LITTER DECOMPOSITION: A GUIDE TO CARBON AND NUTRIENT TURNOVER

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Litter Fall

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I. INTRODUCTION

In forested ecosystems, litter fall is the largest source of organic material that will form humus substances and organic layers. Also, nutrients bound in the litter are deposited into the soil and become associated with the humic substances in the mineral soil and bound in the organic layers where such are found, for example, in most boreal and temperate forests. The chemical composition of plant litter has a large influence on the soil microbial communities and is one of the main factors affecting litter decay rates and the dynamics of soil organic matter. Thus, not only litter-fall quantity but also its quality affects the storage rate of humus and the quantities of released and stored nutrients.

With knowledge about the initial chemical composition of litter and the chemical changes taking place during decomposition, it has been possible to predict not only humus buildup rates (see Chapter 6) but also, for example, the concentration of N in humus formed from a given litter species and thus the buildup rate of N in humus (Chapter 5). With a close connection between the chemical composition of newly shed litter and the relative amount of recalcitrant residual litter (Chapter 6), we may see a direct connection between litter chemical composition and the rate of humus (soil organic matter, [SOM]) buildup. Thus, detailed knowledge about initial litter chemical composition may be a useful tool to estimate humus buildup and nutrient storage. It will, of course, also be possible to estimate the release of some nutrients in the forest floor. There appears, however, to be a severe lack of systematically collected data on the chemical composition of newly shed litter so we are forced to use just a few examples. There is even a lack of generally accepted methodology for sampling litter. This simply means that data given in the literature on this topic has to be studied with some care and results should be evaluated considering the methods used.

The aim of this chapter, which focuses on the foliar litter fall from trees, is to give an insight into the present state of our knowledge on quantitative litter fall and its chemical composition, and also to identify regional factors which may influence both the litter fall quantities and litter chemical composition. To determine the factors regulating the magnitude and the pattern of litter fall may be a complex task and several species-specific properties may influence the outcome. We present here a few main factors.

The chapter has three main sections. The first section presents a general overview to quantitative litter fall; the second gives an overview to litter chemical composition with Scots pine as a case study, followed by other species. The third section presents methods of how to measure litter fall and suggestions on how to sample foliar litter for determination of the

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II. LITTER FALL AMOUNTS—M
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A. Patterns on the Forest Stand Level

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ties, such as stand age, basal area, or
data over larger regions (see Section IV.
either at a stand level or at a local level,

chemical composition. Again, we have used Scots pine as the main example since there is more data available for this species than for any other.

II. LITTER FALL AMOUNTS—MAIN PATTERNS AND REGULATING FACTORS

A. Patterns on the Forest Stand Level

In the boreal and temperate zones, we may distinguish different patterns of foliar litter fall among species. There is not only a difference between the deciduous and the coniferous trees as groups but also among species within each group. No fewer than three main patterns may be distinguished and we have selected some genera and species as examples (Fig. 1). Of the conifers, the pines shed foliar litter in a regular manner, meaning that the oldest shoots still holding needles, normally 2 to 5 years old, shed them in the autumn (see also Section II.B.). Dryness may influence the pattern and cause a fall at other times of the year but normally, for a species like Scots pine, approximately 70% of the needle fall takes place in a short part of the autumn (Fig. 1), with the remaining 30% distributed evenly over the year. The spruce presents an entirely different pattern. Having needles that may remain up to 10 years on the shoots, the trees continuously shed needles of different age classes, that is, needles located on shoots of different years. Thus, in contrast to pines, not all needles on a shoot are shed at the same time but single needles die and stay attached dead for several months before they finally fall. Although dry periods may cause a heavier fall, spruce has no clear litter-fall period but needles are shed about evenly over the year, with a somewhat higher fall in wintertime (Fig 1).

Among the deciduous trees, there is normally a heavy litter fall during a short period in the autumn when the trees shed all their foliage. The timing of litter-fall peak varies, depending on the species (Fig. 1) and geographic location. Further, some species of oak, for example, have a prolonged litter fall over the autumn, winter, and spring. This means that although leaves die in the autumn, they stay attached dead on the twigs and fall occasionally during the winter but a large part stays until spring, to be finally shed when the new buds develop. This may occasionally be seen also with common beech.

Within a group of stands on soils of similar richness and under climatically similar conditions, annual leaf and needle fall may be related to stand properties, such as stand age, basal area, or canopy cover. When investigating data over larger regions (see Section IV.C.), the factors that are important, either at a stand level or at a local level, may become less significant.

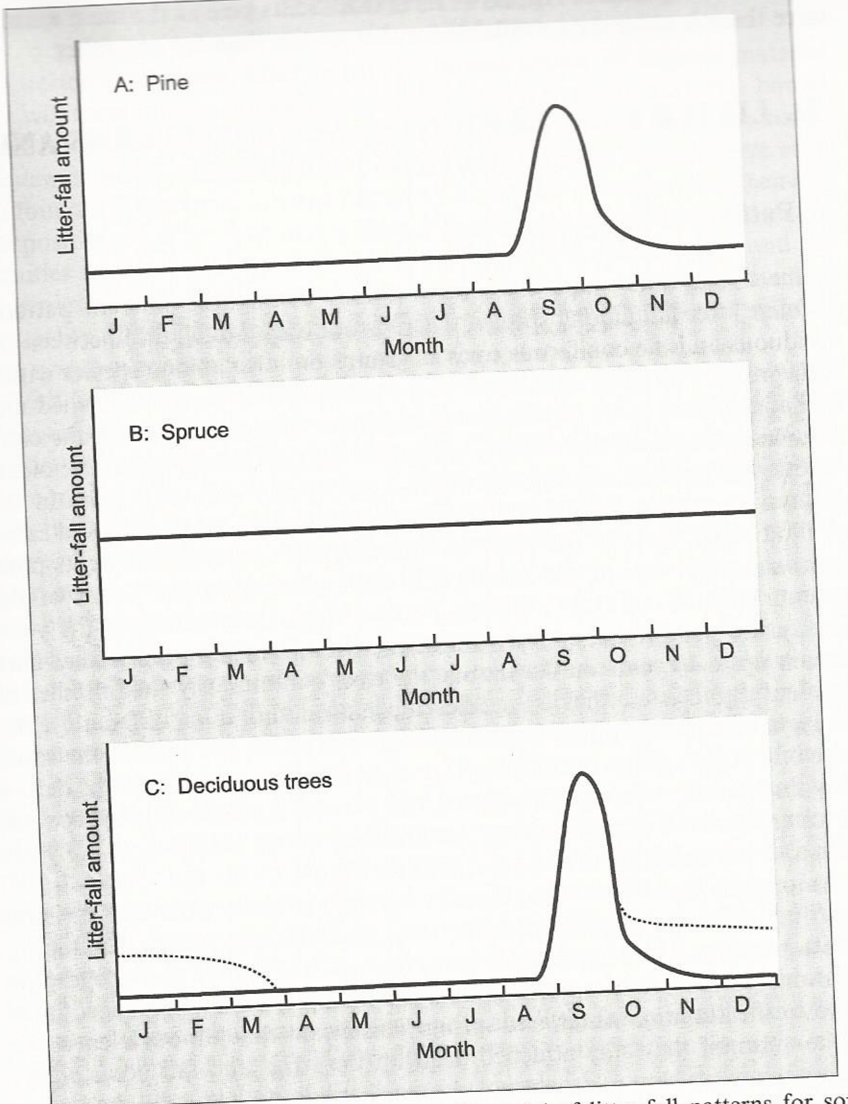

Figure 1 A generalization of typical needle and leaf litter-fall patterns for some coniferous and deciduous tree species. (A) Pines, such as Scots pine, generally have relatively low litter fall over the year and in early to late autumn a sharp peak in fall occurs with about 70% of all needle fall of the year. The peak has a duration of about a month and may occur in August at the northern border for Scots pine, in Europe at approximately 70°N, and as late as November in continental Europe. Under a climate with dry summers, such as the Mediterranean, the litter fall peak may occur in July. (B) Spruce has no pronounced litter-fall period and higher falls occur in connection with events such as drought. (C) Deciduous trees normally shed their foliar litter in a short period in the au[...] depends on latitude and climate. For some [...] not all shed in the autumn but drop during [...] with the development of the new buds (in[...]

nent, and foliar litter fall and woody [...] factors and events. Normally, foliar litter fal[...] this discussion will focus on that subject. T[...] pine and Norway spruce, have provided us wi[...] description of two case studies, both on a loca[...] the temperate regions.

B. Litter Fall Patterns in Scots Pine—A [...]

As a case study, we use an 8-year survey o[...] central Sweden (ca. 61°N), in which litter fa[...] aged 18, 55, and 120 years, at the onset of th[...] even-aged monocultures and the measured [...] cones, bark, and twigs. Over the 8 years, th[...] fall (all litter components combined) in all [...]

In the youngest stand, an increasing trend[...] an increase in total tree biomass. Simila[...] increased in biomass, which was reflected i[...] mature stands, such as those of 120 to 13[...] stable from the point of view of their litter[...] rather constant litter-fall rate. Our case s[...] observed increase in litter fall in this matu[...] However, the increase rate was substanti[...] younger stands. This raises a question abo[...] increase" assumption for mature Scots pi[...] that litter fall is cyclic, with each cycle co[...]

Across the cronosequence, an overall t[...] noted: from the highest proportion of the [...] stand to successively lower proportions o[...] increasing proportions of cones, twigs, an[...] dropped as trees reach their physiological[...] happened when they were approximately [...] falling later, in this cronosequence, at the [...] age of 18 to 25, the needle litter made up [...] at 55 to 61 years, it had decreased to ab[...]

The factors regulating the amount of litter fall vary with the litter component, and foliar litter fall and woody litter are shed due to very different factors and events. Normally, foliar litter fall is the largest component and this discussion will focus on that subject. Two tree species, namely, Scots pine and Norway spruce, have provided us with data allowing for a detailed description of two case studies, both on a local scale and over the boreal and the temperate regions.

B. Litter Fall Patterns in Scots Pine—A Case Study

As a case study, we use an 8-year survey on a Scots pine cronosequence in central Sweden (ca. 61°N), in which litter fall was observed in three stands, aged 18, 55, and 120 years, at the onset of the investigation. The stands were even-aged monocultures and the measured litter-fall fractions were needles, cones, bark, and twigs. Over the 8 years, there was an increase in total litter fall (all litter components combined) in all three stands.

In the youngest stand, an increasing trend in litter fall may be attributed to an increase in total tree biomass. Similarly, the 55-year-old stand also increased in biomass, which was reflected in increased litter fall. In contrast, mature stands, such as those of 120 to 130 years, are normally considered stable from the point of view of their litter production, that is, they have a rather constant litter-fall rate. Our case study was very detailed and the observed increase in litter fall in this mature stand cannot be undermined. However, the increase rate was substantially lower than those in the two younger stands. This raises a question about correctness of the "no litter-fall increase" assumption for mature Scots pine stands or, alternatively, suggests that litter fall is cyclic, with each cycle covering rather long periods.

Across the cronosequence, an overall trend in litter-fall composition was noted: from the highest proportion of the needle component in the youngest stand to successively lower proportions of needles in the older stands and increasing proportions of cones, twigs, and branches. Cones develop and are dropped as trees reach their physiological maturity, which, in our case study, happened when they were approximately 18 years old. Bark and twigs start falling later, in this cronosequence, at the age of about 22 to 23 years. At the age of 18 to 25, the needle litter made up approximately 83% of the litter fall; at 55 to 61 years, it had decreased to about 68%, and at 120 to 126 years, to

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their foliar litter in a short period in the autumn. As for pine, that litter-fall period depends on latitude and climate. For some oak and beech species, the old leaves are not all shed in the autumn but drop during winter until finally all leaves fall in spring with the development of the new buds (indicated with a dotted line).

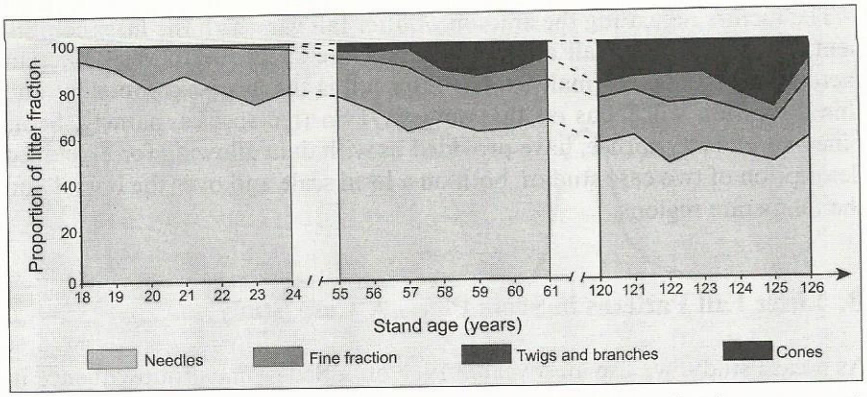

Figure 2 Generalized development of the relative proportions of main components in litter fall (needles, fine litter, twig, and branch litter as well as cones) as observed in a boreal chronosequence of Scots pine. Data from Berg *et al.* (1993a).

58%. This picture, with an increasing proportion of woody parts, is typical for pine stands (Fig. 2) and a high proportion of woody parts and cone litter is characteristic of middle-aged to old stands, in which branch mortality is high.

Needle litter is formed throughout the year, especially during drier periods, and at this latitude (61°N), almost all needles shed come from the 4-year-old shoots. Each stand in this monocultural Scots pine case study site had even-aged trees and the needles of the 4-year-old shoots withdraw their nutrients (Section VI.B.) starting in late July or early August, a process that continues until the needles are shed. In the case of a very dry summer, there may be a summer litter-fall period; otherwise, the main needle fall takes place in September during a relatively short period which produces 70% of the annual needle litter fall. The remaining needle litter is shed, in part, during winter. In younger stands, needle litter fall increases steeply with stand age until the canopy cover is closed (Fig. 3), or until a stage in which the canopies do not develop further and there is no net increase in the green biomass. However, in northern forests like those in the present case study, there is no real canopy closure but rather a maximum canopy size.

For younger stands, it is often possible to create a linear relationship for foliar litter fall versus stand age in the development phase before canopy closure. For older stands which do not develop any further, a decline in needle or leaf fall with age may be observed; still, in our case study, an increase took place over 8 years in the 120- to 130-year-old stand (see previous comments).

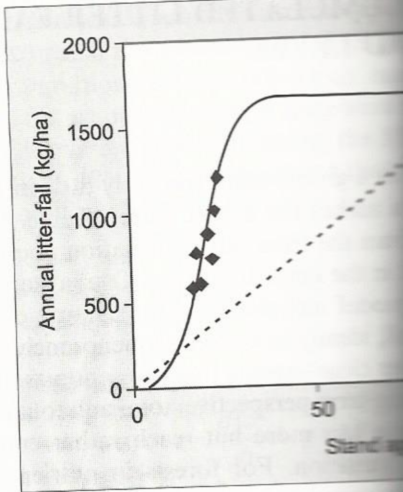

Figure 3 Two simplified models for
Broken line, the model assuming that
canopy closure, in this case study at
line, a logistic, nonlinear model fitted
and 120 to 130 years old. From Berg
Scandinavian Journal of Forest

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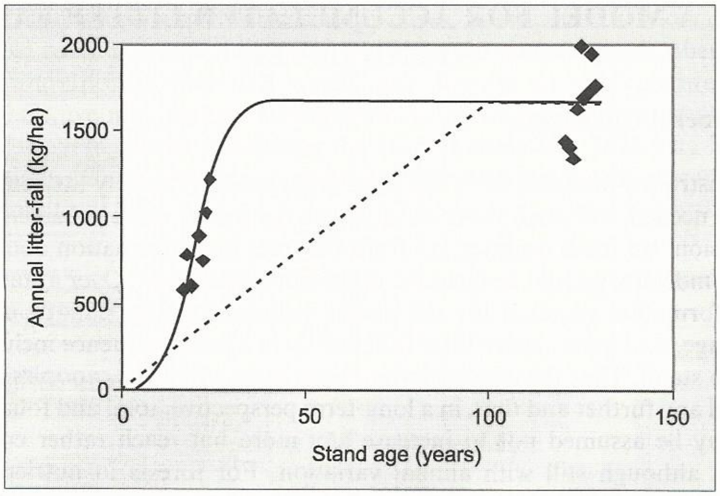

Figure 3 Two simplified models for predicting litter fall of different stand ages. Broken line, the model assuming that litter fall increases linearly with age up to canopy closure, in this case study at 100 years and remains constant thereafter. Solid line, a logistic, nonlinear model fitted to litter fall data for Scots pine stands 18 to 25 and 120 to 130 years old. From Berg *et al.* (1995). Adapted with permission from the Scandinavian Journal of Forest Research.

For mature Scots pine stands, the variation in annual needle litter fall between years is considered rather low. For longer measurement series, the ratio between maximum and minimum annual needle litter fall has been found to be in the range between 1.1 and 2.1. Such comparisons are made within a stand only.

