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**Original article**

# Amounts of litter fall in some pine forests in a European transect, in particular Scots pine

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**Abstract** – Pine litter fall data, mainly needle litter, were available for 64 plots in a transect from the Arctic Circle in Fennoscandia (41 plots) to southern Spain (22 further plots in continental Europe) and one in the American Midwest). Data originated from a total of eight pine species. Regressions were calculated mainly for needle litter fall and to some extent for total litter fall. We obtained a highly significant linear relationship for needle litter fall and latitude ($R^2_{adj} = 0.285$; $n = 58$; $P < 0.001$) when using needle litter fall data from all pine species. Combining sites in the boreal and Atlantic climates gave an $R^2_{adj}$ of 0.732 with $n = 45$ ($P < 0.001$). A multiple linear relationship using stand age, latitude and basal area was highly significant and gave an $R^2_{adj}$ value of 0.412 ($n = 54$; $P < 0.001$). For the amount of Scots pine needle litter in Fennoscandia, the best simple linear relationships were obtained with site index (H 100) ($R^2_{adj} = 0.349$), latitude ($R^2_{adj} = 0.331$) and basal area ($R^2_{adj} = 0.324$) as predictor variables, whereas the regressions on altitude and stand age were significant only with $P < 0.01$. An $X^2$ function for stand age improved the relationship with age to $R^2_{adj} = 0.243$. Multiple regression relationships for Fennoscandia between needle litter fall and latitude plus basal area and that to latitude plus basal area plus age were highly significant ($R^2_{adj} = 0.605$ and 0.661, respectively, with $n = 41$). In a stepwise procedure using data from the same sites, combinations of the factors latitude, site index, basal area and stand age could explain as much as 78 % of the needle litter fall. For total litter fall as measured by the same method as needle litter we related data from 32 sites to that of needle litter fall and obtained highly significant relationships indicating that needle litter fall may be used as an index for total litter fall.


**litter fall / pine / Fennoscandia / Europe / stand age / site index / latitude / basal area**

**Résumé – Chute de litière dans quelques forêts de pins, en particulier du Pin sylvestre, le long d'un transect européen.** Les données de chute de litière, essentiellement des chutes d'aiguilles, étaient disponibles pour 64 sites le long d'un transect depuis le cercle polaire en Scandinavie (41 sites) jusqu'au Sud de l'Espagne (22 sites supplémentaires en Europe continentale) et un site dans le mid-

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ouest américain. Les données proviennent de huit espèces de Pin. Des régressions ont été calculées principalement pour la chute d'aiguilles et dans certains cas pour la chute totale de litière. Il existe une relation linéaire hautement significative entre la chute des aiguilles et la latitude ($R^2_{adj}$ = 0.285 ; n = 58; $p$ < 0,001) lorsque l'ensemble des données pour toutes les espèces sont utilisées. La combinaisons des sites en climat boréal et atlantique donne un $R^2_{adj}$ de 0.732 pour n = 45 ($p$ < 0,001). Une relation linéaire multiple, utilisant l'âge du peuplement, la latitude et la surface terrière est hautement significative et donne un $R^2$~ de 0.412 (n = 54; $p$ < 0.001).
La meilleure relation linéaire, pour les retours d'aiguilles chez le Pin sylvestre en Scandinavie a été obtenue en utilisant comme variables prédictives l'indice de fertilité stationnelle « H 100 » ($R^2_{adj}$ = 0.349), la latitude ($R^{adj}$ = 0331), et la surface terrière ($R^2_{adj}$ = 0.324 ; alors que la régression sur les variables altitudes et âge des peuplements n'était significative seulement à p < 0,01. Une fonction $X^2$ pour l'âge du peuplement améliore la relation avec l'âge, $R^2_{adj}$ = 0,243.
Les relations multiples entre la chute des aiguilles et la latitude associée à la surface terrière et celle associée à la surface terrière plus l'âge, pour les sites Scandinaves, sont hautement significatives ($R^2_{adj}$ = 0,605 et $R^2_{adj}$ = 0,661, respectivement, avec n = 41). La procédure de régression progressive sur les données des mêmes sites, combinaisons des variables latitude, indice de fertilité, surface terrière et âge du peuplement permet d'expliquer 78 % de la variation de la chute des aiguilles.
Des relations hautement significatives ont été calculées sur les données des retours totaux de litière, utilisant la même méthodologie sur 32 des sites. Elles démontrent que la quantité des chutes des seules aiguilles peut être utilisée comme indice pour la chute totale de la litière. 

**chute de litière / pin / Scandinavie / Europe / âge du peuplement / indice de fertilité / latitude / surface terrière**

# 1. Introduction

Litter fall, in most European pine forests dominated by litter from the trees, is the largest natural source for the inflow of organic material and nutrients to the forest floor. The chemical composition of this material, and the temperature and moisture content of the upper soil layers, are the main factors which control the turnover rates of the organic layers, as well as determining both the quantity and quality of nutrient release.

For a long period, there was comparatively little interest in both the amounts and the chemical composition of litter fall. Until the time of the International Biological Programme (IBP) in the 1970s, very few measured litter fall values were published. When major ecosystem projects integrated different scientific disciplines into a combined effort, several weak points were revealed in our knowledge of ecosystems, among others the amount of litter fall and its chemical composition.

