R-07-23

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April 2007

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ISSN 1402-3091
SKB Rapport R-07-23

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Abstract

The Swedish Nuclear Fuel and Waste Management Co (SKB) has performed extensive site investigations in the Forsmark and Oskarshamn areas to provide background data for long-term storage of nuclear waste. The site investigations reported here were conducted to provide data for the comprehensive descriptive ecosystem model that is being constructed. This report provides estimates of annual inputs of aboveground litter from trees (dry mass and amounts of C and N), litter decomposition rates and changes in organic and inorganic components in litter during decomposition.

The study in the Forsmark area comprised two Norway spruce (*Picea abies* (L.) Karst) stands (sites F1 and F3), and a mixed stand of Norway spruce and alder (*Alnus glutinosa* (L.) Gaertn.) (site F2). The study in the Oskarshamn area comprised one common oak stand (*Quercus robur* L.) (site O1), one Scots pine stand (*Pinus silvestris* L.) (site O2) and one Norway spruce stand (site O3).

In the Forsmark area, the aboveground litterfall from trees was of similar magnitude at sites F1 and F2, but considerably lower at site F3. At the former sites the average annual litterfall (including all components) amounted to 195 and 231 gdw m^{-2} respectively, whereas the latter site received only 136 gdw m^{-2}. There was also a large variation in annual litterfall between stands in the Oskarshamn area. The spruce stand at site O3 exhibited the highest litterfall (almost 400 gdw m^{-2}), followed by the oak stand at site O1 (with almost 300 gdw m^{-2}), whereas the pine stand at site O2 had the lowest (less than 150 gdw m^{-2}). The proportion of needles/leaves in the total litterfall varied between 65% and 75% for the stands.

The amount of carbon (C) returned in aboveground litterfall amounted to between 60 and 110 gdw m^{-2} yr^{-1} at the forest sites within the Forsmark area. The corresponding range for the sites in the Oskarshamn area was 70 to 190 gdw m^{-2} yr^{-1}. At sites O1 and O2 in Oskarshamn, about 3.6 gdw m^{-2} yr^{-1} of nitrogen (N) were returned annually to the forest floor by the aboveground litterfall. This was over four times the N amount deposited in the Scots pine stand in the same area (about 0.8 gdw m^{-2} yr^{-1}). At the Forsmark sites, the N return in litterfall varied between 1.1 and 2.6 gdw m^{-2} yr^{-1}, the lower figure for site F3 and the higher for site F2. At site F1, about 1.7 gdw N m^{-2} yr^{-1} was deposited.

The decomposition of the individual site litters was monitored over two years in field studies and the decomposition was predicted for up to 10 years using a dynamic decomposition model. At all three sites in the Forsmark area, the spruce needle litter lost around 33% in mass during the first year and after two years the cumulative mass loss amounted to 45%. The alder leaf litter decomposed more rapidly and lost 60% of mass during the first year and had reached a cumulative mass loss of 73% after two years. Generally, minor differences were noted in the decomposition pattern for the spruce and pine needles at sites within the Oskarshamn area. However, the pine needles started to decompose with a somewhat lower rate than the spruce needles (16% compared with 18% during the first 77 days) but after two years the pine needles had lost significantly more mass than the spruce needles (52% compared with 46% for spruce needles). Overall, the oak and pine litters lost about half their initial mass (51 to 52%) and the spruce litter a somewhat smaller proportion (45%) during two years of decomposition. According to the model predictions, after 10 years about 80% of the initial mass was decomposed from needle litters and oak leaves but over 90% of the initial mass of alder leaves was decomposed.

The rapid mass loss was accompanied by a fast decrease in water–soluble substances and during the first five months all litters in the Forsmark area (except the spruce needles at site F3) generally lost 80–90% of their initial amounts. Thereafter, the level remained fairly constant except in the alder leaf litter, which after two years had lost about 95% of its initial amount of water-solubles. At site F3, about 60% of the initial amount of needles still remained after two years. The ethanol-soluble substances decreased more slowly than the water-soluble substances

and decreased most quickly in the alder leaf litter in the Forsmark area, where only 10% of the initial amount of leaves remained after two years. Although the loss rate of ethanol-soluble components in spruce litter varied between sites, generally about 30% (40% in the Oskarshamn area) of the initial amount remained in the spruce litter at the end of the second year. For the pine needle litter 30% also remained, whereas for the oak litter 50% remained. Lignin generally decomposed slowly and the absolute amount of lignin even increased in the early stages, after which it remained fairly constant until the end of the first year when it started to decompose. In the alder leaf litter and in the F3 spruce needle litter, the lignin fraction showed a consistent pattern and decreased in amount throughout the entire period studied.

Mineralisation of N started immediately from alder leaves, and proceeded at a rapid rate during the first five months, after which it slowed down markedly. Due to its fast initial mineralisation, the alder litter lost about half its original amount of N during these first months. There was also generally a small loss of N from the other litter types during the first months but this loss was minor and never exceeded 10% of the initial N amount in the litter. The first phase of N loss was generally followed by short irregular periods when N was immobilised. Generally, 80–90% of the initial N amount still remained in the coniferous and oak litters after two years of decomposition (100% in the pine needles) whereas alder leaves had lost 60% of their N.

The release of phosphorus (P) started immediately from all litter types and was most rapid from the alder leaf litter, which lost about 60% of its initial amount during the first five months. The other litter types generally lost around 10–20% within the same time period. However, oak leaves and the spruce needles at sites O1 and O3 in the Oskarshamn area exhibited higher losses (30–40% of initial amount). After this initial phase the release rate slowed down and generally about 60–70% of the initial P amount remained in the litters after two years of decomposition. In alder leaves only 20% of the original P amount remained, whereas the pine needle litter had increased its original amount of P by about 20%.

According to the model predictions, after 10 years of decomposition about 60–70% of initial N and 80–90% of initial P was released from the spruce needles and oak leaves. Markedly lower release rates of N and P were predicted for pine needles, 54 and 41%, respectively. The release rate of N and P from alder leaves was predicted to be very high and only a few percent of the initial N and P were predicted to be found in alder leaves after 10 years of decomposition.

Sammanfattning

Föreliggande undersökning ingår i de ekosystemundersökningar som SKB (Svensk Kärnbränslehantering AB) utför i områdena Forsmark och Oskarshamn för att klargöra förutsättningar och fastställa förhållanden inför långtidslagring av använt kärnbränsle. Målet med denna studie var att uppskatta den ovanjordiska produktionen av fallförna från trädskiktet (vikt samt innehåll av C och N) samt beskriva förnans omsättning och kemiska förändring under nedbrytning genom fältstudier under två år och med hjälp av en dynamisk nedbrytningsmodell simulera förnans viktminskning och förlust av kväve och fosfor under en tidsperiod upp till 10 år. Undersökningen utfördes i sex skogsbestånd varav tre var belägna i Forsmarksområdet och tre i Oskarshamn. I Forsmark studerades två granbestånd *(Picea abies (L.) Karst)* (F1 and F3) och ett blandbestånd (F2) av gran och al (*Alnus glutinosa* (L.). Studien i Oskarshamn omfattade rena bestånd av ek *(Quercus robur)*, tall (*Pinus silvestris*) och gran (O1, O2 och O3).

I bestånden F1 och F2 i Forsmark uppskattades det årliga förnafallet (medelvärde för två års mätningar) till 195 respektive 231 gdw m^{-2} och till 136 gdw m^{-2} i bestånd F3. I Oskarshamn var skillnaden mellan bestånden större och det högsta förnafallet (nästan 400 gdw m^{-2}) uppmättes i granbeståndet (O3) följt av ekbeståndet (300 gdw m^{-2}) och tallbeståndet med mindre än 150 gdw m^{-2}. Andelen barr/löv i det totala förnafallet varierade mellan 65 % och 75 % i bestånden.

Mängden kol som tillfördes marken via det årliga förnafallet motsvarande ungefär hälften av fallförnamängderna eftersom halten kol i fallförnan uppgår till ca 50 %. Inom Forsmarksområdet tillfördes beståndet F2 nästan 30 % mer N via det årliga förnafallet än beståndet F1 (2,6 jämfört med 1,7 gdw m^{-2} $år^{-1}$) och mer än 70 % jämfört med beståndet F3 (1,1 gdw m^{-2} $år^{-1}$). Huvuddelen av kvävet i beståndet F2 tillfördes marken via allöv. I Oskarshamnstudien uppmättes ännu större skillnader mellan bestånden där den årligt tillförda kvävemängden via fallförnan uppgick till ca 0,8 gdw m^{-2} i tallbeståndet (O2) och till ca 3,6 gdw m^{-2} i ek- samt i granbeståndet (O1 och O3).

I Forsmark förlorade granbarrsförnan ungefär 33 % av sin ursprungliga vikt under det första nedbrytningsåret och efter två år hade 45 % av den ursprungliga massan försvunnit. Allöven bröts ner snabbare och hade efter ett år förlorat 60 % av ursprunglig vikt och efter två år 73 %. Generellt uppmättes mindre skillnader mellan de olika förnatyperna i Oskarshamn området. Under de första 77 dagarna förlorade tallbarren 16 % i vikt medan granbarren förlorade 18 %. Efter två års nedbrytning hade tallbarren och eklöven förlorat signifikant mer än granbarren i vikt (52 % jämfört med 46 % för granbarren). Simuleringar med den dynamiska nedbrytningsmodellen visade att efter 10 års nedbrytning fanns ca 20 % av den ursprungliga massan kvar hos samtliga förnaslag förutom hos al som nästan helt nedbrutits.

Den snabba initiala viktsminskningen åtföljdes av en hastig minskning av förnans vattenlösliga komponenter med upp till 80–90 % av ursprungligt innehåll under det första halvåret utom i bestånden F3 och O3 där minskningen var lägre (40 % och 50 %). Förnornas innehåll av etanollösliga ämnen förändrades långsammare än de vattenlösliga ämnena. Den hastigaste förändringen skedde i allöven (F2) där endast 10 % av det ursprungliga innehållet fanns kvar efter två år. I övriga förnaslag fanns mellan 30 och 50 % av initial mängd kvar vid samma tidpunkt.

Ligninet uppvisade ett långsamt nedbrytningsförlopp och började vanligtvis brytas ned först under år två, med undantag för allöven (bestånd F2) och granbarren i bestånd F3, där nedbrytningen startade redan under det första året. I de flesta förnorna fanns 80 % till 90 % av det initiala kvävet kvar efter två års nedbrytning (100 % för tallbarren). Allöven hade däremot förlorat 60 % av sitt ursprungliga innehåll av kväve. Frigörelsen av P startade direkt från samtliga förnor och skedde hastigast från allövsförnan som förlorade ca 60 % av sitt ursprungliga innehåll under de första fem månaderna. Övriga förnor förlorade i allmänhet omkring 10–20 % av sitt innehåll under samma tid med undantag för eklöven i bestånd O1 och granbarren i bestånd O3 i Oskarshamn som förlorat 30–40 %. Efter två år hade förnorna i allmänhet förlorat 30–40 % av sin ursprungliga

fosformängd, allöven däremot hela 80 % av sitt innehåll och tallbarren ökat sitt ursprungliga innehåll med ca 20 %. Modellsimuleringarna visade att efter 10 års nedbrytning hade granbarr och eklöv förlorat ca 60–70 % av kvävet och 80 till över 90 % av sitt förråd av P. Tallbarr hade däremot endast förlorat 54 och 41 % av sitt förråd av N och P. Från allöv hade nästan allt kväve och fosfor frigjorts.

Contents

1 Introduction

In 2002, the Swedish Nuclear Fuel and Waste Management Co (SKB) started site investigations in two areas in Sweden (Forsmark and Oskarshamn). The aim of these investigations was to describe the current state and long-term evolution of the biosphere and the geosphere as a basis for the design and safety assessments of a deep repository for spent nuclear fuel.

This document reports results from field measurements of tree litter production and litter decomposition rates in a number of vegetation types in the Forsmark and Oskarshamn areas. Methods used and an analysis of the results are also given. The study complements other studies aimed at generating information on the carbon dynamics in the areas investigated. In some of the vegetation types the net primary production in the field and ground layer has already been estimated /Löfgren 2005/. The work was carried out in accordance with activity plans AP PS 400-03-075 and AP PF 400-03-015, which are SKB's internal control documents. The original results achieved in this study are stored in the primary database (Sicada) and are traceable by the activity plan numbers. Only data in SKB's databases are accepted for further interpretation and modelling. The data presented in this report are regarded as copies of the original data. Data in the databases may be revised, if needed. Such revisions will not necessarily result in a revision of the P-report, although the normal procedure is that major data revisions entail a revision of the P-report. Minor data revisions are normally presented as supplements, available at www.skb.se.

Litter production and litter decomposition are key processes in the cycling of carbon and nutrients in forest ecosystems. Although ground vegetation in sparse open stands can make a substantial contribution to total litterfall in the stand, litter from the trees is generally the largest natural source for the inflow of organic material and nutrients to the forest floor /Berg et al. 1999b/.

The shedding pattern of litter differs among tree species. Differences exist not only between deciduous and coniferous trees, but also among species within the two groups. Of the conifers, pine sheds litter in a regular manner, meaning that the oldest shoots still holding needles, normally 2–5 years old, shed them in the autumn. Dryness may influence the pattern and cause a fall at other times of the year, but normally approximately 70% of the needle fall takes place in the autumn. The remaining 30% is distributed evenly over the year. Spruce behaves in a different way. Since spruce needles may remain for up to 10 years on the shoot, the trees continuously shed needles of different age classes. In contrast to pine, not all needles on a shoot are shed at the same time but single needles die and stay attached dead for several months before the final fall. Although dry periods may cause a heavier fall, spruce has no clear litterfall period. Instead, needles are shed evenly over the year, with a somewhat higher fall in the winter time /Berg and Laskowski 2006/.

Among the deciduous trees, there is normally a heavy litterfall during a short period in the autumn when the trees shed all their leaves. The timing of litterfall peak varies depending on the species and geographical location. Some species of e.g. oak have a prolonged litterfall 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 proportion stay until spring, to be finally shed when the new buds develop. This may occasionally be seen with common beech too /Berg and Laskowski 2006/.

The chemical composition of forest tree litter also varies with tree species. Of the needle/leaf litters produced from the three most common tree species in Sweden (Norway spruce, Scots pine and silver birch), the pine needle litter is the most nutrient-poor type. Birch leaf litter, on the other hand, generally has higher concentrations of nutrients than both the other litter types /Mork 1942, Viro 1956, Berg and Wessén 1983, Johansson 1995/. Besides the nutrient content, the organic chemical composition of forest tree litter also varies with tree species. Spruce needle litter has significantly higher concentrations of lignin than both the other litters and lower levels of ethanol-soluble substances and cellulose than pine needle litter /Johansson 1995/.

Furthermore, birch leaf litter has higher concentrations of water-solubles and lower levels of cellulose and lignin than pine needle litter /Berg and Wessén 1983/.

Chemical composition is one of the main factors controlling the decomposition rate of organic matter, together with environmental factors (temperature, moisture, pH and aeration) and the types of microorganisms present. This was postulated already by /Tenney and Waksman 1929/ and several studies have later stressed the importance of inorganic and organic components in controlling turnover rate of organic matter and release of nutrient elements /Edmonds 1979, Melillo et al. 1982, Berg et al. 1993, Johansson 1994/. Information on levels of inorganic and organic components in tree litterfall is thus of great importance for studying the carbon dynamics in forest ecosystems.

Over the years, numerous studies have been carried out on litter decomposition dynamics. These have involved field measurements using the litterbag approach, as well as incubation experiments in the laboratory /Bocock et al. 1960, Bringmark and Bringmark 1991, Johansson 1994, Karlsson 2000/. This has resulted in a basic understanding of the decom position and transformation processes in boreal and temperate forest systems. Attempts have also been made to describe decomposition using mathematic functions /e.g. Olson 1964/. In addition, during recent years different models have been used to simulate the decomposition process /i.e. Ågren and Bosatta 1998/. These simulations have generally been based on results from short-term decomposition experiments in the field and laboratory and on estimated or measured parameters. In the present study, we combined field measurements conducted during two years with a modelling approach to describe C and N dynamics in decomposing tree litter for a number of vegetation types within the Forsmark and Oskarshamn investigation areas.

2 Investigation areas

The study comprised two investigation areas, Forsmark and Oskarshamn. The Forsmark area is located in east-central Sweden on the Bothnian Sea coast (60°22'N, 18°13'E), south-east of the Forsmark nuclear power plant (Fig. 2-1). The Oskarshamn area is located on the western Baltic Sea coast (57°25'N, 16°33'E), in south-eastern Sweden (Fig. 2-2). The Oskarshamn area has a milder climate than the Forsmark area, with a mean annual temperature of ~ + 6.5°C compared with ~ +5°C at the latter site. Both areas are characterised by a snow-covered winter period lasting from the beginning of December in both areas to March (approx. 75 days) in the Oskarshamn area and to the beginning of April (approx. 125 days) in the Forsmark area. Both areas have fairly dry summers and an increase in runoff after autumn rains and snowmelt periods. Annual precipitation amounts to approx. 700 mm in the Forsmark area and 600 mm in the Oskarshamn area. The soils in both areas are fairly young and the soil material is of till origin that has been affected by sea waves during the transgression of the Baltic Sea /Lundin et al. 2004, 2005/.

In the Forsmark area three sites were studied, two Norway spruce (*Picea abies* (L.) Karst) stands designated F1 and F3 in this report (SKB ID-codes: AFM001068 and AFM001247), and a mixed stand of Norway spruce and alder (*Alnus glutinosa* (L.) Gaertn.), designated F2 in this report (SKB ID-code AFM001076). The study in the Oskarshamn area comprised three sites, one stand of common oak (*Quercus robur* L.), designated O1 in this report (SKB ID-code ASM001426), one Scots pine stand (*Pinus silvestris* L.), designated O2 in this report (SKB ID-code ASM001428), and one Norway spruce stand, designated O3 in this report (SKB ID-code: ASM001440). Additional site information is given in Table 2-1.

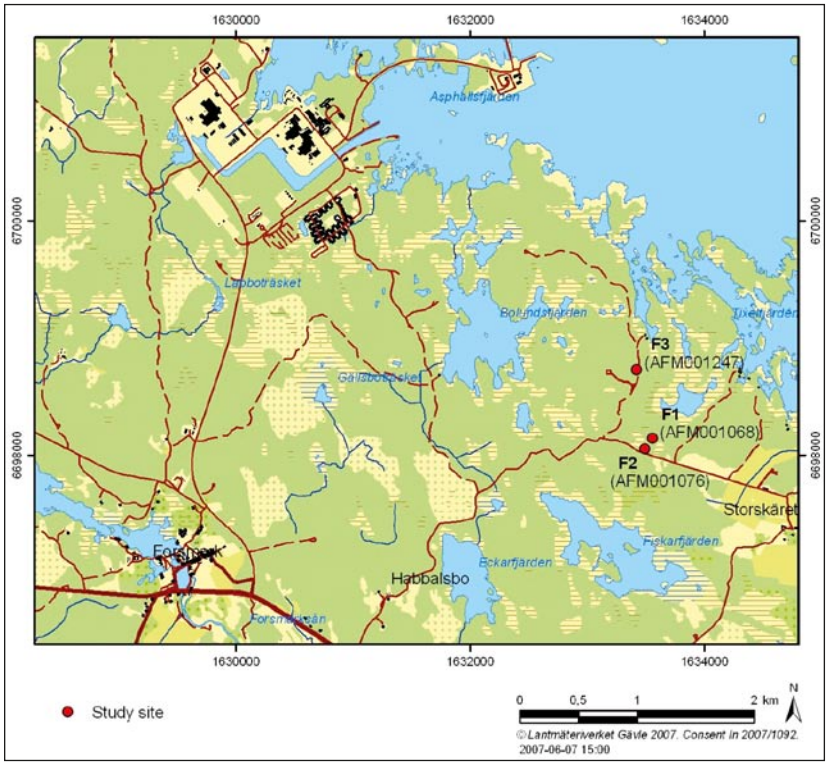

Figure 2-1. *Location of the study sites F1–F3 within the Forsmark investigation area.*

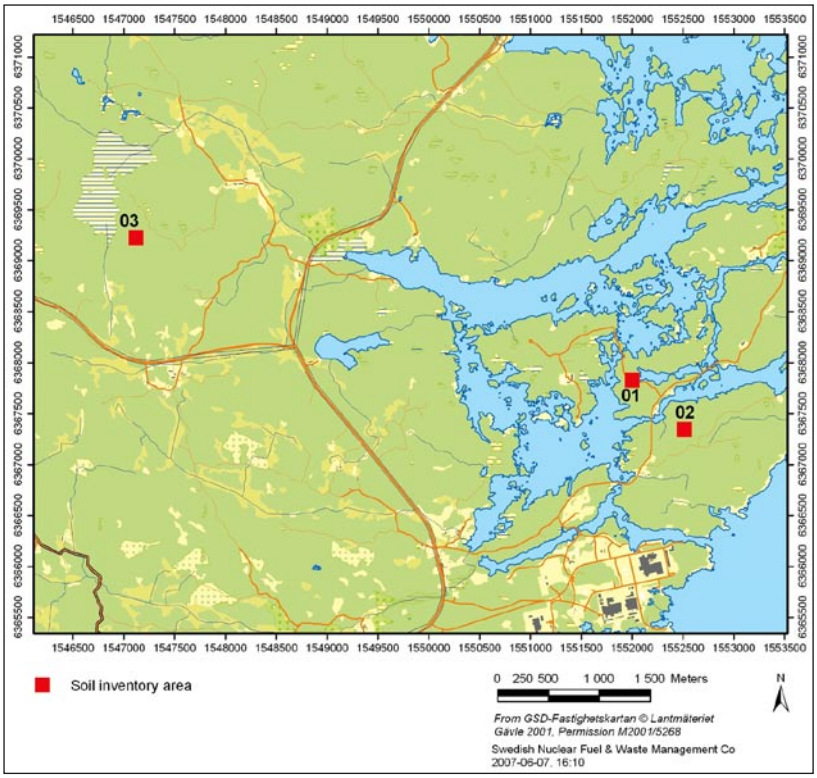

Figure 2-2. *Location of the study sites O1–O3 within the Oskarshamn investigation area.*

Table 2-1. Site information on the forest stands studied in the Forsmark and Oskarshamn investigation areas. All sites except F3 are identical to those described by /Lundin et al. 2004, 2005/.