As can be seen from Fig. 2, litter consists of a number of different fractions that not only look different but also behave in different ways, during both the litter fall and the decomposition. The term "fine litter" is often used as a collective name for a group of small-sized, not well-defined components. "Branch and twig litter" usually does not have any really regular periodic litter fall. Their fall is connected, rather, to specific events such as heavy winds, especially storms, and to heavy rain or snowfall. In turn, the pattern of "cone litter" fall strongly reflects a periodicity in cone production, with peaks at intervals of about 5 years for Scots pine (Flower-Ellis, 1985; Hagner, 1965). Cone production shows a very clear increase with increasing age of the stand, from virtually nil to over 25% of the total litter fall, following a year with high cone production (see the 120- to 130-year-old stand of the case study, Fig. 2). A term such as "cone litter" may seem inappropriate; still, when the cones have fallen to the ground, the main part of the organic matter starts decomposing and should be regarded as litter.

III. A MODEL FOR ACCUMULATED LITTER FALL, STAND LEVEL

A. General Comments

To construct a model of litter fall for a given stand, relatively little information is needed, although more data makes the model more reliable. In our discussion, we focus on litter fall from the trees but information about that of the understory could be included in the same discussion. Over a stand age, the information required for the model includes time for canopy closure, stand age, and quantitative litter fall, ideally in a cronosequence including a mature stand. That the canopy cover closes means that the canopies do not expand any further and that, in a long-term perspective, total and foliar litter fall may be assumed not to increase any more but reach rather constant values, although still with annual variation. For forests in nutrient-poor areas and in many boreal stands, no complete canopy cover is reached but rather a maximum coverage (cf. Fig. 3). In this case, that would correspond to a maximum canopy cover and thus to a maximum litter fall.

We will describe two simple models of litter fall, which we call *linear* and *logistic*. For the linear model, it is assumed that litter fall increases linearly from a stand age of one year up until canopy closure, after which the litter fall may be considered constant. The model would thus be described as two straight linear relationships crossing each other at the time of canopy closure. This model is based on common observations and is sometimes used, for example, in forestry. In the logistic model, litter fall increases initially at an exponential rate until about a maximum canopy cover, when the increase rate slows down approaching an asymptotic level, and litter fall becomes about constant. Both models will be described in detail, using our case study as an example (Fig. 3).

B. A Case Study for a Scots Pine Stand

Litter fall was monitored for 7 to 10 years in each of two adjacent Scots pine stands, initially 18 and 120 years of age, on soil of similar nutrient status. The stands thus represented age periods of 18 to 25 years, and 120 to 130 years, giving a certain age distribution. Detailed measurements and analyses of the total annual litter fall as well as the deposition of single litter components, such as needles, cones, branches, and fine litter, were made providing basic data (Flower-Ellis, 1985; Berg *et al.,* 1993) and some temporal trends were evident within the stands.

The series of observations revealed that total litter fall in the young stand clearly increased with stand age (Fig. 3; cf. Berg *et al.*, 1995). A mature stand

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thus also reach a constant litter fall. Still, a
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tion. The average litter fall during the 10-y
the initially 120-year-old stand and that va
maximum litter fall.

1. A Logistic Model

The logistic model can be stated as:

$$\frac{dLF}{dt} = g \cdot LF \cdot (M$$

and may be developed to

$$LF = \frac{Max \cdot}{LF_0 + (Max - L}$$

where
LF_0 = annual litter fall at $t = 0$; LF = an
Max = maximum ("steady-state") annua
g = constant, intrinsic for rate of increase

Using serial approximations to achieve
stands, the following parameters were de
this model, the value estimated for accum
164,500 kg ha^{-1}. The logistic model pre
stand age of approximately 30 years. W
Chapter 6, Section VI.B., for a discussion

2. A Linear Model

Following the assumptions previously de
case study assumes a linear increase in l
value of 16.2 kg ha^{-1} in year 1 to 162
remaining constant for 20 years thereafte
approximately 116,300 kg ha^{-1} over the
model, with linear increase in litter fall
the observed data well (Fig. 3). In fact,
fall on stand age gives a good relation

should ideally have a maximum canopy cover, not increase its biomass, and thus also reach a constant litter fall. Still, also in mature stands, there is an annual variation in litter fall which may obscure an ideal picture—or a theory. So, we may assume a long-term steady level with an annual variation. The average litter fall during the 10-year study was 1621.5 kg ha^{-1} in the initially 120-year-old stand and that value was used as an average for a maximum litter fall.

1. *A Logistic Model*

The logistic model can be stated as:

$$\frac{dLF}{dt} = g \cdot LF \cdot (Max - LF)$$

and may be developed to

$$LF = \frac{Max \cdot LF_0}{LF_0 + (Max - LF_0) \cdot e^{-g \cdot Max \cdot t}}$$

where
LF_0 = annual litter fall at $t = 0$; LF = annual litter fall
Max = maximum ("steady-state") annual litter fall
g = constant, intrinsic for rate of increase in litter fall with stand age.

Using serial approximations to achieve the best fit to the data from both stands, the following parameters were derived: Max = 1620, g = 0.37. Using this model, the value estimated for accumulated litter fall over 120 years was 164,500 kg ha^{-1}. The logistic model predicted a maximum litter fall at a stand age of approximately 30 years. We have used this litter-fall data in Chapter 6, Section VI.B., for a discussion on humus buildup rates.

2. *A Linear Model*

Following the assumptions previously described, the linear model for this case study assumes a linear increase in litter fall from an estimated initial value of 16.2 kg ha^{-1} in year 1 to 1620 kg ha^{-1} in year 100, with litter fall remaining constant for 20 years thereafter. This model gave an estimate of approximately 116,300 kg ha^{-1} over the 120 years. However, the assumed model, with linear increase in litter fall until canopy closure, does not fit the observed data well (Fig. 3). In fact, the linear regression of needle litter fall on stand age gives a good relationship for the 18-year-old stand for only the 7 years for which data are available but that relationship is much steeper than the assumed model.

The larger estimate produced by the logistic model is due to the fact that this model predicted a much higher litter input in the early years of stand development. The logistic model predicted that the stand reaches its maximum litter production after only 30 years, whereas the linear model assumes that maximum is not attained until year 100 (Fig. 3).

IV. MAIN LITTER-FALL PATTERNS ON A REGIONAL LEVEL: SCOTS PINE AND NORWAY SPRUCE

A. Distribution of Species

In Europe, Scots pine grows from Barents Sea in the north to the Pyrenees in the south, although it forms forests only to about the Alps and the Carpathians. Norway spruce forms forests from about the Arctic Circle to the south side of the Alps. Over such long distances, the magnitude and pattern of litter fall vary with the geographical position and climate. We have chosen to present these two species for case studies since they represent two different types of litter fall. Further, at present, these are the only species for which data on such a broad geographic scale are available.

B. Factors Influencing Amounts of Litter Fall

The factors influencing litter fall may be divided into factors such as climate, which have an influence on a continental to regional scale, and more local factors such as soil nutrient status. Soil nutrients is a factor which can vary substantially on a local scale or stand level. Finally, on forest-stand properties such as basal area and canopy cover, both reflecting the status of stand development. Stand age is often seen as a factor reflect stand development for rather even-aged stands but may be less useful as an index for litter fall in managed forests where, for example, thinnings take place.

Regarding effects of soil nutrient status versus climate, we may take as an example three paired stands of Scots pine, all within a radius of 100 m but growing on different soils with a stand age that can be considered constant (range from 45 to 48 years). The average annual total litter fall was 1360, 1680, and 2084 kg ha^{-1} for a stand on dry and nutrient-poor sandy soil, on a mesic and more nutrient-rich one, and on a very nutrient-rich and moist soil, respectively. Thus, within a rather small area, the litter fall within one species can have a large variability due to site factors, a variability that would correspond to considerable differences in climate if the soil nutrient conditions were constant. Thus, if the lower value of 1360 kg ha^{-1} reflects litter fall at an AET value of 385 mm, the value of 2084 kg ha^{-1} would correspond to an AET value of 490 mm.

Thus, when comparing litter fall on a regional basis in stands under different climates, factors such as soil nutrient status and stand properties must not be neglected. These properties can vary considerably among single stands at similar climatic conditions, enough to cause significant deviations from a general climate-driven trend. As such, they must be considered in litter-fall studies on a regional scale.

C. Needle Litter Fall—Pattern and Quantities: Scots Pine and Other Pine Species

For different species, differences in litter fall may reflect physiological differences, such as species-specific relative distribution of resources to woody and photosynthetic parts. Over a continent, the magnitude of annual foliar litter fall may be related mainly to climate and thus to the productivity of the trees. It may be related to climate (temperature and precipitation) as a main factor and stand density (e.g., basal area) as a second one. The stand density may be a result of different factors, such as soil nutrient level, soil moisture, and solar radiation.

For Scots pine, we describe a transect ranging from Barents Sea to Central Europe, with truly boreal forest in the main part of Fennoscandia and temperate forest in southern Scandinavia and the northern part of the European continent. We also extend the transect to forests of other pine species, reaching as far south as to the subtropical Mediterranean climate (see Fig. 4). In this long transect, the magnitude and pattern of litter fall vary with climate and thus with the geographical position of each stand.

1. The Seasonal Pattern in Pine Litter Fall Varied Over the Transect

Over the range of Scots pine sites, the onset of litter fall in the autumn was related to climate and thus to latitude. In northernmost Finland, close to 70°N and the northern border for this species, the needle litter is shed in early August. About 3° to the south, that is, at the Arctic Circle (about 66°57′N), the litter fall starts in late August, whereas at 60°49′N (Central Sweden), it starts in late September. Further south, for example, at the latitude of Berlin (52°28′N), the main litter fall takes place in late October and early November and in south Poland and south Germany (about 48–49°N) in November. Scots pine stands located in a Mediterranean climate have a different pattern altogether, with the heavy litter fall taking

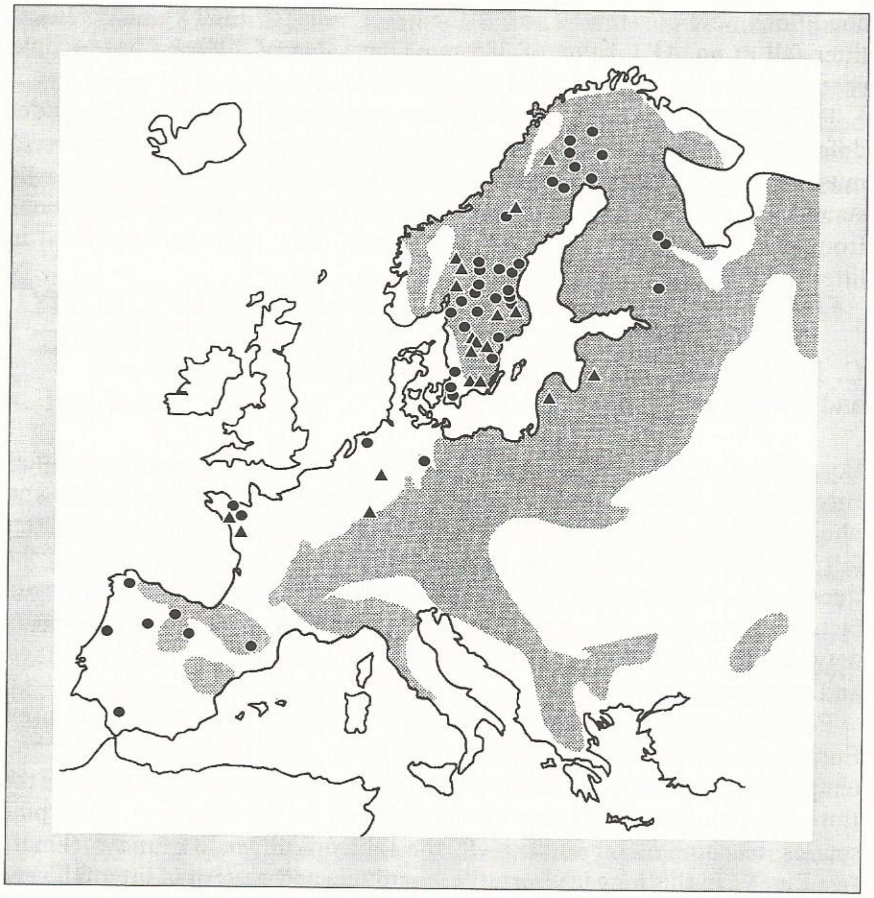

Figure 4 Map of Europe giving approximate locations of the sites used in two transects, one with Scots pine and one with Norway spruce. Pine (●), spruce and fir (▲). The shaded area indicates the extent of main range of Scots pine forests.

place in June owing to the Mediterranean drought period. Other pine species growing in this latter region, such as Aleppo pine, stone pine, and maritime pine, follow about the same pattern.

In boreal systems, Scots pine shows a mean annual needle litter fall ranging from 530 kg ha^{-1} close to the Arctic Circle to 3700 kg ha^{-1} at 57°N, which is approximately 1500 km further south, in southern Scandinavia (Fennoscandia).

The temperate continental pine forests all have a relatively high litter fall as compared to the Scots pine sites in boreal Scandinavia. Thus, a stand of

Austrian pine on the northern coast litter fall of 4400 kg ha^{-1}. Further sou fall for pine was as high as 6604 kg stand in central Portugal, with a mi terey pine, also had a very high needle ha^{-1} at the age of 24 years. In con Mediterranean climate in southern much lower annual needle litter fall main factors influencing the litter fall as far as the data set allows.

An often used climate index for is annual actual evapotranspiration includes both temperature and precip

Textbox 1 Climate indices

The climate indices presented in this biological processes on large geograph an annual basis and below they are pr abbreviations used in the text. As the periods, even within the same site (as a use long-term annual averages.

AET	*Annual actual evapotranspi* ing mainly precipitation and properties may be included are considered). AET is processes. It should be reme does not always reflect exact as an index of ground cond characteristics could thus ha
PET	*Potential evapotranspiration* tion which potentially can ev
AVGT	*Annual average temperature*
JULT	*Average temperature in July* est month of the year in the
PRECIP	*Annual precipitation* (mm).
DEF	*Water deficit* (mm).

Austrian pine on the northern coast of Holland had a high annual needle litter fall of 4400 kg ha^{-1}. Further south in the temperate zone, needle litter fall for pine was as high as 6604 kg ha^{-1} on the French Atlantic coast. A stand in central Portugal, with a mixed culture of maritime pine and Monterey pine, also had a very high needle litter fall, with a bit more than 5005 kg ha^{-1} at the age of 24 years. In contrast, a stone pine stand in a clearly Mediterranean climate in southern Spain (Doñana National Park) had a much lower annual needle litter fall with 1200 kg ha^{-1}. We will present the main factors influencing the litter fall, show available data, and discuss them as far as the data set allows.

An often used climate index for biological activity and productivity is annual actual evapotranspiration (AET) (see Textbox 1). This index includes both temperature and precipitation. In our case study, investigating

Textbox 1 Climate indices

The climate indices presented in this box are often used for analysis of biological processes on large geographic scales. In the book they are used on an annual basis and below they are presented in that way together with the abbreviations used in the text. As the litter fall often is studied over different periods, even within the same site (as are also the decomposition processes), we use long-term annual averages.

AET	*Annual actual evapotranspiration* (mm). A climate index considering mainly precipitation and the energy input at a given site. Soil properties may be included or standardized (e.g. when a set of sites are considered). AET is often used as an index for biological processes. It should be remembered that a calculated AET value does not always reflect exactly the ground climate but rather serves as an index of ground conditions. Forests with different canopy characteristics could thus have different ground climates.
PET	*Potential evapotranspiration (mm).* The amount of the precipitation which potentially can evaporate. PET – DEF = AET
AVGT	*Annual average temperature* (°C).
JULT	*Average temperature in July* (°C). July is thus considered the warmest month of the year in the northern hemisphere.
PRECIP	*Annual precipitation* (mm).
DEF	*Water deficit* (mm).

Table 1 Litter fall for Scots pine and Norway spruce regressed against some commonly used and available parameters[a]

Parameter	r	R^2_{adj}	n	p<
Scots pine:				
Actual evapotranspiration	0.682	0.449	35	0.001
Average annual temperature	0.668	0.429	35	0.001
Latitude	−0.587	0.328	41	0.001
Basal area	0.569	0.307	41	0.001
Stand age	−0.425	0.16	41	0.01
Site altitude	−0.406	0.144	41	0.01
Norway spruce:				
Actual evapotranspiration	0.84	0.679	13	0.001
Latitude	−0.552	0.242	13	ns
Basal area	0.579	0.275	13	0.05
Stand age	−0.598	0.3	13	0.05

[a]The sites used cover Fennoscandia at a range from the Arctic Circle to the latitude of Copenhagen (66°57′N to 55°40′N). Such parameters as latitude and actual evapotranspiration were well correlated. Data from Berg *et al.* (1999) and from Berg and Meentemeyer (2001). The R^2_{adj} transfers the R^2 values to comparable values for different number of degrees of freedom.

Scots pine litter fall in the boreal zone, the best reported relationship for pine needle litter fall to climatic factors was that to AET with an R^2_{adj}* value of 0.449 in a transect with 35 stands (Table 1). The Fennoscandian boreal systems are energy limited, meaning that temperature is a limiting factor and also that variables based on temperature provide good relationships (Berg and Meentemeyer, 2001). Thus, in our case study, annual average temperature alone gave a relationship that was almost as good as AET (Table 2).

