

Testing dependence between growth and needle litterfall in Scots pine—a case study in northern Finland

ALEKSI LEHTONEN,^{1,2} MARKUS LINDHOLM,³ TATU HOKKANEN,¹ HANNU SALMINEN³
and RISTO JALKANEN³

¹ Finnish Forest Research Institute, P.O. Box 18, FI 01301 Vantaa, Finland

² Corresponding author (aleksi.lehtonen@metla.fi)

³ Finnish Forest Research Institute, P.O. Box 16, FI 96301 Rovaniemi, Finland

Received January 9, 2008; accepted July 11, 2008; published online September 2, 2008

Summary Both drought and fungal disease increase needle litterfall of Scots pine (*Pinus sylvestris* L.) trees, but most factors causing annual variation in needle litterfall are poorly understood. We hypothesized that radial growth and weather conditions favorable to growth correlate positively with needle litterfall with a lag equal to the number of needle cohorts (here being 5–6). We studied the time series of needle litterfall, stem increment, pollen cone litter and daily weather conditions in a Scots pine stand over 43 years (1961–2004). The cross-correlations of standardized time series were estimated with various lags. Model predictions of annual needle litterfall were tested against independent data. Changes in annual growth and needle litterfall correlated with lags of 0 and 4 years. The best predictors for needle litterfall were May to mid July temperature sum with a lag of 4 years, May rainfall with a lag of 2 years and September temperature with a lag of 6 years. Pollen cone litter correlated negatively with needle litterfall with a lag of 2 years. The study provided empirical evidence that needle litterfall of Scots pine in northern Finland is influenced by needle production and needle mass development that occurred 4 to 6 years earlier.

Keywords: annual growth, leaf lifespan, needle shed, *Pinus sylvestris*, pollen cones.

Introduction

Needle litter in boreal forests plays an important role in the carbon cycle by providing substantial carbon input to the soil. Changes in soil carbon stock are driven by annual variation in litter input and decomposition (Trumbore and Harden 1997, Liski et al. 2005), but the reasons for the annual variation in needle litterfall are poorly known. Interpretation of carbon flux measurements could be improved by detailed knowledge about drivers of annual variation in needle litter, especially in the boreal zone where soil respiration comprises a considerable part of the carbon flux budget.

Process models that estimate tree growth as a function of photosynthesis, respiration and carbon allocation synthesize

current knowledge of ecosystem function. Mäkelä (1997) has described a carbon balance model for growth that predicts development according to pipe-model theory (Shinozaki et al. 1964), functional balance (Davidson 1969) and an allometric relationship between foliage mass and crown surface area (Zeide and Pfeifer 1991). According to this carbon balance model, foliage growth rate depends on foliage mass, canopy length and rate of self-pruning, where photosynthesis is proportional to foliage mass, and gross growth of woody compartments is a function of foliage mass and stem length. Thus, if stem increment depends on photosynthesis, which in turn depends on foliage mass, favorable years for growth should increase biomass production of needles and stem simultaneously. In contrast, the widely applied 3-PG model (Landsberg and Waring 1997) divides net primary production (NPP) into roots, foliage and stem based on empirical relationships. According to the 3-PG model, an increase in NPP increases the quantity of carbon allocated to stem and to foliage.

Relationships between foliage and stem production in these two models imply that needle litter and stem increment correlate with a lag equal to the number of needle cohorts, assuming that the oldest needle cohort is shed annually. This relationship between NPP and needle production is supported by limited empirical evidence (Waring 1983, Cannell 1989), but has not been tested with appropriate time series of needle litter and tree growth data.

Annual variation in needle litterfall of Scots pine (*Pinus sylvestris* L.) is affected by recent spring and summer temperatures (Kouki and Hokkanen 1992) and by temperature sum (Finér 1996). Between-site variation in needle litterfall is driven by soil fertility, stand age and latitude (Albrektson 1988).

Leaf longevity is closely associated with foliage biomass and NPP. Gower et al. (1993) found that the production efficiency (NPP per leaf area) of trees was inversely related to leaf longevity. Niinemets and Lukjanova (2003), based on Ackerly (1999), concluded that limited shoot growth leads to increased needle lifespan because of reduced self-shading. The concep-

tual model of Reich et al. (1992) links leaf lifespan with growth, which, in turn, is driven by leaf area and carbon gain. Comparison of leaf longevity among species provides insight into ecological strategies, but does not provide tools for testing the reasons for the annual variation in needle longevity or shedding.

We studied factors affecting needle litterfall in a 150-year-old Scots pine stand in northern Finland with modest annual height and crown biomass increments. We modeled variation in needle litterfall with potential evapotranspiration (PET), daily precipitation, daily temperature, radial growth and pollen cone litter with various lags. We hypothesized that radial growth and growth-favoring weather correlate positively with needle litterfall with lags equal to the number of needle cohorts.

Materials and methods

Study site and time-series data

An *Empetrum-Vaccinium*-type (Cajander 1949) Scots pine stand was sampled at the southern edge of the northern Boreal Zone in Lapland, northern Finland (66°36' N, 26°71' E, 130–140 m a.s.l.). The even-aged stand was naturally regenerated after a forest fire in 1854. Scots pine trees in this region have 5–6 needle cohorts.

Time series of needle litter and pollen cone (i.e., male strobilus) litter were collected in 15 litter traps of 0.5 m² in size

(Figure 1). Since 1960, the traps have been emptied monthly from May to September, and the litter accumulated in winter has been sampled each May. The sampling dates varied slightly during these decades. Therefore, the annual estimates of needle and pollen cone litter were aggregated from June 15 in Year 1 to June 14 in Year 2.