Some long-term recordings of litter fall have been carried out, by, for example, Flower-Ellis [13] using Scots pine, and some synthesising studies have been carried out such as that by Bray and Gorham [9] and by Vogt et al. [25], who in their global approach made their synthesis cover numerous different species of both deciduous and coniferous litter. On a more regional scale, Albrektson [1] compared needle litter fall for Scots pine to latitude and forest practice indices.

The aim of the present paper is to identify and present the state of knowledge concerning the amount of litter fall in pine forests in Europe. The study has focused on North-European forest types but Mediterranean sites are also included. Our synthesis includes all available litter fall data for pine forests in order to cover one species and possibly one genus over a broad region. The data for Scots pine were collected from our 3 400-km-long transect ranging from the Arctic Circle to the latitude of Barcelona (Spain) and for all pine species together about 4 000 km with a geographical range from the Arctic Circle to south Spain. This transect almost covers the length of western Europe and probably covers the full climatic range for Scots pine. A similar approach with a smaller data set was made by Berg et al. [5].

We combined litter fall values for the *Pinus* species, Austrian pine (*Pinus nigra* var. austriaca), Corsican pine (*Pinus nigra* var. corsicana), lodgepole pine (*Pinus contorta*), Monterey pine (*Pinus radiata*), maritime pine (*Pinus pinaster*), red pine (*Pinus resinosa*) and stone pine (*Pinus pinea*) with those of Scots pine (*Pinus silvestris*), assuming that the genus *Pinus* shares common characteristics with respect to litter fall. Combining our own data with data from the literature, we obtained a transect with 64 sites and plots and including eight pine species (54 plots with Scots pine, three with Corsican pine, four with Monterey pine and one of each of the other pine species). In all cases, the trapping method used allowed us to rely mainly on the needle litter values; therefore, these have mainly been used in the comparisons. However, in several cases the needle litter was not sorted out and only a combined fraction was obtained.

## 2. Methods

### 2.1. Site descriptions

In this paper only summarised site descriptions are presented (Appendix Ia, b). More full site data are collected in a report in which references to the original descriptions are also given [4]. Sites numbered with digits below 109 are the same as those used and described by Berg et al. [4, 6, 7]. Site numbers preceded by a capital A refer to Anonymous [2]. An overview to the site locations is given in *figure 1.* For four Spanish sites the numbers are the same as those used by Pausas [22].

### 2.2. Plot size and experimental design

The shape of the plots varied and the size ranged from 300 to 1 600 $m^2$, most often approximately 900 $m^2$. The litter traps were set out randomly in most plots with the exception of the plots numbered A 87–A 1012 and 320–325, where the traps were placed systematically. The number of replicate traps varied among the plots. Thus had plots 300, 29 and 308, 20 had replicate litter traps. Plots 313 and 314 had six replicate traps, plot 322 had nine traps, plots 320–321 and 326–327 had 12, 340–344 had five traps and the other plots ten replicate traps each.

### 2.3. Sampling method and treatment of samples

At most sites, circular litter traps were used, with a nominal sampling area of 0.25 $m^2$ [21] or 0.50 $m^2$ for sites 320–325. Traps were mounted at a height of ca 1 m above ground (plots 326 and 327 at 50 cm). The Terylene net used had a mesh size of 1 mm. At sites 313 and 314, the nominal sampling area of each trap was 0.28 $m^2$ and at plots 326 and 327 the quadratic area measured 0.25 $m^2$. At plot 403 the area was 0.145 $m^2$. The sampling frequency varied among the plots. At almost all sites traps were emptied three times a year. At plots 29 and 300, traps were emptied four and five times a year, respectively. At plots 308, 313, 314, 326 and 327 traps were emptied 12 times a year and at site 403 weekly.

The main method of collecting needle fall used at all sites, namely the litter traps of 0.25–0.64 $m^2$, could be expected to give reliable values for needle litter, which is more evenly distributed throughout the stands, whereas, for example, cone and branch litter is less reliably sampled using that method (cf. [14]).

At most sites, litter was sorted into two fractions: needles and a composite fraction consisting of all the other components collected (e.g. seeds, bark, cones, etc.). The fractions were then dried separately at least at 85 °C for 24 or 48 h. After drying, the fractions were weighed individually.

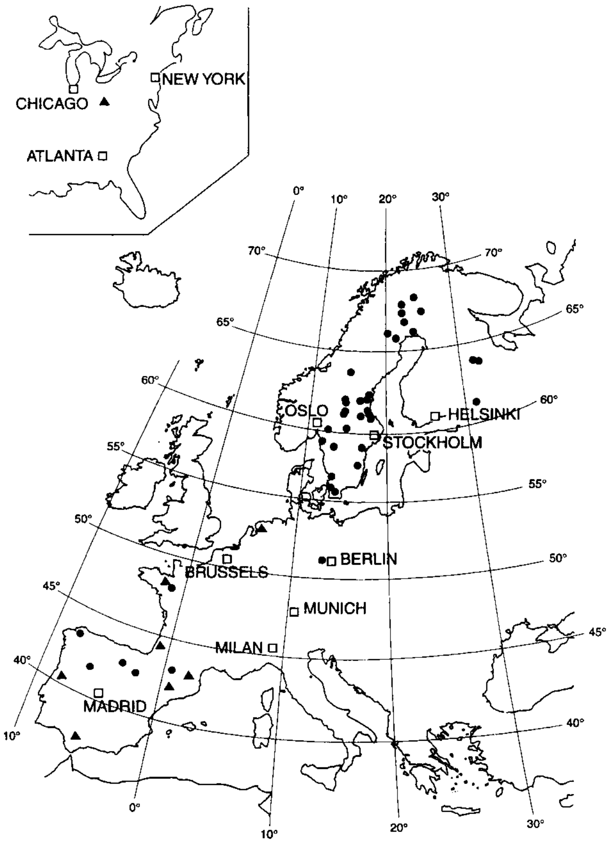



**Figure 1.** Map giving the approximate position of the sampling sites for litter fall. Scots pine stands (●) and stands with other pine species (▲). Please note that a marked site may have several plots.