Also, over larger regions, the best relationships for pine and spruce needle litter fall to climate are those to AET; for combined boreal, temperate, and subtropical (Mediterranean) pine and spruce systems, a very good relationship was seen with a $R^2_{adj} = 0.61$ using data for 64 stands ($p < 0.001$). When we compared litter fall from pine species only, AET gave an R^2_{adj} of 0.578, and average annual temperature gave an R^2_{adj} value of 0.424 (Table 2). Also, the relationships to temperature and to potential evapotranspiration (PET) were almost as good and significant at the level of $p < 0.001$, with values for R^2_{adj} of 0.424 and 0.410, respectively (cf. Textbox 1 and Table 2).

*R^2_{adj} – the determination coefficient (R^2) adjusted for degrees of freedom is more useful and correct for comparing regressions with different number of independent variables.

Table 2 Compilation of needle litter-fall data from a climatic transect covering Europe from the Arctic Circle (66°57′N) to the Mediterranean (37°N)[a]

Parameter	r	R^2_{adj}	n	p<
Actual evapotranspiration[b]	0.766	0.578	48	0.001
Average annual temperature	0.66	0.424	48	0.001
Potential evapotranspiration	0.65	0.41	48	0.001
Latitude[b]	−0.539	0.277	58	0.05
Basal area	0.338	0.098	58	ns
Stand age	−0.52	0.257	58	0.05

[a]Different pine species are combined, namely Austrian pine, Corsican pine, lodgepole pine, maritime pine, Monterey pine, Scots pine and stone pine.
[b]Please note that the relationship between litter fall and latitude given below encompasses all available data for boreal, temperate and Mediterranean forests. Figure 5 shows the same data but divided and that latitude as a parameter gives better relationship where it is related to a climate index.

2. *Latitude*

Although latitude is not a causal factor for litter fall, it is commonly used in the scientific literature since it is often related at least to annual average temperature. Litter fall is thus related to latitude in a general way but with limitations and, since it is not a causal variable itself, it must be used with caution. Using boreal Fennoscandian data for 41 stands gave for our case study a negative relationship between latitude and needle litter fall ($R^2_{adj} = 0.328$; $p < 0.001$) (Table 1). For a longer Scots pine transect, latitude would be acceptable as a regressor as long as it was related to climate indices. Thus, in western Europe, for example, over the boreal and temperate zones, latitude gives an acceptable relationship. However, when including Mediterranean data, this relationship did not hold. We may see this from Fig. 5, in which litter-fall data from the same transect is related to AET and to latitude. When the co-variation between AET and latitude ceases under the Mediterranean climate, the relationship between litter fall and latitude also ceases.

3. *Stand Age*

Age does not give any clear relationship for litter fall in transects, with results actually varying across studies, and Rodin and Basilewich (1967) suggested that no general relationship existed. Some scientists report good relationships, however (Albrektson, 1988). For our case study transect (Barents Sea to Central Europe), we obtained a significant negative

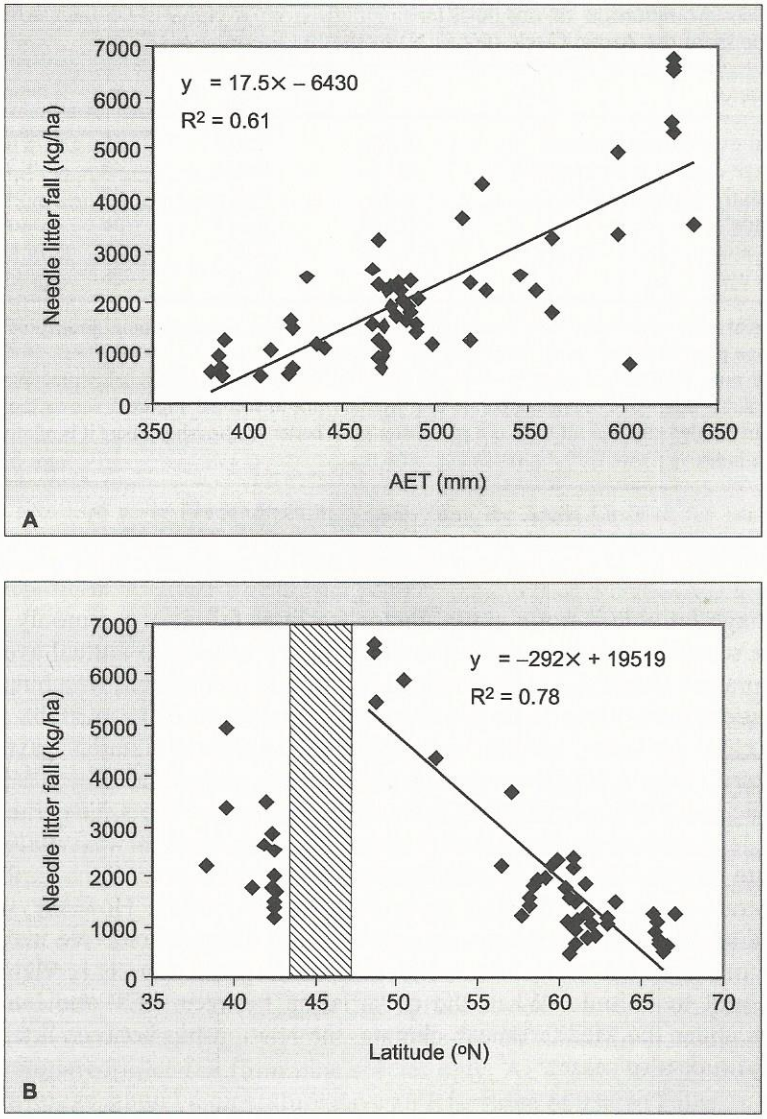

Figure 5 Needle litter fall for some different pine species over Europe related to two different parameters. The two figures give the same data set for litter fall. (A) As compared to actual evapotranspiration (AET). From Berg and Meentemeyer (2000). (B) As compared to latitude. The bar separates the Mediterranean stands from those of temperate and boreal climates. From Berg *et al.* (1999). For the sites on the right-hand side of the bar, latitude and AET are correlated.

relationship with an R^2_{adj} value o
using data from a climate transect
latitude/climate, with trees generall
not reflecting a difference in biomas
lower litter fall at higher latitudes
fall at lower latitudes (younger tre
age may be important for develop
it is probably not correct to use
fact, Liu *et al.* (2003), when comp
climate, excluded younger stands
their data.

D. Basal Area and Canopy Cove

Basal area and canopy cover are e
related to litter fall within at least s
may be described as typical stand
give significant relationships with li
Scandinavia (Table 1). Still, a relati
due to the large climate variation i
over basal area as an index. For 41 s
and $p < 0.001$ (Table 1) as comp
with an R^2_{adj} of 0.429. When usin
probably should be used together
area or canopy cover with climatic
explaining the variation. Thus, in
AET and basal area, R^2_{adj} increase
($n = 45$) with $p <$ 001.

The lowest amounts of annual li
where the basal area would be low
those with till deposits or clays, li
stands on granite sand. Among si
lower for sites situated under drier
than for sites under a higher AET
Amounts of needle litter fall are
66°32'N (AET = 382) and an
These sites had nearly identical
pectively), but the annual needle-li
was only about one-third of the
(1571 kg ha^{-1}). See also the exam

relationship with an R^2_{adj} value of 0.160. Such a negative relationship using data from a climate transect may simply reflect an indirect effect of latitude/climate, with trees generally being older at higher latitudes, age not reflecting a difference in biomass. Thus, in reality, we just compare the lower litter fall at higher latitudes (with older trees) with the higher litter fall at lower latitudes (younger trees). We would conclude that although age may be important for developing younger stands (cf. Section II.B.), it is probably not correct to use it when comparing mature stands. In fact, Liu *et al.* (2003), when comparing litter fall in Europe and Asia to climate, excluded younger stands to avoid this kind of problem with their data.

D. Basal Area and Canopy Cover

Basal area and canopy cover are expressions of the stand biomass and are related to litter fall within at least species and possibly genus. Although both may be described as typical stand properties, basal area has been found to give significant relationships with litter fall over a region the magnitude of Scandinavia (Table 1). Still, a relationship on such a regional level is poor due to the large climate variation in the same region, which may dominate over basal area as an index. For 41 stands over Fennoscandia, R^2_{adj} was 0.307 and $p < 0.001$ (Table 1) as compared to the annual average temperature with an R^2_{adj} of 0.429. When using this variable in a regression model, it probably should be used together with a regional factor. Combining basal area or canopy cover with climatic factors in a model may go a long way in explaining the variation. Thus, in a multiple linear regression combining AET and basal area, R^2_{adj} increased from 0.449 for AET alone to 0.557 ($n = 45$) with $p < 001$.

The lowest amounts of annual litter fall are found at nutrient-poor sites, where the basal area would be low. At more nutrient-rich sites, for example, those with till deposits or clays, litter-fall mass is generally higher than in stands on granite sand. Among sites of similar fertility, needle litter fall is lower for sites situated under drier and colder climate, and thus lower AET, than for sites under a higher AET. This may be illustrated with an example. Amounts of needle litter fall are compared at two sites, one at latitude 66°32'N (AET = 382) and another at latitude 58°07'N (AET = 491). These sites had nearly identical basal areas (17.5 and 18.3 m^2 ha^{-1}, respectively), but the annual needle-litter fall at the northern site (608 kg ha^{-1}) was only about one-third of the amount obtained at the southern one (1571 kg ha^{-1}). See also the example in Section IV.B.

E. Needle Litter Quantities: Norway Spruce

1. Climate Indices

There are few data available for Norway spruce litter fall and, as an example, we have used a transect within all 16 sites across northern Europe. In this case, climate as indexed by AET gave highly significant relationships for all available data, ranging from the Arctic Circle to about the latitude of Paris, Munich, and Budapest, with an R^2_{adj} of 0.778 ($n = 16$) (Table 3). Annual average temperature as a single factor gave an R^2_{adj} of 0.685, which shows that temperature has a strong influence on litter fall for spruce also.

2. Latitude

Latitude did not give a significant relationship for Norway spruce over the range of Fennoscandia alone. However, for a longer transect covering the area from the Arctic Circle to the Alps, an R^2 value of 0.518 was highly significant ($p < 0.001$). This is a substantially weaker relationship than that with AET, a result that should be expected, considering that latitude gives only a rough image of climatic conditions.

F. Comparison of and Combination of Species

Litter-fall measurements including several species may be combined successfully in the same regression model, which indicates that, at least in mature stands with fully developed trees, the foliar litter fall is of similar magnitude across species. Still, there are differences between species and between groups of species (softwoods versus hardwoods; pine versus spruce versus fir, etc.). A number of comparisons of litter fall between species have been made using paired stands with identical environmental conditions such as soil properties, climate, water availability, altitude, and aspect.

Table 3 A comparison of the relationship between actual evapotranspiration (AET) and foliar litter fall for Scots pine and Norway spruce separately and litter fall for the two species combined[a]

	R	R^2_{adj}	n
Norway spruce	0.891	0.778	16
Scots pine	0.868	0.746	38
Data combined	0.877	0.766	54

[a]The geographical extension ranged from the Arctic Circle (66°57′N) to the Alps (47–48°N).

Thus, Berg and Johansson (1994) made such a comparison of Norway spruce and Scots pine in paired stands at eight sites across Sweden and found that Scots pine produced more litter than Norway spruce (measured as "total" litter fall) and that Norway spruce produces more needle litter than Scots pine. Other studies revealed that Norway spruce produced more litter than common beech and lodgepole pine more litter than Scots pine. Still, we have to keep in mind that the litter-fall pattern may vary with stand age. Thus, if one species sheds more litter than another one at a certain age, this difference does not necessarily hold later at a higher stand age. In the examples already given, the litter production was measured over shorter periods, not for whole stand ages.

In a review, Liu *et al.* (2003) compared litter fall in 30-year-old stands of Chinese cork oak and Chinese pine in a temperate forest in China and found an approximately 50% higher litter fall for the former. For the broadleaf species *Castanopsis kawakamii* and quarantine weed, annual litter fall was 13,000 and 7160 kg ha^{-1}, respectively, compared to that of Chinese fir with 4800 kg ha^{-1}, all in paired stands. Thus, the two broadleaf tree species produced more litter than did the coniferous species at the same site. Still, comparisons like these often reflect the conditions for growth for the different species and may depend on factors such as climate and soil fertility. In a critical approach, it would be reasonable to relate litter fall not just to stand age but to a parameter for stand development, for example, basal area.

G. Litter Fall on a Continental to Semiglobal Scale

1. *General Patterns and Amounts*

At regional to global scales, the variation in litter fall is well explained by climate variables such as actual evapotranspiration (AET), annual average temperature and annual precipitation, or climate-related variables such as latitude. In the global model of Meentemeyer *et al.* (1982), AET was used as a predictive variable for total litter fall, with an R^2 value of 0.77 ($n = 81$) thus "explaining"approximately 77% of the variation in litter fall. In another approach, models were established with latitude alone as the independent variable ($R^2 = 0.35$, $n = 242$), or with both latitude and altitude ($R^2 = 0.63$, $n = 181$) (Lonsdale, 1988). However, as already mentioned, latitude is not a causal variable. Using a considerably larger database and a multiple regression model including both coniferous and broadleaf litter with temperature and precipitation as prediction variables, Liu *et al.* (2003) obtained an R^2_{adj} value of 0.53 ($n = 439$) on a Eurasian basis.

In a study covering Europe and Asia, Liu *et al.* (2003) compared broadleaf and coniferous trees and found that broadleaf forests have a higher average total litter fall than do coniferous ones in five biomes out of six (Table 4). Thus, there is a general tendency to higher average litter fall in broadleaf forests except for the boreal ones, where total litter fall in the coniferous forests was about 15% higher than that of the broadleaf ones (Table 4). In four climatic zones, foliar litter fall was higher in broadleaf than in coniferous forests (Table 4). However, this difference was significant ($p < 0.05$ to $p < 0.01$) only for the Asian and European temperate zones and the Asian subtropical and tropical zones. In warm and wet climates, broadleaf forests tend to have a larger variation in both total litter fall and leaf litter fall than do coniferous ones (Fig. 6).

2. *Comparison of the Effects of Temperature and Precipitation*

In the largest study yet done on litter fall, Liu *et al.* (2004) evaluated litter fall for over 400 stands in Europe and Asia. In the boreal zone, with low average temperature and low precipitation, they did not find any significant difference between coniferous and broadleaf forests in regard to the amounts of foliar and total litter fall, although the average litter fall was higher in the coniferous forests (Table 4). With increasing temperature and precipitation, the total litter fall in broadleaf forests increases faster than that in coniferous ones and gradually a significant difference develops.

3. *Litter Fall in Broadleaf Forests Appears to Increase Even when Annual Average Temperature Approaches 30°C*

In a comparison on the effects of temperature and precipitation on total litter fall, Liu *et al.* (2003) found that simple linear relationships provide significant models for total litter fall versus average temperature and annual precipitation. They found that a change in temperature of a standardized unit (see Textbox 2) has a greater impact on total litter fall than a standardized-unit change in precipitation within the observed ranges for the variables, namely, annual average temperature from about −7 to 30°C and, for annual precipitation, from about 350 to 4000 mm. To compare the effects of temperature and precipitation on litter fall, Liu *et al.* (2003) used a logarithmic transformation of data since their data did not have a normal distribution. With temperature as the independent variable, the model for broadleaf litter fall had a significantly higher coefficient for Ln(Temp), showing a faster increase in total litter fall with increasing temperature for broadleaf

Table 4 Annual litter fall, both foliar and "total" litter in coniferous and broadleaf forests in the main climatic zones of Europe and Asia[a]

Forest	Leaf litterfall				Total litter fall			
	Mean value	SE	Range	n	Mean value	SE	Range	n
Boreal forest								
Coniferous	1840	100	320–3300	63	2690	120	580–5080	87
Broadleaf	1930	220	230–3740	17	2260	170	270–5200	28
European temperate forest								
Coniferous	2860[a]	170	1160–4400	26	3470[c]	150	2100–6800	41
Broadleaf	3440[a]	170	2360–5200	20	4420[c]	210	1340–6710	34

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Coniferous	2860[a]	170	1160–4400	26	3470[c]	150	2100–6800	41
Broadleaf	3440[a]	170	2360–5200	20	4420[c]	210	1340–6710	34
European subtropical								
Coniferous	3020	350	1210–5010	11	4090	620	1740–7700	11
Broadleaf	3140	530	800–5300	8	4770	620	2320–6700	8
Asian temperate								
Coniferous	2070[b]	190	790–3340	21	2980[b]	200	910–4990	28
Broadleaf	3320[b]	430	2190–5670	7	4340[b]	440	3000–6670	8
Asian subtropical								
Coniferous	3310[a]	250	940–7040	32	4940	290	1670–9670	32
Broadleaf	4240[a]	210	840–9100	65	5620	300	1010–13,000	69
Asian tropical								
Coniferous	2340[a]	890	1450–3230	2	5010[a]	1350	3000–9000	4
Broadleaf	5400[a]	230	2300–10,750	79	8520[a]	290	3260–15,100	121

[a]Significant differences for pair-wise comparisons between forest types in a climatic zone marked as: *$p < 0.05$.
[b]$p < 0.01$.
[c]$p < 0.001$. From Liu *et al.* (2004).

