1,430 \pm 110$ and $2,300 \pm 180 \text{ kg C ha}^{-1} \text{ year}^{-1}$, respectively) (Table 4).

In Hyytiälä, there were two differentiated seasons regarding the C and N inputs to soil through litterfall: May–October and November–April (paired-samples t tests, $P < 0.001$). Average ($\pm \text{SE}$) C input rates to soil in Hyytiälä were $0.574 \pm 0.039 \text{ g C m}^{-2} \text{ day}^{-1}$ from May to October and $0.204 \pm 0.020 \text{ g C m}^{-2} \text{ day}^{-1}$ from November to April. N input rates for these seasons were 6.48 ± 0.49 and $1.969 \pm 0.037 \text{ mg N m}^{-2} \text{ day}^{-1}$, respectively.

The high rate of twig litterfall of Scots pine exhibited in February 2010 (Fig. 3a) did not remarkably affect the C or N litter contents because of the similar element percentages to those for the needles. In contrast, the high portion of cones and seeds in June and July 2007 in litter (40 % of total litterfall) lowered the total litter N content by 27 % compared with June and July averages for years 2006, 2008 and 2009. Difference in cone and seed production did not affect C content.

The litter C and N content did not show any significant Pearson's linear relationship with the litterfall rate in any of both species ($r^2 < 0.012$). But the litterfall C and N input to soil rates were highly correlated between them, and with the total litterfall and needle litterfall (Table 3).

C content was similar along the litter fractions in both species. In Scots pine, the rest fraction was the richest in N content, followed by the needles (Table 4). In Douglas fir, N content differed between fractions (Table 4). From a temporal view, litter N content fluctuated more along the year in Douglas fir than in Scots pine, which also contained less N (Fig. 5). Douglas fir litter N content in October 2009 and 2010 (1.82 and 1.84 %, respectively) was 16 % higher than in October 2007 and 2008 (1.50 and 1.66 %, respectively), while carbon content was similar (Fig. 5d), and consequently, C/N

Table 3 Equations of linear models ($y=ax+b$) fitted to litterfall characteristics relationships: y correspond to the traits in the second column, x correspond to the titles of the following columns. Scots pine (Jan 2006–Dec 2010) and Douglas fir (Jul 2007–Dec 2010)

Species	Litter traits	LF _{tot}	LF _{nee}	LF _C
Scots pine	LF _{nee}	$0.8895x-0.2023$		
	LF _C	$0.5094x-0.0042$	$0.5190x+0.1355$	
	LF _N	$0.0057x-0.0002$	$0.0061x+0.0012$	$0.0113x-0.0002$
Douglas fir	LF _{nee}	$0.8195x-0.0360$		
	LF _C	$0.5325x+0.0001$	$0.6035x+0.0632$	
	LF _N	$0.0176x-0.0003$	$0.0200x+0.0018$	$0.0328x-0.0002$

LF_{tot} and LF_{nee} are total litterfall and needle litterfall rates (gramme per day); LF_C and LF_N are carbon and nitrogen production rates (gramme per square metre per day)

Parameters are monthly-averaged. The linear regressions are calculated with monthly values ($n=60$ for Scots pine; $n=42$ for Douglas fir)

Pearson's linear correlation coefficients (r^2) are from 0.839 to 0.999, all coefficients are significant at $P<0.001$ (two-tailed)

ratio 14 % smaller (29.3 in 2009 and 28.9 in 2010; Fig. 5f). As a result, the average soil C input rate was 135 % greater (Fig. 6c) in October 2009 and 2010 compared with the same period in 2007 and 2008, whereas the average N input rate average was 167 % greater ($0.046 \text{ g N m}^{-2} \text{ day}^{-1}$ in 2009 and $0.048 \text{ g N m}^{-2} \text{ day}^{-1}$ in 2010; Fig. 6d).