Site	Forest type	Lundin ref.	X	Y	SKB ID-codes
F1	Norway spruce	FG1	6698152	1633558	AFM001068
F2	Norway spruce/ Alder	SS1	6698060	1633495	AFM001076
F3*	Norway spruce	B2	6698733	1633420	AFM001247
O1	Common oak	Löv 1	6367828	1552003	ASM001426
O2	Scots pine	Häll 1	6367322	1552510	ASM001428
O3	Norway spruce	Gran 1	6369225	1547128	ASM001440

* The site was moved about 300 m from that described by /Lundin et al. 2004/, denoted AFM001066.

3 Methods

3.1 Litterfall measurements

Annual litterfall from trees was measured using circular litter traps with a nominal sampling area of 0.32 m^2. Each litter trap consisted of a Terylene net with a mesh size of 0.1 mm and closed at its lower end by a string. The bag was threaded onto a galvanised iron ring (hoop) and kept at a height of 0.9 m by four plastic poles (Fig. 3-1). In June 2004, 10 litter traps were randomly distributed at the edges of a plot measuring 10 × 15 m^2 (in which the litter decomposition studies were conducted) in each stand. The litter traps were emptied three times a year during a two-year period and the litter from each trap was sorted into three fractions: needles, leaves and a composite fraction (other material) consisting of twigs (Ø ≤ 5 mm), cones, bark flakes, seeds, etc. After drying at 85°C for 48 h, each fraction from each trap was weighed individually (after cooling in an desiccator) and then pooled to one composite sample for each collection and fraction. Mean values for each fraction and sampling occasion (N = 10) and year as well as for both years were calculated.

Figure 3-1. *Annual litterfall from trees was measured using litter traps.*

3.2 Litter decomposition – field measurements

Needle/leaf litter was sampled from the forest stands at the different sites during the annual litterfall in the autumn of 2003. Brown needles and yellow-brownish leaves were sampled by placing a tarpaulin on the ground and gently shaking the branches of the trees. The litter was then dried at room temperature to a moisture content of about 5–8%. The dry matter content was determined by drying a subsample of the litter at 85°C for 48 hours. The largest difference in moisture was less than ± 0.5% percentage unit of the average (N=10).

Approximately 1.5 g needles were enclosed in litter bags (measuring 11 × 13 cm^2) made from Terylene net (Fig. 3-2). The exact weight was noted on a piece of plastic tape that was enclosed in the bag. The mesh size of the litter bags was 1 × 1 mm^2 except for those used for spruce needles, which had a mesh size of 1 × 0.5 mm^2. At the start of the experiment (June 2004), the litter bags were placed on the litter layer in each forest within a plot measuring 10 × 15 m^2 in which 25 subplots (1 × 1 m^2) were randomly selected. In each subplot, four litter bags were incubated (eight at site F2 in Forsmark since the decomposition of both alder leaves (four litter bags) and spruce needles (four litter bags) was monitored. The bags were fastened to the ground with metal pins 10–15 cm long. Three times a year during the two-year period (six collections in total) one litter bag (two from site F2) was retrieved from each of the 25 subplots at each site. The litter bags were transported directly to the laboratory, where all moss, lichen, grass and dwarf shrubs were removed. After drying (85°C for 48 hours), the litter samples from each bag were weighed individually and pooled to form one composite sample per set. Individual mass loss values for the 25 litter bags and mean mass loss value for each collection were then calculated.

3.3 Litter decomposition – model simulations

3.3.1 Model for decomposition

The continuous quality theory is extensively described elsewhere /Ågren and Bosatta 1998/. Therefore, only a brief review is given here to introduce the necessary assumptions and equations. The premise is that the decomposer community is carbon-limited and that the growth (and death

Figure 3-2. *Litter decomposition rate was measured using litter bags over a period of two years.*

rate) of decomposers depends on available C sources. Soil C provides the source but all C compounds are not equal with respect to decomposer utilisation but have different qualities. Because of the large number of different C compounds, it is convenient to let the quality become a continuous variable (q), and the amount of C in soil is described by its quality distribution. The C is cycled between the soil organic matter and decomposer biomass. For each cycle, part of the C is lost as respiration. The C returned to the soil has a lower mean quality than the assimilated C. In this assumption, there is no need for a distinction between litter and soil organic matter. Soil organic matter is simply many ages of litter (cohorts) added together.

Starting from an initial mean litter quality q_0, the development of the quality of a litter cohort over time t is given by:

$$q(t) = q_0(1+\beta f_C \eta_{11} u_0 q_0^{\beta} t)^{-1/\beta} \quad (1)$$

where f_C is the C concentration in decomposer biomass. The parameter β is a shape parameter determining how rapidly the growth rate of the decomposer changes with quality. This parameter includes the interaction with soil texture and increases with clay content /Bosatta and Ågren 1997/. The parameter η_{11} describes the rate of change of quality. The parameter u_0 is a basic decomposer growth rate and depends on external factors such as temperature and humidity.

The fraction of C remaining in the litter when quality has decreased to q is given by:

$$C(q) = C_0\left(\frac{q_t}{q_0}\right)^{\frac{1-e_0}{e_0\eta_{11}}} \quad (2)$$

and the fraction of N and P remaining is given by:

$$i(q) = C(q)\left[\frac{f_i}{f_C} - \left(\frac{f_i}{f_C} - r_{i0}\right)\left(\frac{q_t}{q_0}\right)^{\frac{1}{\eta_{11}}}\right]$$

where i is N or P, C_0 is the initial amount of carbon in litter, f_i/f_C the C/N ratio in decomposers and r_{0i} the initial N/C or P/C ratio in litter.

3.3.2 Parameter estimations

Most parameters were given previously estimated values. The parameter β, which has been shown to depend on soil texture (clay content), was given the basic value of β = 7 corresponding to zero clay content /Bosatta and Ågren 1997/. The values of the other decomposer-related parameters e_0 and η_{11} were shown by /Ågren and Bosatta 1996/ to be constant for a large range of litters and physical conditions (e_0 = 0.25, η_{11} = 0.36). The basic decomposer growth rate u_0 for the different litters at the two study sites was estimated using the equation u_0 = 0.0855 + 0.0157(50.6–0.768 Latitude) /Ågren et al. *in press*/. The initial quality q_0 for needle and leaf litters and the decomposer f_i/f_C were obtained by least squares fit of measured and predicted mass losses. The initial N/C and P/C ratios in the needles and leaves were calculated from the measured C, N and P content in those litters. A summary of the parameters used is given in Table 3-1.

Table 3-1. List of parameters used in the model.

Symbol	Meaning	Value	
e_0	Decomposer efficiency	0.25	
u_0	Basic decomposer growth rate (yr^{-1})	Site-specific, see text	
β	Shape of decomposer-quality response	7.00	
η_{11}	Rate of decrease in quality	0.36	
q_0	Initial mean litter quality	Substrate-specific, see text	
f_C	Carbon concentration in decomposer biomass	Measured, this study	
f_N	Nitrogen or phosphorus concentration in decomposer biomass	Estimated	decomposer biomass
r_{0N}	Initial nitrogen or phosphorus concentration in needle or leaf litter	Substrate-specific, see text	in needle or leaf litter

3.4 Chemical analysis

All litter samples were ground in a laboratory mill equipped with a 1 mm screen before chemical analyses. The litter from the litter traps was analysed for contents of C and N and the litter bag samples for C, N, P, water-soluble substances, ethanol-soluble substances and lignin (Klason lignin). Duplicate analyses were consistently used. The total organic C and the total N were analysed using an elemental analyser (LECO CNS-1000). After digestion in 7 M HNO_3 under high pressure, the total P content was determined by ICP.

The analysis of substances soluble in water and ethanol was carried out by sonicating the milled samples in a sonicator bath, first with water and then with ethanol (3 × 20 min for each solvent) and weighing the samples after filtration and drying /Johansson 1995/. Lignin was determined by first removing the solid carbohydrates (cellulose and hemicelluloses) in a sulphuric acid hydrolysis, following the procedure described by /Bethge et al. 1971/. The acid-insoluble residue of the sulphuric acid hydrolysis was weighed and defined as sulphuric acid lignin (Klason lignin).

3.5 Statistical analysis

To test whether litter mass loss values differed significantly between sites within the two areas investigated (Forsmark and Oskarshamn), GLM and Duncan's test for group means were used. All statistical analyses were carried out using SAS 9.1 for Windows (SAS 2004).

4 Results

4.1 Field measurements

4.1.1 The Forsmark area – individual sites

Litterfall – biomass and element return (N and C)

At site F1 the total average litterfall amounted to about 200 gdw m^{-2} yr^{-1} with a small between-year variation of about 10 gdw m^{-2} yr^{-1} (Fig. 4-1). The litterfall was dominated by spruce needles (80 gdw m^{-2}) but birch leaves also made a substantial contribution to total litterfall (about 60 gdw m^{-2}). Other components (small twigs, cones, seeds etc.) accounted for 28% of the total litterfall in the stand.

Of the two elements studied (C and N), a considerably higher amount of C (100 gdw m^{-2}) than of N (1.7 gdw m^{-2}) was returned to the forest floor by the annual litterfall (Figs. 4-2 and 4-3). This was due to a higher concentration of C (about 50%) than of N (0.8 to 0.9%) in the litter. Of the

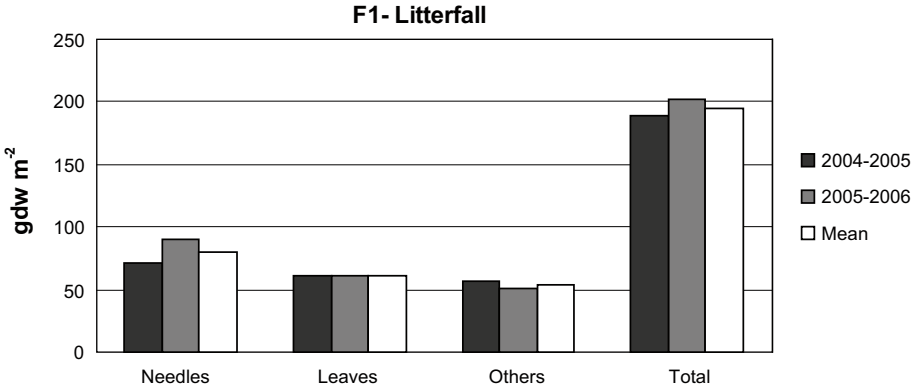

Figure 4-1. *Annual amounts of aboveground tree litterfall (gdw $m^{-2}yr^{-1}$) at site F1 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

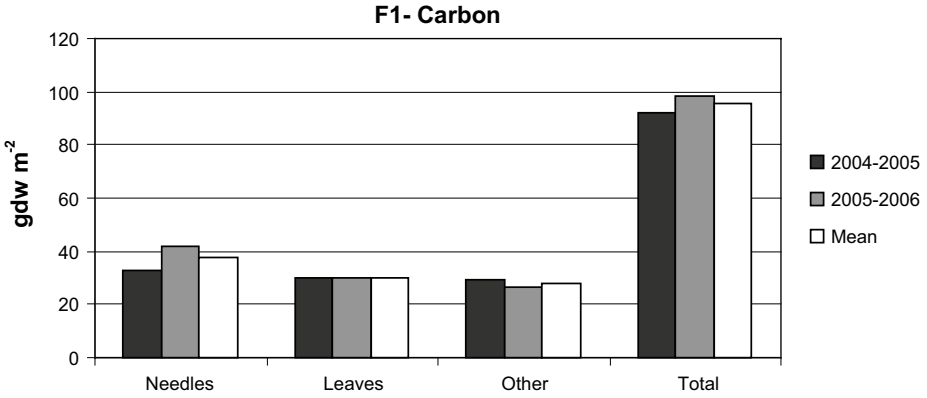

Figure 4-2. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw $m^{-2}yr^{-1}$) at site F1 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

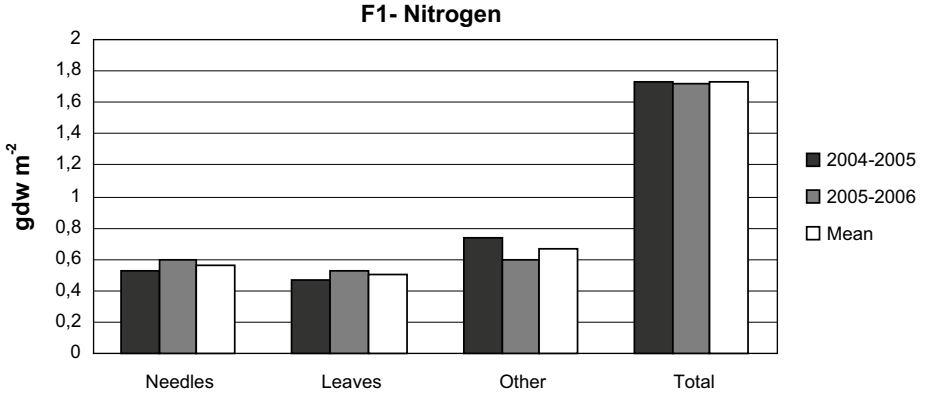

Figure 4-3. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (g $m^{-2}yr^{-1}$) at site F1 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

C returned annually to the forest floor in tree litterfall, around 40 gdw m^{-2} came from needles, 30 gdw m^{-2} from leaves and 30 gdw m^{-2} from other components (Fig. 4-2). The corresponding figures for N were 0.6 gdw m^{-2} from the needles, 0.5 gdw m^{-2} from leaves and 0.7 gdw m^{-2} from other components (Fig. 4-3).

At site F2 the total average litterfall amounted to about 230 gdw m^{-2} yr^{-1}, with a somewhat larger variation between years (about 25 gdw m^{-2}) than at site F1 (Fig. 4-4). Leaves, mainly alder leaves, accounted for a larger proportion of the total litterfall than needles (90 compared with 80 gdw m^{-2} yr^{-1}) and the weight of other components was 65 gdw m^{-2} yr^{-1}. Needles, leaves and other components accounted for 34%, 38% and 28%, respectively, of the total average litterfall (Fig. 4-4).

The average annual input of C via the total litterfall amounted to 110 gdw m^{-2}, of which needles and leaves contributed 40 gdw m^{-2} each and the 'others' fraction contributed 30 gdw m^{-2} (Fig. 4-5).

About 50% of the N returned to the forest floor by the annual litterfall (2.6 gdw m^{-2}) was deposited with the leaf fraction (1.4 gdw m^{-2}), while the needles and 'others" fractions contributed 0.5 gdw m^{-2} and 0.8 gdw m^{-2} each (Fig. 4-6).

At site F3, which was a pure spruce stand, the litterfall consisted solely of needles and other components. The total average litterfall was low and amounted to 135 gdw m^{-2}, of which needles contributed 100 gdw m^{-2} and the fraction 'others' 35 gdw m^{-2} (Fig. 4-7). Other components (small twigs, cones, seeds etc.) thus accounted for 26% of the total litterfall in the stand.

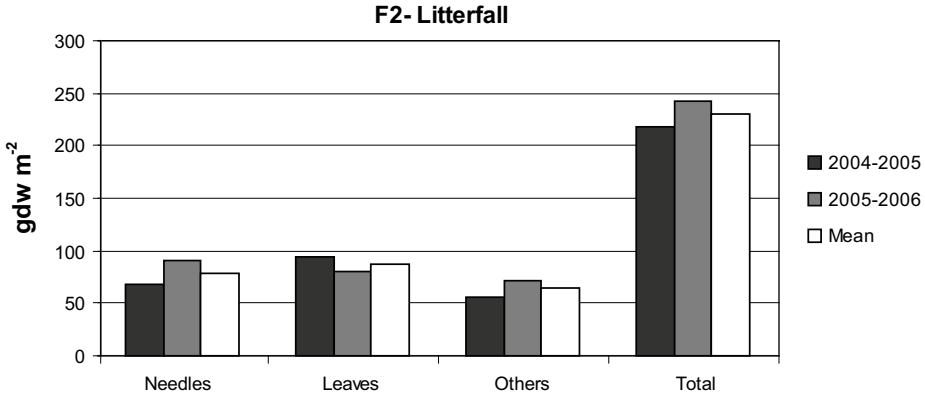

Figure 4-4. *Annual amounts of tree aboveground litterfall (gdw m^{-2} yr^{-1}) at site F2 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

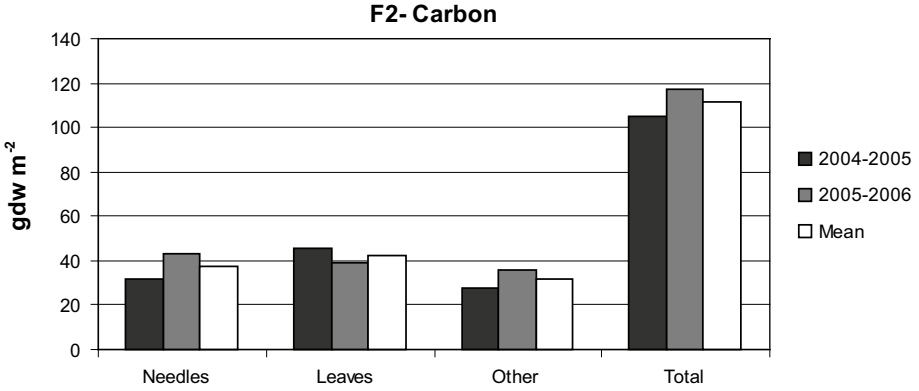

Figure 4-5. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site F2 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

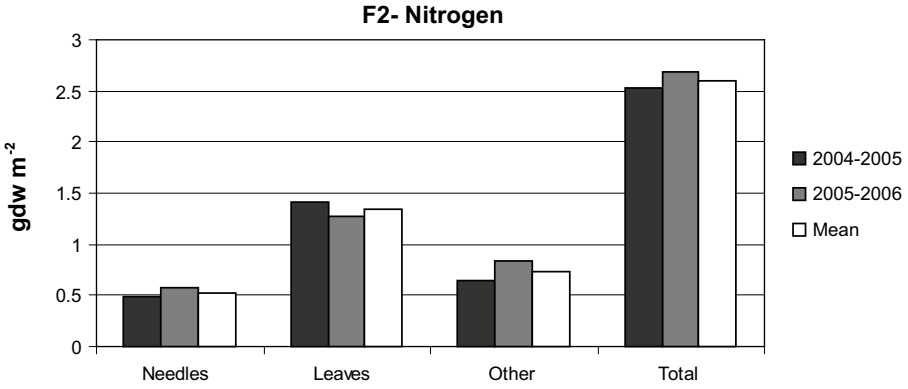

Figure 4-6. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site F2 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

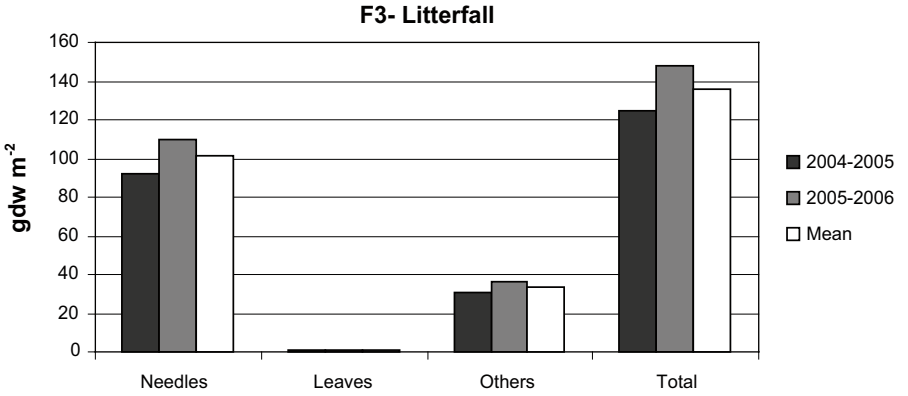

Figure 4-7. *Annual amounts of aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site F3 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

On average for the two years studied, about 65 g dw m^{-2} of C and 1.1 g dw m^{-2} of N were returned annually to the forest floor in the litterfall (Figs. 4-8 and 4-9). The amounts were somewhat larger during the second year than during the first due to the higher litter production during the second year. Of the C annually returned to the forest floor in tree litterfall, around 50 gdw m^{-2} on average came from needles and 15 gdw m^{-2} from other components (Fig. 4-8). The corresponding figures for N were 0.7 gdw m^{-2} from needles and about 0.4 gdw m^{-2} from other components (Fig. 4-9).