### 2.4. Duration of the measurements

Litter fall was mainly followed for 1–10 years at the Scots pine sites (Appendix IIa, b). Three-year measurements were carried out at site 101, 4-year measurements at sites 100–106 and 10:1 and at sites 2, 3:1, 3:2, 3:3 and 107 litter fall was measured over 5 years. Sites 321 and 322 were sampled for 9 and 4 years, respectively, while the sites 323–325 and 337–343 for 2 years, and plots 326 and 327 for 4 years. The plots with Austrian pine, maritime pine, Monterey pine and stone pine were sampled for 1 year only.

### 2.5. Literature data

In the search for literature data clear quality requests have been set and the following criteria have been used for acceptance of the different studies. Samplings should be made at least three times a year and the size of the needle litter collector should be at least 0.25 $m^2$. On a plot of 40 m × 40 m there should be at least eight replicate litter traps.

### 2.6. Statistical analysis

To compare the coefficient of determination among regressions with different numbers of parameters we have used the adjusted $R^2$ ($R^2_{adj}$). It has been shown by Ekbohm and Rydin [11] that mean square error and $R^2_{adj}$ are equivalent as criteria of goodness of fit. The formula $R^2_{adj} = 1 - (1 - r^2)(n - 1)/(n - p)$ where p equals 2 for straight lines has been used.

### 2.6. Terminology and definitions

We have used some geographical concepts subdividing the regions of western Europe at which our sites were found; Fennoscandia, encompassing the Scandinavian peninsula and Finland, the Iberian peninsula encompassing Spain and Portugal, and continental Europe, in our case referring to sites in France, Germany and Holland. The sites were located in the boreal, Atlantic and Mediterranean climate zones and in transition zones between them. No site had a really continental climate.

The term 'site index' (H 100) has been used. This index, based on soil data and climate is species specific and gives the estimated tree height at an age of 100 years [16].

## 3. Results and discussion

### 3.1. Comments to the synthesis and to the sampled fractions

The analysis was mainly carried out in the following two steps.

I) The combined studies on litter fall of Scots pine are referred to as 'the Scots pine transect'. This data set has an emphasis on the methodologically very homogeneous Fennoscandian sites with a long period of recording litter fall.

II) We combined data from Scots pine with data of seven other pine species ('the all pine transect').

**Table I.** List of variables and their abbreviations.

| | |
|---|---|
| LITT | Annual needle litterfall (kg $ha^{-1}$) |
| LITO | Annual total litterfall (kg $ha^{-1}$) |
| LATI | Latitude (°N) |
| ALTI | Altitude (m above sea level) |
| AGE | Stand age (years) |
| SITI | Site index (–) |
| BASA | Basal area ($m^2$ $ha^{-1}$) |

The comparisons were made between annual needle litter fall (LITT), and stand age (AGE), basal area (BASA), site index (SITI) and latitude (LATI), using available data (*table I*).

We have focused this synthesis towards needle litter and in a few cases compared with recorded values for other litter fractions.

### 3.2. Litter fall patterns over the whole region

The pattern in litter fall varied over the transect. Over the range of Scots pine sites the onset of litter fall in the autumn was related to latitude. Thus, in northernmost Finland, close to 70 °N and the northern border for this species the needle litter was shed in early August. In the northern part of our transect, viz. at the Arctic Circle (about 66°57'N), the litter fall started in late August, whereas at, for example, site Jädraås (60°49'N) it starts in late September and about 80 % of the annual needle litter fall takes place within about 3 weeks [13, 14]. Further south, for example at the latitude of Berlin (52°28'N), the main litter fall takes place in late October/November (W. Kratz, unpubl.) and in south Poland and south Germany (about 48–49°N) in November. The Scots pine sites located in a Mediterranean climate, such as 337–344 (cf. Appendix I) have a different pattern altogether, with the heavy litter fall taking place in June owing to the Mediterranean draught period. The other pine species followed about the same pattern when in the Mediterranean region.