After air-drying at room temperature for 12–36 months, the litter was separated into the following fractions: needles, pollen cones and their remains, cones, seeds, branches, insects and their faeces, and others. The fractions were then weighed to the nearest 0.1 mg.

Stocking density of the stand has been relatively constant since the first measurements (Table 1). The point method was used to determine crown closure with a Cajanus cylinder (Sarvas 1953). Random stratified sampling was applied to produce tree-ring time series: nine sample trees from each of five equally wide diameter classes were cored at breast height in autumn 2005, resulting in a sample of 45 out of 89 pines. Annual ring widths were measured to the nearest 0.01 mm. These series were then cross-dated visually and checked by standard methods of dendrochronology (Fritts 1976), computing cross-correlations between individual series and the master chronology. These cross-correlations were studied to obtain the annual resolution for each increment core.

Pre-whitening

The time series of needle litter, radial growth and pollen cone litter were standardized by standard procedures of dendro-

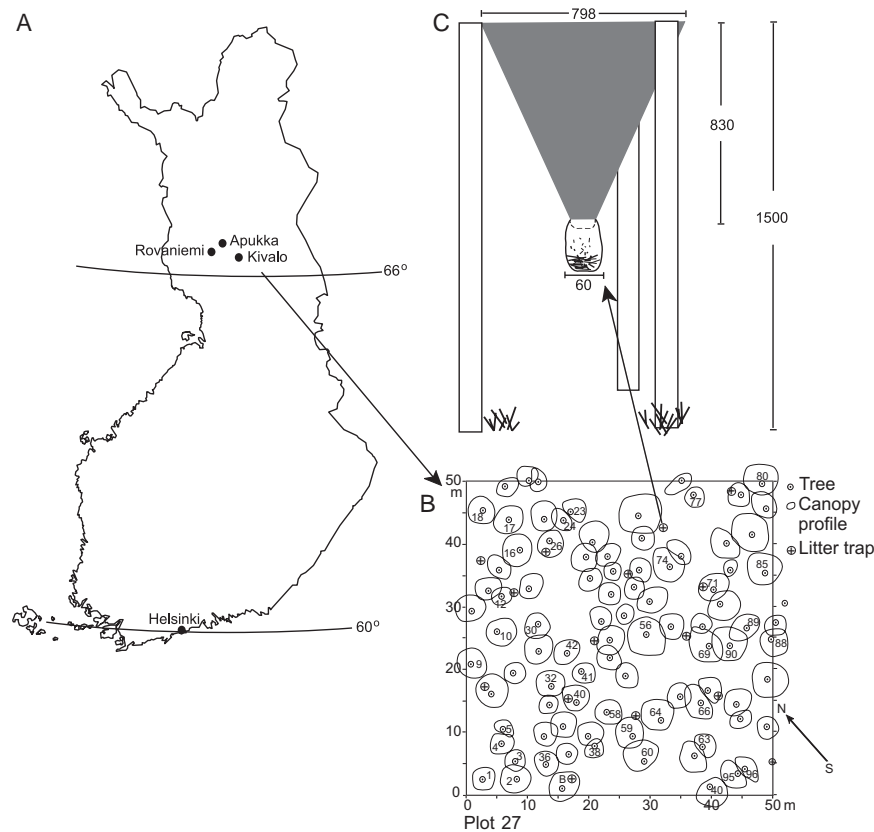


Figure 1. (A) Kivalo research area and the weather station at Apukka in Finland. (B) The measured sample plot (2500 m²) including canopy profiles of trees and litter traps (trees cored for increment are numbered). (C) Litter trap dimensions (mm).

Table 1. Characteristics of the experimental stand at Rovaniemi, Finland.

Year	Stand density (stems ha ⁻¹)	Stem volume (m ³ ha ⁻¹)	Dominant height ¹ (m)	Dominant diameter ² (cm)	Crown closure (%)	Stand age (years)
1961	384	175	22.0	29.8	44	103
1967	376	175	22.8	29.8	36	109
1972	376	198	23.0	30.3	–	114
1991	360	243	23.9	35.6	45	133
2001	356	266	24.4	37.5	53	143

¹ Mean height of trees with largest diameter (100 ha⁻¹).

² Mean diameter of trees with largest diameter (100 ha⁻¹).

chronology (Cook and Peters 1981). This was done to ensure that the effects of trend-like changes in biomass, stand age and soil fertility on litterfall were removed, our focus being the causes of annual variation in litter. Trends in radial growth were modeled and then removed with flexible 33% spline functions (Cook and Peters 1981). These splines retain 50% of the variance in the series at frequencies greater than one third of the series length. Previously, similar splines were shown to preserve the annual to decadal timescales in the resultant chronologies (Lindholm et al. 2000, 2001). Because our focus was on the high and medium frequencies, we assumed that the low frequency variance removed consisted mainly of noise. The time series of needle and pollen cone litter were indexed with splines with four degrees of freedom (Figures 2 and 3).

The needle litter index was tested and found to be stationary (single mean) and white noise (no significant autocorrelation). Indexed radial growth showed significant autocorrelation at lags of 1 and 2 years ($r = 0.61$ and 0.46 , respectively), and therefore a differenced radial growth index was used ($dG = \text{indexed growth}_t - \text{indexed growth}_{t-1}$). The pollen cone litter index showed autocorrelation at a lag of 2 years ($r = -0.34$). Cross-correlation of the pollen cone index and needle litter index was studied, where needle litter was white noise. When cross-correlation of two time series is studied, at least one should be white noise (Chatfield 2004), and therefore autocorrelation in the pollen cone litter index was not removed. The correlation between differenced needle litter index and differenced radial growth index was also studied.