Litter decomposition and chemical changes

At the F1 site, as well as at the other sites within the Forsmark area, there was a rapid loss of mass from spruce needle litter during the two years studied. The needle litter lost as much as 33% in mass during the first year and after two years the cumulative mass loss amounted to 45% (Fig. 4-10).

The rapid loss in mass was accompanied by a fast decrease in amounts of water-soluble and ethanol-soluble substances (Fig. 4-10). The water-soluble fraction, which started with an amount of 166 mg g^{-1}, dropped to 48 mg g^{-1} during the first three months and to 29 mg g^{-1} by the end of the study (Fig. 4-11). This corresponds to a decrease of 83% in the initial amount of water-soluble substances during the first two years of the decomposition (Fig. 4-10). The amount of ethanol-soluble substances decreased from 41 mg g^{-1} to 9 mg g^{-1} over the two years

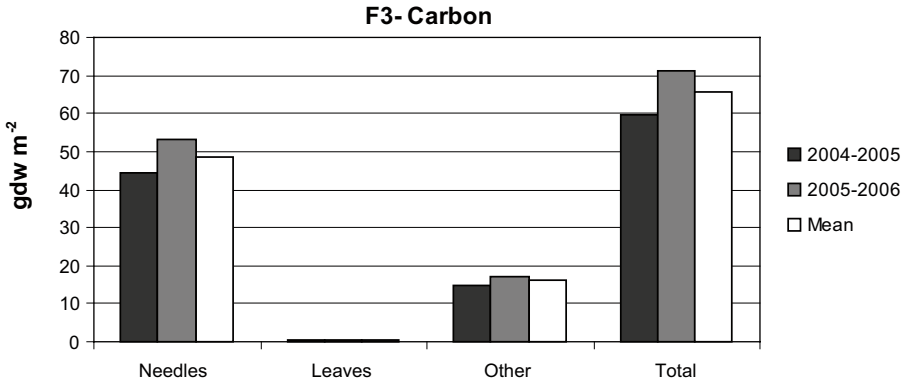

Figure 4-8. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site F3 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006,) as well as the mean for these two years.*

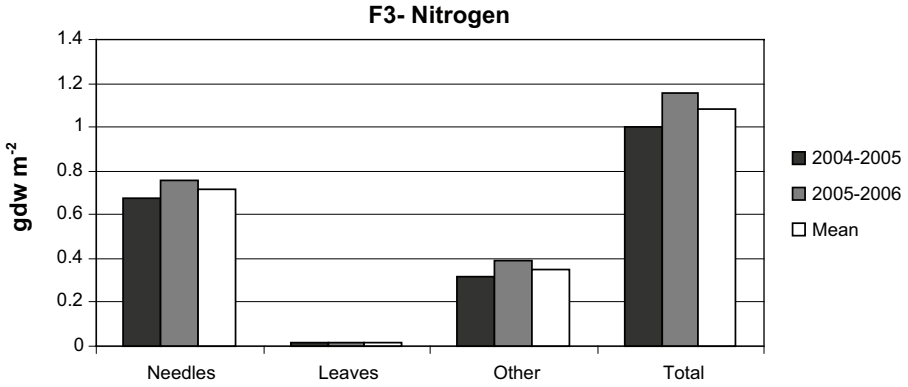

Figure 4-9. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site F3 within the Forsmark investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

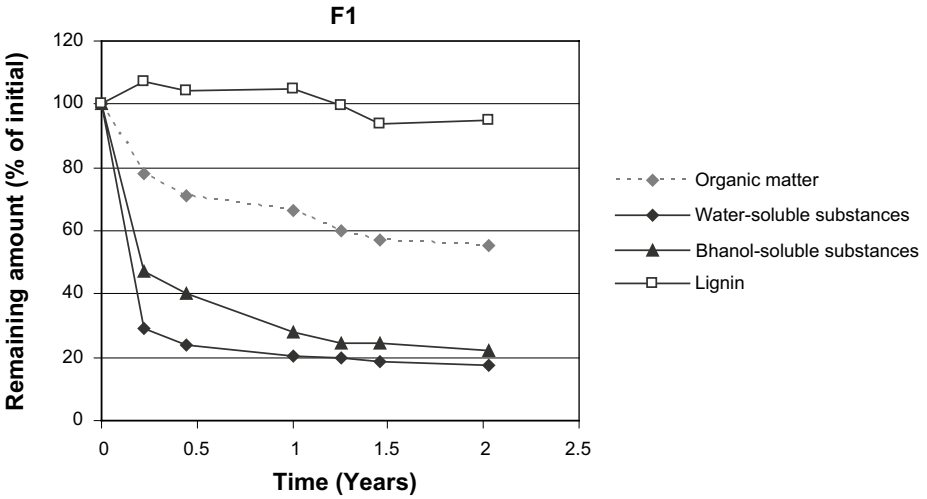

Figure 4-10. *Remaining amount (% of initial) of organic matter (spruce needle litter mass), soluble substances (water and ethanol) and lignin after different times of decomposition.*

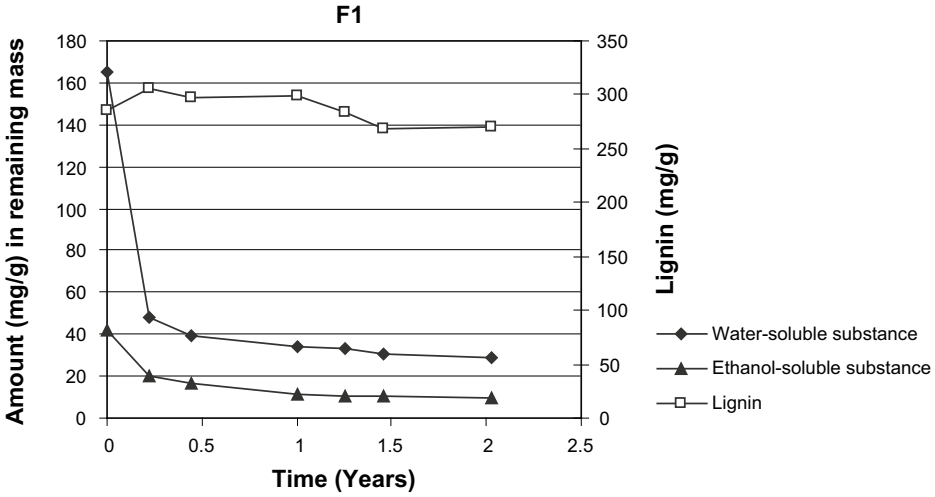

Figure 4-11. *Changes in absolute amounts of solubles (water and ethanol) and lignin with time in an initial 1,000 mg of Norway spruce needle litter incubated at site F1 in the Forsmark area.*

(Fig. 4-11), which is equivalent to a loss of 78% of the initial amount (Fig. 4-10). During the first three months the absolute amount of lignin increased from 290 mg g^{-1} to 310 mg g^{-1} (up to 107% of initial amount) and then remained fairly constant until the end of the first year, when it started to decompose. The decomposition proceeded slowly, however, and after two years the amount had decreased to 270 mg g^{-1}, resulting in a loss of only 5% of the initial lignin amount (Fig. 4-10 and Fig. 4-11).

The C amount followed the mass loss pattern of the litter, starting at 461 mg g^{-1} and ending at 252 mg g^{-1}, which corresponds to a loss of 45%. The N amount decreased by 10% during the first three months (from 7.5 mg g^{-1} to 6.7 mg g^{-1}) and showed only a slight further decrease down to 6.5 mg g^{-1} until the end of the second year. The P followed the same trend, with the largest decrease during the first three months from an initial amount of 0.38 mg g^{-1} down to 0.33 mg g^{-1}. This corresponds to a loss of about 13% of the initial P pool stored in the litter. However, the P amount continued to decrease between month three and the end of the study and ended up at 0.27 mg g^{-1}, resulting in a total loss of 29% of the initial amount (Figs. 4-12 and 4-13).

At the F2 site, the spruce needle litter lost 22% in mass during the first 80 days (Fig. 4-14), which is identical to the mass loss of the spruce needle litter at the F1 site (Fig. 4-12). After one

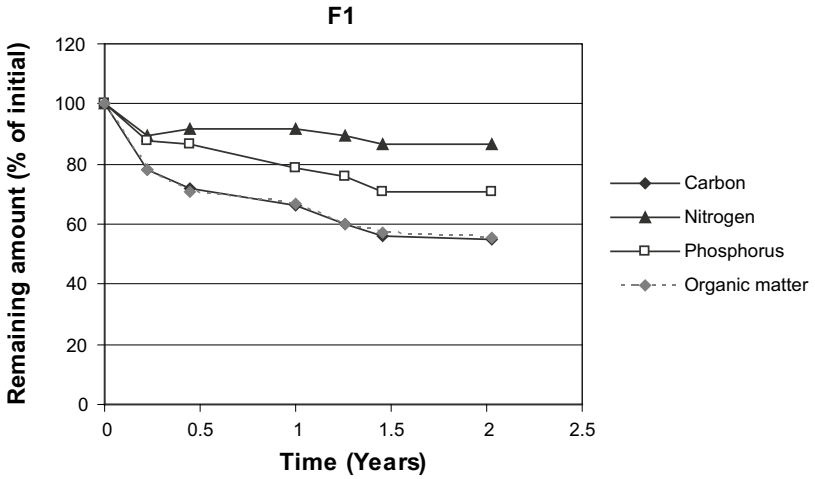

Figure 4-12. *Remaining amount (% of initial) of needle litter mass, carbon, nitrogen and phosphorus after different times of decomposition at site F1 in the Forsmark area.*

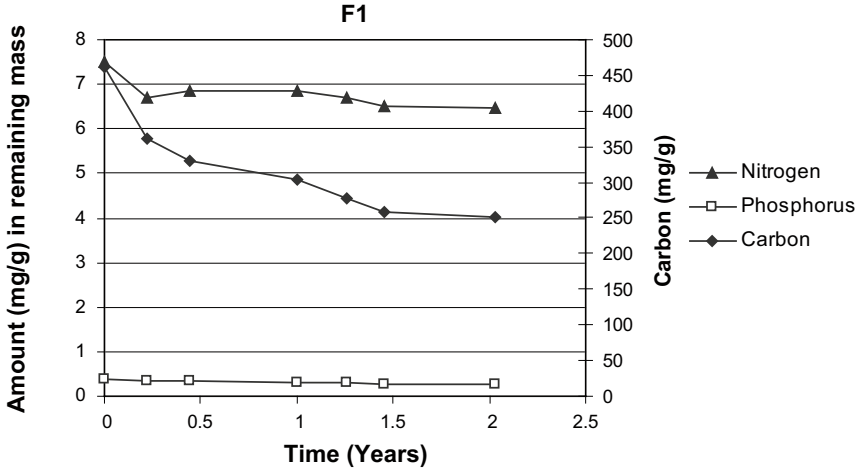

Figure 4-13. *Changes in absolute amounts of carbon, nitrogen and phosphorus with time in an initial 1,000 mg of Norway spruce needle litter incubated at site F1 in the Forsmark area.*

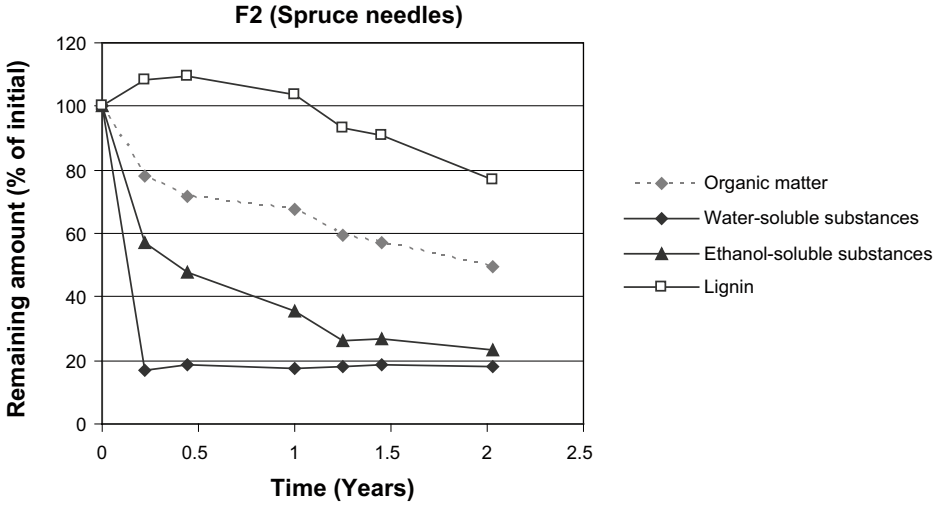

Figure 4-14. *Remaining amount (% of initial) of organic matter (spruce needle litter mass), soluble substances (water and ethanol) and lignin after different times of decomposition at site F2 in the Forsmark area.*

year of decomposition the cumulative mass loss amounted to 33% and after two years to 49%. This means that about 50% of the initial mass of the litter remained after two years in the field (Fig. 4-14).

As at site F1, the rapid loss in mass of the needle litter was accompanied by a fast decrease in water-soluble and ethanol-soluble substances (Fig. 4-14). The water-soluble fraction, which initially amounted to 199 mg g^{-1}, dropped to 35 mg g^{-1} during the first year and to 36 mg g^{-1} at the end of the study (Fig. 4-15). This corresponds to a decrease of 82% of the initial amount of water-soluble substances during the first two years of the decomposition (Fig. 4-14).

The ethanol-soluble substances in the litter decreased more slowly than the water-soluble substances and made up a considerably lower amount of the fresh needle litter than the latter fraction (about one-quarter of the concentration) (Fig. 4-15). Of the initial amount (52 mg g^{-1}) as much as nearly 60% remained after 80 days of decomposition, 38% after one year and 23% after two years (Fig. 4-14). By this time, the absolute amount of ethanol-soluble substances had decreased down to 12 mg g^{-1} (Fig. 4-15).

The initial lignin level of the spruce needle litter was 300 mg g^{-1}, while it amounted to 225 mg g^{-1} after two years (Fig. 4-15). Lignin increased in amount during the first five months (up to about 110% of initial amount), after which it started to decompose. However, at the end of the study about 80% of the initial lignin amount still remained in the litter (Fig. 4-14).

The loss of C followed the mass loss pattern of the litter. From an initial level of 472 mg g^{-1}, the amount decreased down to 229 mg g^{-1} during the two years studied (Fig. 4-17). This corresponds to a loss of about 50% of the initial amount (Fig. 4-16).

Nitrogen had a lower loss rate than the organic matter and was efficiently retained in the litter during the first year. After a minor release during the first month from about 7.2 to 6.9 mg g^{-1}, the N amount increased again. During the second part of year two the first release took place and the amount stabilised at 6.5 mg g^{-1}. Not more than 10% of the initial amount was released during two years (Figs. 4-16 and 4-17).

Phosphorus also had a lower loss rate than the organic matter but was released faster than N. During the first year 25% of the initial P amount was released. After two years the P level had dropped down to 0.25 mg g^{-1} from the initial level of 0.40 mg g^{-1} and 60% of the initial P amount remained in the litter (Figs. 4-16 and 4-17).

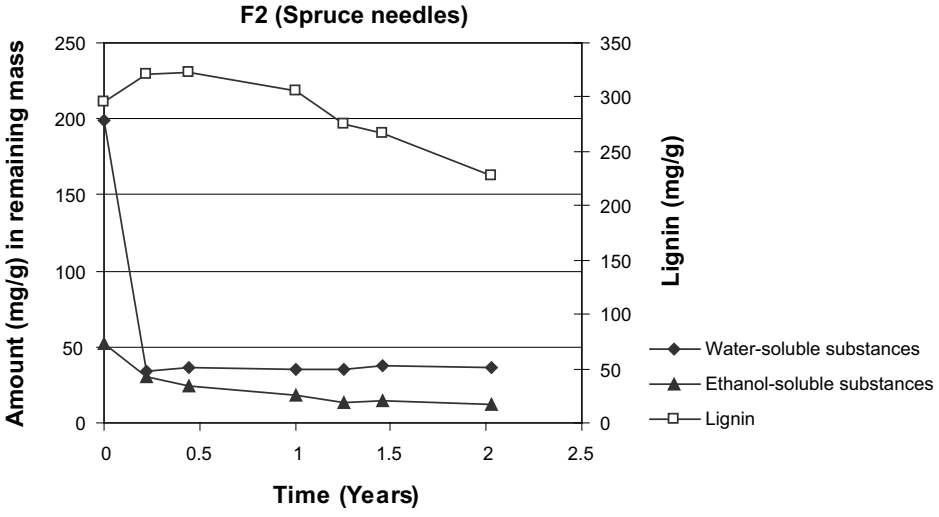

Figure 4-15. *Changes in absolute amounts of solubles (water and ethanol) and lignin with time in an initial 1,000 mg of Norway spruce needle litter incubated at site F2 in the Forsmark area.*

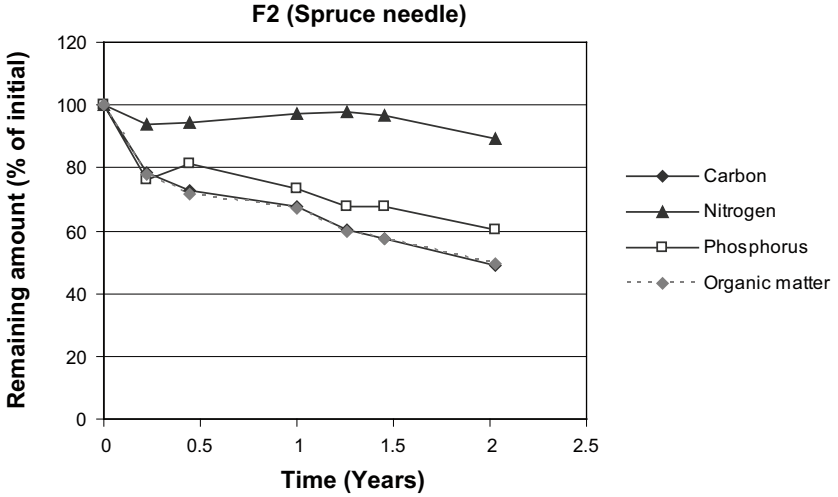

Figure 4-16. *Remaining amount (% of initial) of needle litter mass, carbon, nitrogen and phosphorus after different times of decomposition at site F2 in the Forsmark area.*

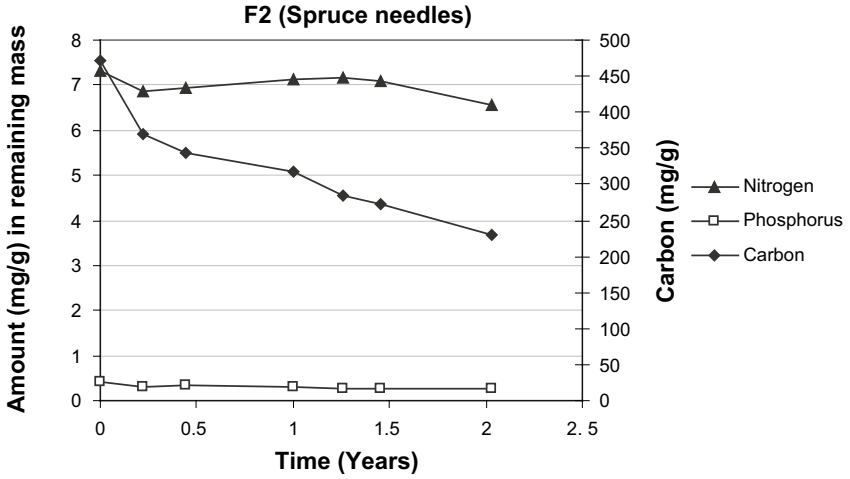

Figure 4-17. *Changes in absolute amounts of carbon, nitrogen and phosphorus with time in an initial 1,000 mg of Norway spruce needle litter incubated at site F2 in the Forsmark area.*

At the F2 site, the alder leaf litter decomposed rapidly and lost 60% in mass during the first six months and had reached an cumulative mass loss of 73% after two years (Fig. 4-19).

The water-soluble substances were decomposed faster than the organic matter and the amount decreased from 210 mg g^{-1} (initial level) down to 40 mg g^{-1} in three months and to 12 mg g^{-1} by the end of the second year (Figs. 4-18 and 4-19). The rapid loss resulted in less than 20% of the initial water-soluble amount remaining in the litter after the first 80 days and only about 5% after two years (Fig. 4-18).

The ethanol-soluble substances also showed a faster decomposition rate than the organic matter (Fig. 4-18). The initial amount of 46 mg g^{-1} dropped to 13 mg g^{-1} during the first three months and stabilised at 5 mg g^{-1} during the second year (Fig. 4-19). Thus, only a minor proportion (11%) of the initial amount remained in the litter after two years of decomposition (Fig. 4-18).

Lignin showed a steady decrease during the first six months (from 225 mg g^{-1} to 160 mg g^{-1}) and then stabilised at this level (Fig. 4-19). The lignin fraction decomposed rapidly and already during the first six months 30% of the initial lignin amount was lost. The decomposition followed that of the organic matter and after two years only 50% of the initial lignin amount remained in the alder leaf litter (Fig. 4-18).