Textbox 2 Standardized climatic indices

To compare the effects of two variables such as "annual average temperature" and "annual precipitation" on foliar and total litter fall, these may be transformed to standardized units. The standardized temperature and precipitation are dimensionless with a mean of zero and a standard deviation of one. Thus, the values of the coefficients for temperature and precipitation in a multiple regression equation indicate their contributions to the model explaining the variation in foliar and total litterfall in terms of a relative unit change. Most statistical software packages can make such transformations, and some even calculate standardized regression coefficients by default. Using standardized temperature and precipitation in a multiple regression (Table 5) resulted in a significantly larger coefficient (steeper slope) for temperature than for precipitation in the model for total litter fall in broadleaf forests. This indicates that for broadleaf forests, temperature has a stronger effect on total litter fall than precipitation on a relative basis and within the present ranges.

forests than for coniferous forests. This relationship was generally valid over all the biomes (Table 5).

Further, the total litter fall in broadleaf forests tends to decrease at a precipitation above about 2500 mm (Fig. 6). The negative effect of high precipitation on litter production is possibly due to a higher number of cloudy days and lower solar radiation, which can reduce tree photosynthesis and result in lower productivity and litter fall. For the relationships between leaf litter fall and climatic factors, the pattern was generally similar to that of total litter fall.

V. THE FIBER STRUCTURE AND ORGANIC–CHEMICAL COMPONENTS OF PLANT LITTER

A. The Fiber

In the plant fibers, the cellulose, the hemicellulose (together called holocellulose), and the lignin molecule are not only combined physically but normally more or less encrusted. The formation of lignin in the fibers (lignification) of the live plant is a slower process than the formation of cellulose and hemicelluloses and the result is that the last formed parts of the fiber structure may be very low in lignin or not lignified at all and the older parts richer, thus causing a lignin "cover" for part of the holocelluloses.

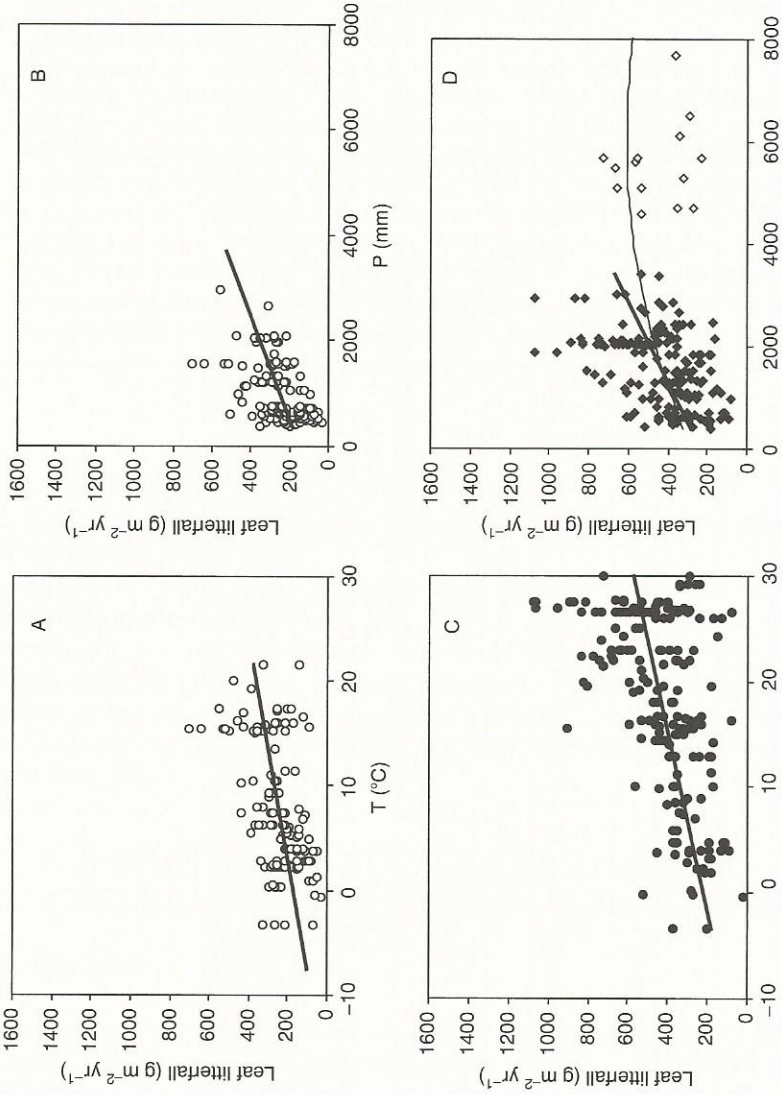
Table 5 Multiple linear regressions relating the logarithms for total litter fall ln(total) to standardized ln(temp) and ln(precip)[a]

Forest type	Constant		ln(Temp)		ln(Precip)		n	R^2_{adj}
	Intercept	p	Slope	p	Slope	p		

Table 5 Multiple linear regressions relating the logarithms for total litter fall ln(ltotal) to standardized ln(temp) and ln(precip)[a]

	Constant		ln(Temp)		ln(Precip)			
Forest type	Intercept	p	Slope	p	Slope	p	n	R^2_{adj}
Broadleaf	6.3	<0.001	0.298	<0.001	0.11	<0.005	240	0.498
Coniferous	5.71	<0.001	0.169	<0.001	0.116	<0.002	199	0.272
Broadleaf and coniferous	6.032	<0.001	0.331	<0.001	0.13	<0.001	439	0.535

[a]The litter fall data originating from Europe and Asia covered the latitudes from ca. 7°S to 69°N, a temperature range from ca. −7°C to 30°C, and a precipitation range from approximately 350 to 10,400 mm. Intercepts between broadleaf and coniferous litter fall were significantly different, as were the coefficients for temperature between broadleaf and coniferous litter fall. Data from Liu *et al.* (2004).



The wood cell is composed of various
tissue. In the wood cell, the middle lame
compound middle lamella, which is loc
adjacent cells (Core *et al.*, 1979). The c
(P) and a secondary wall (S), which ha
S3 (Fig. 7). The S3 layer is located clo
thickest layer is the middle layer (S2),
secondary wall. These layers are distin
lose occurs in different microfibrillar o

In the wood, lignin is distributed th
the compound middle lamella, with the
lamella. The secondary wall makes up
and most of the cell wall lignin (60–80
Thomas, 1982a,b). The hemicelluloses
within the wall (Parameswaran and Li
microfibrils, which, in their turn, occu
the cell wall, cellulose forms microfib
fibrils.

There is a tremendous diversity in w
grow in the boreal and temperate zones
1980) and the example of a wood cell g
our purpose is to give an overview o
decomposers.

B. The Organic–Chemical Compon

Together with lignin, which is a compl
ic rings, the polymer carbohydrates for
common organic components in plant
as cellulose and hemicelluloses. The
them, the cellulose, is made up of
forming long straight chains of mole
turn, organized into fibers. Cellulose m
the litter mass (Table 6).

Figure 6 Variation of foliar litter fall
annual precipitation (mm) in coniferous
precipitation (D) leaf litter fall in broad
when including all data. However, when
excluded, a linear relationship held on (fr

The wood cell is composed of various layers (Fig. 7) of cells combined into tissue. In the wood cell, the middle lamella and the primary wall make up the compound middle lamella, which is located between the secondary walls of adjacent cells (Core *et al.*, 1979). The cell wall is made up of a primary wall (P) and a secondary wall (S), which has three layers designated S1, S2, and S3 (Fig. 7). The S3 layer is located closest to the lumen (L). Normally, the thickest layer is the middle layer (S2), and S1 is the outermost layer of the secondary wall. These layers are distinct from each other because the cellulose occurs in different microfibrillar orientations.

In the wood, lignin is distributed throughout the secondary (S) wall and the compound middle lamella, with the highest concentration in the middle lamella. The secondary wall makes up a large part of the total cell wall area and most of the cell wall lignin (60–80%) is located in this region (Saka and Thomas, 1982a,b). The hemicelluloses are distributed parallel to the lignin within the wall (Parameswaran and Liese, 1982) and surround the cellulose microfibrils, which, in their turn, occupy spaces between the fibrils. Within the cell wall, cellulose forms microfibrils, which are organized into bigger fibrils.

There is a tremendous diversity in wood structure among tree species that grow in the boreal and temperate zones of the world (Panshin and de Zeeuw, 1980) and the example of a wood cell given in Fig. 7 is thus not general. Still, our purpose is to give an overview of the environment for the microbial decomposers.

B. The Organic–Chemical Components

Together with lignin, which is a complex polymer formed mainly by aromatic rings, the polymer carbohydrates form the plant fiber structures. The most common organic components in plant litter are such polymer carbohydrates as cellulose and hemicelluloses. The quantitatively most common among them, the cellulose, is made up of glucose units connected 1–4 bonds, forming long straight chains of molecules (Fig. 8) with the chains, in their turn, organized into fibers. Cellulose may constitute between 20 and 30% of the litter mass (Table 6).

Figure 6 Variation of foliar litter fall with mean annual temperature (°C) and annual precipitation (mm) in coniferous (A, B) and broadleaf forests (C, D). For precipitation (D) leaf litter fall in broadleaf forests had a non-linear relationship when including all data. However, when stands with precipitation >4000 mm were excluded, a linear relationship held on (from Liu *et al.*, 2004).

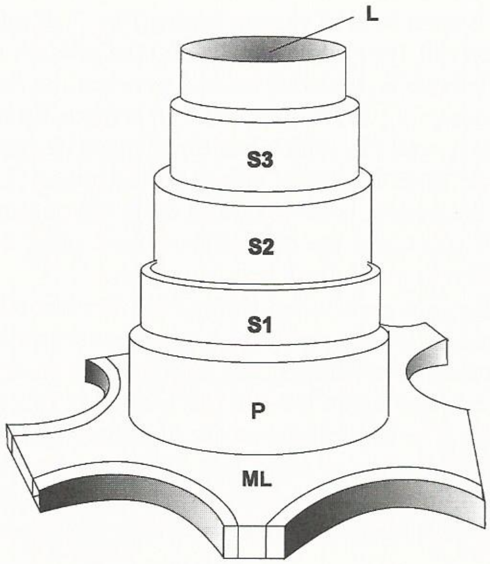


Figure 7 A model for a cell wall and the arrangement of cellulose, hemicelluloses, and lignin in the secondary wall. ML, middle lamella; P, primary wall; S1, S2, and S3, layers of the secondary wall; L, lumen. Each layer has a different microfibrillar orientation and thickness. Based on Eriksson *et al.* (1990).

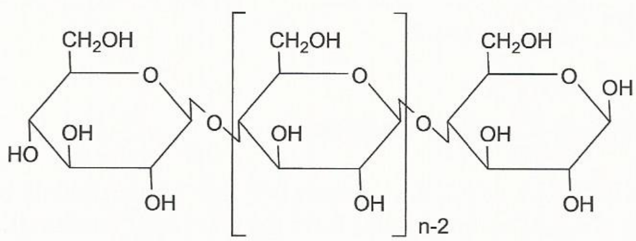


Figure 8 The cellulose made of glucose units form long chains of *n* identical molecules. Carbon atom numbers 1 and 4 are connected with an oxygen bridge giving a 1 to 4 bond.

The hemicelluloses are polymers of sugars other than glucose which form long chains of molecules, which are built into the fiber with names related to the corresponding simple sugars, namely mannan, galactan, arabinan, xylan, and others. Together, they may make up as much as 30 to 40% of the fiber, and are normally present in the range between 1 and 10% each (Table 6). It appears that the molecules of the different sugars are mixed and thus the chains are not always homogeneous. The chains may also be branched.

Lignin often makes up between 15 and 40% of the litter mass, but, in some extreme cases, we may find foliar litter with very low lignin contents (e.g., 4%

Table 6 Comparison of the major organic–chemical compounds in a few boreal litter types[a]

Litter type	Water soluble	Ethanol soluble	Lignin	Cellulose	Mannans	Xylans	Galactans	Arabinans	Rhamnans	Ratio hemicellulose to cellulose
	Concentration of compound (mg g^{-1})									
Deciduous										
Leaf litter										
Silver birch	241	57	330	166	14	77	44	49	16	1.2
Grey alder	254	39	264	116	10	30	32	44	9	1.08
Wood										
Silver birch	[illegible]	[illegible]	217	351	9	207	[illegible]	[illegible]	[illegible]	[illegible]

Table 6 Comparison of the major organic–chemical compounds in a few boreal litter types[a]

Litter type	Concentration of compound ($mg\ g^{-1}$)									Ratio hemicellulose to cellulose
	Water soluble	Ethanol soluble	Lignin	Cellulose	Mannans	Xylans	Galactans	Arabinans	Rhamnans	
Deciduous										
Leaf litter										
Silver birch	241	57	330	166	14	77	44	49	16	1.2
Grey alder	254	39	264	116	10	30	32	44	9	1.08
Wood										
Silver birch			217	351	9	207				
Trembling aspen			220	462	16	189				
Red alder			246	470	4	176				
Coniferous										
Needle litter										
Scots pine	164	113	231	245	75	23	32	36	3	0.69
Lodgepole pine	103	42	381	254	90	34	46	48	6	0.88
Norway spruce	32	48	318	288	105	33	28	40	7	0.74
Wood										
Scots pine			300	383	111	65				
Red pine			279	449	123	84				
Norway spruce			271	416	136	52				

[a]Foliar litter data from Berg and Ekbohm (1991), wood data from Eriksson *et al.* (1990).

in leaf litter of flowering dogwood) and values as high as 50% have been recorded for leaves of common beech from temperate forests. The structure of lignin molecules varies among plant species, and one example is illustrated in Fig. 9. Even if some basic structural elements are common across species, probably each plant species has its own variety of lignin, with varying amounts of smaller groups, such as the methoxyl groups and other substituents (Fig. 9), located at different sites in the molecule.

The terminology pertaining to lignin and its transformation products is not always clear. Different analytical methods may produce different results. The name of the analytical method is important since it specifies more exactly what "kind" of lignin was analyzed. Furthermore, the native lignin of different species may be specified by the name of the plant species, for example, Norway spruce lignin. Another complicating factor is that when the lignin molecules start decomposing, the structure changes and the term "lignin" has been questioned for such modified lignin (see Textbox 3).

The lignin content of hardwoods is generally lower than that of softwoods, although the range is wide in both groups. Generally, the types of lignin formed in coniferous trees and in deciduous trees are different. Whereas the deciduous lignin contains varying ratios of syringyl and guaiacyl units (Fig. 10), the coniferous ones have mainly guaiacyl lignin (Fengel and Wegener, 1983). These components, being important building units, have properties that affect the basic structure of lignin, which may be of importance for the microbial attack on lignin and thus on the litter as a whole (see Chapter 3).

Litter contains quantitatively large groups of more low-molecular substances too, such as amino acids, simple sugars, lower fatty acids, and lower phenolic substances. More complex compounds, such as high-molecular fatty acids and phenolic compounds, are also found and probably some hundred different molecules can be distinguished within these groups. Often, they are analyzed as water-solubles for the former group and ethanol or acetone solubles for the latter. Although many of these have been identified and described, no clear functional roles can be seen for particular compounds in the decomposition process. One notable exception is the large group of phenolics of different kinds (for example, benzoic acid) which suppress microbial activity.