Generally, there were two periods during the year at the Douglas fir site when C and N were released to the topsoil from the canopy litter (Fig. 6c, d), while there was only one period at the Finnish site (Fig. 6a, b). Litter C production rate (Fig. 6a, c) followed the same pattern as the total litter production rate (Fig. 3a, b), reflecting the circumstance that litter C concentration almost did not vary during the year (Fig. 5a, d). Despite, Scots pine litter C (50.74 ± 0.27 %; Fig. 5a) and N content (0.642 ± 0.025 %; Fig. 5b) had maxima in September. Litter was richer in N with a minimum C/N ratio

in September (79.1 ± 2.8 ; Fig. 5c), where the smallest yearly standard deviation was found.

4 Discussion

4.1 Litterfall characteristics

At the Hyytiälä site, the inter-annual variations in litter production emphasize the importance of long study periods (Fig. 2). Measurements repeated on the same trees revealed a fluctuating pattern (Fig. 2a): after one period with higher canopy litterfall succeeded another period with smaller amount and vice versa. These fluctuations can be consequences of annual irregularities in the climate, which can create a higher needle loss with nutritional problems for the

Fig. 4 Annual dynamics of litterfall fractions for the periods 1999 to 2011 in Scots pine (a, b, c, d), and July 2007 to December 2010 in Douglas fir (e, f, g, h)

Table 4 Average ($\pm$ SE) litter mass fractionation, litter C and N contents, and annual inputs of biomass, C and N to the forest soil in Hyytiälä (Jan 1999–Dec 2010) and in Speulderbos (Jan 2008–Dec 2010)

Species	Litter fraction	Mass percentage	C content	N content	Annual biomass soil input	Annual C soil input	Annual N soil input
		(%)	(%)	(%)	(kg ha ⁻¹ year ⁻¹)	(kg C ha ⁻¹ year ⁻¹)	(kg N ha ⁻¹ year ⁻¹)
Scots pine	Needle	61 $\pm$ 8	51.16 $\pm$ 0.19	0.663 $\pm$ 0.038	1,600 $\pm$ 120	800 $\pm$ 70	9.1 $\pm$ 1.3
	Twigs	14 $\pm$ 6	49.40 $\pm$ 0.15	0.454 $\pm$ 0.047	580 $\pm$ 190	180 $\pm$ 90	2.3 $\pm$ 0.9
	Bark	11.8 $\pm$ 2.2	49.20 $\pm$ 0.40	0.416 $\pm$ 0.016	290 $\pm$ 11	141 $\pm$ 6	1.31 $\pm$ 0.14
	Cones and seeds	7 $\pm$ 5	47.07 $\pm$ 0.26	0.228 $\pm$ 0.031	200 $\pm$ 29	93 $\pm$ 13	0.70 $\pm$ 0.16
	Rest	6.5 $\pm$ 0.8	50.32 $\pm$ 0.25	1.278 $\pm$ 0.049	166 $\pm$ 7	83 $\pm$ 4	2.05 $\pm$ 0.11
	Total	100	50.27 $\pm$ 0.24	0.601 $\pm$ 0.036	2,860 $\pm$ 220	1,430 $\pm$ 110	15.9 $\pm$ 1.5
Douglas fir	Needle	78.9 $\pm$ 1.9	53.19 $\pm$ 0.27	1.80 $\pm$ 0.23	3,420 $\pm$ 310	1,820 $\pm$ 80	62 $\pm$ 7
	Twigs	14.33 $\pm$ 0.39	53.0 $\pm$ 0.6	1.07 $\pm$ 0.37	620 $\pm$ 5	330 $\pm$ 29	6.6 $\pm$ 1.8
	Bark	0.45 $\pm$ 0.13	52.8 $\pm$ 0.9	1.055 $\pm$ 0.041	20 $\pm$ 5	10.6 $\pm$ 4.2	0.21 $\pm$ 0.05
	Cones and seeds	6.3 $\pm$ 2.1	53.2 $\pm$ 2.6	2.0 $\pm$ 1.4	265 $\pm$ 32	140 $\pm$ 80	5.3 $\pm$ 4.5
	Total	100	53.1 $\pm$ 1.1	1.7 $\pm$ 0.5	4,340 $\pm$ 330	2,300 $\pm$ 180	75 $\pm$ 8