### 3.3. Needle litter fall in the Scots pine transect

The locations for the Scots pine sites ranged from the Arctic Circle (66°57'N) to about the latitude of Barcelona (42°12'N). Most of them were found in the Nordic countries and only 12 plots were located in continental Europe and the northern part of the Iberian peninsula. This means that the main part of the sites had a boreal climate or were located in a transition zone to an Atlantic climate with a few sites with a clearly Atlantic climate. The mean annual needle litter fall varied from 490 and 555 kg·ha$^{-1}$ (sites A629 and 324 in northern Fennoscandia) to 6 604 kg·ha$^{-1}$ (plot 334 on the French Atlantic coast) – a variation with a factor of 12–13 (Appendix II). The lowest amounts were found at nutrient-poor sites, generally with sandy sediment soil, in the north. Litter fall mass was higher at more fertile sites with till deposits and with a warmer and wetter climate. Among sites of similar fertility, the amount of needle litter fall was lower for sites situated in the north than for sites with a more southern location. Thus, two of the sites, 106 (latitude 66°32'N) and 107 (latitude 58°07'N) had nearly identical site indices (SITI) (H100, 17 and 16 m, respectively) and basal areas (BASA) (17.5 and 18.3 m$^2$·ha$^{-1}$, respectively) but the needle litter fall at the northern site (608 kg·ha$^{-1}$·year$^{-1}$) was only about one third of the amount obtained at the site located in the south (1 571 kg·ha$^{-1}$·year$^{-1}$). Increases with site quality (site index) but decreases with increasing latitude were earlier observed by Albrektson [1] who reported this phenomenon in needle litter fall in stands of Scots pine in Sweden.

The variation in needle litter fall between years was rather low. Ratios of maximum to minimum annual needle litter fall ranged between 1.1 and 2.1, but for the majority of sites it was less than 1.3. These ratios were much lower than those reported by Bray and Gorham [9], who found ratios with values up to 5.1 (for gymnosperms) when reviewing a number of studies where litter fall had been monitored for over 4 years. As observed at 14 stands that were monitored during a long period (generally 1978–1983), needle litter fall was lowest during the year 1979/1980 at 12 of the 14 studied sites. Some of the sites situated in the south of Sweden (sites 101–104) showed a steady increase in needle litter fall during the period 1979/1980 to 1981/1982. The increase was generally rather small, about 20–30 %. At one site, however, it was more marked (site 103) and amounted to 50 %. During the last sampling year (1982/1983), litter fall decreased again.

### 3.4. Scots pine needle litter fall versus latitude, site index, stand age, basal area, and altitude

A comparison of LITT to AGE, using all available Scots pine data gave an $R^2_{adj}$ value of 0.269 ($n = 56$; $P < 0.001$) in a linear regression and a negative relationship (*table II*). In the Fennoscandian part of the transect we obtained an $R^2_{adj}$ of 0.160 ($n = 41$) which was significant at the $P < 0.01$ level (*table III*). Considering the distribution of needle litterfall over stand ages (*figure 2*) we used

**Table II.** Some simple and multiple relations for average annual amounts of needle litterfall (kg ha$^{-1}$) as dependent on latitude, stand age, site index, and basal area in Scots pine stands. All available data were used (Appendix II).

| | Coefficient(SE) | Intercept(SE) | $R^2$ | $R^2_{adj}$ | n | p < |
|---|---|---|---|---|---|---|
| **Simple linear relations** | | | | | | |
| AGE | −11.1 (3.9) | 2243.8 (981.4) | 0.278 | 0.265 | 56 | 0.001 |
| LATI | −173.6 (36.4) | 12242.8 (856.2) | 0.190 | 0.173 | 51 | 0.01 |
| BASA | 264.2 (984.5) | 51.2 (18.5) | 0.190 | 0.174 | 54 | 0.01 |
| SITI | | | | 0.049 | 40 | n.s. |
| **Multiple linear relationsm** | | | | | | |
| LATI plus | −167.2 (32.7) | 10722.6 (767.9) | 0.505 | 0.479 | 41 | 0.001 |
| BASA | 46.7 (14.4) | | | | | |
| SITI plus | 67.4 (20.6) | −707.7 (539.2) | 0.432 | 0.398 | 36 | 0.001 |
| BASA | 23.9 (12.4) | | | | | |
| LATI plus | −38.2 (31.1) | 2051.6 (556.3) | 0.395 | 0.339 | 36 | 0.001 |
| SITI | 76.9 (20.2) | | | | | |
| LATI plus | −43.9 (29.8) | 2239.0 (529.8) | 0.468 | 0.401 | 36 | 0.001 |
| SITI plus | 56.9 (21.6) | | | | | |
| BASA | 25.6 (12.2) | | | | | |
| LATI plus | 39.2 (28.4) | 2844.1 (503.5) | 0.535 | 0.475 | 36 | 0.001 |
| BASA plus | −5.6 (2.6) | | | | | |
| AGE plus | 27.3 (24.8) | | | | | |
| SITI | 32.1 (12.0) | | | | | |

**Table III.** Simple and multiple linear relations for average annual amounts of needle litterfall (kg $ha^{-1}$) as dependent on latitude, stand age, site index and basal area in the methodologically homogeneous Fennoscandian Scots pine stands (Appendices I and II).