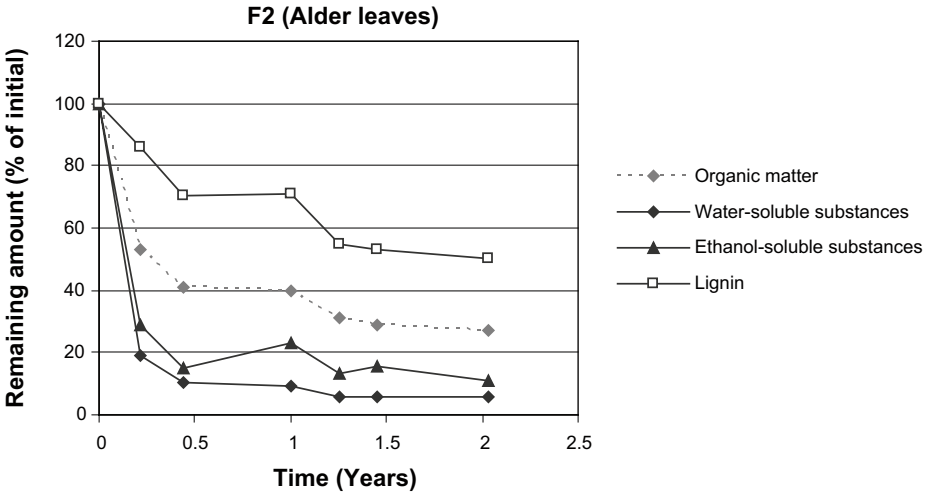

Figure 4-18. *Remaining amount (% of initial) of organic matter (alder leaf litter mass), soluble substances (water and ethanol) and lignin after different times of decomposition at site F2 in the Forsmark area.*

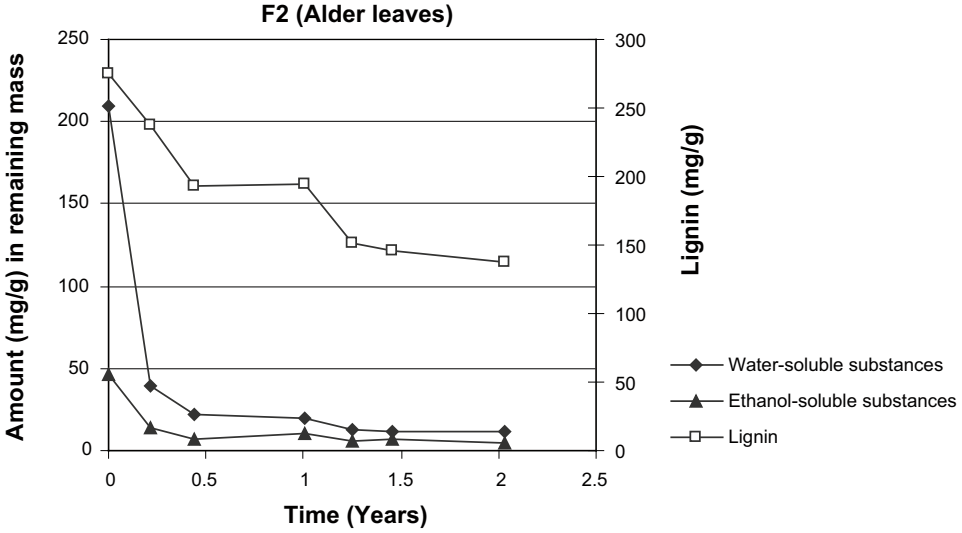

Figure 4-19. *Changes in absolute amounts of solubles (water and ethanol) and lignin with time in an initial 1,000 mg of alder leaf litter incubated at site F2 in the Forsmark area.*

Carbon decreased at the same rate as the organic matter, whereas N was released somewhat slower and P somewhat faster (Fig. 4-20). The C amount was initially 480 mg g^{-1} and ended up at 131 mg g^{-1} (Fig. 4-21), which resulted in a loss of 70% (Fig. 4-20). The initial N level was high (25 mg g^{-1}) and after the two years had decreased down to 9.5 mg g^{-1}, which corresponds to a loss of 62% of the initial amount. Phosphorus, present in a considerably lower concentration than N in the litter (0.86 mg g^{-1}), decreased down to 0.18 mg g^{-1} in two years (Fig. 4-21). Only a minor proportion (about 20%) of the initial P amount in the alder leaf litter remained at the end of the study (Fig. 4-20).

At the F3 site, the spruce needle litter lost 32% in mass during the first year. After two years, the cumulative mass loss amounted to 44%, resulting in 56% of the initial mass remaining (Fig. 4-22).

The spruce needle litter was poor in water-soluble substances. This fraction only amounted to 64 mg g^{-1} in the litter at the start of the experiment. Despite the low initial level, the absolute amount of water-solubles showed a rapid decrease during the first six months down to 40 mg g^{-1}, after which it showed a more irregular pattern. At the end of the second year the amount was down to 37 mg g^{-1}, which corresponds to a loss of 42% of the initial amount (Figs. 4-22 and 4-23).

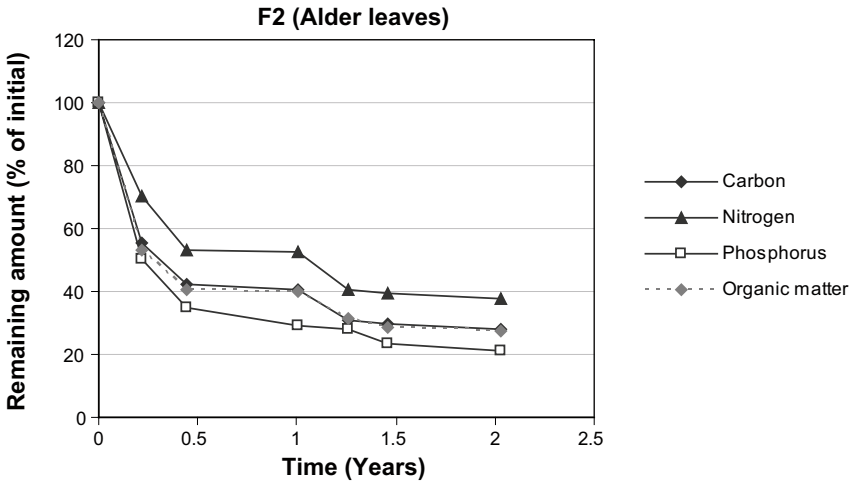

Figure 4-20. *Remaining amount (% of initial) of alder leaf litter mass, carbon, nitrogen and phosphorus after different times of decomposition at site F2 in the Forsmark area.*

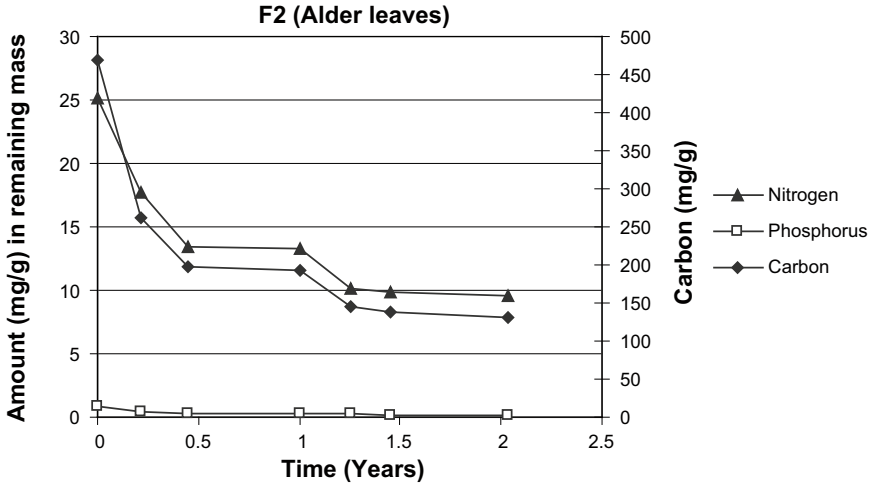

Figure 4-21. *Changes in absolute amounts of carbon, nitrogen and phosphorus with time in an initial 1,000 mg of alder leaf litter incubated at site F2 in the Forsmark area.*

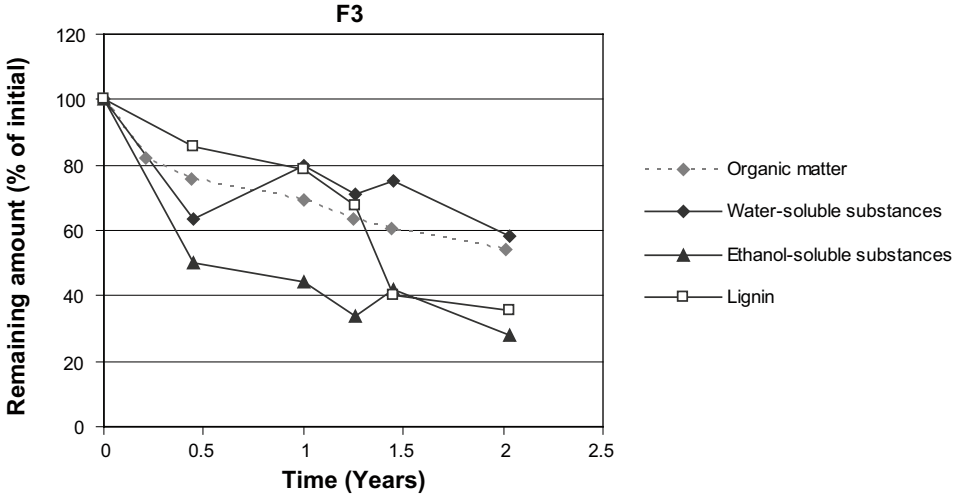

Figure 4-22. *Remaining amount (% of initial) of organic matter (spruce needle litter mass), soluble substances (water and ethanol) and lignin after different times of decomposition at site F3 in the Forsmark area.*

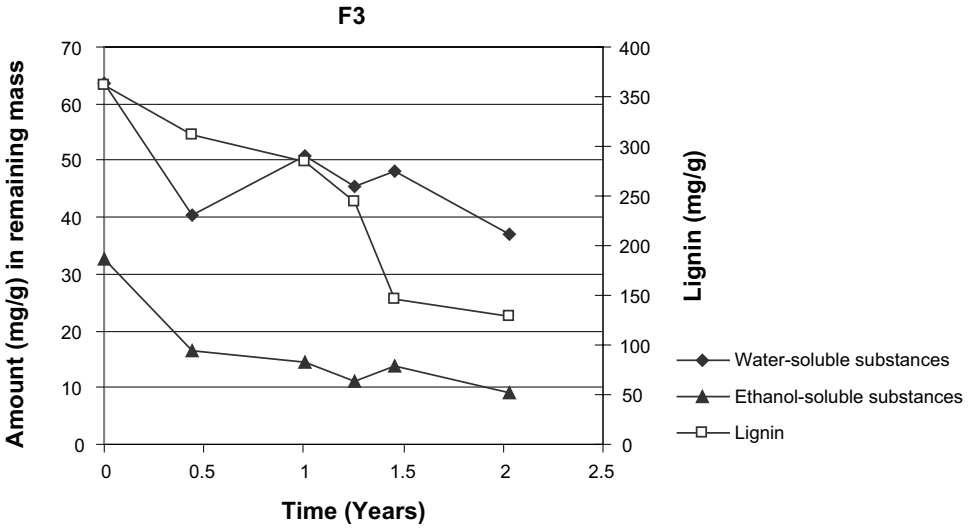

Figure 4-23. *Changes in absolute amounts of solubles (water and ethanol) and lignin with time in an initial 1,000 mg of Norway spruce needle litter incubated at site F3 in the Forsmark area.*

The ethanol-soluble substances showed a more uniform decomposition pattern and decreased from an initial amount of 33 mg g^{-1} to 9 mg g^{-1} within two years (Fig. 4-23). This decrease corresponds to a loss of 72% of the initial amount during two years in the field (Fig. 4-22).

A decrease in the absolute amount of lignin was seen during the first five months, from 360 mg g^{-1} to 320 mg g^{-1}, after which it stabilised until the second year when it further decreased to 120 mg g^{-1} (Fig. 4-23). The total decrease in lignin during two years amounted to 64% of the initial amount (Fig. 4-22).

Carbon in the spruce needle litter deceased from an initial amount of 471 mg g^{-1} to 208 mg g^{-1} during the two years (Fig. 4-25). Thus, 44% of the initial C amount remained after two years of decomposition (Fig. 4-25).

Nitrogen was released more slowly than C, which followed the mass loss pattern of the litter. From an initial level of 9.1 mg g^{-1} the amount decreased down to 6.8 mg g^{-1} during the two years studied (Fig. 4-25). This corresponds to a loss of about 25% of the initial amount in the litter (Fig. 4-24).

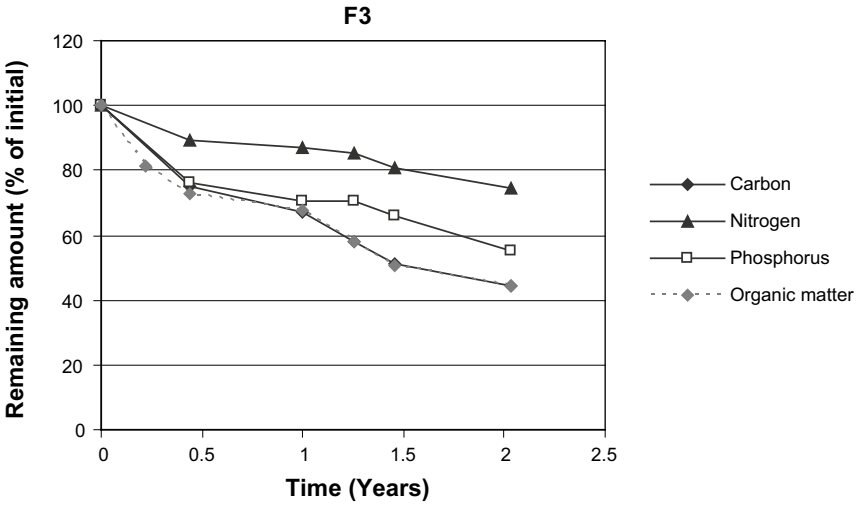

Figure 4-24. *Remaining amount (% of initial) of needle litter mass, carbon, nitrogen and phosphorus after different times of decomposition at site F3 in the Forsmark area.*

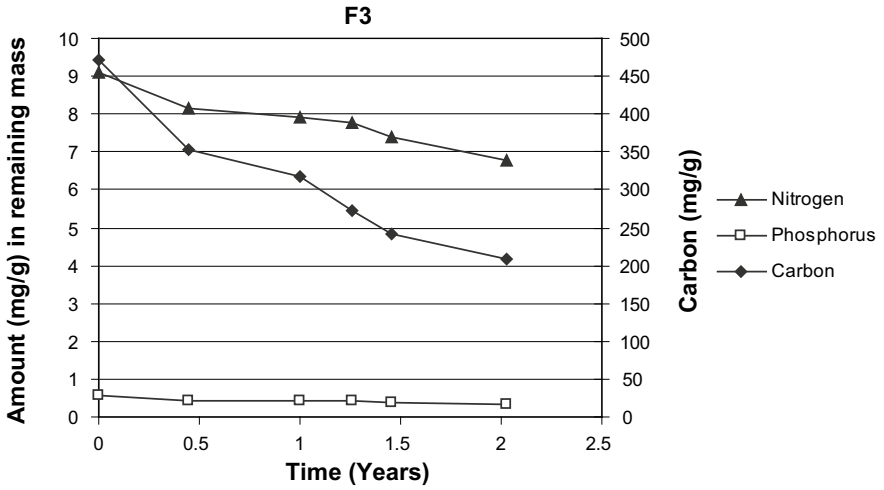

Figure 4-25. *Changes in absolute amounts of carbon, nitrogen and phosphorus with time in an initial 1,000 mg of Norway spruce needle litter incubated at site F3 in the Forsmark area.*

Phosphorus was present in considerably lower amounts than N in the litter. The fresh needle litter contained 0.6 mg g^{-1} of P, which was one-sixteenth of the N amount (9.1 mg g^{-1}). On the other hand, the P release was much faster and about half the original amount was released in two years (Figs. 4-24 and 4-25).

4.1.2 The Oskarshamn area – individual sites

Litterfall – biomass and element return (N and C)

At site O1 the total litterfall (mean for two years) amounted to about 290 gdw m^{-2} yr^{-1}, with a between-year variation of about 50 gdw m^{-2} (Fig. 4-26, Appendix A1). Since this was an almost pure deciduous stand (mainly oak), needle litter only accounted for 1% of the total litterfall. The leaf fraction, on the other hand, accounted for 64% of the average total litterfall, whereas other components contributed about 35% (100 gdw m^{-2} yr^{-1}).

The mean annual input of C was 140 gdw m^{-2} and that of N 3.6 gdw m^{-2} (Figs. 4-27 and 4-28). Of the carbon, about 90 gdw m^{-2} originated from the leaves and about 50 gdw m^{-2} from the other components. The major proportion of the N was also deposited with the leaf fraction (2.0 gdw m^{-2} yr^{-1}). However, the amounts of N transferred to the forest floor with leaves did not differ between each specific year although the leaf fall varied between years (Figs. 4-26 and 4-28). This indicates that N concentrations in the leaf litter varied between years.

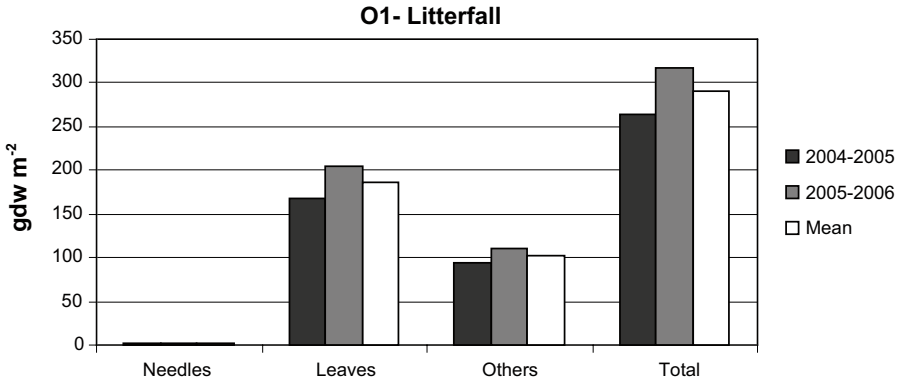

Figure 4-26. *Annual amounts of aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O1 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

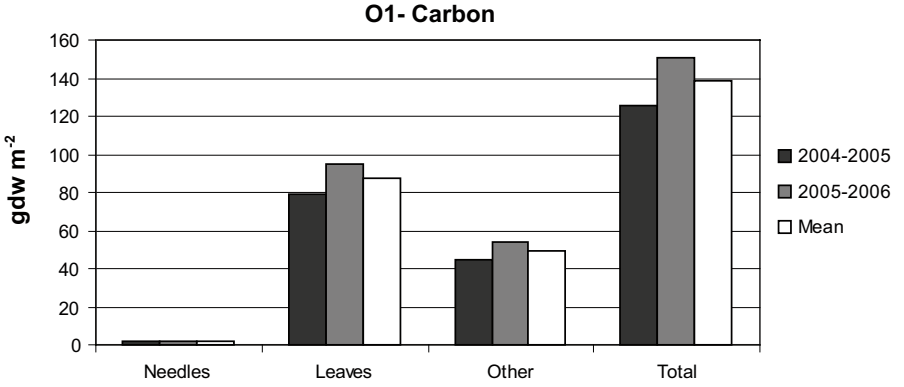

Figure 4-27. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O1 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

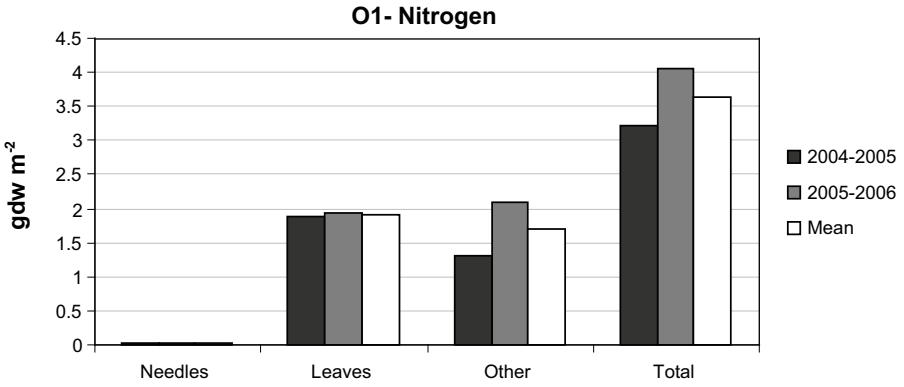

Figure 4-28. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O1 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

At the O2 site**,** which consisted of a pine stand, the total average litterfall was low and amounted to about 140 gdw m^{-2}, of which pine needles contributed 100 gdw m^{-2} and the 'others' fraction 40 gdw m^{-2} (Fig. 4-29). Other components (small twigs, cones, seeds etc.) thus accounted for 29% of the total litterfall. The variation in total litterfall between years amounted to about 30 gdw m^{-2} and was mainly due to a higher needle litter production during 2004–2005 (Fig. 4-29).

The average annual input of C through the total litterfall amounted to 70 gdw m^{-2}, of which 50 gdw m^{-2} (70%) originated from needles and 20 gdw m^{-2} (30%) from the 'others' fraction (Fig. 4-30).