The mass fractions and elemental contents among the litter components within species were compared by one-way ANOVA, showing significant differences ($P<0.001$)

The averages shown in the table are calculated from 3-months intervals collected litter during 1999–2005 and monthly intervals during 2006–2010

trees in the subsequent period; or longer-term variations like drought years period or plagues. As we cannot control every climatic and physiological parameters, it is important to identify whether the data outliers were produced by sampling errors or by actual variations in litterfall. Outliers removal, numerical transformations or other data processing

Fig. 5 Litterfall quality (C and N content, and C/N ratio) of Scots pine (1999–2009) in Hyytiälä and Douglas fir (July 2007 to December 2010) in Speulderbos. Data correspond to monthly averages during the study period. Data were fitted by third-order polynomial regressions; all are significant at $P<0.001$

Fig. 6 Carbon and nitrogen production rate in litterfall of Scots pine (1999–2009) in Hyytiälä and Douglas fir (July 2007 to December 2010) in Speulderbos. Data of Scots pine were fitted by third-order polynomial regression and those in Douglas fir by fifth-order polynomial regressions

methods must be done with extreme caution because the results can be modified drastically and interesting litterfall events might be ignored.

The Eq. 1 showed that the increasing number of data yields to a less deviated mean if compared to the mean over the years (Fig. 2b). The Eq. 1 permitted to highlight the biased viewpoint of short-term studies on the annual average litterfall. The annual litterfall of a stand is far from being a steady value (Kouki and Hokkanen 1992; Reyer et al. 2003), it fluctuates. Depending of the length of the study period, scientists may calculate different average values for annual litterfall in the same stand. As an example, Ranger et al. (2003) reported big variations in Douglas fir annual litterfall (from ca. 2.5 to 6 Mg ha⁻¹ year⁻¹) during a 7-year study in France. Fig. 2b showed the importance of long-term studies concerning litterfall. However, climatic factors, extreme weather events, stand growth, or forest management practices like thinning will play an important role on the litterfall rates. This is why litterfall averages of long-term studies must be used carefully. Understanding the processes which affected them and the status of the stand can be more important than the litterfall average itself. In the other hand, the average annual litterfall in Speulderbos can be taken only as a first-stage estimate; this is why this article studies more the intra-annual characteristics for the Speulderbos stand.

Although being both monoculture conifer forests and having installed a double amount of litter traps of similar size in Hyytiälä, CV between litter traps was relatively high. The Scots pine stand was partially thinned during the experiment, which can explain the spatial differences in litterfall. Also, the CV values can reflect the more open

canopy of the Scots pine stand in contrast to the Douglas fir stand, with 6.5 m² m⁻² (all-sided) LAI (Kolari et al. 2009) and 7.8 to 10.5 m² m⁻² (projected) (Van Wijk et al. 2000), respectively. Nonetheless, McShane et al. (1983) found a high CV between litter traps while studying a Douglas fir stand. In addition, despite a similar twig mass was produced in both stands, the bigger pine twig size enhanced the CV, producing less single pieces with higher mass each and higher difference in the collected litterfall between litter traps.

4.2 Correlations of litter production with environmental drivers and effects of extreme events

Climatic parameters had an important effect on litterfall dynamics. Extreme values were especially important to understand unusually high peaks of litterfall production (i.e. drought effect in 2002 and 2006, early frosts and snow damage at Hyytiälä, and wind gusts effect on Speulderbos).

At Hyytiälä site, wind speed did not reach as high values as at Speulderbos. Data showed that Douglas fir litterfall was affected by high wind speeds (maximum wind gusts). In addition to wind-influenced litterfall, wind may damage the internal structures of the branches. This effect decreases the tree growth rate and needle production in the subsequent years, which will decrease the needle litter production in a short term. Nevertheless, damaged twigs are shed later on. In conclusion, these damages can create a biased disturbance in the litterfall rates of stands frequently affected by phenomena such as wind damage, etc.