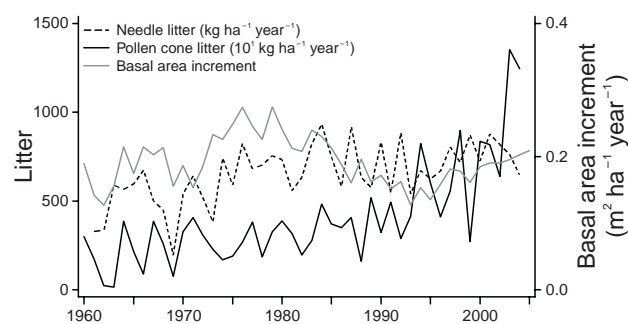


Figure 2. Variations in needle litter, pollen cone litter and basal area increment of a *Pinus sylvestris* stand at Kivalo, Rovaniemi from 1961 to 2004. Basal area increment is based on cored trees.

Meteorological data

Air temperature and precipitation measured at 3-h intervals were obtained from the nearest official weather station, located at 102 m a.s.l. and 38 km northwest of the litter-collection stand (Figure 1). Daily potential evapotranspiration (PET) measurements were obtained from the airport at Rovaniemi (available for the growing seasons 1960–1997). The correlation between indexed needle litter and weather variables was studied at lags from 0 to 6 years.

In addition to annual and monthly weather data, an iteration method based on statistical fit was used to find predictors of the needle litter index among the weather variables. A large set of PETs, snowfall and rainfall, and temperature sums with 0, 5, 15 and -15 °C thresholds were calculated varying the starting (s) day in a year and the length of the summation period (p). The lengths of these time periods varied from $p = 7$ to 120 days, and the starting date was run daily throughout the year ($s = 1$ to 358). Pearson's correlation coefficients between the needle litter index time series (Y_t) and various weather parameter time series (X_{t-l}) with lags of l ($l = 0 \dots 6$) were estimated as:

$$\rho = \text{corr}(Y_t, X_{t-l}) \quad (1)$$

where

$$X_{t(s,p)} = \sum_{i=1}^s \sum_{j=7}^p X_{ij} \quad (2)$$

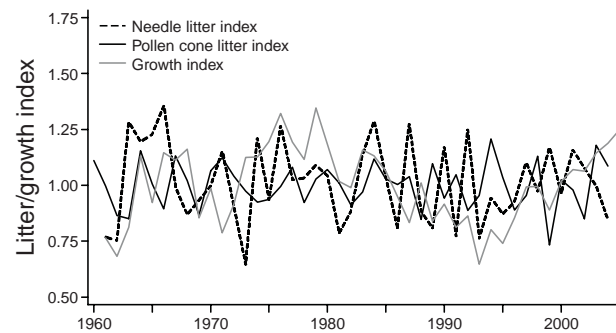


Figure 3. Time series of indices of needle litter, pollen cone litter and radial growth of a *Pinus sylvestris* stand at Kivalo, Rovaniemi from 1961 to 2004.

where x_{ij} is either daily precipitation below 0 °C (SF, snowfall), daily precipitation above 0 °C (RF, rainfall), mean daily temperature above 0 °C threshold (DD0), mean daily temperature above 5 °C threshold (DD5), mean daily temperature above 15 °C threshold (DD15), mean daily temperature below -15 °C threshold (DD-15) or potential evapotranspiration (PET).

The PET, precipitation and temperature sum periods that showed statistically significant correlations with the needle litter series were chosen for further analysis. Time series that had more than three observations with values of zero were removed because of the possibility of high and misleading correlations (e.g., DD0 in January or snowfall (SF) during summer).

Models

The time series of indexed radial growth, pollen cone litter and weather variables were used to model the needle litter index. Four subjectively selected models were applied, one using a radial growth index as a predictor, another using a radial growth index and pollen cone litter index, a third using weather variables, and the fourth being a full model including weather variables and pollen cone litter index (Tables 2 and 3). All models had the form:

$$Y_t = \beta_1 x_{1t} + \beta_2 x_{2t} + \dots + \beta_m x_{mt} + Z_t, \quad t = 1 \dots N \quad (3)$$

where Y_t is the dependent variable (needle litter index), β is a vector of coefficients of the explanatory variables $x_1 \dots x_m$ (with

varying lags) with N observations, and Z is the random error. The parameter values were estimated following the principles of Chatfield (2004). The same predictors were used to model differenced needle litter index (the four models mentioned above were estimated), to study the effect of differencing on the results.

Testing models

The applied iterative selection of weather variables was based on the statistical significance of their cross-correlation with the needle litter time series. Thus, there is a risk that some weather variables correlate with the needle litter index by chance. Therefore, the weather and the full model were tested with independent but similarly collected litter material at another Scots pine stand, 4.5 km southwest of the experimental stand (Plot 29), hereafter called the modeled stand. The modeled 150-year-old stand had only 172 stems ha^{-1} , whereas the experimental stand had 356 stems ha^{-1} . The time series of needle and pollen cone litter, covering the period 1984–1999, was treated in the same way as the data from the experimental stand.

Results

Mean (\pm standard deviation) annual amount of needle litter was $65.3 \pm 16.3 \text{ g m}^{-2}$. The amount of pollen cone litter showed high annual variation, from 0.14 g m^{-2} in 1963 to 13.5 g m^{-2} in 2003, with a mean of $4 \pm 2.8 \text{ g m}^{-2}$. The amount of pollen cone litter increased after the mid-1990s (Figure 2).