On average, about 0.8 gdw m^{-2} of the N was returned to the forest floor by the annual litterfall, of which the needle fraction accounted for 0.45 gdw m^{-2} and other components for 0.35 gdw m^{-2} (Fig. 4-31).

At the O3 site**,** a substantial amount of litter fell to the ground. The mean for the two years was 390 gdw m^{-2}, of which needles contributed 70% and other components 30% (Fig. 4-32). The between-year variation was large (about 170 gdw m^{-2}), which meant a variation of 64% (Appendix A1).

The average annual input of C amounted to 190 gdw m^{-2}, of which as much as 130 gdw m^{-2} was deposited with needles and 60 gdw m^{-2} with the 'others' fraction (Fig. 4-33). The C input was highly variable between years due to the uneven litterfall.

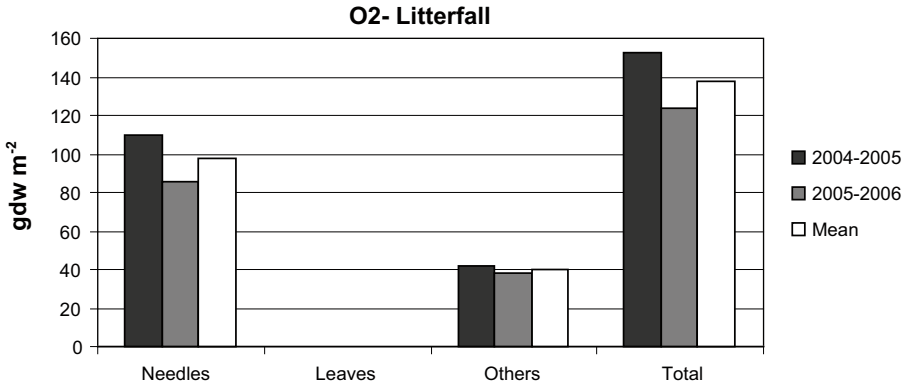

Figure 4-29. *Annual amounts of aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O2 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

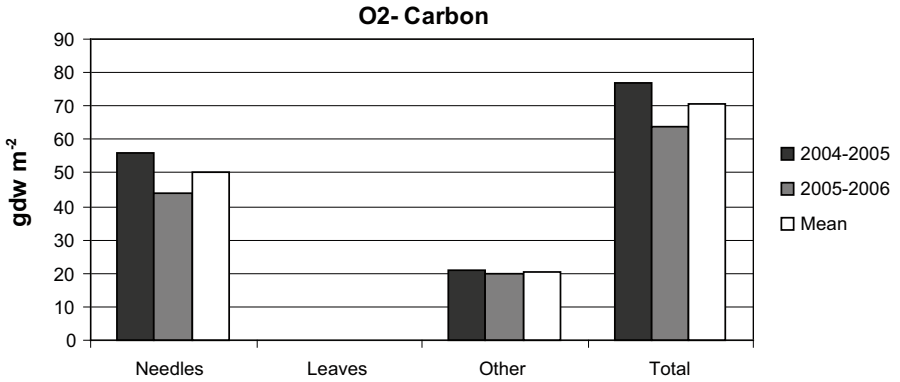

Figure 4-30. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O2 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

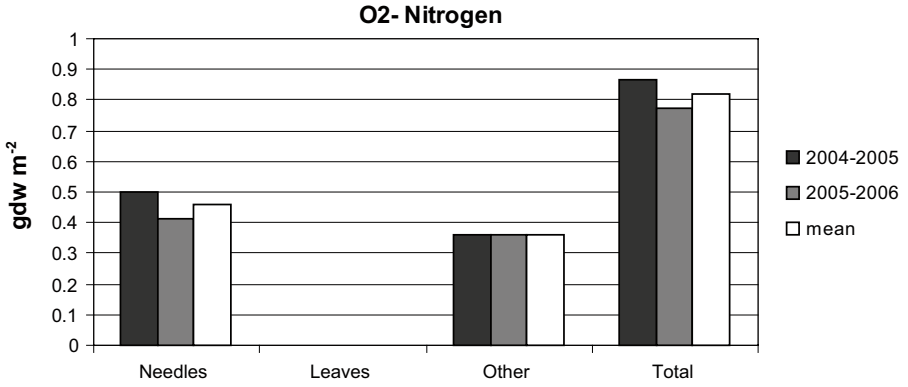

Figure 4-31. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O2 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

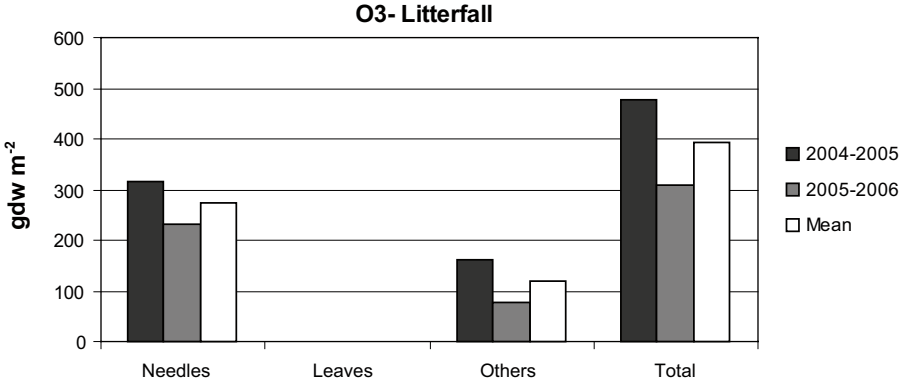

Figure 4-32. *Annual amounts of aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O3 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

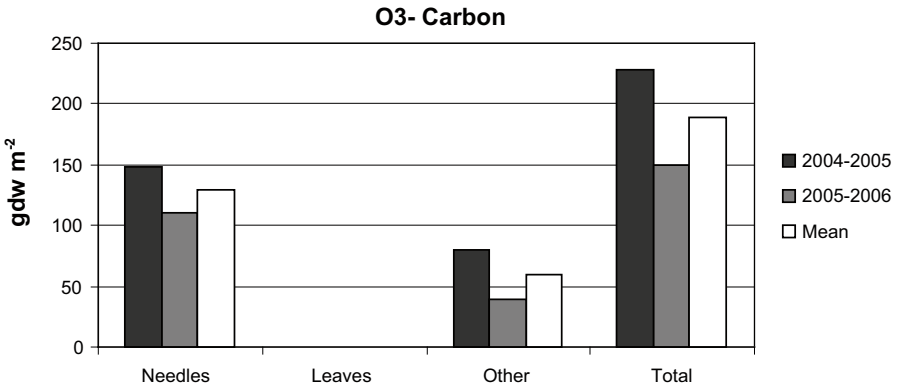

Figure 4-33. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O3 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

About 70% of the N returned to the forest floor by the annual litterfall (3.5 gdw m^{-2}) was deposited with the needle litter fraction (2.5 gdw m^{-2}), whereas the leaves and 'others' fractions contributed 30% (1 gdw m^{-2}) (Fig.4-34).

Litter decomposition and chemical changes

At site O1, the initial content of water-soluble substances in oak litter was 184 mg g^{-1}. During the first six months it dropped to 37 mg g^{-1} and after two years it had decreased to 23 mg g^{-1} (Fig. 4-36). This corresponds to an 87% decrease in the initial amount (Fig. 4-35). The ethanol-soluble substances decreased from 23 mg g^{-1} to 12 mg g^{-1} in the two years (Fig. 4-36), representing a loss of 50% of the initial amount (Fig. 4-35).

The lignin fraction showed a consistent pattern with decreasing absolute amounts, from 350 mg g^{-1} initially to 240 mg g^{-1} after two years of decomposition (Fig. 4-36). The decomposition was slow during initial stages and not more than 10% of the initial lignin amount was decomposed during the first year. After two years, however, the lignin fraction had decreased by about 30% (Fig. 4-35).

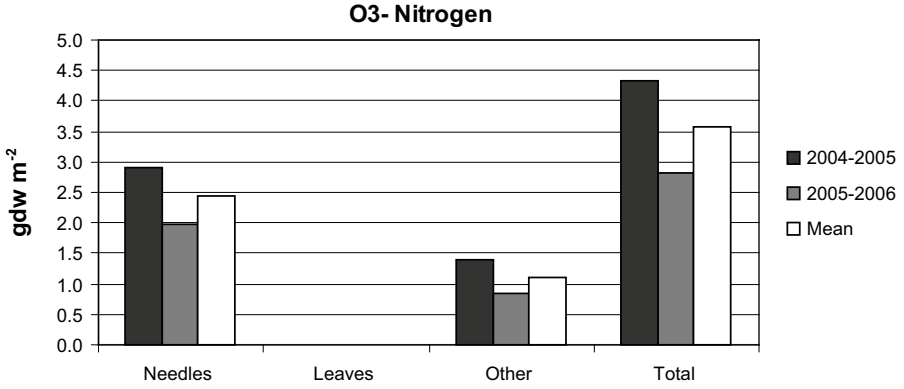

Figure 4-34. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at site O2 within the Oskarshamn investigation area. Results from two consecutive years are given (June 2004 – June 2005 and June 2005 – June 2006), as well as the mean for these two years.*

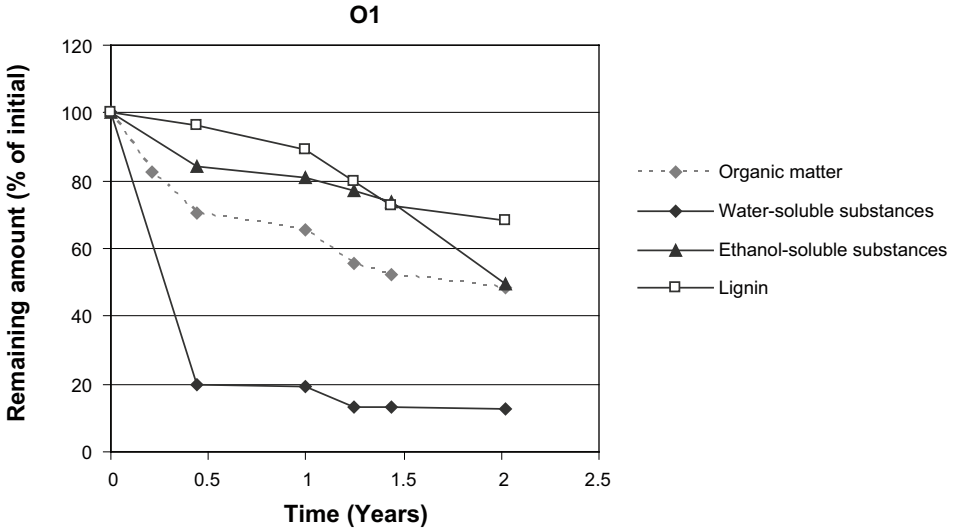

Figure 4-35. *Remaining amount (% of initial) of organic matter (oak leaf litter mass), soluble substances (water and ethanol) and lignin after different times of decomposition at site O1 in the Oskarshamn area.*

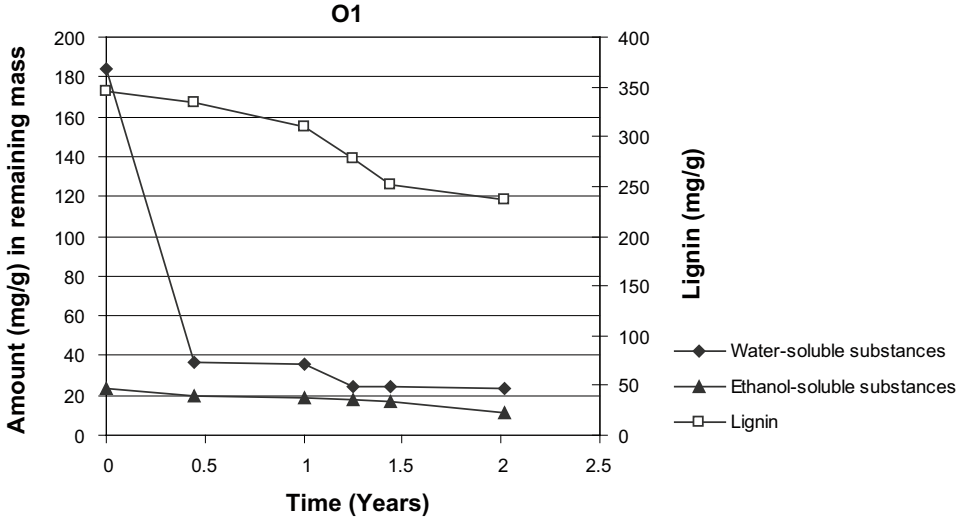

Figure 4-36. *Changes in absolute amounts of solubles (water and ethanol) and lignin with time in an initial 1,000 mg of oak leaf litter incubated at site O1 in the Oskarshamn area.*

The absolute amount of C in oak leaf litter at the O1 site decreased from 472 mg g^{-1} to 217 mg g^{-1} during the two years (Fig. 4-38), which corresponds to a decrease of 54% in the initial C amount (Fig. 4-37). The decomposition of C followed the decomposition curve of the organic matter. Nitrogen was initially present at an amount of 11 mg g^{-1} and did not change during the first year. At the end of the study the amount had decreased to 9 mg g^{-1} (Fig. 4-38), which is equivalent to a loss of 20% of the initial amount (Fig. 4-37). Compared with N and C, the P level was low, starting at 0.6 mg g^{-1} and ending at 0.3 mg g^{-1} (Fig. 4-38), which represents a loss of 42% of the initial amount during the two years (Fig. 4-37).

At the O2 site, the initial amount of water-soluble substances in pine needles was 145 mg g^{-1}. The amount decreased rather rapidly and was down at 34 mg g^{-1} already after some months (Fig. 4-40). Thereafter, the level remained fairly constant and at the end of the study about 20% of the water-solubles present initially were left (Fig. 4-39). The ethanol-soluble substances decreased from about 100 mg g^{-1} to 31 mg g^{-1} during the two years (Fig. 4-40), which means that about 40% of the initial amount still remained in the litter (Fig. 4-39). The lignin fraction also decreased from an initial amount of 260 mg g^{-1} to 190 mg g^{-1} during two years (Fig. 4-40). At the end of the study, about 70% of the initial lignin amount remained in the litter (Fig. 4-39).

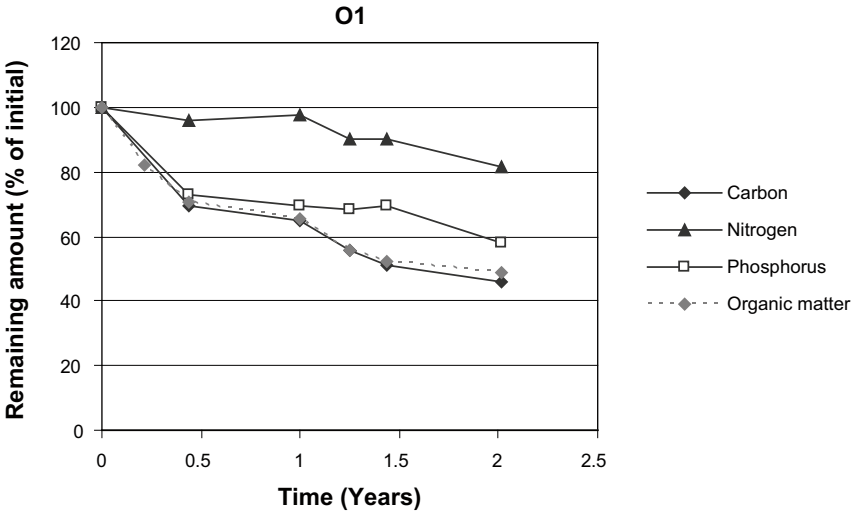

Figure 4-37. *Remaining amount (% of initial) of organic matter (oak leaf litter mass), carbon, nitrogen and phosphorus after different times of decomposition at site O1 in the Oskarshamn area.*

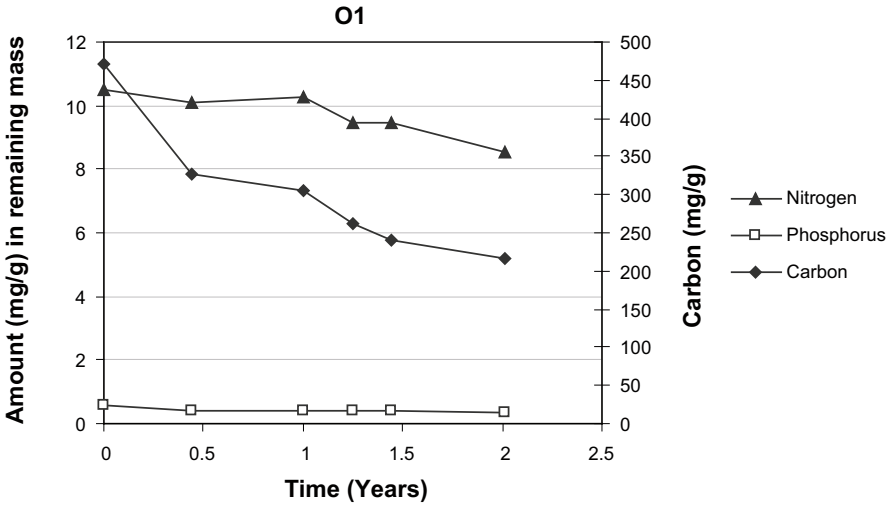

Figure 4-38. *Changes in absolute amounts of carbon, nitrogen and phosphorus with time in an initial 1,000 mg of oak leaf litter incubated at site O1 in the Oskarshamn area.*

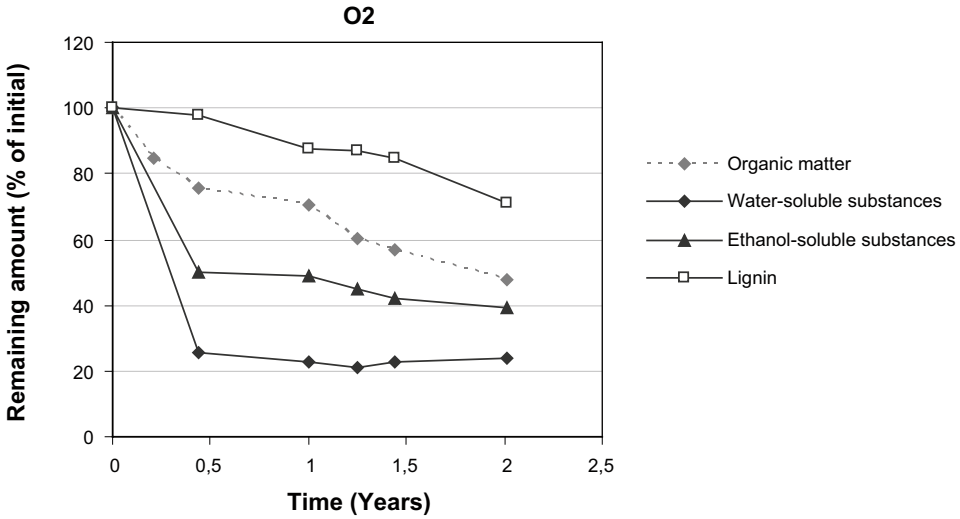

Figure 4-39. *Remaining amount (% of initial) of organic matter (pine needle litter mass), soluble substances (water and ethanol) and lignin after different times of decomposition at site O2 in the Oskarshamn area.*

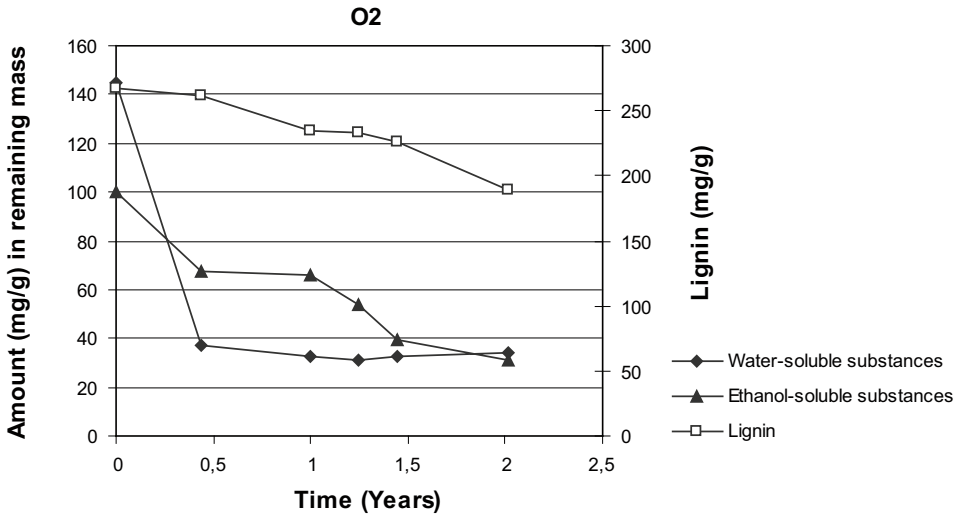

Figure 4-40. *Changes in absolute amounts of solubles (water and ethanol) and lignin with time in an initial 1,000 mg of Scots pine needle litter incubated at site O2 in the Oskarshamn area.*

The amount of C in the pine litter decreased by 52% during two years and the loss followed the pattern of the organic matter (Fig. 4-41). Initially, 507 mg g^{-1} of C were present in the litter and at the end the absolute amount was 242 mg g^{-1} (Fig. 4-42). The N amount increased in the litter after a minor loss during the first months and was at the same level as initially after two years (4 mg g^{-1}) (Fig. 4-42). Phosphorus followed a similar pattern (Fig. 4-42) but was present in a higher amount at the end of the decomposition period studied (0.3 mg g^{-1}) than initially (0.25 mg g^{-1}). Thus, the final amount was 121% of the original amount (Fig. 4-41).