Premature needle abscission can be responsible for lower resorption rates. The early frosts that occurred at Hyytiälä

had a direct effect on litter N content enhancement (Fig. 6b), associated to the highest values of minimum annual needle N concentration. Also, the early frosts in 2008 and 2009 could have affected the secondary growth of Scots pine, finding less cone production in the subsequent years.

Table 3 showed that the litterfall production rates and the C and N soil input rates were correlated. Despite isolated events of high litterfall and C and N soil input, the linear models shown in Table 3 were highly significant.

4.3 Litter production and fractional composition of litter

Similar values for annual Scots pine litter production have been reported by Berg et al. (1999) and Starr et al. (2005) in stands with similar age in similar latitudes. In the natural environment of Douglas fir, McShane et al. (1983) found similar annual litterfall values in a stand of similar age. Also, Ranger et al. (2003) reported similar values for a 40-year stand in France. In Speulderbos, when the stand was 35 years old, Koopmans et al. (1996) calculated a N input to soil of 51 kg N year⁻¹ (ca. 0.014 g N m⁻² day⁻¹), and our results give an input of 0.019 g N m⁻² day⁻¹. This increase can be interpreted as a result of the stand growth (Ukonmaanaho et al. 2008).

Our study demonstrates that sorting the litterfall in fractions allows to gaining important insight into the determinants of inter-annual and seasonal variations in litter production rate and chemistry. Litter production rates for different litter components were statistically different. This is important as the fractional composition of litter directly determines which type of litter is added to the forest soil in every period of the year. Regarding the physical characteristics (toughness, shape, or amount) and chemical composition of the litterfall, and the meteorological and biological status of the soil, it influences the litter decomposability and nutrient release to the soil.

The maximum litterfall rates in summer of cones at both stands (Fig. 4c, g), bark and rest, may suggest that trees shed the materials *unused* during the growth season. The stem and branches could increase the bark litterfall in Scots pine as they grow and increase their diameter. The resin droplets of the rest fraction in Scots pine are secondary products of tree metabolism, and principally produced in that season. And mature cones could be liberated in summer in favor of higher priority processes like maintaining photosynthetic needles.

4.4 Seasonality of leaf litterfall

Deciduous trees in the climates of this study (i.e. oak, beech, maple and birch) have a strategy of building one-season leaves, which grow and senesce in some months. It is in autumn, where conditions get unfavorable for the net primary production (colder temperatures and less light), that

leaves senesce and fall to the topsoil, generating the annual maximum N input to these soils (excluding sites with high atmospheric N deposition). Situation in evergreen conifers (i.e. the species of this study, pine trees and firs) is different: they support several cohorts of leaves on their canopy lasting several years. The leaf longevity of Scots pine and Douglas fir at the study sites is about 2 to 3 years (Wang et al. 2012). Leaf longevity in these species is variable inside the same tree: new leaves are produced in spring and old leaves are shed during the whole year, although there are leaf litter production peaks. Evergreen broad-leaved Mediterranean species (i.e. cork oak, olive, *Arbutus* and *Nerium oleander*) conserve leaves for more than one growing season, but the shedding of leaves occurs during the hot and dry summer months.

Despite similar physiological characteristics in both our species, litterfall seasonality was different (Fig. 3). During winter in Hyttiälä, the needles are in dormant phase and it is beneficial for the plants to drop the needles right before this phase. Therefore leaf litter production in winter is normally small and presumably caused mainly by physical damage to the trees. At Speulderbos, which has warmer climate, the rate of litter production processes only decreased during winter (Fig. 3). Speulderbos conditions generated an overall higher leaf litter production and it presented higher leaf area index, helped by the higher and moderate temperatures by the latitude and maritime influences.