Table 2. Models for needle litter index, parameter estimates and their standard errors. Abbreviations: Int, integer (constant of the regression); PC, pollen cone litter index; RF_{135,7}, rainfall over 7 days beginning Day of year 135; DD0_{127,68} and DD0_{250,19}, mean daily temperatures above 0 °C threshold over 68 days beginning Day of year 127 and over 19 days beginning Day of year 250, respectively; AIC, Akaike Information Criterion; SEE, standard error of estimate; dG, difference in growth index; and Lag, delay in years. Variance estimate of the needle litter index is 0.0399.

Variable	Full model					Weather model				
	Estimate	SE	P	Lag	Effect ¹	Estimate	SE	P	Lag	Effect ¹
Int	1.3577	0.3355	0.000	–	–	0.4375	0.2447	0.074	–	–
PC	-0.6686	0.1892	0.000	2	-0.048	–	–	–	–	–
RF _{135,7}	-0.0085	0.0023	0.000	2	-0.053	-0.0096	0.0026	0.000	2	-0.060
DD0 _{127,68}	0.0008	0.0003	0.002	4	0.050	0.0011	0.0003	0.000	4	0.069
DD0 _{250,19}	-0.0018	0.0005	0.001	6	-0.048	-0.0015	0.0006	0.017	6	-0.039
AIC	-60.01					-49.82				
SEE	0.103					0.120				
Variable	Growth and pollen cone litter model					Growth model				
	Estimate	SE	P	Lag	Effect ¹	Estimate	SE	P	Lag	Effect ¹
Int	1.8294	0.2714	0.000	–	–	0.9877	0.0292	0.000	–	–
dG	0.4730	0.1890	0.012	0	0.055	0.3880	0.2216	0.080	0	0.045
dG	–	–	–	–	–	0.3931	0.2002	0.050	4	0.046
MF	-0.8354	0.2718	0.002	2	-0.060	–	–	–	–	–
AIC	-24.73					-19.35				
SEE	0.176					0.182				

¹ Effect on predicted needle litter index if the value of the predictor increases from its mean to the third quartile.

Table 3. Correlations of the full model variables. Abbreviations: Int, integer (constant of the regression); PC, pollen cone litter; RF_{135,7}, rainfall over 7 days beginning Day of year 135; DD0_{127,68} and DD0_{250,19}, mean daily temperatures above 0 °C threshold over 68 days beginning Day of year 127 and over 19 days beginning Day of year 250, respectively; and Lag, delay in years.

	Int	PC	RF _{135,7}	DD0 _{127,68}	DD0 _{250,19}	Lag
Int	1					–
PC	–0.776	1				2
RF _{135,7}	0.101	–0.134	1			2
DD0 _{127,68}	–0.824	0.330	–0.033	1		4
DD0 _{250,19}	–0.507	0.185	–0.315	0.382	1	6

Current-year differenced radial growth index, May temperature, September temperature sum, summer rainfall and winter snowfall correlated positively with needle litter index, whereas May rainfall and PET were negatively correlated (Figure 4). The number of frost-free days, the number of precipitation days, and spring rainfall with a 1-year lag correlated positively with needle litter index, whereas autumn rainfall of the previous year correlated negatively. Needle litter index correlated negatively with events having a lag of 2 years such as spring-time (April–May) rainfall and pollen cone litter index (Figure 4).

In addition to recent weather variations, events with lags of

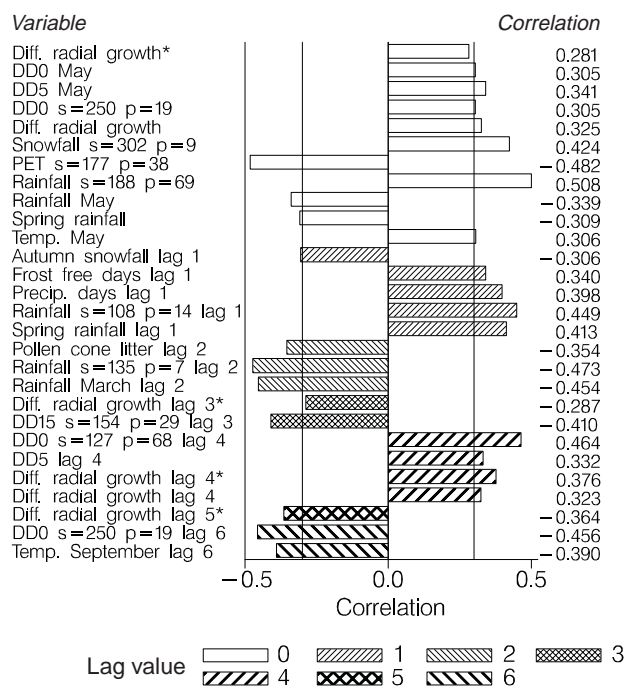


Figure 4. Correlations between needle litter index and other variables. Vertical lines indicate the limit of significance. Abbreviations: DD0, DD5 and DD15, mean daily temperatures above 0, 5 and 15 °C thresholds, respectively; PET, measured potential evapotranspiration; and s, starting day (day of year) of period with length p. Asterisks (*) indicate correlations between differenced needle litterfall and differenced radial growth.

4 and 6 years affected the quantity of needle litter. Spring temperatures, temperature sums (both annual and May to mid July) and differenced radial growth index with a lag of 4 years correlated positively with needle litter index, whereas autumn temperature with a lag of 6 years correlated negatively with needle litter index. Differenced needle litterfall also correlated with differenced radial growth with lags of 0, 3, 4 and 5 ($r = 0.281, -0.287, 0.376$ and -0.364 , respectively) (Figure 4).

Extreme weather periods had little effect on needle litterfall. Only periods with high temperature during June with a lag of 3 years reduced current-year needle litterfall (Figure 4), whereas cold periods during winter had no effect on needle litterfall.