| | Coefficient(SE) | Intercept(SE) | $R^2$ | $R^2_{adj}$ | n | p < |
|---|---|---|---|---|---|---|
| **Simple linear relationships** | | | | | | |
| SITI | 85.29 (19.17) | –520.0 (560.39) | 0.368 | 0.349 | 36 | 0.001 |
| LATI | –131.92 (29.29) | 9544.4 (563.27) | 0.345 | 0.331 | 41 | 0.001 |
| BASA | –48.69 (11.43) | 188.97(573.94) | 0.324 | 0.305 | 41 | 0.001 |
| AGE | –7.36 (2.58) | 1874.2 (632.90) | 0.181 | 0.160 | 41 | 0.01 |
| ALTI | –3.07 (1.107) | 1806.8 (631.16) | 0.165 | 0.144 | 41 | 0.01 |
| **Simple $X^2$ relationship** | | | | | | |
| AGE plus | –33.954 (13.113) | 3275.4 (570.12) | 0.286 | 0.229 | 41 | 0.001 |
| $AGE^2$ | 0.1039 (0.0610) | | | | | |
| **Multiple linear relationships** | | | | | | |
| LATI plus | –123.40 (22.54) | 7918.67 (432.36) | 0.625 | 0.605 | 41 | 0.001 |
| BASA | 45.30 (8.63) | | | | | |
| LATI plus | –101.90 (27.72) | 6455.90 (479.08) | 0.552 | 0.525 | 36 | 0.001 |
| SITI | 56.9 (18.12) | | | | | |
| SITI plus | –101.91 (27.72) | –785.79 (532.43) | 0.446 | 0.412 | 36 | 0.001 |
| BASA | 28.43 (13.17) | | | | | |
| LATI plus | –102.29 (22.53) | 6906.04 (402.78) | 0.686 | 0.661 | 41 | 0.001 |
| BASA plus | 46.40 (8.05) | | | | | |
| AGE | –4.53 (1.76) | | | | | |
| **A stepwise procedure** | | | | | | |
| LITT = | 1.882 SITI×BASA | 331.841 | 0.479 | | 36 | 0.001 |
| LITT = | –103.223 LATI | 6985.98 | 0.690 | | 36 | 0.001 |
| | 1.4658 SITI×BASA | | | | | |
| LITT = | –98.408 LATI | 7058.72 | 0.735 | | 36 | 0.001 |
| | 1.4328 SITI×BASA | | | | | |
| | –0.2347 SITI×AGE | | | | | |
| LITT = | –2231.27 LATI | 73116.60 | 0.777 | | 36 | 0.001 |
| | 17.175 $LATI^2$ | | | | | |
| | 1.510 SITI×BASA | | | | | |
| | –0.2778 SITI×AGE | | | | | |

an $X^2$ function in an analysis of variance which improved the relationship ($R^2_{adj}$ = 0.229 with $n$ = 41) (*table III*). The $(AGE)^2$ variable was significant on the $P < 0.1$ level only.

Albrektson [1] related annual amounts of needle litter fall to AGE using 16 sites in a transect across Sweden, obtaining a negative relationship with an $r^2$ value of 0.46 ($P < 0.001$). Earlier comparisons between litter fall and age show ambiguous relationships and, for example, Rodin and Bazilevich [23] claimed that no relationship between stand age and litter fall exists. On the other hand, they worked on a global scale and lumped several species, whereas the present study focused on one species only and was carried out over a smaller region. With a mainly north–south transect there was a clearly significant and positive relationship between LATI and AGE ($R^2$ = 0.154; $n$ = 58; $P < 0.01$) indicating that the older stands were found at the northern latitudes.

We obtained a negative relationship between LATI and LITT with $R^2_{adj}$ = 0.173; $n$ = 51; $P < 0.01$) using all Scots pine data (*table II*). This may be compared with the results of Albrektson [1], who also obtained a negative relationship ($R^2_{adj}$ = 0.42; $n$ = 16; $P < 0.01$) using a smaller data set. In our case the Scots pine transect ranged over a wider area, also including continental plots, which

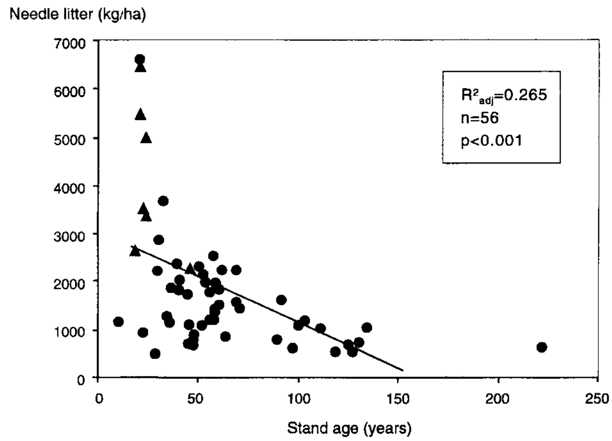
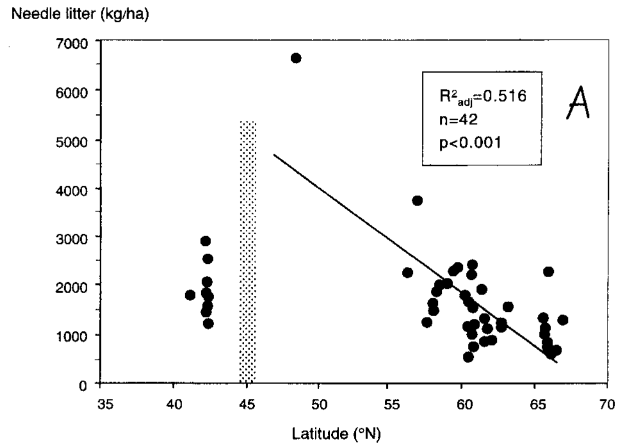



**Figure 2.** Needle litter fall for all Scots pine stands as compared to stand age (cf. *table II*). Scots pine (●) and other pine species (▲).

appeared to have a strong influence on the relationship. We compared 41 Fennoscandian sites and plots and obtained a highly significant linear relationship between litter fall and LATI with an $R^2_{adj}$ value of 0.331 ($P < 0.001$) (*table III*). However, when all Scots pine data for needle litter fall were used, excluding the few sites with a Mediterranean climate (*figure 3a*), the relationship was much improved ($R^2_{adj} = 0.516$; $n = 42$; $P < 0.001$). This improvement depended on one site, though, viz. the one at Bretagne (at 48°28'N; 01°29'W), apparently with a favourable climate for tree growth.