VI. NUTRIENTS

A. General Features

The chemical composition of live leaves and needles is also reflected in the litter formed. This applies to several compounds, such as the relative composition of hemicelluloses, cellulose, and lignin, as well as to chemical

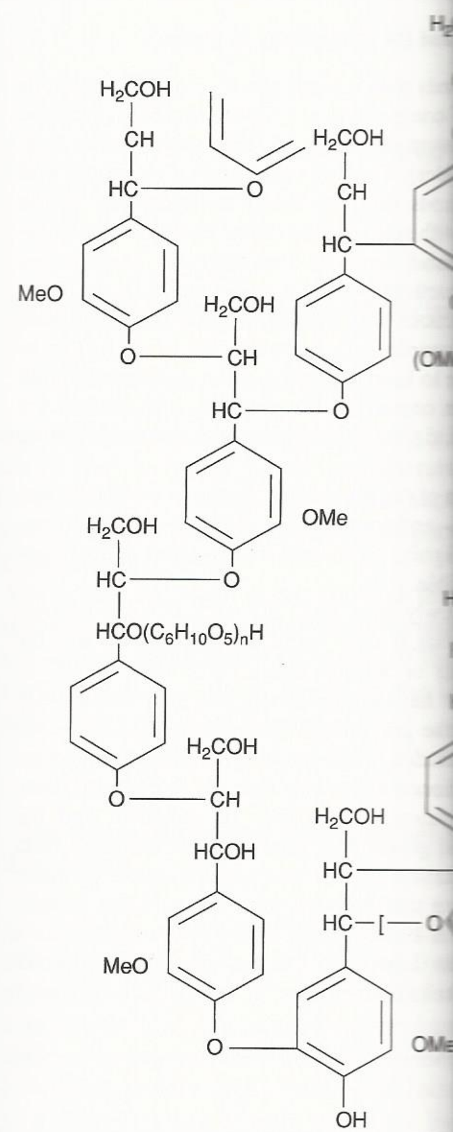


Figure 9 Lignin molecule

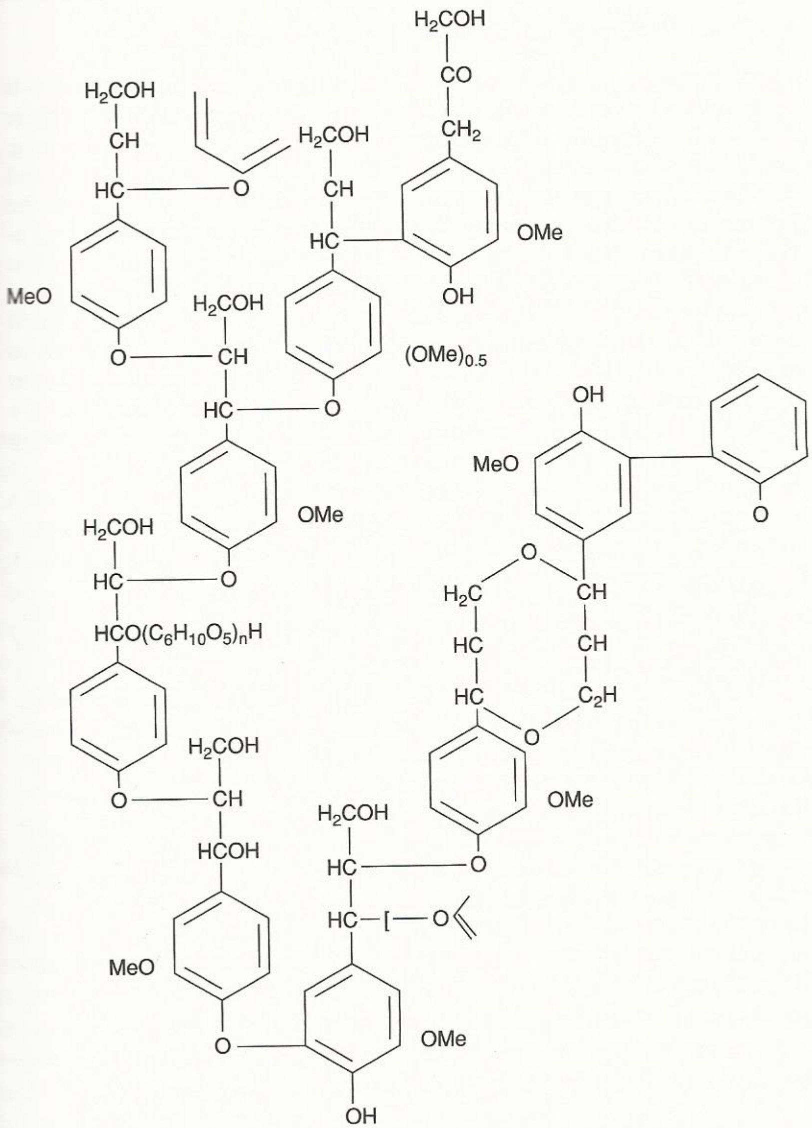


Figure 9 Lignin molecule from Norway spruce.

elements. The nutrients found in newly shed plant litter have their origin in the strictly controlled structures of live plant parts, and a nutrient such as nitrogen could be found, for example, in membranes, nucleic acids, and proteins. When a leaf starts dying and turns into litter, these structures

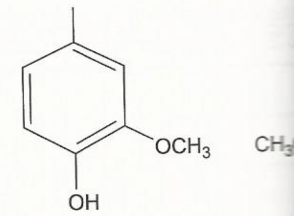
Textbox 3 Different lignin names and the terminology of lignins

Lignin is rather a group of compounds than a single specific one. The methods to determine lignins as a group of compounds are numerous. Most of these methods have been intended to determine lignin in fresh plant matter (e.g. newly harvested wood or fresh fodder). That was the original intention, and there are several gravimetric methods that are based on hydrolysis of the polymer carbohydrates, normally with sulfuric acid. Some examples are sulfuric-acid lignin (Klason lignin), Effland lignin or acid-detergent lignin, often called ADL. There are also other methods, such as milled wood lignin based on, among others, numerous extractions with dioxan. Further methods based on extensive oxidation, using for example CuO, hydrolyze the lignin further to more basic units. However, we have to keep in mind that the gravimetric lignin may also contain "ash", which can consist of, for example, silicates that are not hydrolyzed in the sulfuric acid and whose contents increases during decomposition.

The authors have compared some of the gravimetric methods using the same substrate—Scots pine needle litter—and found about the same lignin concentration for Klason lignin, Effland lignin, ADL, and milled-wood lignin. Thus these methods were rather compatible.

If we apply these methods to newly shed litter the term *lignin* is correct. Considering the number of methods it may be better, though, to use the method's name (e.g. Effland lignin or Klason lignin). For the "lignin" in partly decomposed litter we do not have any generally accepted terminology and it appears that when we use the gravimetric methods more compounds than native (original) lignin are included in the fraction determined that way. Of course the "ash" fraction mentioned above can increase in concentration, but also products of the humification process may be included, and the concentration of N increases in the gravimetric lignins as the decomposition process proceeds. So far determination of this combined fraction of lignin plus humification products has been useful in decomposition studies, in spite of the fact that the terminology is controversial. We have suggested as a provisional term "the NIT–Lignin complex" for this fraction in decomposing litter, a term that indicates the inclusion of newly formed humic substances.

break up, at least in part, and some part of each nutrient is retrieved to the live plant while another part remains in the newly dead material. What is often measured as just a mineral nutrient, say, nitrogen, is thus bound in different chemical structures in the litter, such as partly decomposed proteins and nucleic acids. In part, it becomes tied to lignin, which has started to be modified as the humification process has begun. Thus, it is found in compounds with different properties. In foliar litter, nitrogen can be found in



Guaiacyl

Figure 10 Guaiacyl and syringyl, the

amounts between around 2 and 30 mg
such as that in branches, the concentr
(Table 8). Phosphorus is bound in n
proteins, among other molecules (for p
ple, Stevenson, 1994).

When the microbial ingrowth and
distribution of nutrients in different co
tions will be very different from that of
we will not discuss the nutrients in th
rather as just chemical elements.

B. The Trees Withdraw Nutrients b Foliar Litter

Many genera, such as pine, growin
which, in addition, often are drained
retrieve the main part of nutrients b
"inner circulation" is a conserving me
al differs among nutrients as well as a
the N_2-fixing genera such as alder and
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In the case of Scots pine, silver birch
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(Table 9; Fig. 11). This retrieval p
possibly by an early frost, which occ

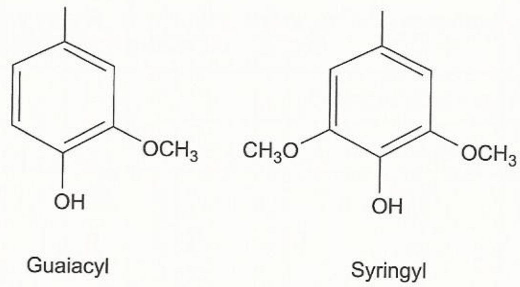

Figure 10 Guaiacyl and syringyl, the important structural units of lignin.

amounts between around 2 and 30 mg g^{-1} (Table 7). In woody structures, such as that in branches, the concentration may be as low as 0.4 mg g^{-1} (Table 8). Phosphorus is bound in nucleic acids, and sulfur is found in proteins, among other molecules (for phosphorus and sulfur see, for example, Stevenson, 1994).

When the microbial ingrowth and the decomposition have started, the distribution of nutrients in different compounds as well as their concentrations will be very different from that of the original material. In this chapter, we will not discuss the nutrients in the form of their structural origin but rather as just chemical elements.

B. The Trees Withdraw Nutrients before Shedding their Foliar Litter

Many genera, such as pine, growing on relatively nutrient-poor soils, which, in addition, often are drained from nutrients by repeated wildfires, retrieve the main part of nutrients before shedding the foliar litter. This "inner circulation" is a conserving mechanism for nutrients. This withdrawal differs among nutrients as well as among species. Extreme examples are the N_2-fixing genera such as alder and locust producing leaf litter that has as high a concentration of nitrogen as the live leaves.

In the case of Scots pine, silver birch, and trembling aspen, the concentration of N may decrease to about one-third of that in live leaves when the leaves and needles are shed in the autumn. For example, for Scots pine, the concentration may decrease from about 12 to 14 mg g^{-1} to about 3 to 4 mg g^{-1} (Table 9; Fig. 11). This retrieval process may, of course, be disturbed, possibly by an early frost, which occasionally would give extreme levels of

Table 7 Concentrations of some major nutrients, ash, and lignin in some selected boreal and temperate foliar litter species

Litter type	Concentration of nutrient (mg g^{-1})									Reference
	N	P	S	K	Ca	Mg	Mn	Ash	Lignin	
Deciduous leaf litter										
Grey alder	30.7	1.37	6.12	15.6	12.3	2.32	0.1	42.4	–	(1)
Silver birch	7.7	1.05	0.8	4.66	11.8	3.3	1.23	22.4	294	(2)
Ash	8.63	1.96	–	15.3	33.2	2.28	0.03	12.2	–	
Mountain ash	7.12	0.31	–	10.8	12.4	2.86	0.3	5.5	–	
Trembling aspen	8.15	0.93	–	5.09	29.9	4.69	0.53	9.3	–	(3)
European maple	5.07	3.15	–	13.1	20.4	1.46	0.12	11.9	–	(5)
Common beech	9.5	1.4	1.3	2.3	7.4	1.2	1.9	n.d.	–	(4)
Coniferous needle litter										
Spruce										
Norway spruce	4.9	0.45	0.73	0.72	17.9	0.65	–	–	–	(6)
Pines										
Scots pine	4.8	0.33	0.55	1.07	4.42	0.49	0.79	10.5	261	(2)
Lodgepole pine	3.9	0.34	0.62	0.56	6.35	0.95	1.79	13.6	–	(2)
Maritime pine	6.8	0.54	1.01	1.95	3.1	1.9	0.59	22	–	(4)
Red pine	6	0.36	0.73	1.4	8.9	2	0.73	36	–	(4)
White pine	5.9	0.21	0.68	0.7	7.2	1.1	0.8	28	–	(4)
Jack pine	7.8	0.64	0.77	2.3	4	2.1	0.25	23	–	(4)
Limber pine	4.3	0.43	0.52	1.1	5.3	1.1	0.21	24	–	(4)

(1) Berg and Ekbohm (1991), (2) Reurslag and Berg (1993), (3) Berg *et al.* (2003), (4) B. Berg and C. McClaugherty (unpublished), (5) Bogatyrev *et al.* (1983), (6) Berg and Tamm (1991).

Table 8 Concentrations of nitrogen, water soluble compounds, and sulfuric-acid lignin in wood from some tree species[a]

Species	Concentration (mg g^{-1})		
	N	Water solubles	Lignin
Norway spruce	0.39	37	271
Common beech	0.92	35	228
Silver birch	0.64	26	195
Trembling aspen	0.55	39	197

[a]Data in part from Staaf and Berg (1989) and Eriksson *et al.* (1991).

N (Table 10). Norway spruce appears to differ from the Scots pine with N concentrations often decreasing to about 50% of that in live needles.

The range in concentrations of remaining P is wider than for N, from 15 to 50%, and in the case of S, the concentration in litter is approximately 38 to 73% of that in the original green needles. For K, there is a difference between coniferous and deciduous trees, with the latter having clearly higher proportions of original contents when shed, that is, concentrations have decreased to a range of 40 to 50% as compared to less than 25% on average for the spruce group, and for pines even less.

Trees not only withdraw part of the nutrients before shedding leaves. At the same time, different soluble carbon components, such as sugars and phenolics, are withdrawn. As a result, the total leaf mass decreases, and as a consequence, the basis for calculation of concentrations changes. This may result in an increase in concentration for those nutrients that are withdrawn only to a low extent (e.g., Ca) and a decrease for those that have been withdrawn to a higher extent. There may also be an influence of soil type, and low pH has been found to have a negative effect on Ca withdrawal. Thus, at sites with a lower soil pH, there is a lower withdrawal, an effect seen only for Ca though (Staaf, 1982).

A study on leaves of common beech (Staaf, 1982) indicates that the withdrawal of nutrients is positively related to the concentration of the element in green leaves (Fig. 12). This relationship was especially steep for N (Fig. 12A), indicating a high withdrawal, while for Ca, the relationship was rather flat (Fig. 12E), indicating lower withdrawal. Thus, calcium was retrieved in relatively small amounts and the net result was an increase in concentration in all cases (to 115–220% of the initial concentration). In the same study, magnesium concentrations ranged from 43 to 113% of the initial concentrations, indicating a high variability in relative withdrawal (Fig. 12F).

The few data on heavy metals indicate that their concentrations increase in senescing leaves before these are shed. Storage of metals in senescent tissues is

Table 9 Concentrations of some nutrients and heavy metals in green leaves collected in July and the corresponding "brown" litter shed some months later (B. Berg, unpublished)[a]

Litter species (type) and % change in concentration from green to brown leaves	Concentration of a nutrient									
	mg g^{-1}							mg kg^{-1}		
	N	P	S	K	Ca	Mg	Mn	Fe	Zn	Cd
Scots pine (green)	12.1	1.36	0.809	5.9	3.9	0.79	0.53	64	49.4	0.1
Scots pine (brown)	3.6	0.2	0.444	0.5	5.6	0.34	1.19	79	48.3	0.1
Concentration change (%)	−70	−85	−45	−92	+44	−57	+125	+23	−2	0
Lodgepole pine (green)	10.5	0.82	1.17	3.84	3.99	0.93	0.82	–	–	–
Lodgepole pine (brown)	3.1	0.29	0.441	0.5	8.7	1.06	2.03	–	–	–
Concentration change (%)	−70	−65	−62	−87	+118	+14	+148	–	–	–
Norway spruce (green)	8.5	1.32	–	4.01	11.3	1.22	1.07	–	–	–
Norway spruce (brown)	4.2	0.41	–	0.97	13.1	0.89	1.32	–	–	–
Concentration change (%)	−51	−69	–	−76	+16	−27	+23	–	–	–
Silver birch (green)	24.3	1.96	1.535	9	9.5	3.37	0.76	53	140	0.2
Silver birch (brown)	7.7	1.05	0.8	4.66	11.8	3.3	1.23	61	340	0.8
Concentration change (%)	−68	−46	−48	−48	+24	−2	+62	+15	+143	+300
Trembling aspen (green)	24.2	2.12	1.87	14.2	8.4	2.29	0.1	44	107.1	0.3
Trembling aspen (brown)	6.8	0.63	1.369	6.3	17.1	2.13	0.15	46.4	126.1	0.5
Concentration change (%)	−72	−70	−27	−56	+104	−7	+50	+5	+18	+67
Common beech (green)	22.6	1.44	1.18	5.42	7.7	1.67	–	–	–	–
Common beech (brown)	9.1	0.63	1.21	2.7	10	1.7	–	–	–	–
Concentration change (%)[b]	−60	−56	+3	−50	30	+2	–	–	–	–

[a] The difference between green and brown leaves in their chemical composition is also reported as the percentage concentration change.
[b] Data for common beech from Staaf (1982).

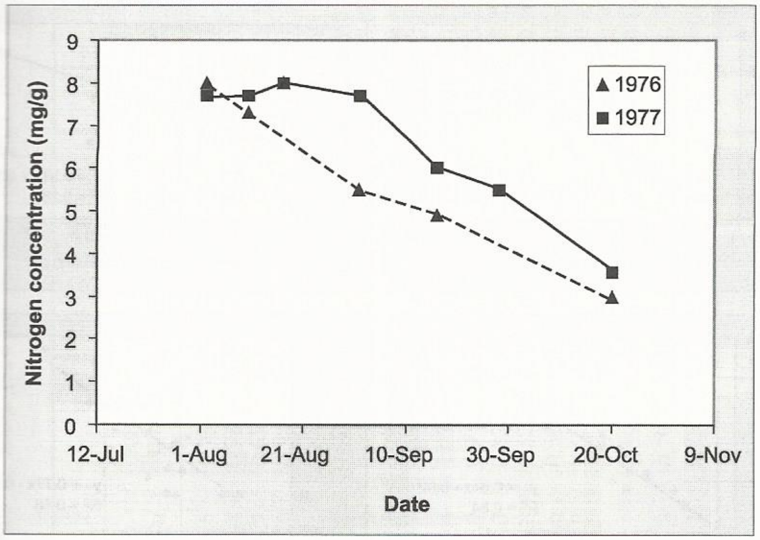

Figure 11 The withdrawal of nutrients for the major nutrients normally results in a decrease in concentration. The figure shows the change in concentration of N in Scots pine needles during the months before shedding.

interpreted sometimes as a "detoxification mechanism" (Ernst, 1998). For example, Dahmani-Muller *et al.* (2000) found that Zn, Cd, Pb, and Cu concentrations in brown leaves of Sea Pink growing near a former metal smelter were 3 to 8 times higher than those in green leaves.