Variance in the needle litter index decreased from $(0.202)^2$ to $(0.103)^2$ when the full model was applied, implying that 74% of the variance was explained by the predictors (Figures 5 and 6). The weather model, which lacked the pollen cone litter index as a predictor (Table 2), explained 65% of the original variance. The predictors of the full model correlated weakly with each other (Table 3, Figure 6). The model based on differenced radial growth index explained only 19% of the variance, whereas the differenced radial growth index and the pollen cone litter index together explained 25% of the variance (Figure 6, Table 2).

Both the full model and the weather model gave good predictions of variation in needle litter in the parameterized model stand, catching the peaks in litterfall, although some peaks were overestimated. Based on the analysis, model residuals were white noise, but the residuals of the full model had a nonsignificant autocorrelation of -0.29 with a lag of 4 years.

Developed models were tested against independent measurements—predictions of all models were weakest for 1989, the year when needle litter was underestimated. The full model gave the best predictions with pollen cone production from the experimental stand (i.e., parameterized site), with a root-mean-square error (RMSE) of 0.136. The second best was the weather model with an RMSE of 0.138, whereas the full model with the pollen cone litter of the modeled stand (i.e., independent site) gave the poorest results with an RMSE of 0.194 (Figure 7).

Results changed when the differenced needle litter index

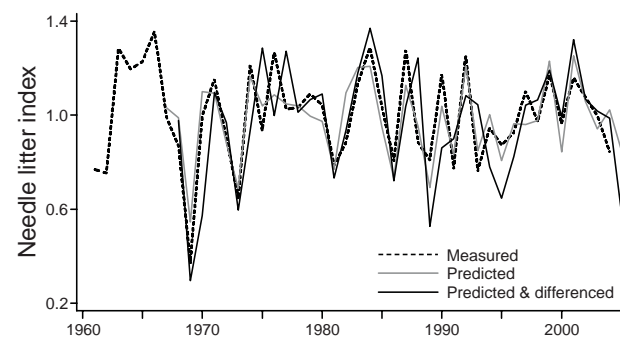


Figure 5. Measured and predicted needle litter index based on the full model (including model predictions for both needle litter index and for its difference).

was used as the response. The full model was then able to explain only 45% of the variability of the original series (differenced needle litter index) (Figure 5). Changing the response to differenced needle litter index reduced the P -value of the summer temperature sum with a lag of 4 years ($P = 0.12$, Table 4). According to the Akaike Information Criterion, the order of model performance remained the same, but the overall performance of predictors was weaker with the differenced needle litter index than with the non-differenced needle litter index.

Discussion

Cross-correlation analysis showed that the variables significantly correlated with needle litter could be grouped according to the lag at which they correlated. Variables that were statistically significant at lags of 4 and 6 years influenced needle production, whereas the variables that were effective at lags between 0 and 2 years directly influenced needle shedding.

We found that radial growth correlated positively but weakly with needle litter (lags of 0 and 4 years). According to the analysis, we can reject our hypothesis that growth-favoring conditions 5–6 years previously (equivalent to the quantity of needle cohorts) increase needle litter. On the contrary, our analysis indicated that conditions favoring photosynthesis 4 years previously correlated with needle litter. This finding corroborates earlier studies showing that the quantity of needles is predetermined in the bud and that the unit mass of needles increases during the summer after needle elongation (Kramer and Kozlowski 1979). Our results showed that the simplified assumptions of the process models (direct link be-

tween NPP and carbon allocated to stem and to foliage and eventually to foliage litter) (Waring 1983, Mäkelä 1997) do not hold for our Scots pine site in northern Finland where annual needle litterfall dynamics is a more complex phenomenon.

Radial increment correlated with needle litter, but it did not qualify as a predictor for the full model based on the weather data and pollen cone litter. The full model explained 78% of the variance in needle litter. This model included pollen cone litter with a lag of 2 years and three weather variables—rainfall between May 15 and 22 with a lag of 2 years, temperature sum between May 7 and July 14 with a lag of 4 years, and temperature sum between September 7 and 26 with a lag of 6 years. An increase in pollen cone litter reduced needle litter after 2 years, indicating that carbohydrate and nutrient allocation in the tree are linked and covary between different uses. Many textbooks (e.g., Oliver and Larson 1996) state that trees allocate carbon for reproduction before tree growth. Increased reproduction may reduce both tree growth and needle litter, because tree growth is dependent on photosynthetic production. Flower-Ellis and Olsson (1978) report that the number of needles in Scots pine shoots was reduced by two-thirds in years when pollen production was high; the more pollen cone positions there were per shoot, the fewer the needles produced.

According to Jalkanen (1998), Scots pine trees in our study area had five to six needle cohorts in the branches between 1990 and 1997. We found that a high temperature sum between September 7 and 26 with a lag of 6 years reduced the amount of needle litter, perhaps indicating that a warm Sep-