4.5 Litter chemistry

Nutrients lost in litterfall are a cost to a tree, as they have to be substituted to maintain primary productivity (Lin et al. 2003). Boreal soils are typically N limited (Priha and Smolander 1999); climate presents lower temperatures and longer and colder winters. Our results of Scots pine needle N content are in concordance with Ukonmaanaho et al. (2008), which reported a mean of 0.49 % in senescent needles in Finnish forests. The narrow fluctuation range and low annual average of Scots pine litter N concentration observed is typical for a species adapted to N limited ecosystem, even lower than the N content reported by Niinemets et al. (2001) (0.86±0.12 %) in an infertile site in Estonia. Concerning Douglas fir, Turner and Olson (1976) reported a value of 0.57 % for a 42-year-old Western Washington stand. Reyer et al. (2003) found litter N concentrations of 0.91–1.38 % in a 7-year study in France, with a seasonal dynamic similar to our study. Our values are still higher possibly because of the chronic N deposition, which could have increased needle N concentration (Turner 1977). Furthermore, Simpson et al. (2006) found Speulderbos site to be particularly affected by N deposition, while Hyttiälä belonged to the less affected areas in Europe.

648 4.6 Nutrient resorption efficiency and nutrient losses
 649 by litter

650 According to Killingbeck (1996), leaf litter N concentra-
 651 tions observed during the year and its minimum (NRP)
 652 indicated very good capacity for senescent leaf nutrient
 653 resorption ($\text{NRP} < 0.7\%$ N) in the Scots pine stand
 654 (Fig. 5b). This is typical of a species adapted to low-
 655 fertility soils (Pensa and Sellin 2003) and high-stress envi-
 656 ronmental conditions. Similar NRP values (0.50 and
 657 0.52 %) were reported by Killingbeck (1996), and even
 658 lower NRP values (0.44 % N) in Scots pine grown on
 659 podzols in Estonia were found by Pensa and Sellin (2003).
 660 In contrast, Douglas fir stand performed in every year an
 661 incomplete N resorption ($\text{NRP} < 1\%$ N), but its favorable
 662 site conditions regarding soil N availability, higher temper-
 663 ature and light may compensate this inefficacy, and help the
 664 stand reaching high growth rates per year. A most exhaust-
 665 ive sampling of senescent needles during nutrient resorp-
 666 tion period might reveal a most accurate NRP value.

667 The storm episodes in 2009 and 2010 in Speulderbos led to
 668 an increase in annual litterfall. The loss of cones, the loss of
 669 twigs as support structures for potential new needles and the
 670 loss of needles itself during the nutrient retranslocation period
 671 resulted in an incomplete nitrogen resorption, if compared
 672 with previous years NRP values (2007 and 2008).

673 5 Conclusion

674 These data collectively demonstrated that there were large
 675 inter- and intra-annual variations in canopy litterfall. Longer
 676 study period will produce better result on the site litterfall
 677 average calculation. Inter-annual fluctuations in litterfall
 678 may lead to biased values in the annual litterfall estimates
 679 if the study period is short.

680 Weather conditions played a big role on litterfall. These
 681 importantly altered litter production and litter quality. Both
 682 species had different meteorological conditions and were
 683 affected differently by meteorological events. Scots pine
 684 litterfall in Hyytiälä was affected by annual low precipita-
 685 tion, early frosts and snow load. Douglas fir litterfall was
 686 mostly affected by wind gusts. A principle of effect of
 687 unexpected premature leaf shedding on leaf nitrogen resorp-
 688 tion efficiency was found in this study; senescent leaf min-
 689 imum N concentration was found to increase in Douglas fir
 690 after significantly high leaf fall events, if compared with
 691 other years. This particular subject needs further research.

692 When studying litterfall, researchers must pay attention
 693 to the climatic variables and single events which could
 694 affect it. Litterfall rates usually vary largely from year to
 695 year. More studies about the causes of these differences are
 696 needed to properly model the nutrient cycling in forests.

Acknowledgements We fully thank to the anonymous reviewers
 who helped to improve the manuscript.

Funding The funding for the study was provided by the European
 Commission (FP6 framework IP NitroEurope and the Center of
 Excellence in Environmental Adaptation supported through the
 European Regional Fund, and Internationalization Program DoRa for
 doctoral studies supported through the European Social Fund) and the
 Estonian Ministry of Science and Education (grant SF1090065s07).