In their synthesis, Vogt et al. [25] found a clear negative relationship between litter fall (leaves and needles) and latitude. Whereas their plots located between the equator and about 65°N and with leaf and needle litter fall gave a relationship with an $R^2$ value of 0.58 they obtained a more narrow interval for needle litter (about 32°N–65°N) and an $r^2$ of 0.22 ($n = 120$) with different genera and species. They concluded that litter production in broad-leaved forests may be more sensitive to climatic factors than in coniferous forests. They also made a comparison with other climatic factors and found that annual mean temperature could explain 36 % of the needle litter fall.

For BASA, the data from the Scots pine transect gave an $R^2_{adj}$ value of 0.174; $n = 54$; $P < 0.01$ (*table II*). The majority of sites were subject to silvicultural practices, such as thinning, which decreased the basal area of the stand. For the more homogeneous Fennoscandian sites a highly significant relationship between BASA and LITT ($R^2_{adj} = 0.305$; $n = 41$; $P < 0.001$) was found (*table III*).



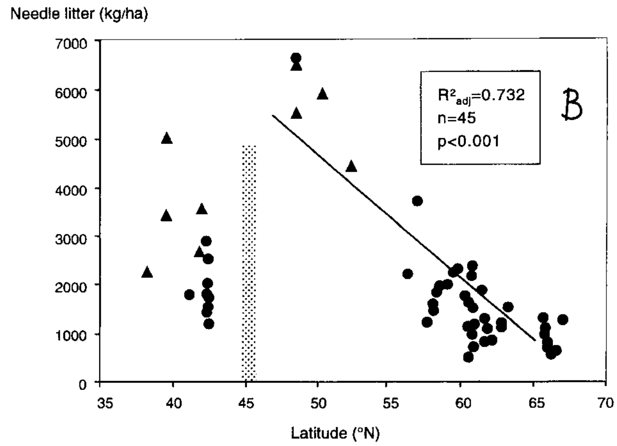




**Figure 3.** Linear relation for needle litter fall in pine stands as compared to latitude above 45°N(cf *table II*). Scots pine (●), other pine species (▲). A. All Scots pine stands except for those with a Mediterranean climate. B. All pine species and stands.

SITI values were available for 40 stands. A regression of SITI and litter fall, using all available Scots pine data gave an $R^2_{adj}$ value of 0.049 which was not significant (*table II*). For the Fennoscandian sites an $R^2_{adj}$ value of 0.349 ($n = 36$) (*table III*) was obtained. In the studies of Albrektson [1] an $R^2$ value of 0.65 ($R^2_{adj} = 0.63$; $n = 16$) was reported making it the superior relationship in his study.

ALTI alone gave a significant and negative relationship to LITT for the Fennoscandian part of the Scots pine transect with an $R^2_{adj}$ of 0.144; $n = 41$; $P < 0.01$ (*table III*).

### 3.5. Multiple linear relationships

Simple linear relationships could explain a certain portion of the litter fall and to obtain a better model we combined several variables. Linear two-factor relationships including LATI gave the best-fitted models (*table II*) using all Scots pine data. Thus LATI plus BASA gave the best fit ($R^2_{adj}$ = 0.479; *n* = 41; *P* < 0.001) for a two-factorial model, followed by SITI plus BASA ($R^2_{adj}$ = 0.398; *n* = 36; *P* < 0.001). When we combined LATI with SITI this improved the single relationship ($R^2_{adj}$ = 0.339; *n* = 36; *P* < 0.001). The combined variables LATI plus SITI plus BASA gave an $R^2_{adj}$ of 0.401 which was lower than that for LATI and SITI alone, possibly due to a lower number of measurement points (*n* = 36) since site indices were not available in all cases. The best fitted model included all four variables ($R^2_{adj}$ = 0.475; *n* = 36; *P* < 0.001) (*table II*).

Data obtained from the Fennoscandian sites gave similar results as above but with higher $R^2_{adj}$ values. The best two-factor model combining LATI and BASA (*table III*) gave an $R^2_{adj}$ value of 0.605 (*n* = 41) followed by the combination of LATI plus SITI with an $R^2_{adj}$ value of 0.525 (*n* = 36). Finally, SITI plus BASA gave an $R^2_{adj}$ value of 0.412 (*table III*). An attempt to combine ALTI with LATI did not improve the relationships. Although ALTI was a significant factor alone (*P* < 0.01), and not significantly related to LATI, the covariation was close to significant which may explain the weak combined relationship. The three-factor models improved the relationship giving an $R^2_{adj}$ of 0.661 for LATI plus BASA plus AGE thus explaining 66 % of the variation.

We also tried a stepwise regression procedure and found a good relationship between LITT and SITI × BASA (*table III*) which gave an $R^2$ value of 0.479 (*n* = 36; *P* < 0.01). In the second step LATI was added, improving the relationship to $R^2$ = 0.690 (*P* < 0.01). In a third step the combined factor SITI × AGE was added and in the fourth step $LATI^2$, increasing the $R^2$ value to 0.735 and 0.777, respectively. The factor SITI × AGE was significant at the *P* < 0.05 level and in the fourth step the addition of $SITI^2$ was significant at the *P* < 0.05 level. The factor SITI × BASA was present in all cases that the model selected. By using these four factors about 78 % of the variance in needle litter fall in Fennoscandia could be explained (*table III*).