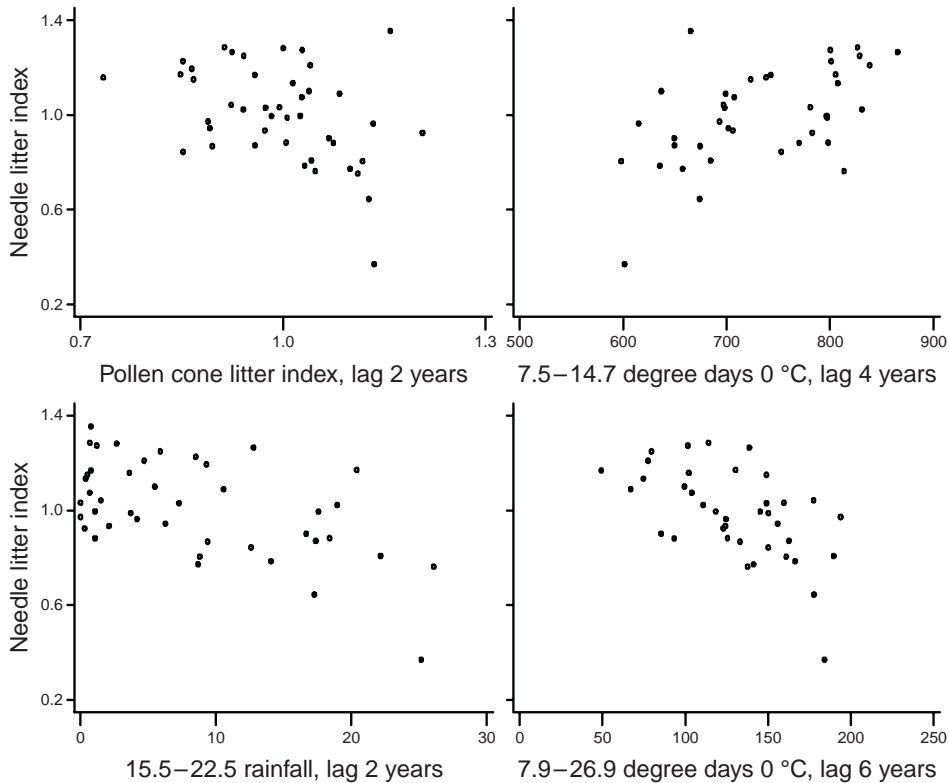


Figure 6. Scatter plots for needle litter index on the y-axis and predictors of the full model on the x-axis: pollen cone litter lag 2 years; 7.5–14.7 degree days 0 °C lag 4 year; 15.5–22.5 rainfall lag 2 years; and 7.9–26.9 degree days 0 °C lag 6.

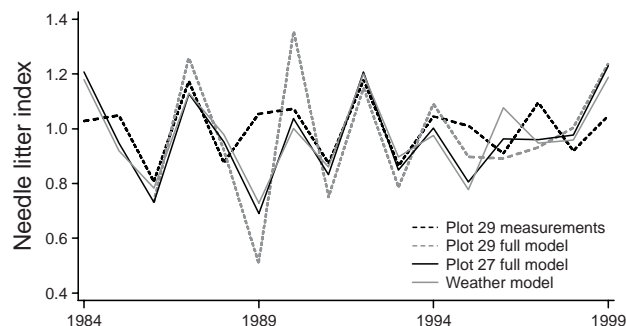


Figure 7. Tests of models against independent measurements (Plot 29). The full model was applied with data from an independent site (Plot 29) and from parameterization of the measurement site (Plot 27). The climate model was applied based on data from the nearest weather station (same data as used for parameterization).

tember decreases the mass of new needles that grow during the following summer, to be shed after 5 years. We speculate that this dependence is associated with reduced resources for forthcoming needles because a warm autumn causes both increased resource use for maintenance respiration and reduced resource supply as a result of the later senescence of older needles (Cannell 1989, Atkin et al. 2005).

The temperature sum between May 7 and July 14 with a lag of 4 years correlated positively with needle litterfall. This correlation likely relates to needle mass increase during needle aging (Viro 1956), when more favorable growth conditions result in increases in the length and mass of 1-year-old needles that will be shed after 4 years (Junttila 1986). Similarly Brix

and Ebell (1969) found that fertilization increased the mass of needles by increasing needle dimensions especially in the year after fertilization. Scots pines derived from seed originating at Rovaniemi and planted in 1931 at Tuusula (23 km north of Helsinki) have 2–4 needle cohorts instead of 5–6 (typical at Rovaniemi), implying that Scots pines with similar genetics reduce the number of needle cohorts under warmer conditions, a finding that is also supported by the study of Reich et al. (1996). The ability to reduce the quantity of needle cohorts according to climate demonstrates the adaptability of Scots pine to local conditions.

Rainfall at the start of the height increment (May 15–22) reduced the amount of needle litter with a lag of 2 years (all periods with lengths between 7 and 18 days after mid May had a significant negative correlation with needle litter). Drenkhan et al. (2006) found that 1–2-year-old needle cohorts were responsible for most of the Scots pine growth in southern Finland. Cloudy weather during height growth and branch formation apparently reduce potential self-shading through decreased growth. The link between poor height growth and reduced needle litter supports the assumption that trees tend to maintain a constant amount of foliage (Pensa and Jalkanen 2005).

All four models were parameterized for the differenced needle litter index. We found that *P*-values of predictors were weaker for the differenced response than for the non-differenced response. Temperature sum of summer 4 years ago was a nonsignificant (*P* = 0.12) predictor in the full model (including the differenced pollen cone litter index as a predictor). In the weather model, temperature sum of summer 4 years ago

Table 4. Models for differenced needle litter index, parameter estimates and their standard errors. Abbreviations: Int, integer (constant of the regression); dPC, difference in pollen cone litter index; RF_{135,7}, rainfall over 7 days beginning Day of year 135; DDO_{127,68} and DDO_{250,19}, mean daily temperatures above 0 °C threshold over 68 days beginning Day of year 127 and over 19 days beginning Day of year 250, respectively; AIC, Akaike Information Criterion; SEE, standard error of estimate; dG, difference in growth index; and Lag, delay in years. Variance estimate of the differenced needle litter index is 0.0807.