Reference

- Aerts R (1997) Climate, leaf litter chemistry and leaf litter decompo-
 sition in terrestrial ecosystems: a triangular relationship. *Oikos*
 79:439–449. doi:10.2307/3546886
 Aerts R, Berendse F (1989) Above-ground nutrient turnover and net
 primary production of an evergreen and a deciduous species in a
 heathland ecosystem. *J Ecol* 77:343–356
 Álvarez JA, Villagra PE, Rossi BE, Cesca EM (2009) Spatial and
 temporal litterfall heterogeneity generated by woody species in
 the Central Monte desert. *Plant Ecol* 205:295–303. doi:10.1007/
 s11258-009-9618-z
 Berg BA, Albrektson A, Berg MP, Cortina J, Johansson MB, Gallardo
 A, Madeira M, Pausas J, Kratz W, Vallego R, McClaugherty C
 (1999) Amounts of litter fall in some pine forests in a European
 transect, in particular Scots pine. *Ann For Sci* 56:625–639
 Drebs A, Nordlund A, Karlsson P, Helminen J, Rissanen P (2002)
 Climatological statistics of Finland 1971–2000. Finnish Meteorological
 Institute, Helsinki
 Ganjegunte GK, Condon LM, Clinton PW, Davis MR, Mahieu N
 (2004) Decomposition and nutrient release from radiata pine
 (*Pinus radiata*) coarse woody debris. *Forest Ecol Manag*
 187:197–211. doi:10.1016/S0378-1127(03)00332-3
 Ilvesniemi H, Levula J, Ojansuu R, Kolari P, Kulmala L, Pumpanen J,
 Launiainen S, Vesala T, Nikinmaa E (2009) Long-term measure-
 ments of the carbon balance of a boreal Scots pine dominated
 forest ecosystem. *Boreal Environ Res* 14:731–753
 Killingbeck KT (1996) Nutrients in senesced leaves: keys to the search
 for potential resorption and resorption proficiency. *Ecology*
 77:1716–1727. doi:10.2307/2265777
 Kolari P, Kulmala L, Pumpanen J, Launiainen S, Ilvesniemi H, Hari P,
 Nikinmaa E (2009) CO₂ exchange and component CO₂ fluxes of
 a boreal Scots pine forest. *Boreal Environ Res* 14:761–783
 Koopmans CJ, Tietema A, Boxman AW (1996) The fate of ¹⁵N
 enriched throughfall in two coniferous forest stands at different
 nitrogen deposition levels. *Biogeochemistry* 34:19–44
 Kouki J, Hokkanen T (1992) Long-term needle litterfall of a Scots pine
Pinus sylvestris stand: relation to temperature factors. *Oecologia*
 89:176–181
 Lehtonen A, Sievänen R, Mäkelä A, Mäkipää R, Korhonen KT,
 Hokkanen T (2004) Potential litterfall of Scots pine branches in
 southern Finland. *Ecol Model* 180:305–315. doi:10.1016/
 j.ecolmodel.2004.04.024
 Lin KC, Hamburg SP, Tang S, Hsia YJ, Lin TC (2003) Typhoon effects
 on litterfall in a subtropical forest. *Can J Forest Res* 33:2184–2192
 Lodge DJ, Scatena FN, Asbury CE, Sánchez MJ (1991) Fine litterfall
 and related nutrient inputs resulting from hurricane Hugo in
 subtropical wet and lower montane rain forests of Puerto Rico.
Biotropica 23:336–342
 McShane MC, Carlile DW, Hinds WT (1983) The effect of collector
 size on forest litter-fall collection and analysis. *Can J Forest Res*
 13:1037–1042