C. Scots Pine—A Case Study

1. Annual Variation in Chemical Composition at One Site

Even in a given stand, there is a clear variation in the chemical composition of the newly shed needle litter among years. This is illustrated in an investigation in which some nutrients in Scots pine needle litter were followed for 17 consecutive years (Table 10). A clear difference may be seen among years, but still no pattern in the variation in concentrations could be distinguished. A trend analysis did not reveal any significant change in nutrient concentrations over time.

At the site of our case study, the average concentration for nitrogen in needle litter was 4.2 mg g^{-1}, varying between years from 3.8 mg g^{-1} up to an exceptionally high value of 10.4 mg g^{-1} (Table 10). Compared with other years, such a value is disproportionately high also in relation to concentrations of other elements, such as phosphorus and sulfur, in the same year. The

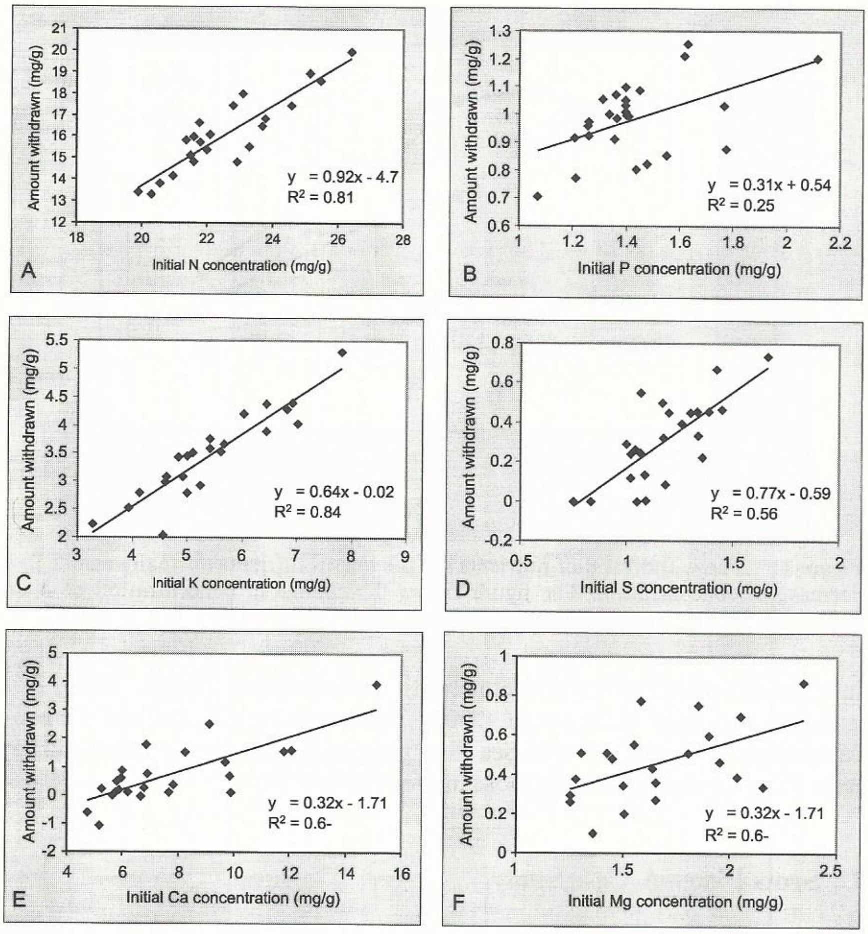

Figure 12 The linear relationships between concentrations of nutrients (N, P, K, S, Ca, and Mg) in green leaves of common beech and the amount of nutrients withdrawn from the leaves during senescence. Each dot represents a sampling in a separate forest (from Staaf, 1982).

frequency of occurrence of such high values has not been established and may be regarded as a consequence of an unknown extreme event. Even excluding that extreme value, with the next highest value being 4.8 mg g^{-1}, there is still a considerable year-to-year variation (a range factor of 1.3) in nitrogen concentration. The reason for this variation is not yet known.

The concentration of phosphorus varied between 0.17 and 0.33 mg g^{-1}, with a factor of 2.5. For sulfur, the range was from 0.29 to 0.78 mg g^{-1}, also with a factor of 2.5. Within the same site, the annual variation for calcium

Table 10 Annual variation in concentrations of solubles, lignin, and nutrients of Scots pine needle litter (in part, from Berg *et al.*, 1993)[a]

Sampling year	Concentration (mg g^{-1})											
	Water solubles	Ethanol solubles	Lignin	N	P	S	Ca	K	Mg	Mn	Ash	N:P:S
1973	92	120	223	3.8	0.19	0.42	6.5	0.73	0.38	1.55	23	1:0.050:0.111
1974	145	84	276	4.2	0.22	0.29	5.4	0.71	0.49	n.d.	24	1:0.052:0.069
1975	172	107	238	3.4	0.2	0.32	4.7	0.61	0.39	n.d.	19	1:0.048:0.094
1976	151	89	255	4	0.21	0.36	4.9	0.53	0.42	n.d.	n.d.	1:0.053:0.090
1977	202	102	224	4.1	0.19	0.38	6	0.87	0.42	1.02	n.d.	1:0.046:0.093
1978	164	96	257	3.8	0.21	0.33	5.5	0.62	0.55	1	20	1:0.055:0.087

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	Concentration (mg g^{-1})											
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1974	145	84	276	4.2	0.22	0.29	5.4	0.71	0.49	n.d.	24	1:0.052:0.069
1975	172	107	238	3.4	0.2	0.32	4.7	0.61	0.39	n.d.	19	1:0.048:0.094
1976	151	89	255	4	0.21	0.36	4.9	0.53	0.42	n.d.	n.d.	1:0.053:0.090
1977	202	102	224	4.1	0.19	0.38	6	0.87	0.42	1.02	n.d.	1:0.046:0.093
1978	164	96	257	3.8	0.21	0.33	5.5	0.62	0.55	1	20	1:0.055:0.087
1979	129	95	288	10.4	0.29	0.78	2.3	0.97	0.39	0.31	12	1:0.028:0.078
1980	180	102	246	3.8	0.18	0.5	6.1	1.72	0.53	0.77	17	1:0.047:0.132
1981	213	94	231	3.9	0.28	0.61	7.1	1.02	0.58	1.17	23	1:0.072:0.152
1982	164	113	231	4.8	0.33	0.55	4.4	1.07	0.49	0.79	19	1:0.069:0.115
1983	178	112	229	3.8	0.3	0.45	5.9	0.9	0.39	1.08	26	1:0.079:0.118
1984	82	116	288	3.7	0.21	0.47	6.3	0.82	0.44	1.12	22	1:0.057:0.127
1985	182	94	241	3	0.19	0.45	4.8	0.52	0.38	1.24	18	1:0.063:0.150
1986	170	89	257	4	0.23	0.44	5.6	0.58	0.57	1.13	20	1:0.058:0.110
1987	162	100	250	3.8	0.21	0.42	4.9	0.55	0.41	1.18	18	1:0.055:0.111
1988	165	94	247	3.8	0.21	0.39	5	0.67	0.38	1.18	19	1:0.055:0.106
1989	n.d.	n.d.	n.d.	3.6	0.17	0.38	4	0.59	0.42	0.92	n.d.	1:0.047:0.106
Mean:	159	100	249	4.2	0.23	0.44	5.3	0.79	0.45	1.03	20	1:0.055:0.105
S.D.:	35	11	21	1.6	0.05	0.12	1.1	0.29	0.07	0.27	3.5	

[a] The data show a certain interannual variation. A value for N as high as 10.4 mg g^{-1} probably should be regarded as caused by an event disturbing the retrieval process.

concentrations ranged from 2.3 to 7.1 mg g^{-1}, with a factor of 3.1, a relatively large variation, considering several investigations indicating that Ca concentration in leaves is strongly dependent on soil properties. For potassium, the mean value was 0.79 mg g^{-1} and the range from 0.52 to 1.72 mg g^{-1}, giving a factor of 3. For magnesium, the mean was 0.45 mg g^{-1}, and the range from 0.38 to 0.58 mg g^{-1}—a factor of 1.5. The highest variability, with a factor of 5, was found for manganese: the mean value was 1.03 mg g^{-1} and the range was from 0.31 to 1.55 mg g^{-1}.

The concentrations of the main nutrients, N, P, and S, were in the average proportions of 1:0.055:0.105. As we will see later, especially N and P have been ascribed the role of being rate limiting for decomposition (Chapter 4). When we relate both P and S to N, the relative proportions are seen to vary considerably—for P from 0.028 to 0.079 and for S from 0.069 to 0.156 (Table 10). This variation in relative proportions between years may decide which nutrient is rate regulating in a particular year (see Chapter 4).

Ash content in the collections of Scots pine needle litter, with an average of 20 mg g^{-1}, was relatively low as compared with those of other tree species (Bogatyrev *et al.*, 1983). Concentrations of water-soluble substances ranged from 82 to 213 mg g^{-1}, with the average value of 159 mg g^{-1}, and lignin concentrations ranged from 223 to 288 mg g^{-1} with an average value of 249 mg g^{-1}, a range factor of about 1.2.

2. *Variation among Scots Pine Stands and in a Transect of Forests*

In Europe, Scots pine grows mainly from Barents Sea in the north to the Mediterranean in the south, although it forms forests to about the latitude of the Alps and the Carpathians. Scots pine may grow on nutrient-poor granite sand and on clayey soil. On a European scale, the magnitude and pattern of litter fall varies with the geographical position and climate (see Section IV.C.). The chemical composition of foliar litter varies also with the site's geographical position and climate (Berg *et al.*, 1995a). A study along a transect ranging from Barents Sea in the north to about the Carpathian Mountains in the south, encompassing half the length of Europe, shows a clear trend in chemical composition with climate (Fig. 13). Along this climatic gradient, concentrations of nitrogen, phosphorus, sulfur, and potassium are positively related to AET. This behavior appears to be general over the genus *Pinus* and has been found also when different pine species were combined in a regression. Nitrogen levels range from about 3 mg g^{-1} close to Barents Sea to about 9 mg g^{-1} at the more southern locations (Fig. 13). In contrast, for manganese, a weak relationship is negative, meaning that the highest manganese concentrations were found at low AET values in the north, and the lowest at the southern sites with high AET. Whereas there may be an

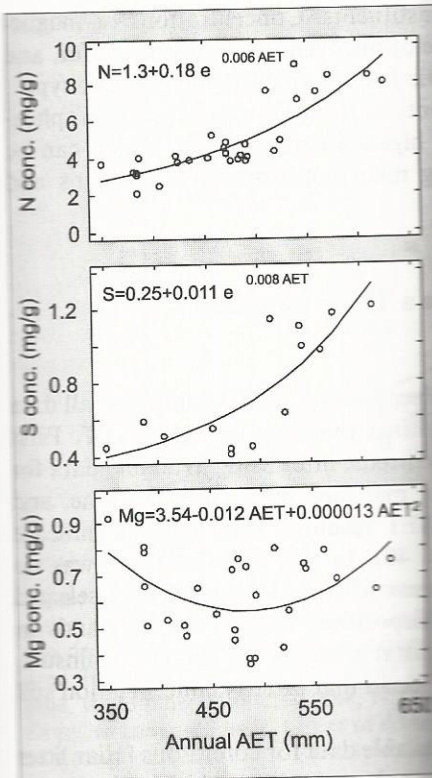

Figure 13 Relationships between actual e
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explanation related to climate for nit
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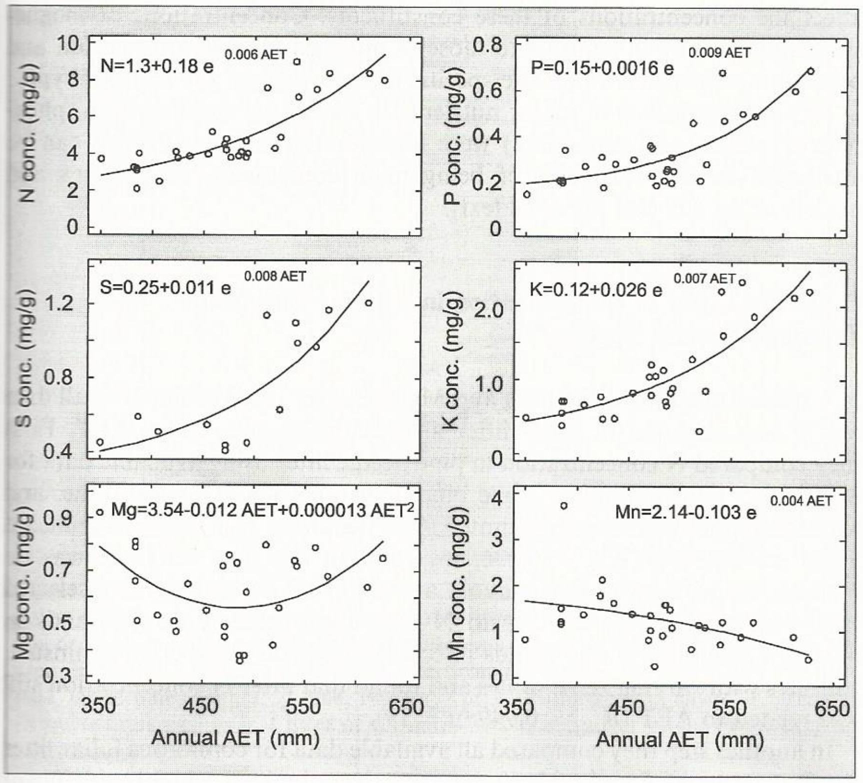

Figure 13 Relationships between actual evapotranspiration (AET) and concentrations of N, P, S, K, Mg, and Mn in newly shed Scots pine needle litter collected in a transect from Barents Sea to the Alps and the Carpathians in the south (from Berg *et al.*, 1995).

explanation related to climate for nitrogen and, consequently, also for phosphorus and sulfur, an explanation related to manganese may be less evident and possibly AET is just an indirect index. The warmer sites with higher precipitation, having higher AET values, thus produced litter rich in nitrogen, phosphorus, sulfur, and potassium and poor in manganese.

These increases in concentrations of N, P, S, and K in litter with increasing AET and decreasing latitude may very well reflect a direct or an indirect effect of climate on litter quality. Direct effects may be related to differences in physiological requirements for these nutrients in live leaves and possibilities of allocating them in larger quantities due to, for example, warmer and wetter growing seasons in the southern end of the Scots pine area.

Calcium and magnesium did not exhibit any correlation with latitude or with other nutrients within Scots pine. The lack of any relationship for calcium and magnesium to AET indicates that factors other than climate affect the concentrations of these constituents. Concentrations of magnesium and calcium, in contrast to those of nitrogen, phosphorus, sulfur, and potassium, depend more on site-specific factors, mainly, the bedrock type.

The concentrations of major nutrients in fresh litter fall (nitrogen, phosphorus, sulfur, and potassium) were highly intercorrelated, which can be attributed to their property of being main constituents of proteins and nucleic acids, etc. (see previous text).

D. Foliar Litter N Concentration in a Trans-European Transect, Several Species

In a trans-European study Berg and Meentemeyer (2001) compared all data for N concentration in foliar litter against the climatic index AET. First they compared N concentration in pine needle litter using available data for Scots pine, lodgepole pine, stone pine, maritime pine, Corsican pine, and Monterey pine with average annual AET resulting in a highly significant linear relationship ($R^2_{adj} = 0.536$; $n = 40$). In this data set there was no relationship with latitude. To avoid areas with N deposition they selected sites with clearly very low or no N deposition, namely forest stands in northern Scandinavia and stands in coastal areas on the Iberian peninsula, still sites with varying AET values and found that litter N concentration still was related to AET ($R^2_{adj} = 0.749$: $n = 19$).

In another step they compared all available data for coniferous foliar litter for Europe to AET and with 60 data sets they obtained a highly significant relationship with $R^2_{adj} = 0.370$. In addition to the above pine species this data set included Norway spruce, Sitka spruce, silver fir, grand fir, and Douglas fir. Adding available data for deciduous foliar litter did not change the relationship ($R^2_{adj} = 0.344$; $n = 68$; Fig. 14) and the data for deciduous litter alone formed a significant relationship ($R^2_{adj} = 0.800$; $n = 8$) between N and AET although based on a small number of samples.

It thus appears that there may be a certain generality to the relationship between climate and litter N concentration at least for the boreal, temperate and Mediterranean climatic zones.