It appears that the exclusion of some sites, viz. those on continental Europe and thus investigating only Fennoscandian data, strongly affected the relationship. This may be due to some differences in methodology but it could also reflect that the environmental factors we have used cannot fully explain the variance in litter fall over a broad range in climate.

### 3.6. Needle litter fall at all sites in the 'all pine transect'

We attempted to generalise the results of the Scots pine transect (*table IV*) and combined the LITT data for Austrian pine, Corsican pine, lodgepole pine, Monterey pine, maritime pine, red pine and stone pine with those of Scots pine, assuming that species within the genus *Pinus* share common characteristics with respect to litter fall.

**Table IV.** Simple and multiple relations for average annual amounts of needle litterfall (kg $ha^{-1}$) as dependent on latitude, stand age, site index and basal area for stands of different pine species over northern, western, and Mediterranean Europe. All available values for Austrian pine, Corsican pine, lodgepole pine, maritime pine, Monterey pine, Scots pine, and stone pine were used.

| | Coefficient(SE) | Intercept(SE) | $R^2$ | $R^2_{adj}$ | n | p < |
|---|---|---|---|---|---|---|
| **Simple linear relationships** | | | | | | |
| LATI | –78.8 (16.2) | 6302.8 (1143.8) | 0.298 | 0.285 | 58 | 0.001 |
| AGE | –19.0 (4.0) | 3041.0 (1180.6) | 0.270 | 0.265 | 56 | 0.001 |
| BASA | 47.7 (18.1) | 527.4 (1227.1) | 0.114 | 0.098 | 56 | 0.05 |
| **Multiple linear relations** | | | | | | |
| LATI plus | –65.4 (17.1) | 6361.1 (1054.4) | 0.436 | 0.403 | 56 | 0.001 |
| AGE | –12.5 (3.9) | | | | | |
| LATI plus | –44.8 (18.6) | 4101.5 (999.6) | 0.456 | 0.412 | 54 | 0.001 |
| AGE plus | –13.4 (3.9) | | | | | |
| BASA | 43.1 (16.9) | | | | | |

We thus obtained a transect from the Arctic Circle to south Spain.

The sites on continental Europe all had relatively high litter fall values as compared to the Scots pine sites in Fennoscandia (Appendix II). For needle litter fall the range was from 1 210 kg·ha$^{-1}$·year$^{-1}$ at site Donana with stone pine to above 6 600 kg·ha$^{-1}$ year$^{-1}$ in Bretagne on the English Channel.

### 3.7. Litterfall versus latitude

When all pine needle litter fall data were compared according to latitude we obtained an $R^2_{adj}$ value of 0.285 with $n$ = 58 which was highly significant (*table IV*). On the other hand, in *figure 3b* we may see that the sites with a Mediterranean climate deviated and that a linear relationship would be more optimal from 48°N. Such a relationship was considerably better and had a value for $R^2_{adj}$ of 0.732. We may see that the addition of three plots with three further species did not change the pattern obtained for Scots pine alone. For sites north of ca 48°N a linear increase took place with decreasing latitude. The sites used in that relationship were located in boreal or Atlantic climates or in zones with a transitional climate. The slope of this increase was not significantly different from that for Scots pine. At all latitudes below 48°N there was no relationship to latitude.

The 'all pine transect' covered a broad geographical range of latitudes from about 67°N to about 38°N and we may, therefore, compare the results with those of Vogt et al. [25]. They found a clear negative relationship between needle litter fall and latitude for a latitudinal range that was slightly larger (about 32–65°). Combining different genera and species they obtained an $R^2$ value of 0.22 ($n$ = 120). One significant difference to the present study may be that we have investigated litter fall in the genus *Pinus* only, whereas their study encompassed several coniferous species.

### 3.8. Litter fall versus age

Litter fall was negatively related to AGE and we found an $R^2_{adj}$ value of 0.265 ($n$ = 56; $P < 0.001$), a value that was higher than for the Scots pine transect alone (*table IV*). Almost all our stands had closed canopy covers or the canopies had reached their maximum coverage. In their paper Berg et al. [5] presented data for a stand at site Jädraås showing that at an age of 120 years or more needle litter fall decreased with age. We may expect that the significant negative relationships seen here would reflect such a degeneration on a larger scale giving a negative relationship over a region. Also in this case there was a positive relationship between LATI and AGE (cf. above).

### 3.9. Litterfall versus basal area and site index

The relationship between LITT and BASA was not as good as the other simple linear relationships with an $R^2_{adj}$ value of just 0.098 and with $n$ = 56 it was barely significant. The SITI scales differed between species so it was not possible to extend this comparison beyond that already observed (above).

### 3.10. Multiple linear relationships

These relationships did not improve much as compared to the Scots pine transect. LATI plus AGE was the best two-factor relationship and could explain about 40 % of the variation. When adding a third factor the relationship was not greatly improved ($R^2_{adj}$ = 0.412;$n$ = 54 (*table IV*).