Variable	Full model				Weather model			
	Estimate	SE	<i>P</i>	Lag	Estimate	SE	<i>P</i>	Lag
Int	-0.2377	0.4645	0.609	–	-0.6858	0.4628	0.138	–
dPC	-0.6528	0.2572	0.011	2	–	–	–	–
RF _{135,7}	-0.0094	0.0047	0.046	2	-0.0124	0.0049	0.012	2
DDO _{127,68}	0.0008	0.0005	0.120	4	0.0014	0.0005	0.008	4
DDO _{250,19}	-0.0025	0.0011	0.024	6	-0.0019	0.0012	0.095	6
AIC	-6.15				-1.38			
SEE	0.210				0.226			

Variable	Growth and pollen cone litter model				Growth model			
	Estimate	SE	<i>P</i>	Lag	Estimate	SE	<i>P</i>	Lag
Int	-0.0080	0.0402	0.842	–	-0.0177	0.0423	0.676	–
dG	0.4469	0.2834	0.115	0	0.5142	0.3213	0.109	0
dG	–	–	–	–	0.6741	0.2903	0.020	4
dPC	-0.7773	0.2658	0.003	2	–	–	–	–
AIC	8.66				9.63			
SEE	0.259				0.264			

was a significant predictor, indicating that the cross-correlation of 0.33 between current-year pollen cone litter and temperature sum of summer 2 years ago (Table 3) affects the appropriate combination of predictors. This interaction between warm summer and future pollen cone litter hints that warm periods will increase future pollen cone litter, and that both variables correlate with needle litter (Figure 6).

Results of the growth model changed when the differenced needle litter index was predicted with differenced growth: the differenced growth 4 years ago explained most of the variability but current-year differenced growth was nonsignificant, indicating the importance of growth conditions 4 years ago for current-year needle litterfall.

July and August PET correlated negatively with needle litterfall, whereas rainfall in the same period correlated positively with needle litterfall, indicating that the site is not water limited. This finding also indicates that rainfall plays a role as a mechanism that removes dead needles from the canopy to the soil. The negative relationship reported in this study contrasts with that found by Berg and Meentemeyer (2001), who reported a high positive correlation between actual evapotranspiration (AET) and needle litterfall based on mean values of different sites across Europe (from Spain to Sweden). Our PET and needle litterfall results are supported by the study of Starr et al. (2005) showing a correlation of -0.5 between needle litterfall and evapotranspiration index (ratio between rainfall and effective temperature sum) based on 34 Scots pine sites across Finland.

Predictions made with the weather model agreed well with measurements from the modeled stand (i.e., independent site), although the full model with pollen cone data from the modeled stand was less accurate than the weather model. The relationship between tree flowering and needle litter varied among the stands. It has been shown that needles are shed from various cohorts simultaneously (Jalkanen 1998), which may confound the relationship between pollen cone litter and needle litter. All models failed to predict needle litterfall in 1989 at the independent site, likely because of frost damage during the 1986–1987 winter that severely reduced tree growth in Lapland during the late 1980s.

We found a weak correlation between radial growth and needle litter, refuting our original hypothesis of a tight link between NPP and foliage litterfall. Similarly Wirth et al. (2002) and Martinez-Alonso et al. (2007) reported that needle litterfall did not correlate with tree growth. These studies were both based on a short time series and therefore the statistical analyses were restricted. Nevertheless, these shorter time series provide an important source of information for calibrating process models (e.g., Corbeels et al. 2005).

Kouki and Hokkanen (1992) found in their study (series of 24 years) that needle litter of Scots pine in southern Finland was positively dependent on the mean temperature of current-year July and March–April, and negatively with July temperature of the previous year. The effect of the March–April temperature on needle litter was related to tree transpiration and the lack of water. Similarly, we found a positive relationship between current-year May temperature sum and needle

litter. However, in contrast to Kouki and Hokkanen (1992), we found no correlation between current-year July temperatures and needle litter, but we observed that summer rainfall (July–August) increased needle litterfall. A similar relationship between summer rainfall and needle litter was found near Krasnoyarsk, Russia by Elagin and Cherkashin (1988), who reported that the duration of rainfall at the end of the vegetation period and the relationship between summer rainfall and summer temperatures influence needle litter variability with a lag of 3–4 years. Kouki and Hokkanen (1992) also reported an autoregressive relationship in needle litter with a lag of 4 years, suggesting that this phenomenon is related to the number of needle cohorts.

Our results indicate that needle shedding in northern Finland is influenced by needle production and development of needle mass 4 and 6 years earlier, and that weather as a proxy for needle production and development correlated with annual needle litterfall of Scots pine. If future years have higher summer temperatures, extreme rainfall episodes and longer growing seasons, needle turnover may be accelerated.

Acknowledgments

The authors thank the Academy of Finland for financing project 108328. We acknowledge Mr. Jaakko Heinonen, Dr. Mikko Peltoniemi, Dr. Raisa Mäkipää and Mr. Mikko Kukkola for valuable comments, Mr. Tauno Luosujärvi for tree-ring analysis and Mr. Timo Haapakoski for tree-ring measurements.