- Melillo JM, Aber JD, Linkins AE, Ricca A, Fry B, Nadelhoffer KJ (1989) Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. *Plant Soil* 115:189–198. doi:10.1007/BF02202587
- Morillas L, Gallardo A, Portillo-Estrada M, Covelo F (2012) Nutritional status of *Quercus suber* populations under contrasting tree dieback. *Forestry* 85:369–378. doi:10.1093/forestry/cps035
- Niinemets Ü, Ellsworth DS, Lukjanova A, Tobias M (2001) Site fertility and the morphological and photosynthetic acclimation of *Pinus sylvestris* needles to light. *Tree Physiol* 21:1231–1244
- Owen SM, Leaver DS, Bealey WJ, Wilson R, Reis S, Sutton M (2011) A new database for time-series monitoring data: the NitroEurope approach. *IForest* 226–232. doi: 10.3832/for0595-004
- Pensa M, Sellin A (2003) Soil type affects nitrogen conservation in foliage of small *Pinus sylvestris* L. trees. *Plant Soil* 253:321–329. doi:10.1023/A:1024884516655
- Pérez-Suárez M, Arredondo-Moreno JT, Huber-Sannwald E, Vargas-Hernández JJ (2009) Production and quality of senesced and green litterfall in a pine-oak forest in central-northwest Mexico. *Forest Ecol Manag* 258:1307–1315. doi:10.1016/j.foreco.2009.06.031
- Priha O, Smolander A (1999) Nitrogen transformations in soil under *Pinus sylvestris*, *Picea abies* and *Betula pendula* at two forest sites. *Soil Biol Biochem* 31:965–977. doi:10.1016/S0038-0717(99)00006-1
- Ranger J, Gerard F, Lindemann M, Gelhaye D, Gelhaye L (2003) Dynamics of litterfall in a chronosequence of Douglas-fir (*Pseudotsuga menziesii* Franco) stands in the Beaujolais mounts (France). *Ann For Sci* 60:475–488. doi:10.1051/forest:2003041
- Reyer C, Lasch P, Mohren GMJ, Sterck FJ (2010) Inter-specific competition in mixed forests of Douglas-fir (*Pseudotsuga menziesii*) and common beech (*Fagus sylvatica*) under climate change—a model-based analysis. *Ann For Sci* 67:805. doi:10.1051/forest/2010041
- Sanford RLJ, Parton WJ, Ojima DS, Lodge DJ (1991) Hurricane effects on soil organic matter dynamics and forest production in the Luquillo experimental forest, Puerto Rico: results of simulation modeling. *Biotropica* 23:364–372
- Simpson D, Butterbach-Bahl K, Fagerli H, Kesik M, Skiba U, Tang Y (2006) Deposition and emissions of reactive nitrogen over European forests: a modelling study. *Atmos Environ* 40:5712–5726
- Starr M, Saarsalmi A, Hokkanen T, Merilä P, Helmisaari HS (2005) Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. *Forest Ecol Manag* 205:215–225
- Su Z, Timmermans WJ, Van Der Tol C et al (2009) EAGLE 2006—multi-purpose, multi-angle and multi-sensor in-situ and airborne campaigns over grassland and forest. *Earth* 13:833–845. doi:10.5194/hessd-6-1797-2009
- Turner J (1977) Effect of nitrogen availability on nitrogen cycling in a Douglas-fir stand. *Forest Sci* 23:307–316
- Turner J, Olson PR (1976) Nitrogen relations in a Douglas-fir plantation. *Ann Bot-London* 40:1185–1193
- Ukonmaanaho L, Merilä P, Nöjd P, Nieminen TM (2008) Litterfall production and nutrient return to the forest floor in Scots pine and Norway spruce stands in Finland. *Boreal Environ Res* 13:67–91
- Van Wijk MT, Dekker SC, Bouten W, Bosveld FC, Kohsiek W, Kramer K, Mohren GMJ (2000) Modeling daily gas exchange of a Douglas-fir forest: comparison of three stomatal conductance models with and without a soil water stress function. *Tree Physiol* 20:115–122
- Vitousek PM, Gerrish G, Turner DR, Walker LR, Mueller-Dombois D (1995) Litterfall and nutrient cycling in four Hawaiian montane rainforests. *J Trop Ecol* 11:189–203
- Wang L, Ibrom A, Korhonen JFJ, Frumau AKF, Pihlatie M, Schjoerring JK (2012) Interactions between leaf nitrogen status and longevity in relation to N cycling in three contrasting European forest canopies. *Biogeosciences Discuss* 9:9759–9790. doi:10.5194/bgd-9-9759-2012