### 3.11. Total litter fall

We made some regressions between available parameters and litter fall using 'total' litter fall in the 'all pine transect'. Total litter fall was made up of needle litter and a fraction here called 'other litter'. This fraction 'other litter' which in this study consisted of fine litter, cones and small twigs, varied for Scots pine from 85 kg·ha$^{-1}$·year$^{-1}$ (site 324, Tammela) to 1 916 kg·ha$^{-1}$·year$^{-1}$ (site 101). The proportion of 'other litter' in the total litter fall (in our case excluding larger twigs and branches), varied between 25 and 67 % in the stands studied. However, in most of the stands the 'other litter' fraction accounted for about 40–50 % of the total annual litter fall. There was a tendency towards a lower proportion of 'other litter' in the total litter fall in older stands than in younger ones. In stands aged about 70 years and more (e.g. sites 2, 106, 108 and 107) the 'other litter' fraction accounted for between 25 and 33 % of the total annual litter fall. This should not be interpreted as indicating that there was a larger proportion of needles in older stands but could be due to the fact that larger twigs and branches were not included in the results, which probably was a consequence of the type of trap employed. The situation seems to be quite the opposite as judged from a careful method study [13, 14]. The results obtained in a cronosequence of Scots pine stands at the site Jädraås [13,14] point to that there was a successively lower proportion of needles and a larger proportion of twigs and branches in older stands. Thus, in a Scots pine stand, initially 18 years old the average percentage of needle litter fall as followed over a 7-year period was 84.5 % of the total litter fall, in a stand initially aged 55 years the average fraction of needle litter over a 10-year period was 68.2 % and in an initially 120-year-old stand the fraction was 57.3 %. Over the two younger stands, in which measurements spanned 17 years and which could represent stand ages up to 65 years at that site, a highly significant linear relationship was found between age and the fraction of needle litter in total litter fall.

The needle litter fall was significantly related to 'total' litter fall. All Scots pine data as well as those for the Fennoscandian part of the Scots pine sites gave highly significant relationships ($R^2$ = 0.795 and 0.828, respectively, with $n$ = 31 and 22). The slope coefficients were 0.483 and 0.469. Using all data, thus including eight plots with other species the slope increased to 0.788 ($R^2$ = 0.844; $n$ = 39; $P < 0.001$); however, that graph became curved giving a high negative intercept. When estimating the fraction of needle litter as compared to the total we obtained for Scots pine 67 and 69 % using linear relationships for the all Scots pine transect and that for Fennoscandia. We may compare that to the estimate for the mature stand at site Jädraås in which needle litter was 57.3 % when compared to total tree litter fall data measured in an extensive way (data from [13]).

The good relationships indicate that although the sampling method applied for needle litter fall does not give correct values for total litter fall the needle litter fall may serve as an index also for total litter fall.

## 4. Conclusions

For Fennoscandia, using needle litter fall and Scots pine only simple linear regressions gave highly significant relationships with latitude and site index ($R^2_{adj}$ = 0.331 and 0.349, respectively). In a stepwise procedure using combinations of latitude, basal area, site index, and age as much as about 78 % of the variation could be explained.

No single one of the investigated factors gave an appropriate level of explanation to the magnitude of litter fall, although we investigated the needle litter fraction and in particular investigated a transect that was homogeneous in methodology. We may not exclude that in the future a direct inclusion of climatic factors may increase the level of explanation.

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**Appendix Ia.** Some basic data for the sites used for litterfall measurements.

| Site No./Name | Lat/long | Humus form/Soil texture | Stand age (yr) | Basal area ($m^2\ ha^{-1}$) | Site index (–) | Lit ref |
|---|---|---|---|---|---|---|
| **Scots pine** | | | | | | |
| A951 | 66°57'N; 23°48'E | sandy till | 55 | 32.7 | 21 | [1] |
| 106 Skällarimsheden | 66°32'N 20°11'E | mor/sandy till | 97 | 17.5 | 17 | [5] |
| A612 | 66°28'N 20°29'E | fine sandy till | 221 | 27.3 | 15 | [1] |
| 2 Harads | 66°08'N 20°53'E | mor/fine sand | 118 | 9.7 | 12 | [5] |
| A613 | 65°57'N 20°15 E | sandy till | 130 | 32.1 | 14 | [1] |
| 3:1 Manjärv | 65°47'N 20°37'E | mor/fine sand | 45 | 16.1 | 24 | [5] |
| 3:2 Manjärv | 65°47'N 20°37'E | mor/silt | 48 | 22.3 | 25 | [5] |
| 3:3 Manjärv | 65°47'N 20°37'E | mor/silt | 47 | 18.6 | 26 | [5] |
| A 87 | 65°45'N 21°16'E | sandy till | 134 | 30.7 | 21 | [1] |
| A629 | 65°41'N 18°48'E | sand | 127 | 27.2 | 16 | [1] |
| 108 Västbyn | 63°13'N 14°28'E | mor/clayey till | 70 | 36.0 | 24 | [5] |
| A681 | 61°37'N 16°54'E | gravelly till | 34 | 29.4 | 23 | [1] |
| A965 | 61°25'N 16°31'E | fine sand | 36 | 34.0 | 29 | [1] |
| A983 | 60°54'N 14°21'E | sandy till | 51 | 23.0 | 21 | [1] |
| A106 | 60°53'N 14°24'E | sandy till | 29 | 26.7 | 27 | [1] |
| A787 | 60°48'N 17°12'E | fine sand | 39 | 43.9 | 30 | [1] |
| A987 | 60°47'N 17°17'E | fine sandy till | 52 | 37.3 | 26 | [1] |