E. Several Deciduous and Coniferous Leaf Litters

1. Nutrients in Litter Fall—Similarities and Differences among Species

To make a thorough overview of the chemical composition of the most common litter types in a given ecosystem is not yet possible due to the lack of basic information. We may distinguish some main patterns,

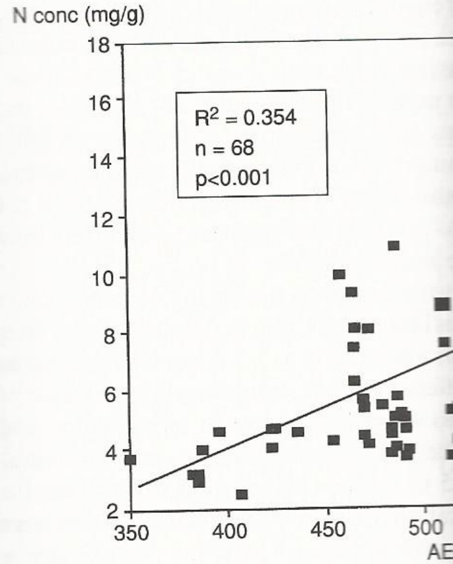

Figure 14 A linear relationship between cli
ration (AET) and N concentration in foliar
and deciduous litter across Europe from Bar
used. Included in the data set is foliar litter fr
pine, stone pine, Monterey pine, Norway s
Douglas fir as well as leaf litter of common
Meentemeyer (2001).

though, which we may relate to tree
patterns.

Litter chemical composition may be
nutrient supply, climate, and tree speci
north European tree species will illustr
there are general differences between th
trees (Table 7), one difference being the
(Table 6), there are also clear difference
main groups.

Average values from a large set of da
indicate a clear tendency in nutrient ri
rally, leaves of silver birch are more
beech, followed by those of Norway
Scots pine needles (Table 7), which are
picture applies to most of the measured
nitrogen, birch and beech leaf litter ha
spruce and beech have similar levels. T

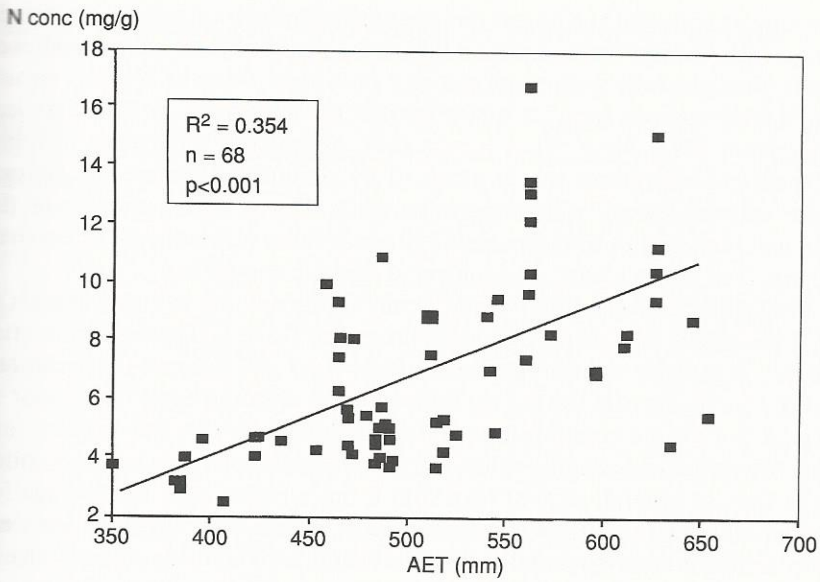

Figure 14 A linear relationship between climate as indexed by actual evapotranspiration (AET) and N concentration in foliar litter. All available data on coniferous and deciduous litter across Europe from Barents Sea to the Mediterranean area were used. Included in the data set is foliar litter from Scots pine, lodgepole pine, maritime pine, stone pine, Monterey pine, Norway spruce, Sitka spruce, silver fir, grand fir, Douglas fir as well as leaf litter of common beech, and silver birch. From Berg and Meentemeyer (2001).

though, which we may relate to tree genera/species and their nutritional patterns.

Litter chemical composition may be related to a few factors such as soil nutrient supply, climate, and tree species, and a set of data covering some north European tree species will illustrate some basic differences. Although there are general differences between the groups of deciduous and coniferous trees (Table 7), one difference being the contents of hemicelluloses and lignin (Table 6), there are also clear differences among species within each of these main groups.

Average values from a large set of data for some major boreal tree species indicate a clear tendency in nutrient richness among genera/species. Generally, leaves of silver birch are more nutrient-rich than those of common beech, followed by those of Norway spruce. The most nutrient-poor are Scots pine needles (Table 7), which are close to those of lodgepole pine. This picture applies to most of the measured nutrients (N, Mg, K, Mn). Regarding nitrogen, birch and beech leaf litter have similar levels, and for phosphorus, spruce and beech have similar levels. This set of data originates from stands growing on soils and at climates representative for the species but is confirmed by pair-wise comparisons made on the same soil and climate where needles of Scots pine generally were more nutrient poor than those of Norway spruce and a tendency was seen for spruce needles to be less nutrient rich than leaf litter from silver birch. That means that, aside from differences in foliar nutrient concentrations that are caused by climatic or site-specific factors, clear between-species differences also exist. The results demonstrate the inherent tendency of some species to produce more nutrient-rich litters than others, even under identical edaphic and climatic conditions.

The coniferous foliar litter, on the whole, appears poorer in nutrients such as N, P, Ca, and K than do the deciduous litters (see Table 7). The coniferous litter species, in general, had nitrogen levels under 7 mg g^{-1}, whereas the deciduous levels were higher and the groups differed in phosphorus levels by a factor of at least 3. Calcium concentration was exceptionally low in pine needles, and Norway spruce had a higher value, whereas the deciduous trees had concentrations that, in general, were at least 5 to 6 times higher than the average for coniferous litter. In contrast, concentrations of magnesium and manganese were more similar in coniferous and deciduous foliar litter. There was even a tendency for Mn to be lower in the deciduous leaves as compared to pine needle litter.

2. *Chemical Composition across Climatic Transects*

Not only Scots pine appears to exhibit variation in litter chemical composition with climate. For other pine species, available data for nitrogen in foliar litter indicate that they follow the same pattern as Scots pine and all available data for AET and foliar litter including pine, spruce, and deciduous trees manifest the same pattern. Thus, the finding that N concentration in litter fall can be related to climate has a higher generality (Fig. 13). In that comparison, N_2-fixing species were excluded. For Mn, there was a general negative relationship to AET, also similar to Scots pine. However, no such general relationships have yet been found for other nutrients, such as P, S, and K.

3. *Chemical Composition as Influenced by Soil Properties*

The influence of soil chemical composition and nutrient availability on litter chemical composition is well illustrated by a study on common beech leaves in 24 stands in a climatologically homogeneous area. Ten plots with mull soils had significantly higher humus pH, and the shed litter had higher concentrations of Ca and Mg than litter at those with a mor soil. In contrast, the concentrations of N, P, S, and K were not affected by soil type (Table 11). The author (Staaf, 1982) did not mention the chemical composition of the mineral soil.

Table 11 Variation in nutrients composi

Plot no.	N	P
Mor humus		
15	9.1	0.49
19	9.4	0.41
23	9.2	0.41
14	9.9	0.54
6	8	1.42
20	9.2	0.56
21	9.2	0.4
9	8.7	0.56
18	9.7	0.54
24	8.6	0.36
10	10.1	0.82
8	9.2	1.16
5	8.7	0.54
7	7.8	1.01
Average	9.06	0.66
SD	0.43	0.1
Mull humus		
3	8.3	0.49
1	9.1	0.45
2	9.9	0.56
4	8.1	0.58
13	8.6	0.42
12	8.9	0.82
11	9.3	0.56
16	9.6	0.45
17	9.5	1.03
22	9.1	0.44
Average	9.04	0.58
SD	0.33	0.04
t-test (p value)	>0.05	>0.05

[a]The litter was sampled from stands within a li
differences between the mor and mull humus ty
Staaf (1982) and from H. Staaf, personal comm

The effect related to by humus type
small, with mean Ca concentrations of
(mor soil) and for Mg 2.0 versus 1.5
differences were statistically significan
litter (Table 10), the annual variation
the range between litter from the two

Table 11 Variation in nutrients composition for leaf litter of common beech[a]

	Concentration (mg g^{-1})					
Plot no.	N	P	S	Ca	Mg	K
Mor humus						
15	9.1	0.49	0.98	10.13	1.9	2.3
19	9.4	0.41	0.98	8.01	1.35	1.38
23	9.2	0.41	1.26	8	1.83	2.9
14	9.9	0.54	1.24	9.82	1.98	2.22
6	8	1.42	1.19	9.63	1.45	2.56
20	9.2	0.56	1.13	7.69	1.23	1.96
21	9.2	0.4	1.09	7.63	1.3	3.34
9	8.7	0.56	1.3	8.19	1.23	2.16
18	9.7	0.54	1.3	7.5	1.5	2.4
24	8.6	0.36	1.04	7.69	1.57	2.26
10	10.1	0.82	1.33	8	1.14	2.92
8	9.2	1.16	1.32	9.63	1.65	2.38
5	8.7	0.54	1.25	8.88	1.47	3.36
7	7.8	1.01	1.09	8.75	1.38	4.18
Average	9.06	0.66	1.18	8.54	1.5	2.59
SD	0.43	0.1	0.02	0.85	0.04	0.49
Mull humus						
3	8.3	0.49	1.06	14.82	2.08	2.46
1	9.1	0.45	1.27	16.38	2.39	3.6
2	9.9	0.56	1.34	12.63	1.9	3.2
4	8.1	0.58	0.77	12.88	1.99	3.84
13	8.6	0.42	1.17	11.69	2.17	2.48
12	8.9	0.82	1.41	13.26	1.89	2.84
11	9.3	0.56	1.46	9.63	1.92	2.1
16	9.6	0.45	1.55	10.25	1.9	2.74
17	9.5	1.03	1.36	9.88	1.7	2.38
22	9.1	0.44	1.2	8.32	1.78	2.78
Average	9.04	0.58	1.26	11.97	1.97	2.84
SD	0.33	0.04	0.05	6.3	0.04	0.31
t-test (p value)	>0.05	>0.05	>0.05	<0.0001	<0.0001	>0.05

[a]The litter was sampled from stands within a limited geographical region. Significance level for differences between the mor and mull humus types is also reported for each nutrient. Data from Staaf (1982) and from H. Staaf, personal communication.

The effect related to by humus type (directly or indirectly) was apparently small, with mean Ca concentrations of 12.0 mg g^{-1} (mull soil) and 8.5 mg g^{-1} (mor soil) and for Mg 2.0 versus 1.5 mg^{-1}, respectively. Nevertheless, these differences were statistically significant. Still, when comparing to Scots pine litter (Table 10), the annual variation at the Scots pine stand was as large as the range between litter from the two previously mentioned soils.

4. *A Case Study on K Concentrations in Foliar Litter*

In a large study on K concentrations in boreal and temperate foliar litter fall, a statistically significant ($p < 0.0001$) difference in average initial K concentrations between coniferous and deciduous litters was seen (1.03 versus 4.52 mg g^{-1}, respectively; Berg *et al.*, 1995). The litter types investigated covered the most common litter types found in forests of Northern and Central Europe and some major North American species. Of investigated boreal species, lodgepole pine needle litter had the lowest initial concentrations followed by those of Scots pine. Both these litter types had lower initial K concentrations than those found in the leaf litter of Norway spruce, oak–hornbeam, and silver birch. The highest average value was that for grey alder leaves (8.3 mg g^{-1}) followed by that for silver birch leaves (5.0 mg g^{-1}). In contrast, leaves of common beech with 1.7 mg g^{-1} were in the same range as the coniferous litter.

5. *Some Types of Woody Litter*

Wood is largely made up of cellulose, lignin, and hemicelluloses in different proportions (Table 6). As a whole, the woody parts of the tree are poorer in nutrients than the photosynthesizing parts. We may see (see Tables 7 and 8) that nitrogen concentrations in woody parts may be lower than those in foliar litter by a factor of at least 10 within the species, for example, Norway spruce, trembling aspen, silver birch, and common beech.

VII. ANTHROPOGENIC INFLUENCES

In this section, we compare the effects on litter chemical composition of modified soils with artificially raised levels of nitrogen and soils with increased levels of heavy metals. We have used examples which are applicable to deposition of nitrogen as well as sulfur and several heavy metals.

A. Nitrogen-Fertilized Scots Pine and Norway Spruce Monocultures

Fertilization of forest soils as well as deposition of nitrogen add significant amounts of nitrogen to the ground, resulting in higher concentrations as compared to those in the original soil. In the examples reported in the following text, the trees have simply taken up more of both nitrogen and some other nutrients with a high availability, resulting in higher concentrations in the foliage. At retrieval, before the needles are shed, a certain fraction of the

needles' nutrients is retrieved and a certain
concentrations in the foliar litter as compar
For both Scots pine and Norway sp
chemical composition of needle litter wi
Textbox 4; Fig. 15). In general, the conce
sulfur, and potassium increased as a con
and the effect on the concentration of n
contrast, the concentration of calcium de
species (Fig. 15), and, for magnesium, no
for Scots pine while its concentration inc
Increased uptake of nitrogen in N-ferti
concentrations of nitrogen in the freshly f
phenomena, observed in a number of stu
and Miller, 1976). The former authors, u
fertilization experiment (dosage details
nitrogen additions at an annual dosag
statistically significant increase in litter-N
of 40 kg ha^{-1} yr^{-1} did not have any si
of additions. The range of the increa
one experimental site was from about
The variation in N concentration w
in concentrations of other nutrients a
balanced nutrient composition.
Norway spruce needle litter followe
pine, although the needle litter had si
all measured nutrients throughout the
Also, the rate of concentration chang

Textbox 4 Nitrogen fertilization experi

The fertilization experiments were perfo
needle litter fall sampled in 1983 and 19
litter fall sampled in 1975 and 1976) in
plots were fertilized annually with dose
spruce and 40, 80, and 120 kg ha^{-1} f
ammonium nitrate. Chemical composit
during the two consecutive years at e
experiment with Norway spruce there w
while only one replicate per dose was
analysis presented (Fig. 15) the averag
Norway spruce plots were used.

needles' nutrients is retrieved and a certain fraction is left, resulting in higher concentrations in the foliar litter as compared to the natural system.

For both Scots pine and Norway spruce there was a clear trend in chemical composition of needle litter with increasing fertilizer doses (see Textbox 4; Fig. 15). In general, the concentrations of nitrogen, phosphorus, sulfur, and potassium increased as a consequence of nitrogen fertilization, and the effect on the concentration of nitrogen was most pronounced. In contrast, the concentration of calcium decreased in litter produced by both species (Fig. 15), and, for magnesium, no significant relationship was found for Scots pine while its concentration increased in Norway spruce litter.

Increased uptake of nitrogen in N-fertilized plots and resulting enhanced concentrations of nitrogen in the freshly formed litter were the most obvious phenomena, observed in a number of studies (Berg and Staaf, 1980a; Miller and Miller, 1976). The former authors, using Scots pine needle litter from a fertilization experiment (dosage details given by Tamm, 1991) found that nitrogen additions at an annual dosage of 80 kg N ha^{-1} resulted in a statistically significant increase in litter-N concentrations, whereas a dosage of 40 kg ha^{-1} yr^{-1} did not have any significant effect, even after 10 years of additions. The range of the increase measured over several years at one experimental site was from about 3.6 to 8.5 mg N g^{-1} needle litter. The variation in N concentration was accompanied by a variation in concentrations of other nutrients as well, to some extent producing a balanced nutrient composition.

Norway spruce needle litter followed a similar pattern as that of Scots pine, although the needle litter had significantly higher concentrations of all measured nutrients throughout the whole gradient of fertilizer doses. Also, the rate of concentration change (regression slope) differed between

Textbox 4 Nitrogen fertilization experiments

The fertilization experiments were performed on Norway spruce (started 1967, needle litter fall sampled in 1983 and 1984) and Scots pine stands (started 1969, litter fall sampled in 1975 and 1976) in boreal forests in central Sweden. The plots were fertilized annually with doses of 60 and 90 kg N ha^{-1} for Norway spruce and 40, 80, and 120 kg ha^{-1} for Scots pine, in both cases given as ammonium nitrate. Chemical composition of foliar litter fall was analyzed for during the two consecutive years at experimental and control plots. In the experiment with Norway spruce there were five replicate plots for each N dose, while only one replicate per dose was used for the Scots pine stands. For the analysis presented (Fig. 15) the average values of the second year data for the Norway spruce plots were used.