At the O3 site, there was a rapid decrease in both water-soluble and ethanol-soluble substances from the spruce litter (Fig. 4-43 and 4-44). The first fraction, which was initially present in an amount of 104.4 mg g^{-1}, decreased to 48.8 mg g^{-1} in six months, and ended at 34 mg g^{-1} after two years (Fig. 4-44). This corresponds to a decrease of 67% in the initial amount of water-soluble substances during the first two years of decomposition (Fig. 4-43). The ethanol-soluble substances decreased from 41 to 16 mg g^{-1} in the two years and already after six months the amount had decreased down to 20 mg g^{-1} (Fig. 4-44). After two years about 40% of the initial amount of

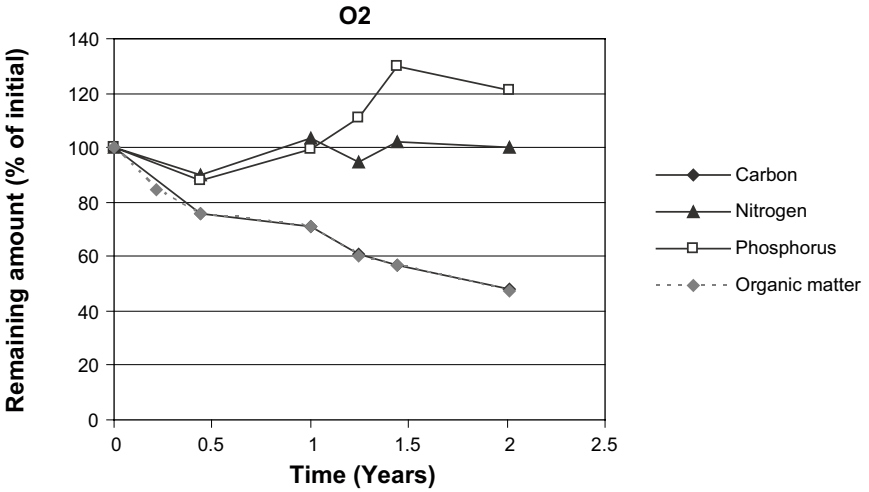

Figure 4-41. *Remaining amount (% of initial) of organic matter (pine needle litter mass), carbon, nitrogen and phosphorus after different times of decomposition at site O2 in the Oskarshamn area.*

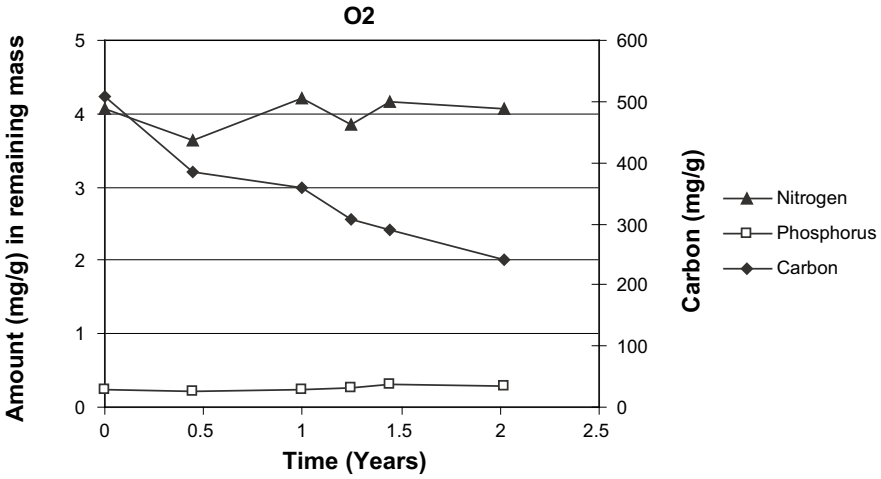

Figure 4-42. *Changes in absolute amounts of carbon, nitrogen and phosphorus with time in an initial 1,000 mg of Scots pine needle litter incubated at site O2 in the Oskarshamn area.*

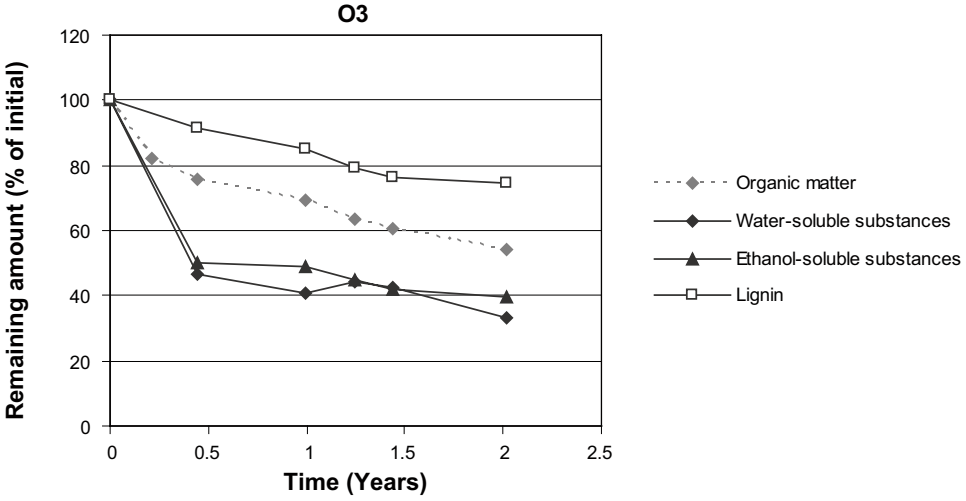

Figure 4-43. *Remaining amount (% of initial) of organic matter (spruce needle litter mass), soluble substances (water and ethanol) and lignin after different times of decomposition at site O3 in the Oskarshamn area.*

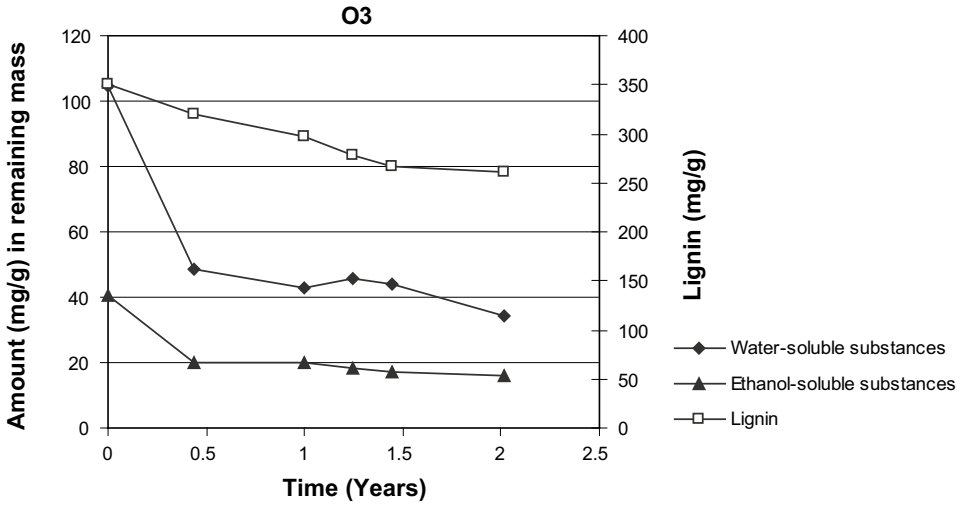

Figure 4-44. *Changes in absolute amounts of solubles (water and ethanol) and lignin with time in an initial 1,000 mg of Norway spruce needle litter incubated at site O3 in the Oskarshamn area.*

ethanol-soluble substances remained in the spruce litter (Fig. 4-43). The decomposition of lignin started immediately and during the first year about 15% of the original amount was decomposed, while after two years 25% was decomposed (Fig. 4-43). During the same time the lignin amount decreased from 350 mg g^{-1} to 260 mg g^{-1} (Fig. 4-44).

The C in the litter decreased from 461 mg g^{-1} to 247 mg g^{-1} in two years (Fig. 4-46) which corresponds to a loss of 46% of the initial amount (Fig. 4-45). Nitrogen decreased from 8 mg g^{-1} to 7 mg g^{-1} in the first six months, after which the level stabilised (Fig. 4-46). This means that about 10% of the original N amount was released during the first two years of decomposition. Phosphorus, which initially was present in an amount of 0.6 mg g^{-1} in the litter, decreased down to 0.3 mg g^{-1} after two years (Fig. 4-46) which is equivalent to a loss of 45% (Fig. 4-45).

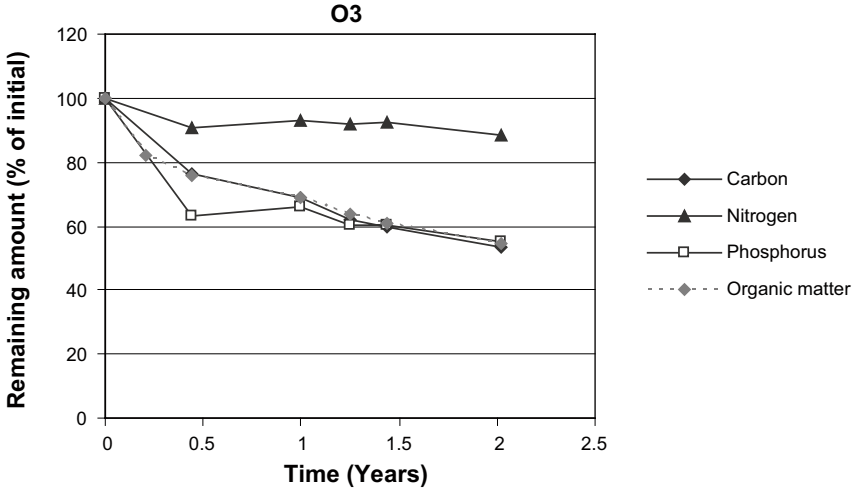

Figure 4-45. *Remaining amount (% of initial) of organic matter (spruce needle litter mass), carbon, nitrogen and phosphorus after different times of decomposition at site O3 in the Oskarshamn area.*

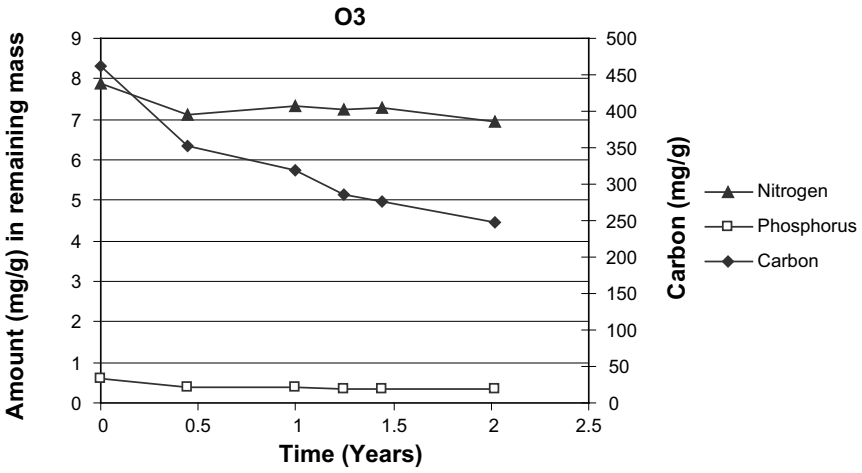

Figure 4-46. *Changes in absolute amounts of carbon, nitrogen and phosphorus with time in an initial 1,000 mg of Norway spruce needle litter incubated at site O3 in the Oskarshamn area.*

4.2 Model simulations of decomposition and nutrient dynamics

There was generally a good fit between the measured and predicted mass loss and N and P dynamics in litter materials. Mass loss was slightly underestimated initially and overestimated at later stages for alder leaves at the site F2 in Forsmark (Figure 4-47).

Litter can lose mass and nutrients through decomposition but also through leaching, especially of water-soluble compounds /Berg et al. 1982a, Johansson 1994/. In the litter bag method these two processes cannot be separated and because the model predicts only mass loss through decomposition, the initial mass loss might be underestimated for litters with a high content of water-soluble compounds. During the first two years of decomposition, 45–55% of the initial mass was lost from needle litters and oak leaves, while markedly higher mass loss was observed for alder leaves. According to the model predictions, after 10 years about 80% of the initial mass was decomposed from needle litters and oak leaves but over 90% of the initial mass of alder leaves was predicted to be decomposed (Figure 4-48).

The dynamics of N and P in decomposing needles and leaves are shown in Figures 4-49 and 4-50. Alder leaves had the highest initial content of N and P, followed by spruce needles and oak leaves. The content of those elements was lowest in pine needles. There was no marked difference in the element content between the different sites for the different tree species. Mineralisation of N started immediately from alder leaves, while the other litter types showed a short period of N immobilisation (Fig. 4-49 and 4-50). The release of P started immediately for all the litter types except for pine needles. Element accumulation in litters is generally associated with low initial element content, while a marked release of elements is typical for litters with high initial element content /Berg and Staaf 1980b, Johansson 1992, Ågren and Bosatta 1998/.

The release of N and P from the litter materials was slower compared with mass loss, and N was released at a lower rate than P. After 10 years of decomposition, about 60–70% of the initial N and 80–90% of the initial P was released from the spruce needles and oak leaves. Markedly lower release rates of N and P were predicted from pine needles, 54 and 41%, respectively. The release rate of N and P from alder leaves was predicted to be very high and only a few percent of the initial N and P were predicted to be found in decomposed alder leaves. However, considering the amount of N and P after 10 years of decomposition, the differences between the litter types had decreased. About 3 mg N and 0.08 mg P were predicted to be found in the decomposed spruce needles and oak leaves. The amount of N was lower in decomposed alder leaves (1.5 mg), and pine needles (2 mg) (Figs. 4-49 and 4-50). The amount of P in pine needles (145 mg) was twice as high as in the other litter types, but as shown in Fig. 4-49, the agreement between the measured and predicted P dynamics was not as good for P in pine needles as for P and N in the other litter types.

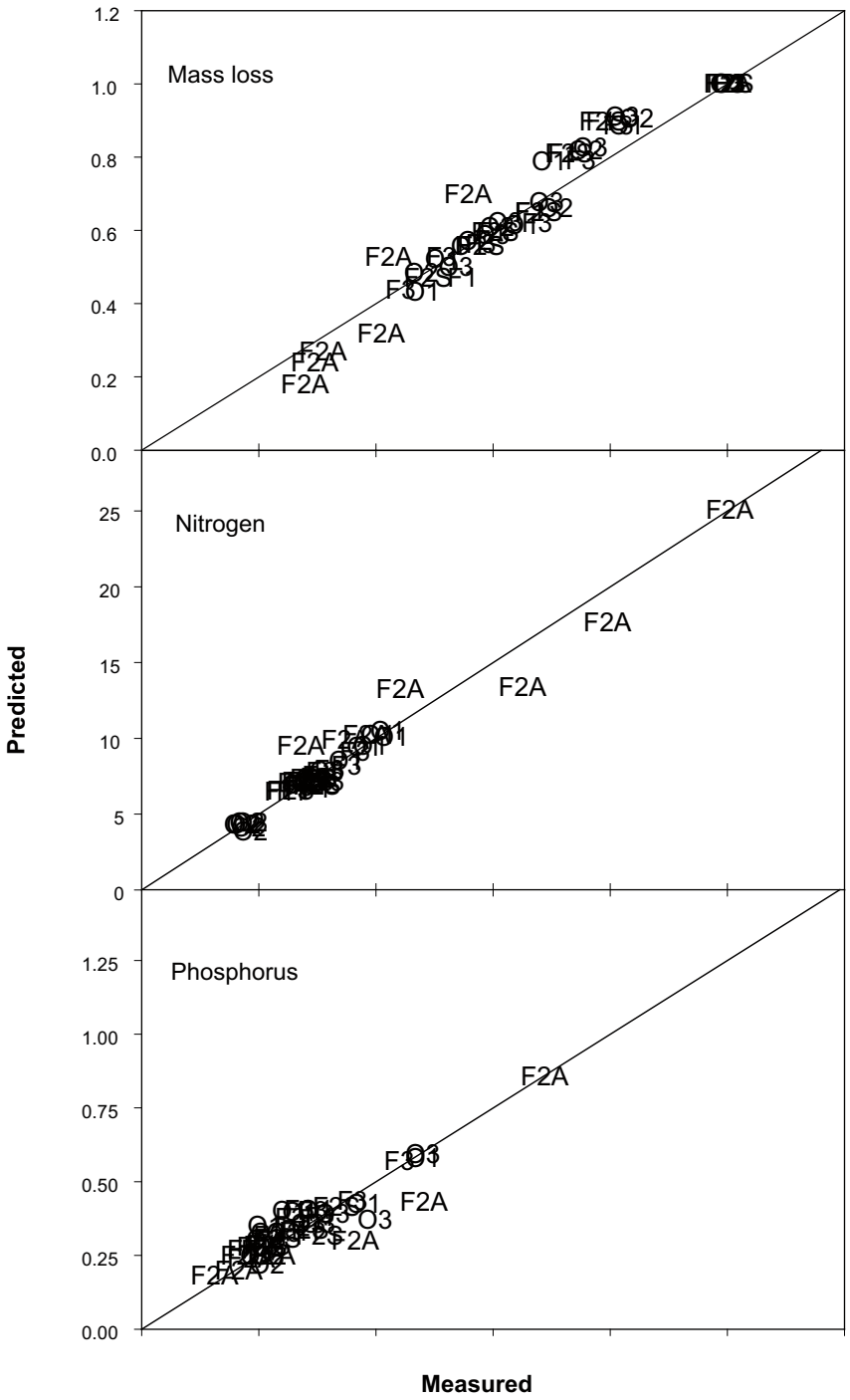

Figure 4-47. *Predicted and measured dynamics of mass loss and C, N and P in the different litter types. F1 and F3 are the spruce sites and F2A the alder part of the spruce/alder site at Forsmark. O1 denotes the oak site, O2 the pine site and O3 the spruce site at Oskarshamn.*

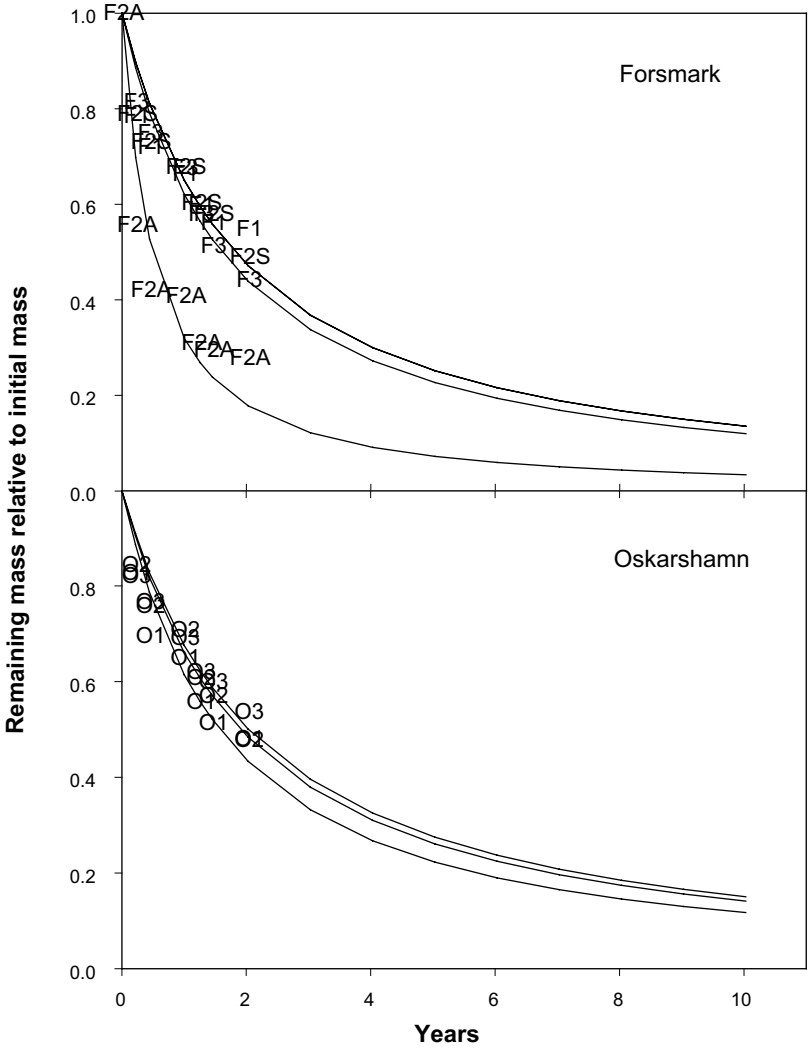

Figure 4-48. *Dynamics of remaining mass during decomposition relative to the initial amount. F1 and F3 are the spruce sites and F2A the alder part of the spruce/alder site in Forsmark. O1 denotes the oak site, O2, the pine site and O3 the spruce site in Oskarshamn.*