References

- Ackerly, D. 1999. Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia* 119:300–310.
- Albrektson, A. 1988. Needle litterfall in stands of *Pinus sylvestris* L. in Sweden, in relation to site quality, stand age and latitude. *Scand. J. For. Res.* 3:333–342.
- Atkin, O.K., D. Bruhn, V.M. Hurry and M.G. Tjoelker. 2005. Evans Review No. 2: The hot and the cold: unravelling the variable response of plant respiration to temperature. *Funct. Plant Biol.* 32: 87–105.
- Berg, B. and V. Meentemeyer. 2001. Litter fall in some European coniferous forests as dependent on climate: a synthesis. *Can. J. For. Res.* 31:292–301.
- Brix, H. and L.F. Ebell. 1969. Effects of nitrogen fertilization on growth, leaf area, and photosynthesis rate in Douglas-fir. *For. Sci.* 15:189–196.
- Cajander, A.K. 1949. Forest types and their significance. *Acta For. Fenn.* 56:1–71.
- Cannell, M.G.R. 1989. Physiological basis of wood production: a review. *Scand. J. For. Res.* 4:459–490.
- Chatfield, C. 2004. The analysis of time series: an introduction. CRC Press, 333 p.
- Cook, E.R. and K. Peters. 1981. The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull.* 41:45–53.
- Corbeels, M., R.E. McMurtrie, D.A. Pepper and A.M. O'Connell. 2005. A process-based model of nitrogen cycling in forest plantations: Part II. Simulating growth and nitrogen mineralisation of *Eucalyptus globulus* plantations in south-western Australia. *Ecol. Model.* 187:449–474.

- Davidson, R.L. 1969. Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. *Ann. Bot.* 33:561–569.
- Drenkhan, R., T. Kurkela and M. Hanso. 2006. The relationship between the needle age and the growth rate in Scots pine (*Pinus sylvestris*): a retrospective analysis by needle trace method (NTM). *Eur. J. For. Res.* 125:397–405.
- Elagin, I.N. and V.P. Cherkashin. 1988. Structure and dynamics of litter in iris-cowberry pine forest. *Sov. J. Ecol.* 18:196–199.
- Finér, L. 1996. Variation in the amount and quality of litterfall in a *Pinus sylvestris* L. stand growing on a bog. *For. Ecol. Manage.* 80:1–11.
- Flower-Ellis, J.G.K. and L. Olsson. 1978. Litterfall in an age series of Scots pine stands and its variation by components during the years 1973–1976. SLU, Uppsala, pp 1–62.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, London, 567 p.
- Gower, S.T., P.B. Reich and Y. Son. 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiol.* 12:327–345.
- Jalkanen, R. 1998. Fluctuation in the number of needle sets and needle shed in *Pinus sylvestris*. *Scand. J. For. Res.* 13:284–291.
- Junttila, O. 1986. Effects of temperature on shoot growth in northern provenance of *Pinus sylvestris* L. *Tree Physiol.* 1:185–192.
- Kouki, J. and T. Hokkanen. 1992. Long-term needle litterfall of a Scots pine *Pinus sylvestris* stand: relation to temperature factors. *Oecologia* 89:176–181.
- Kramer, P.J. and T.T. Kozlowski. 1979. *Physiology of woody plants*. Academic Press, New York, 703 p.
- Landsberg, J.J. and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95:209–228.
- Lindholm, M., H. Lehtonen, T. Kolström, J. Meriläinen, M. Eronen and M. Timonen. 2000. Climatic signals extracted from ring-width chronologies of Scots pine from the Northern, Middle and Southern parts of the boreal forest belt in Finland. *Silva Fenn.* 34: 317–329.
- Lindholm, M., Ö. Eggertsson, N. Lovelius, O. Raspopov, O. Shumilov and A. Läänelaid. 2001. Growth indices of North European Scots pine record the seasonal North Atlantic Oscillation. *Boreal Environ. Res.* 6:1–10.
- Liski, J., T. Palosuo, M. Peltoniemi and R. Sievänen. 2005. Carbon and decomposition model Yasso for forest soils. *Ecol. Model.* 189:168–182.
- Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. *For. Sci.* 43:7–24.
- Martinez-Alonso, C., F. Valladares, J.J. Camarero, M.L. Arias, M. Serrano and J.A. Rodriguez. 2007. The uncoupling of secondary growth, cone and litter production by intradecadal climatic variability in a mediterranean Scots pine forest. *For. Ecol. Manage.* 253:19–29.
- Niinemets, U. and A. Lukjanova. 2003. Total foliar area and average leaf age may be more strongly associated with branching frequency than with leaf longevity in temperate conifers. *New Phytol.* 158: 75–89.
- Oliver, C.D. and B.C. Larson. 1996. *Forest stand dynamics*. John Wiley & Sons, New York, 518 p.
- Pensa, M. and R. Jalkanen. 2005. Variation in needle longevity is related to needle-fascicle production rate in *Pinus sylvestris*. *Tree Physiol.* 25:1265–1271.
- Reich, P.B., M.B. Walters and D.S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62:365–392.
- Reich, P.B., J. Oleksyn, J. Modrzyński and M.G. Tjoelker. 1996. Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. *Tree Physiol.* 16:643–647.
- Sarvas, R. 1953. Measurement of the crown closure of the stand. *Comm. Inst. For. Fenn.* 41.6:1–13.
- Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964. A quantitative analysis of plant form: the pipe model theory. I. Basic analyses. *Jpn. J. Ecol.* 14:133–139.
- Starr, M., A. Saarsalmi, T. Hokkanen, P. Merilä and H.-S. Helmisaari. 2005. Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. *For. Ecol. Manage.* 205:215–225.
- Trumbore, S.E. and J.W. Harden. 1997. Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area. *J. Geophys. Res.* 102:28,817–28,830.
- Viro, P.J. 1956. Investigations on forest litter. *Comm. Inst. For. Fenn.* 45.6:1–142.
- Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res.* 13:327–354.
- Wirth, C., E.D. Schulze, V. Kuznetsova, I. Milyukova, G. Hades, M. Siry, B. Schulze and N.N. Vygodskaya. 2002. Comparing the influence of site quality, stand age, fire and climate on aboveground tree production in Siberian Scots pine forests. *Tree Physiol.* 22: 537–552.
- Zeide, B. and P. Pfeifer. 1991. A method for estimation of fractal dimension of tree crowns. *For. Sci.* 37:1253–1265.