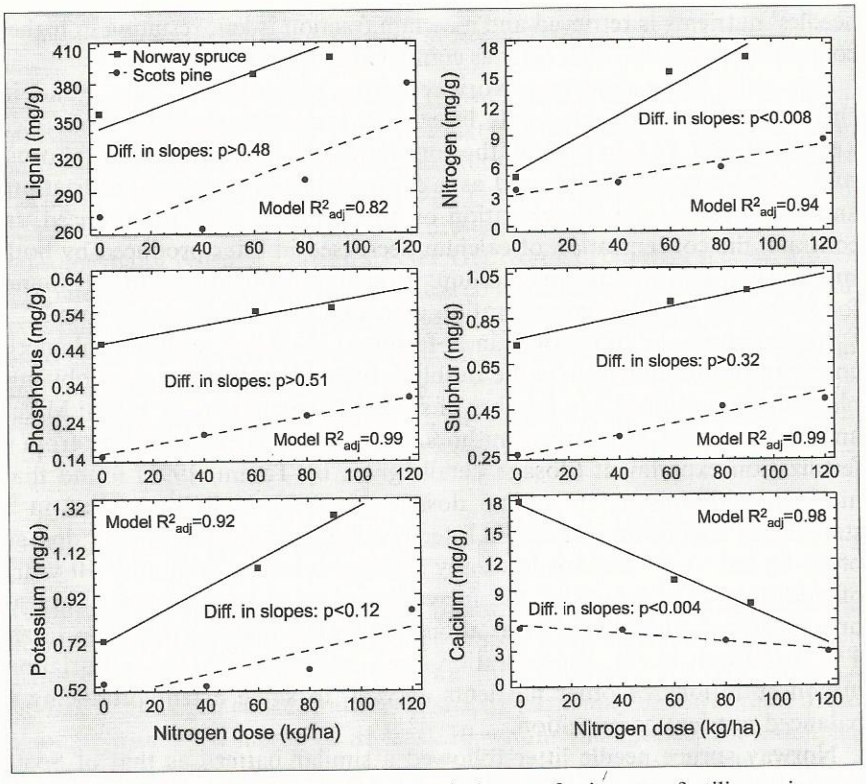

Figure 15 Relationships between annual doses of nitrogen fertilizer given as ammonium nitrate and concentrations of lignin, nitrogen, phosphorus, sulfur, potassium, and calcium in newly shed litter of Norway spruce and Scots pine (Norway spruce, [■] and full line; Scots pine, [●] and dashed line). All models are significant; the p-values indicate the significance level for the difference in slopes between Scots pine and Norway spruce. Despite a nonsignificant difference for potassium, regression lines with different slopes are shown because of the higher R^2 (see text for more information).

the species for some nutrients (see Textbox 5). Thus, in Norway spruce litter, nitrogen concentration increased significantly faster than in Scots pine, while calcium concentration decreased significantly faster. For potassium, statistical tests did not detect significant difference in slopes. However, a due to substantially higher R^2_{adj} for the model with different slopes, a low number of data points, and still quite low p value for the difference in slopes, we may expect that the rates of increase in potassium concentration are rather different among the species (see Fig. 15). A substantial difference was also noted for magnesium; its concentration

Textbox 5 Comparing regression lines

Regression analysis is a powerful tool allowing us to describe mathematically the relationship between one dependent variable and one or more independent variables. Specific tests have been developed to test the significance of the model as a whole as well as of its particular parameters. In this book regression analysis is used frequently to describe such phenomena as, for example, relationship between accumulated mass loss and lignin concentration, nutrient contents or pollution level. However, finding such a relationship and describing it by a mathematical function is often only a first step in data analysis. If a significant relationship is found, the next obvious question is whether the same relationship applies over a broad range of systems. In our case these could be represented by different forest types (e.g., deciduous vs. coniferous) or species (e.g., Scots pine vs. silver birch). In statistical terms such a question is equivalent to asking if regression parameters can be considered the same over the systems (species) studied, or the if difference between them is large enough to be considered significant. The latter case means that a common regression does not describe the systems (species) studied adequately, and the regression parameters should be estimated for each case separately. The central question here is when the regression parameters should be considered significantly different.

The method to test for significance is the regression analysis with so-called "dummy variables" (D), sometimes called also "indicator variables" as their only purpose is to indicate separate categories that we are comparing in the analysis. For the sake of simplicity, we will describe the concept using a simple linear regression as an example. In litter decomposition studies such a regression may describe, for example, how the concentration of nitrogen (Y) depends on litter accumulated mass loss (x):

$$Y = a + bx$$

where a is the regression intercept and b is the slope (rate of concentration change). If we make similar studies on a number of species named 1, 2, ..., n, we would obtain n regressions:

$$\begin{aligned} Y_1 &= a_1 + b_1 x \\ Y_2 &= a_2 + b_2 x \\ &\dots \\ Y_n &= a_n + b_n x \end{aligned}$$

Having n such equations, we want to know whether the estimated regressions are really different or are similar enough to be combined into one common model for all species studied. We thus need a statistical tool that would let us separate the models if they are significantly different, and combine them to a common model if differences are nonsignificant.

With the dummy variable method, we start with adding additional n (or n–1, depending on details of the method) variables that consist only from 1s and 0s. Thus, using as an example the set of linear regressions as above, the first dummy variable (D1) has 1s for species 1 and 0s for all other species, the second dummy variable (D2) has 1s for the species 2 only, and 0s for the remaining species, and so on up to the last species (n) taken into account in the comparison. Now, we construct a common linear regression model which distinguishes the species thanks to the dummy variables created:

$$Y = a + bx + D_1a_1 + D_1b_1x + D_2a_2 + D_2b_2x + \ldots + D_na_n + D_nb_nx$$

The reasoning in interpreting results of such a regression analysis is quite straightforward: if a common model (the first part of the equation, $Y = a + bx$) describes the relationship adequately, then all remaining terms in the equation will be nonsignificant because none of them introduces significant information to the model. Thus, if the only significant parameters in the regression above are a and b, then we conclude that a common model is sufficient and no significant differences among species exist. If, however, any other parameter appears significant, then the common model cannot be used—in our example that would mean that nitrogen dynamics differs significantly between species. Note that we have separate parameters for each species, thus looking at significance levels for each case, we may distinguish the species that do not fit to the common model from those that do. Thus, the dummy variable regression is a powerful method, allowing to test for differences between different groups of data (populations) in their relation to some independent variable(s). The method can be extended also to nonlinear models, but the interpretation of the results gets more complicated.

increased in Norway spruce litter, whereas no fertilization effect was found in Scots pine.

It is noteworthy also that concentrations of lignin increased with dosage of N fertilizer both for Scots pine and Norway spruce. For Scots pine, the lignin concentrations increased with those of N from 270 to 380 mg g^{-1}. For Norway spruce, the increase was of a similar rate (Fig. 15) with the range from 242 to 407 mg g^{-1}. This kind of effect seems to vary with the type of system and appears to be indirect. This may be related to deficiency of boron in the soil, a phenomenon that may be of interest, though not being a direct causal relationship. It is possible that the high dosage of nitrogen fertilizer forced the trees to grow so quickly that the supply of some essential nutrients became insufficient as their mobile pool in the soil became exhausted. The weathering apparently could not provide a good enough supply and therefore some nutrients became limiting. Boron has an important role for the formation of an enzyme transporting phenols out from the needles. The lack of boron probably resulted in accumulation of phenolics in the needles and thus caused a higher synthesis of lignin.

B. The Effect of Heavy Metal Pollution

Scots pine needle litter has been investigated as regards pollution in a transect from a smelter. The chemical composition of newly shed, locally collected needles in the pollution transect varied with the distance from the smelter (Fig. 16; Table 12). A significant positive relationship ($p < 0.05$) was found between the distance from the smelter and Mg concentrations in the fresh litter and the same tendency was also observed for Mn (Fig. 16) meaning that concentrations of these nutrients increased with the distance from the smelter. Of the pollutants, Pb and Zn concentrations showed a strong decrease with distance from the smelter ($p < 0.01$). The same trend was noted for Fe and Cu ($p < 0.05$; Fig. 16) and also, although less marked, for S and Cd ($p < 0.1$; Fig. 16). The concentrations of organic compounds, on the other hand, seemed largely unaffected. The completely unpolluted litter (Table 12) had somewhat lower lignin and higher N and P concentrations than the needles (Berg *et al.*, 1991).

In the case of metals originating from industrial activity, the majority of their contents in foliage can be deposited as particles on leaf surfaces. For example, according to Kozlov *et al.* (2000), as much as about 80% of nickel and copper in leaves of mountain birch, growing in the area polluted by a nickel-and-copper smelter, were found as dust particles on the leaf surface.

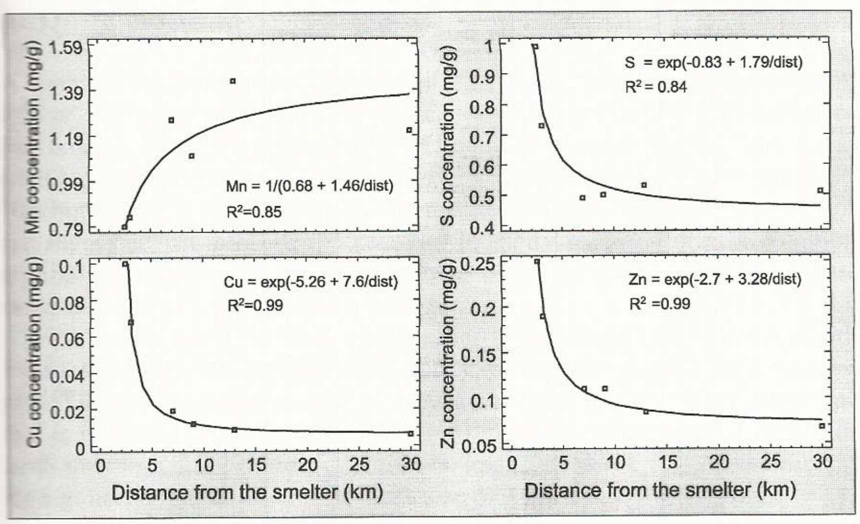

Figure 16 Concentrations of manganese (Mn), sulfur (S), copper (Cu), and zinc (Zn) in Scots pine needle litter collected at different distances from a smelter.

Table 12 Concentrations of plant nutrients, and heavy metals in fresh needle litter of Scots pine sampled at six study plots in a smelter pollution transect in Northern Sweden (local litter) and needle litter sampled at an unpolluted site[a]

Distance from the smelter (km)	Chemical element (mg g^{-1})										
	N	P	S	K	Ca	Mg	Mn	Fe	Zn	Cu	Pb
Local litter from a transect											
2.5	3.78	0.26	0.99	1.43	5.23	0.47	0.79	0.38	0.25	0.1	0.311
3	3.73	0.24	0.73	1.01	5.7	0.53	0.83	0.36	0.19	0.068	0.191
7	3.25	0.19	0.49	0.7	6.11	0.46	1.26	0.14	0.11	0.019	0.044
9	3.71	0.26	0.5	1.08	4.65	0.56	1.1	0.27	0.11	0.012	0.034
13	3.66	0.25	0.53	1.23	5.65	0.66	1.43	0.12	0.084	0.009	0.022
30	4.4	0.22	0.51	0.98	5.7	0.67	1.21	0.11	0.068	0.006	0.012
Litter from a clean area											
	4.8	0.35	0.41	1.2	5.26	0.49	1.35	0.06	0.051	0.002	0.0011

[a]Concentrations of Na, Al, B, Ni, Mo, Sr, and Cd did not exhibit any trend along the transect. From Berg *et al.* (1991).

It seems that metals available through so
nal chemical composition of live leaves sig
et al. (2003) found no increase in concentr
downy oak growing in a district of centurie
and Zn. Arsenic was the only element exhi
leaves from sites with deposits of metal
around abandoned smelting plants. It ha
incorporation of heavy metals into live p
on soil properties, the acidity (pH) bein
addition to metal concentration. Thus, in
neutral soil reaction, where only minor fr
soil are bioavailable, leaves may not accu
of metals. However, at acidic stands, the
For example, Blake and Goulding (2002)
ately contaminated areas contained ten t
Ni, and three times more Cd at pH 4 than
clearly that concentrations of metals in
litter fall depend not only directly on
specific properties, such as soil pH in p
also on other pollution effects, such as
NO_x emissions.

VIII. METHODS FOR LI

A. Quantities

A common method to sample litter fall is
0.25 m^2, mounted at an height of ca 1 m a
bag being a loosely hanging net on a m
were recommended already in the Interna
Newbould 1967). Although in the literat
are suggested per plot, it appears that
number is between 10 and 20 replicat
ranging between 2500 m^2 and a hectare.
With needle and leaf litter being rath
litter traps intended to collect foliar litt
plot. The net mesh size should be consi
that is collected. For example, for litter
larch the mesh size should preferably be
for e.g. beech and oak leaves a mesh siz
Other litter components such as twigs
like cones or acorns have no even dis

It seems that metals available through soil do not necessarily affect internal chemical composition of live leaves significantly. For example, Bargali *et al.* (2003) found no increase in concentration of most metals in leaves of downy oak growing in a district of centuries-long mining of Fe, Ag, Cu, Pb, and Zn. Arsenic was the only element exhibiting increased concentrations in leaves from sites with deposits of metal sulfide ores or As-polluted soils around abandoned smelting plants. It has to be stressed, however, that incorporation of heavy metals into live plant tissues may depend heavily on soil properties, the acidity (pH) being the most important factor in addition to metal concentration. Thus, in forest stands with approximately neutral soil reaction, where only minor fractions of metals accumulated in soil are bioavailable, leaves may not accumulate significant concentrations of metals. However, at acidic stands, the situation may be quite different. For example, Blake and Goulding (2002) found that oak leaves in moderately contaminated areas contained ten times more Mn, four times more Ni, and three times more Cd at pH 4 than at pH 7. The latter results indicate clearly that concentrations of metals in leaves and, consequently, in leaf litter fall depend not only directly on pollution level but also on site-specific properties, such as soil pH in particular, and possibly indirectly also on other pollution effects, such as acidification caused by SO_2 and NO_x emissions.

VIII. METHODS FOR LITTER COLLECTION

A. Quantities

A common method to sample litter fall is to use circular litter traps, often of 0.25 m^2, mounted at an height of ca 1 m above the ground, with the collector bag being a loosely hanging net on a metal or wooden frame. Such traps were recommended already in the International Biolpgical Programme (IBP; Newbould 1967). Although in the literature different numbers of such traps are suggested per plot, it appears that in many recent studies a common number is between 10 and 20 replicate traps per stand, with plot sizes ranging between 2500 m^2 and a hectare.

With needle and leaf litter being rather evenly distributed over a stand, litter traps intended to collect foliar litter can be placed randomly over the plot. The net mesh size should be considered with respect to the litter type that is collected. For example, for litter types such as needles of spruce or larch the mesh size should preferably be less than ca 0.2×0.2 mm whereas for e.g. beech and oak leaves a mesh size of 1 cm could do.

Other litter components such as twigs, branches and most fruiting bodies like cones or acorns have no even distribution over the ground but fall directly below the canopy. Thus, traps for these components could ideally be placed to reflect the canopy projections on the ground. This means either randomly, depending on canopy density, or directly under the canopies. Of course, a high enough number of traps randomly placed and reflecting also the canopy distribution can be used. For cones and nuts an often used type of a seed trap measures 1 × 1 m.

For twigs and large branches a successful approach was made using low "bed-like" traps with a crude steel net, measuring at least 1 × 1m (Flower-Ellis, 1985). In that case the mesh size should be selected to let finer material out and retain twigs of the wanted size. Also the sides need to have a fence or net structure to prevent falling branches from bouncing off.

Sampling periods and frequency vary according to the literature and may be adapted to whether foliar litter only or other, additional litter components should be sampled. For foliar litter from conifers or evergreens, e.g., needle litter from pine and spruce, with litter fall distributed over the whole year, a sampling frequency of every one to three weeks is often used throughout the year. In contrast, for those deciduous species that shed the main part of their foliar litter during a shorter period only, e.g., aspen, birch, chestnut in central Europe between July and December, and birch in Scandinavia from August through October, samplings may be carried out during a more limited period. The sampling frequency is important from both the point of view of quality and quantity since, e.g., nutrients and soluble compounds may be leached out by rain and a wet litter may start decomposing and thus lose mass.

Regarding collection of woody components in litter fall the sampling may continue over the whole year since twigs and branches rather fall in connection to events such as storms, snowfall or heavy rains.

There is also a considerable variation among years and samplings should never be made for one year only, even in mature stands in which litter fall often is considered to be "constant". Even if the tree biomass is actually more or less constant in mature stands, there is still a considerable between-year variation in the litter fall. There does not seem to be any general recommendation about the duration of a measurement and we refer to a ten-year long measurement in a mature Scots pine stand, in which the litter fall was considered to be constant. Over the ten years the ratios between highest and lowest amount of needle litter fall was considerable, with 1.9 for needle litter, 5.0 for cones, 2.4 for twigs and 1.5 for total. The only general recommendation we can make is to continue with the sampling for as long as possible, keeping in mind that just one or two years measurements may give values that are distant from a long-term average.

Qualitative Sampling

in Fig. 11, the chemical compositi
change with time before abscission
result in a litter sample that
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for spruce, for example. We cannot
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investigator.

B. Qualitative Sampling

As seen in Fig. 11, the chemical composition of the leaves or needles to be shed do change with time before abscission takes place. A too early sampling may thus result in a litter sample that is not representative. The *ideal representation is thus the litter that has been shed* naturally, namely that has fallen itself and not been *picked from the trees.*

Still, such collections are not always possible to do and we may therefore suggest two alternative approaches. In both cases we suggest that for a sample representative of the selected stand at least 20 trees are used. Today we still do not know the variation in chemical composition of litter fall among individual trees so this number is selected out of a general statistical principle.

In the case of natural litter fall, sheets of plastic or cloth are spread under the 20 or more trees and the shed litter is collected daily. As an alternative, limbs of the trees are shaken gently and the shed leaves are collected on sheets. Often part of the shed needles would be green, a phenomenon often seen for spruce, for example. We cannot give advice about that here but a decision about what to include in the samples in terms of green litter is up to the investigator.