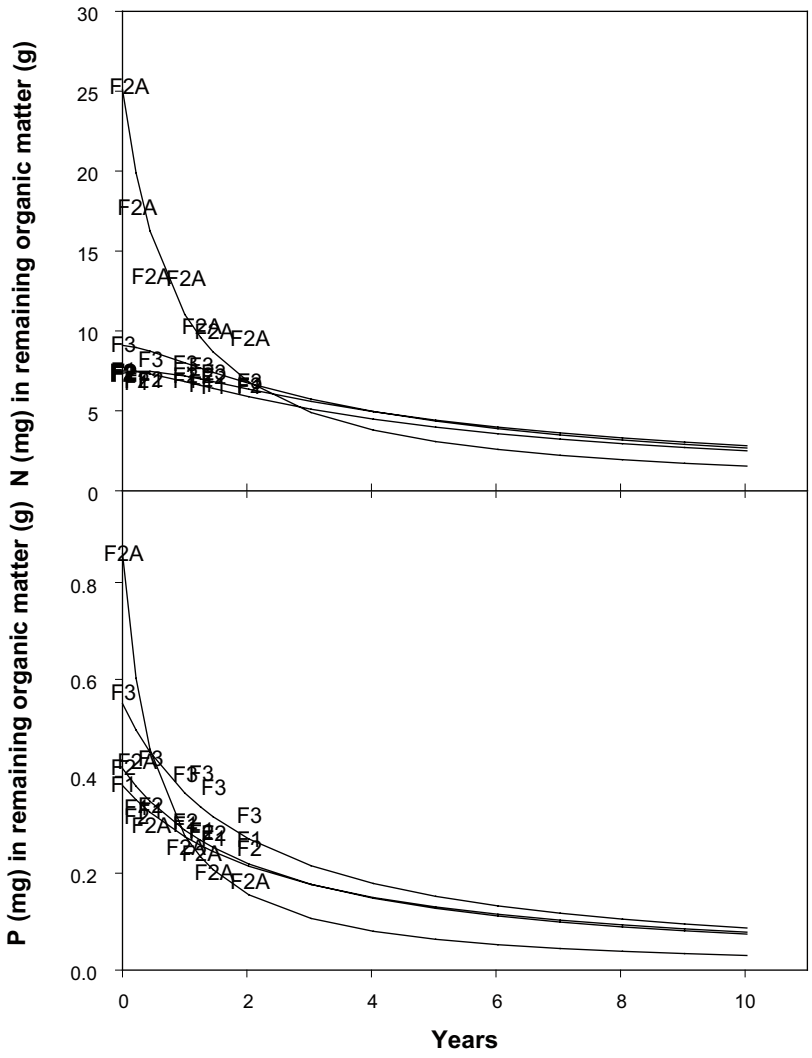

Figure 4-49. *Dynamics of N (mg) and P (mg) in remaining mass (g C) of the different litter types. F1 and F3 denote the spruce sites and F2A the alder part of the spruce/alder site at Forsmark.*

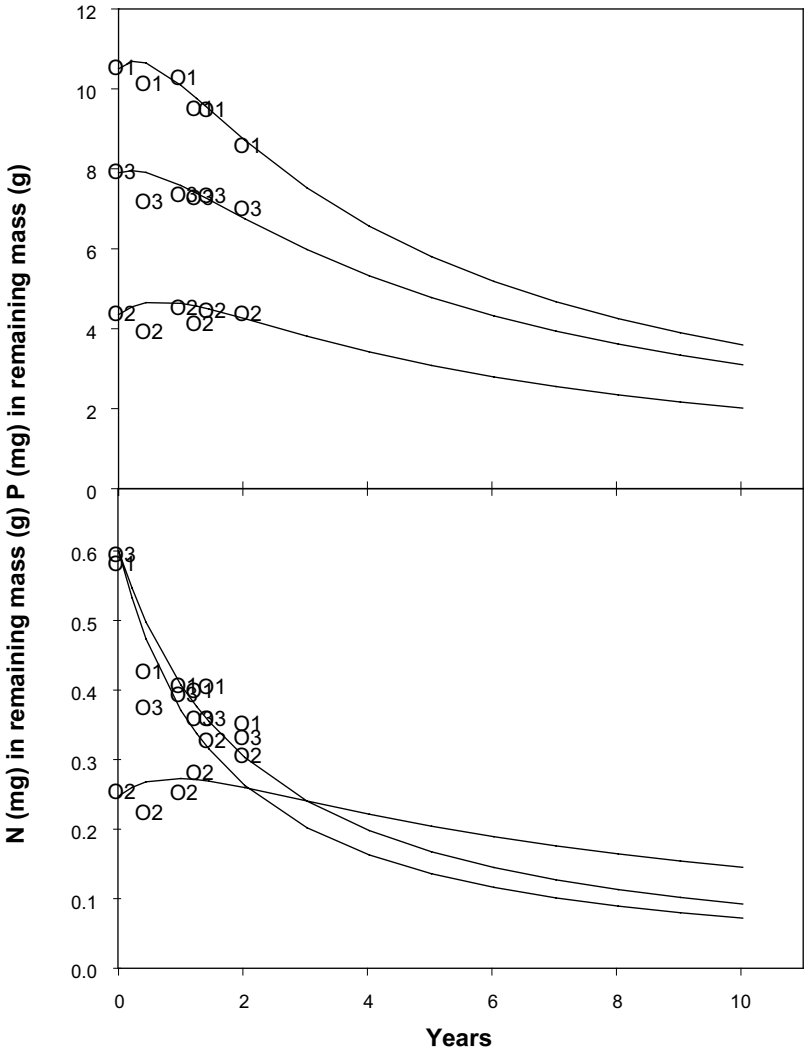

Figure 4-50. *Dynamics of N (mg) and P (mg) in remaining mass (g C) of the different litter types. O1 denotes the oak site, O2, the pine site and O3 the spruce site at Oskarshamn.*

5 Discussion

5.1 Litterfall biomass and element return in litterfall

In the Forsmark investigation area, the aboveground litterfall from trees was of similar magnitude at sites F1 and F2 but considerably lower at site F3 (Fig. 5-1). At the former sites the average annual litterfall (including all components) amounted to 195 and 231 gdw m^{-2}, whereas the latter site only received 136 gdw m^{-2}. The measurements also revealed that leaves accounted for almost the same proportion as needles in the litterfall at sites F1 and F2. For site F1 this was unexpected, since the stand was considered an almost pure spruce stand. However, some large birch trees were found in the part where the litter traps were placed and contributed a large amount of leaf litter.

In the Oskarshamn investigation area too, there was a large variation in annual litterfall between stands (Fig. 5-2). The spruce stand at site O3 exhibited the highest litterfall (almost 400 gdw m^{-2}), followed by the oak stand at site O1 (almost 300 gdw m^{-2}), while the pine stand at site O2 had the lowest litterfall (less than 150 gdw m^{-2}). At site O3 the litterfall was markedly higher during the first year of measurement than during the second (a difference of about 170 gdw m^{-2}) (Fig. 4-32). This between-year variation in litterfall may have been the result of the storm 'Gudrun', which hit Götaland in January 2005. Although the most severe forest damage occurred in other parts of Småland, the storm event also affected the Oskarshamn region. Storm events and other fluctuations in environmental factors such as cold temperatures or drought can result in enhanced litterfall /Bornebusch 1937, Mork 1942/. During the first year of measurement, a slightly higher litterfall was also observed in the pine stand (O2) (Fig. 4-29) but not in the oak stand (O1) (Fig. 4-26). The lack of increase in the latter stand was probably due to the fact that the oak trees were already defoliated when the storm came in January.

Good growth conditions caused by a favourable climate in individual years can also result in increased tree biomass production and increased litterfall production. The increase in litter production may occur several years after the increased biomass production, since the life-time of the foliage varies with tree species and also between different geographical locations. Although the between-year variation in litterfall can be very high due to fluctuations in environmental factors, it was rather low in both areas investigated in this study. The ratio of maximum to minimum annual total litterfall within a site ranged between 1.2 and 1.6 gdw m^{-2}. These values are somewhat lower than those reported by /Berg et al. 1999b/ for 12 stands located from Norrbotten in the north of Sweden to Blekinge in the south, where total litterfall was measured during 4 years. The ratios observed ranged between 1.1 and 2.1 gdw m^{-2}. This indicates that aboveground litterfall has to be monitored over several years to get a high accuracy in the estimates.

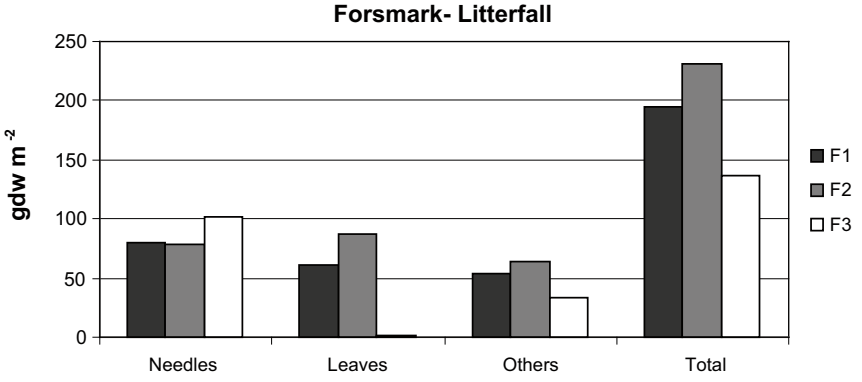

Figure 5–1. *Annual amounts of aboveground tree litterfall (gdw m^{-2} yr^{-1}) at sites F1, F2 and F3 within the Forsmark investigation area. Results are given as the mean for the two years (June 2004 – June 2005 and June 2005 – June 2006).*

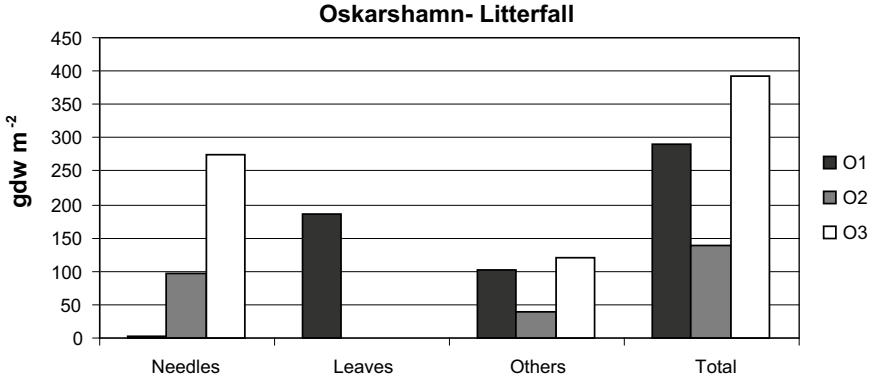

Figure 5-2. *Annual amounts of aboveground tree litterfall (gdw m^{-2} yr^{-1}) at sites O1, O2 and O3 within the Oskarshamn investigation area. Results are given as the mean for the two years (June 2004 – June 2005 and June 2005 – June 2006).*

The proportion of needles/leaves in total litterfall varied between 65% and 75% in the stands studied here. In the aforementioned study by /Berg et al. 1999b/, the proportion in Norway spruce stands varied between 56% and 84% but in most stands the needle fraction accounted for about 70% of the total annual litterfall. In a similar study dealing with Scots pine stands /Berg et al. 1999a/, the proportion of needles in total litterfall varied between 33% and 75%. However, in most of the stands the needle fraction accounted for about 55% of the total litterfall. Our figures are thus in agreement with those reported in the literature.

Whether the measured litterfall amounts in the stands studied here are in agreement with previously reported figures is more difficult to assess. In the literature, the litterfall in forests has successfully been related to site factors such as site index (positive relationship), stand age (negative relationship), basal area (positive relationship), latitude (negative relationship), annual temperature (positive relationship), and annual precipitation (positive relationship) /Bonnevie-Svendsen and Gjems 1957, Mälkönen 1974, Albrektson 1988, Berg et al. 1999ab/. In the stands in the present investigation, none of the stand-related parameters given above were estimated, so it is difficult to identify discrepancies in relation to literature values. However, present values can be compared with ranges given in the literature for litterfall amounts in stands of different tree species.

In the present study the average total litterfall in spruce stands ranged from 136 gdw $m^{-2}yr^{-1}$ at site F3 in Forsmark to 400 gdw $m^{-2}yr^{-1}$ at site O3 in Oskarshamn. This is within the range (120 to 452 gdw $m^{-2}yr^{-1}$) reported by /Berg et al. 1999b/ for Norway spruce stands located from the Arctic Circle in the north of Sweden to the latitude of Malmö in the south. The high litter production at site O3 compared with site F3 can probably be explained by fertility differences between the sites. Site O3 is a drained peatland with spruce on a fresh to fresh-moist soil. These kind of soils can provide high yields /Lundin et al. 2005/ and thus have a high litter production. Site F3, on the other hand, is a poorer and less productive soil, which can explain the low litterfall at the site. The litterfall amount produced in the Scots pine stand at site O2 within the Oskarshamn investigation area (about 150 gdw m^{-2} yr^{-1}) is also within the range (74 to 420 gdw m^{-2} yr^{-1}) reported for Scots pine stands in Sweden /Berg et al. 1999a/. However, the litterfall is lower than for pine stands of 'normal fertility', which generally have a litter production of around 300 gdw m^{-2} yr^{-1} /Berg et al. 1999a/. The Scots pine stand at site O2 is probably growing on a soil of lower fertility since the soil cover is rather thin (0.3–1.0 m) and the soil is a fairly coarse sandy and sandy-silty till /Lundin et al. 2004/. The stem density was also very low, resulting in a low basal area, which in turn gives rise to a low litter production /Berg et al. 1999a/.

The amounts of C and N returned to the forest floor by the annual litterfall in the stands are given in Figures 5-3 to 5-6. Since the C concentration in litter is about 50%, the amount of C deposited is about half the litterfall amount. The pattern of C return thus follows the pattern of

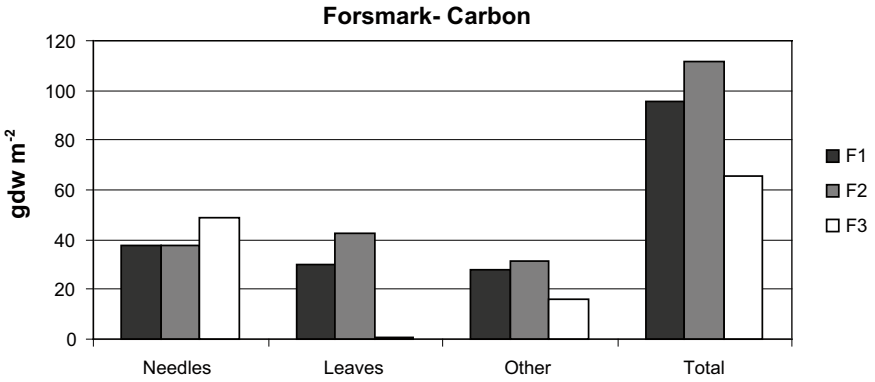

Figure 5-3. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at sites F1, F2 and F3 within the Forsmark investigation area. Results are given as the mean for the two years (June 2004 – June 2005 and June 2005 – June 2006).*

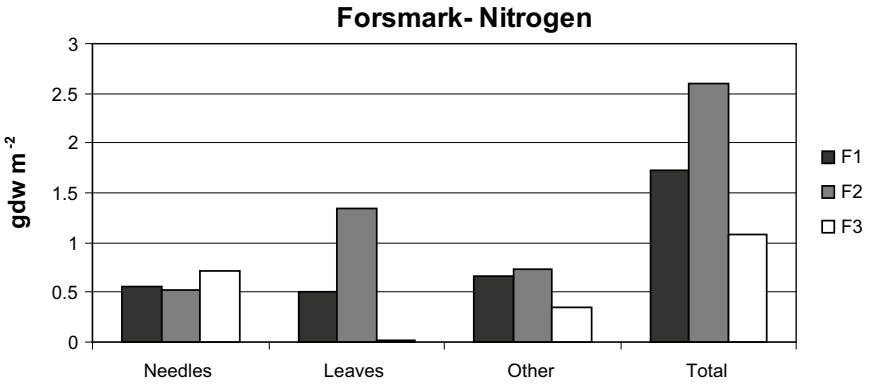

Figure 5-4. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at sites F1, F2 and F3 within the Forsmark investigation area. Results are given as the mean for the two years (June 2004 – June 2005 and June 2005 – June 2006).*

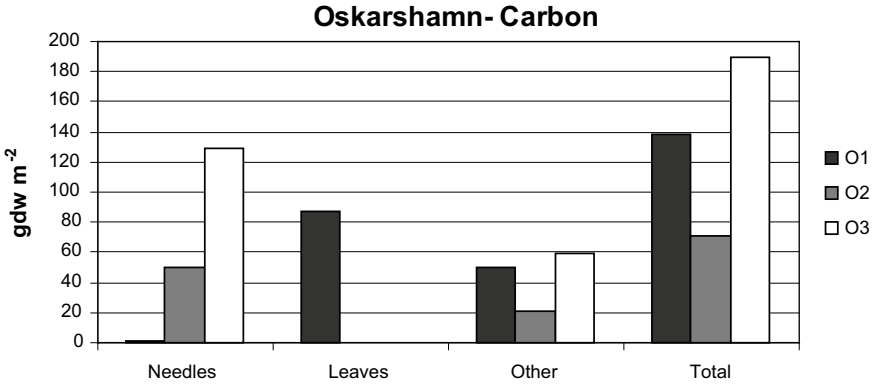

Figure 5-5. *Quantity of carbon returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at the sites O1, O2 and O3 within the Oskarshamn investigation area. Results are given as the mean for the two years (June 2004 – June 2005 and June 2005 – June 2006).*

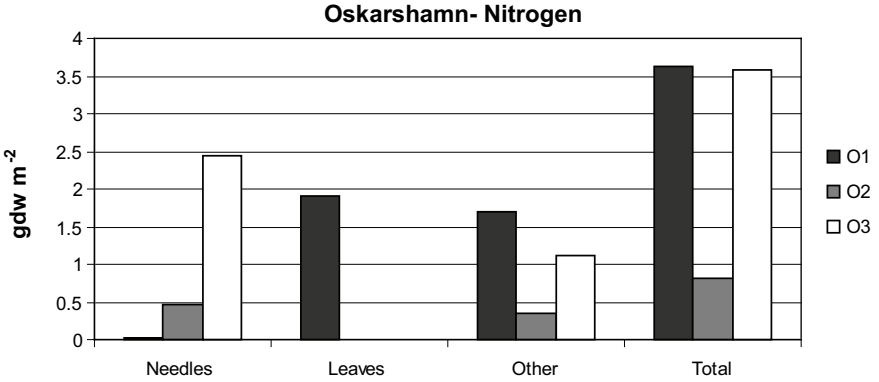

Figure 5-6. *Quantity of nitrogen returned to the forest floor annually in aboveground tree litterfall (gdw m^{-2} yr^{-1}) at sites O1, O2 and O3 within the Oskarshamn investigation area. Results are given as the mean for the two years (June 2004 – June 2005 and June 2005 – June 2006).*

litterfall, with a C input varying between about 60 to 110 gdw m^{-2} yr^{-1} in the forests within the Forsmark investigation area. Corresponding figures for the forests in the Oskarshamn area are about 90 to 190 gdw m^{-2} yr^{-1}. Concentrations of N are much more variable among litter types than those of C. A high concentration of N is found in alder leaf litter (about 25 mg g^{-1}) and a very low concentration in pine needle litter (4 mg g^{-1}). Thus, the amounts of N returned in the stands do not always correspond with litterfall amounts. This was evident from the Oskarshamn area, where litterfall at sites O1 and O2 differed considerably (Fig. 5-2) but amounts of N returned were of similar magnitude (Fig. 5-6). This was due to a high N return by the 'others' fraction in the O1 stand, which had a high N concentration (1.7 mg g^{-1}). In these two stands about 3.6 gdw m^{-2} yr^{-1} of N were returned to the forest floor by the annual litterfall (Fig. 5-6). This is four times more than that deposited in the Scots pine stand in the Oskarshamn area (about 0.8 g N dw m^{-2} yr^{-1}) (Fig. 5-6). Although the difference is large, the figures are in agreement with results from other studies. For spruce stands a N return in litterfall varying between 3.2 and 6.2 gdw m^{-2} yr^{-1} has been reported by /Johansson and Lundmark 1986/ and /Johansson and Gralls 1989/. For Scots pine stands, /Lundmark et al. 1982/ reported an N return of 0.6 gdw m^{-2} yr^{-1} in relatively young stands located in Central Sweden. Furthermore, /Lundmark 1988/ (as a mean for five middle-aged stands) found that 0.8 g dw N m^{-2} yr^{-1} was deposited with the needle fraction. In the Forsmark investigation area the N return in litterfall varied between 1.1 and 2.6 gdw m^{-2} yr^{-1}, the lower figure for site F3 and the higher for site F2. At site F1 about 1.7 gdw m^{-2} yr^{-1} was deposited (Fig. 5-4). The relative order of the deposited N amounts followed the litterfall pattern, although the N return was somewhat higher than expected from just litterfall amounts. This was due to the high N concentration in the alder leaves. That site F2 consists of a mixed spruce/alder stand is evident from the size of the N return in litter. It is much lower than the figure reported by /Johansson and Gralls 1989/ for a pure alder stand (6.6 compared with 2.6 g dw N m^{-2} yr^{-1}).

5.2 Litter decomposition and chemical changes

5.2.1 Litter decomposition

Within the Forsmark investigation area, the mass loss pattern differed considerably between the alder leaf litter and the spruce needle litters, with the former exhibiting the highest mass loss rate (Figure 5-7). On the other hand, the mass loss pattern of the spruce needle litter was very uniform among the spruce sites studied during the first 15 months of decomposition (Fig. 5-7). By this time, 40–42% of the initial mass had been lost from spruce needles at all three sites. However, later the mass loss pattern of the spruce needle litter also started to differ between spruce sites. After 531 days the needles at the F3 site had lost significantly more ($p < 0.05$, $N = 75$) mass than the needles at the other sites (49% compared with 43%). Furthermore, two-year values for mass loss at sites F2 and F3 were significantly higher ($p < 0.05$, $N = 75$) than

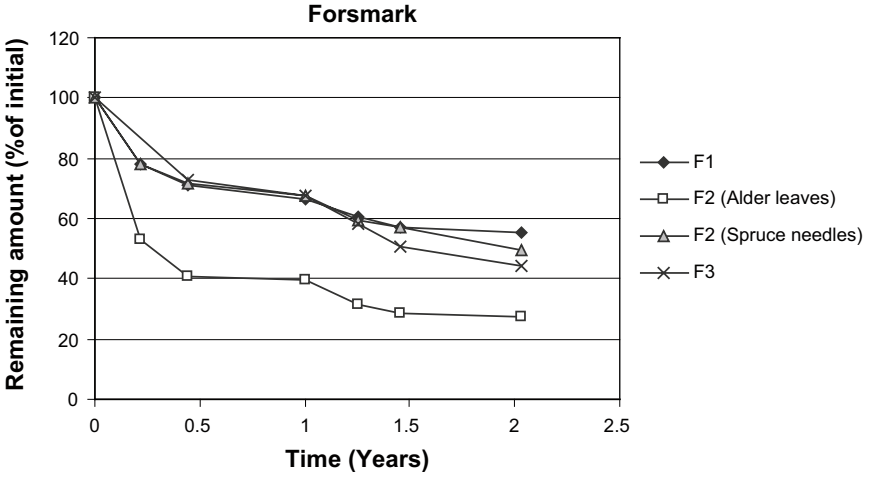

Figure 5-7. *Remaining amount (% of initial) of organic matter at sites F1, F2 (alder leaves), F2 (spruce leaves) and F3 within the Forsmark investigation area, after different times of decomposition.*

those at F1 (Appendix A2). The difference was also very high especially between sites F1 and F2 (45% compared with 60%) and somewhat less pronounced between sites F1 and F3, with a difference in mass loss of 15 percentage-units (Appendix A2).

In the Oskarshamn investigation area, the mass loss pattern of the oak litter generally differed from the other two litter types. Apart from in the initial stages (up to 77 days of decomposition), the oak leaf litter exhibited a significantly higher mass loss rate ($p < 0.05$, $N = 50$) than the spruce needle litter. Furthermore, the oak litter decomposed significantly faster ($p < 0.05$, $N = 50$) than the pine needle litter up to 456 days, after which the mass loss rates for the two litter types did not differ significantly (Fig. 5-8). Generally, minor differences were noted in the decomposition pattern for the spruce and pine needles within this investigation area. However, the pine needles started to decompose with a somewhat lower rate than the spruce needles (16% compared with 18% during the first 77 days) but after two years the pine needles had lost significantly more mass than the spruce needles (52% compared with 46% for spruce needles). Thus, the oak and pine litters had lost about half their initial mass (51 to 52%) and the spruce litter a somewhat smaller proportion (45%) during two years of decomposition. That pine needles have a slightly

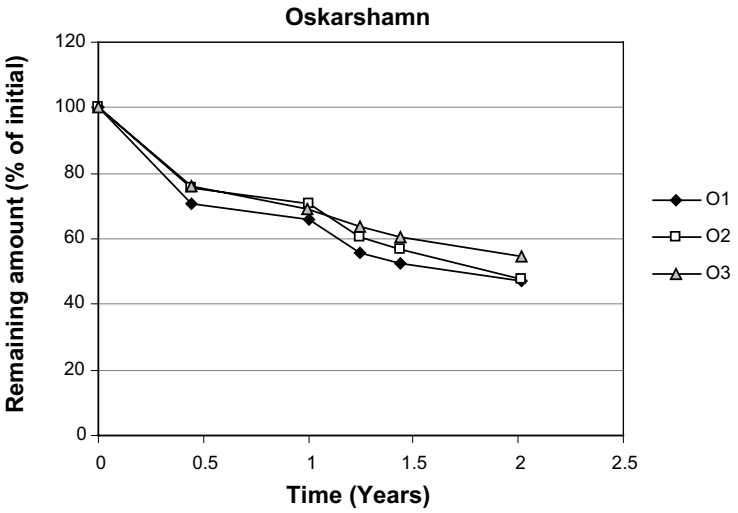

Figure 5-8. *Remaining amount (% of initial) of organic matter at sites O1, O2 and O3 within the Oskarshamn investigation area, after different times of decomposition.*

higher decomposition rate than spruce needles is a well known phenomenon /Johansson et al. 1986, Berg et al. 1996/ and has been ascribed to a lower concentration of lignin and a higher concentration of ethanol-solubles in pine needles than in spruce needles. The initial lignin levels in the oak and the spruce litters in the Oskarshamn area were similar (35%) but the oak leaves exhibited a significantly higher mass loss rate than the spruce needles. This can probably be explained by the higher level of solubles in the oak litter (20% compared with 14% in spruce litter). Compared with other deciduous leaf litters, oak leaves have a rather slow decomposition pattern due to a thick wax layer and high concentrations of polyphenolic substances that do not appeal to decomposers.

The extremely high mass loss rate shown by the alder leaf litter within the Forsmark investigation area, close to 50% in just 90 days and about 70% after two years, was probably due to a favourable chemical composition that promoted decomposition. High contents of N and calcium (Ca) in litter are known to stimulate the decomposing microorganisms /Yamaya and Branch 1968/. Furthermore, high contents of water-soluble substances, which are easily lost from the leaves through leaching, result in a fast mass loss of the litter. Calcium content was not determined, but determination of N and water-soluble substances revealed high contents of both fractions. The N content amounted to 25 mg g^{-1}, which was over three times the levels in spruce needle litter at the same site (7 mg g^{-1}) and the other spruce sites (7–9 mg g^{-1}) studied in Forsmark (Figs. 4-13, 4-17, 4-19 and 4-25).

The mass loss rates obtained for spruce needle litter in both investigation areas in this study were higher than those generally reported in the literature /Johansson and Lundmark 1986, Johansson and Grälls 1989/. Furthermore, in a study encompassing 14 different spruce forests located from Halland in the south of Sweden to Norrbotten in the north, /Berg et al. 2000/ found that spruce needle litter lost between 22% and 33% of mass during one year of decomposition. The mean value was 28% and the mass loss only exceeded 30% at one site.

The decomposition of litter is controlled by many factors, among them the chemical composition of the litter, climate, nutrient availability, communities of soil organisms and site-specific factors. First-year mass losses for Scots pine needle litter have been related to climatic factors /Fox and van Cleve 1984, Berg et al. 1993, Johansson 1994, Johansson et al. 1995/ whereas litter chemical variables (concentrations of water-soluble substances, manganese (Mn) and lignin) have been identified as key factors for Norway spruce needle litter decomposition /Berg and Tamm 1991, Berg et al. 2000/. Manganese is needed for the growth of Mn-peroxidase, a lignin-degrading enzyme, and is also involved in the regulation of other lignolytic enzymes such as laccase and lignin peroxidase /Archibald and Roy 1992, Perez and Jeffries 1992/. The concentrations of water-soluble substances (17–20%) and of lignin (29%) in the needle litter at sites F1 and F3 in Forsmark were somewhat higher and somewhat lower, respectively, than the mean values for 13 spruce sites (water-solubles 13% and lignin 32%) presented by /Johansson 1995/. No information on the Mn concentration in the litter from the Forsmark area is available. One can however speculate that levels are elevated, since Mn is related to site-specific factors such as soil fertility /Berg et al. 1995/. In soils with high pH, Mn exists in the form of Mn^{3+} or Mn^{4+}, both of which are insoluble in water and Mn is protected from being leached from the soil /Marshner 1995/. Thus in Sweden, the Mn concentration in litter increases with latitude and the possibility cannot be excluded that the litter produced at the calcareous soils (with high pH values) within the Forsmark area are rather rich in Mn. The pH value for the upper part of the mineral soil varied between 7.0 and 7.2 /Lundin et al. 2004/ amongst the Forsmark sites (which is high for forest soils in general but occurs in areas with calcareous deposits). However, no clear effect on the lignin decomposition in the spruce needles was seen except at site F3, where only 40% of the initial lignin amount remained after two years (Fig. 5-13). The high initial concentration of lignin (Fig. 4-23) together with the low concentration of water-solubles (Fig. 4-23) indicates that the F3 needles were partly decomposed on the trees before they were shed.

The high mass loss rates of the spruce needle litter in the Oskarshamn area, as well as the fast decomposition of the lignin fraction, cannot be attributed to a higher Mn concentration in the litter since the soils are not calcareous in this region. The pH in the mineral soil was not recorded

in the site description by /Lundin et al. 2005/ since the humus layer was very thick and classified as peat. However, the humus layer was very acidic, with pH values of 3.9 in the upper 30 cm of the peat layer and 4.7 in the 40–60 cm layer. Nevertheless, the decomposition level reached by the spruce litter at this site (46%) after two years of decomposition was in agreement with that found by Johansson (unpublished) for spruce needles (45%) at a site with similar conditions (a drained peatland with spruce on fresh and fresh-moist soils) close to Uppsala. In addition, the lignin decomposition was of the same magnitude at both sites, resulting in 73–80% of the initial lignin amount remaining after two years.

Within both investigation areas, a clear seasonal trend in the decomposition pattern was observed. During the second and the third collection of litter bags, as well as between the fifth and sixth, the decomposition stagnated due to lower temperatures in the winter period (Appendix A2). This of course affects the decomposer organisms, the activity of which is determined by a number of factors, of which one is the temperature. It can also be seen that the inhibitory effect on the decomposition during the winter period was not as strong in the Oskarshamn area as in the Forsmark area (Figs. 5-7 and 5-8). This is probably due to the more southerly location of the Oskarshamn site, with less harsh winter periods.

The model simulation showed that the relative order recorded for the litters during the two-years measurement period will be maintained during the following eight years of decomposition. According to the model predictions, about 80% of the initial mass was decomposed from needle litters and oak leaves after 10 years but over 90% of the initial mass of alder leaves (Fig. 4-48).

5.2.2 Changes in organic and inorganic components

The organic-chemical components disappeared in the order generally observed when litter is decomposed /Berg 1986, Johansson 1994/. Thus, water-soluble components disappeared faster than ethanol-soluble substances and lignin showed the slowest decrease rate. Within the Forsmark area, the water-soluble fraction in the litter showed a similar pattern at sites F1 and F2, but behaved in a quite different way at site F3 (Fig. 5-9). At the former sites, where the initial concentration for spruce litter varied between 170 and 200 mg g^{-1} and was 210 mg g^{-1} for alder leaves, the fraction decreased very rapidly during the first three months down to an absolute amount of 40–50 mg g^{-1} (Appendix A2). These initial concentrations for spruce litter are somewhat higher than the average (130 mg g^{-1}) but within the range (65–200 mg g^{-1}) reported by /Johansson 1995/ for spruce needle litter. The decrease in amount corresponds to a loss of about 70–80% of the initial amount of water-soluble substances in the litter (Fig. 5-9). Thereafter, the level remained fairly constant except in the alder leaves, where it further decreased down to 12 mg g^{-1}, resulting in a loss of about 95% of the initial amount. While the litters at these two sites lost the main part of their water-soluble substances already within the first months of decomposition, about 60% of the initial amount of water-soluble components in needles still remained at site F3 after two years (Fig. 5-9). The reason for this was the very low initial concentration of water-soluble substances in this litter (only 64 mg g^{-1}), which is close to the concentrations found in the other litters after three months of decomposition (Appendix A2). The low initial concentration of water-soluble substances together with the high initial concentration of lignin indicates that the needles were partly decomposed on the trees before they were shed. This phenomenon was also observed in the study by /Berg et al. 2000/.

In the Oskarshamn area too, the water-soluble fraction in the litters decreased very rapidly during the first months (Fig. 5-10) and after 161 days the absolute amount was 30–50 mg g^{-1} (Figs. 4-36, 4-40 and 4-44). After this the level remained fairly constant and after two years all litters had amounts varying between 20 and 40 mg g^{-1}. The oak and the pine litter lost about 80% of their initial amount of water-soluble substances within the first 161 days and after two years the oak litter had lost a further 10%. In contrast, the spruce litter at the O3 site only lost about 50% of its initial amount of water-solubles during the first 161 days and only a further 15% until the end of the second year. This resembles the pattern shown by the F3 needle litter in the Forsmark area (see above), although the initial concentration of water-soluble substances in the O3 litter (104 mg g^{-1}) was not as low as in the F3 litter (64 mg g^{-1}). Furthermore, the O3

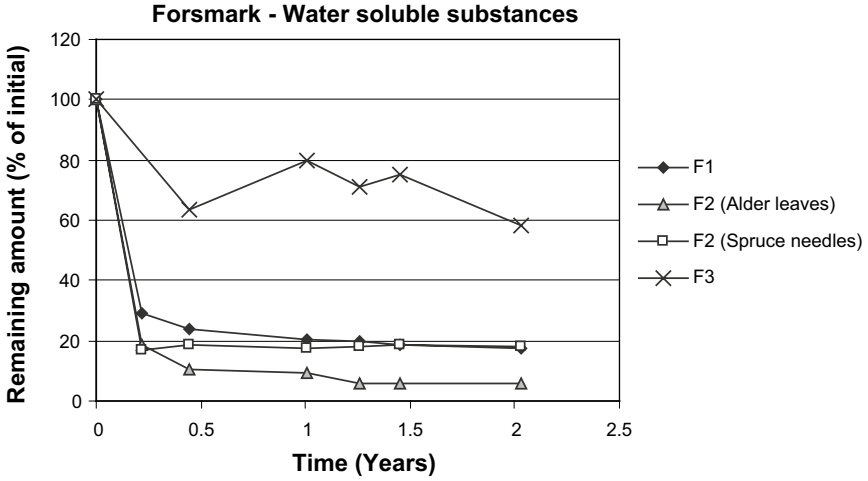

Figure 5-9. *Remaining amount (% of initial) of water-soluble substances at sites F1, F2 (alder leaves), F2 (spruce needles) and F3 within the Forsmark investigation area, after different times of decomposition.*

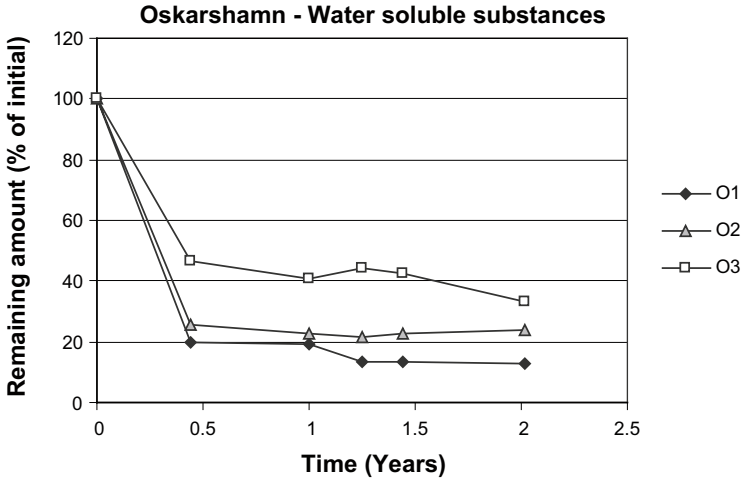

Figure 5-10. *Remaining amount (% of initial) of water-soluble substances at sites O1, O2 and O3 within the Oskarshamn investigation area, after different times of decomposition.*

litter also had a high initial concentration of lignin, a fact indicating that the litter might have already been partly decomposed on the trees before it was shed.

Ethanol-soluble components in litter, which comprise fats, waxes and resins /Alexander 1977/, make up a smaller part of the litter than the water-soluble substances. As with the water-soluble substances, the decrease in ethanol-soluble components contributes to the mass loss in the early stages of the decomposition process. Most of the litters in the Forsmark area had initial concentrations of around 40 to 50 mg g^{-1} (Fig. 5-11), while the F3 litter had a lower content (about 30 mg g^{-1}) probably due to the fact that these needles had already been decomposed to a certain degree on the trees (see above). In the Oskarshamn area the initial concentrations of ethanol-solubles in litter were much more variable (from 20 to 100 mg g^{-1}) due to the presence of Scots pine needles and oak litter, the former being rich in this component (100 mg g^{-1}) and the latter being poor (20 mg g^{-1}). However, the concentrations for the spruce and pine needle litters are in agreement with the averages reported by /Johansson 1995/ (48 mg g^{-1} for spruce needle litter and 100 mg g^{-1} for Scots pine needle litter).

The ethanol-soluble fraction of the litter generally had a lower disappearance rate than the water-soluble fraction and decreased most quickly in the alder leaf litter in the Forsmark area,

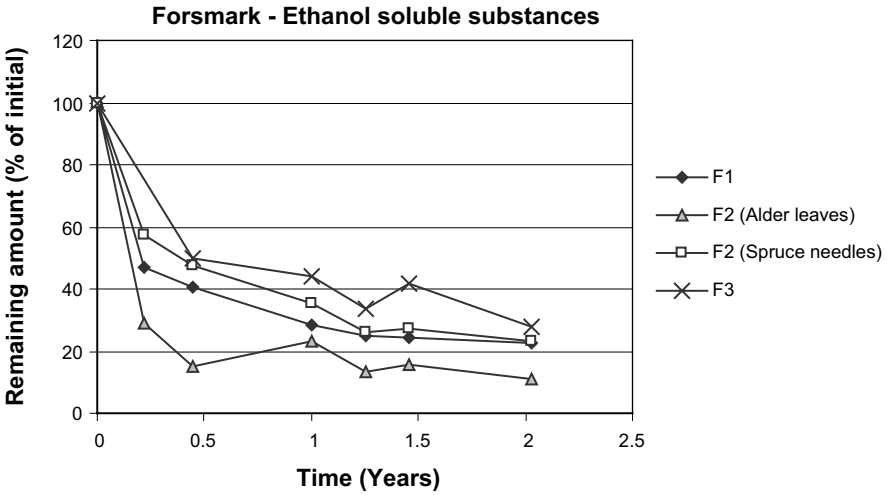

Figure 5-11. *Remaining amount (% of initial) of ethanol-soluble substances at sites F1, F2 (alder leaves), F2 (spruce needles) and F3 within the Forsmark investigation area, after different times of decomposition.*

where only 10% of the initial amount in leaves remained after two years. Although the loss rate of ethanol-solubles in spruce litter varied between sites, generally about 30% (40% in the Oskarshamn area) of the initial amount was left at all spruce sites by the end of the second year. In the pine needle litter 30% also remained, whereas the oak litter had only reduced its original amount by 50% (Figure 5-12).

Lignin is the most resistant component in litter to decomposition. The influence of lignin on the decomposition rate is so strong that the effect of climate is not only suppressed but appears to disappear completely when the lignin concentration is sufficiently high /Johansson 1994, Johansson et al. 1995/. The lignin content especially determines the mass loss rate in the latter stages of the decomposition process /Fogel and Cromack 1977, Berg and Staaf 1980a, Johansson 1994/.

Two of the litters in the Forsmark area (spruce litter incubated at sites F1 and F2) showed a completely different pattern as regards the decomposition of the lignin fraction. In these litters the absolute amount of lignin increased in the early stages (up to 107% of the initial amount at site F1 and up to about 110% at site F2 during the first three to five months), after which it remained fairly constant until the end of the first year, when it started to decompose (Fig. 5-13).

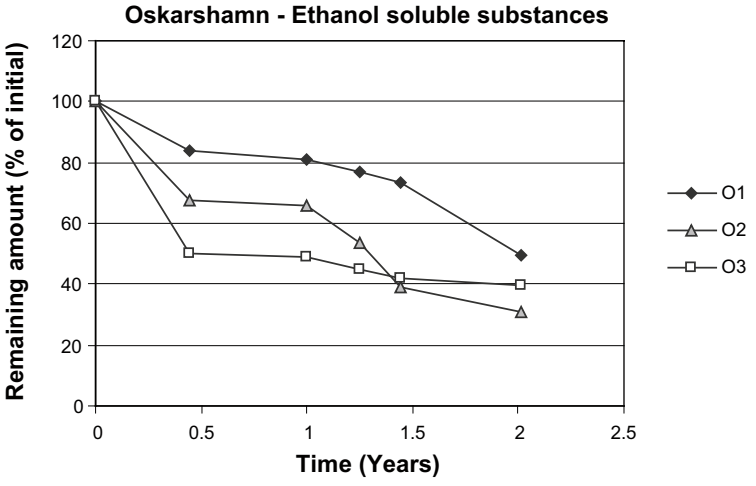

Figure 5-12. *Remaining amount (% of initial) of ethanol-soluble substances at sites O1, O2 and O3 within the Oskarshamn investigation area, after different times of decomposition.*

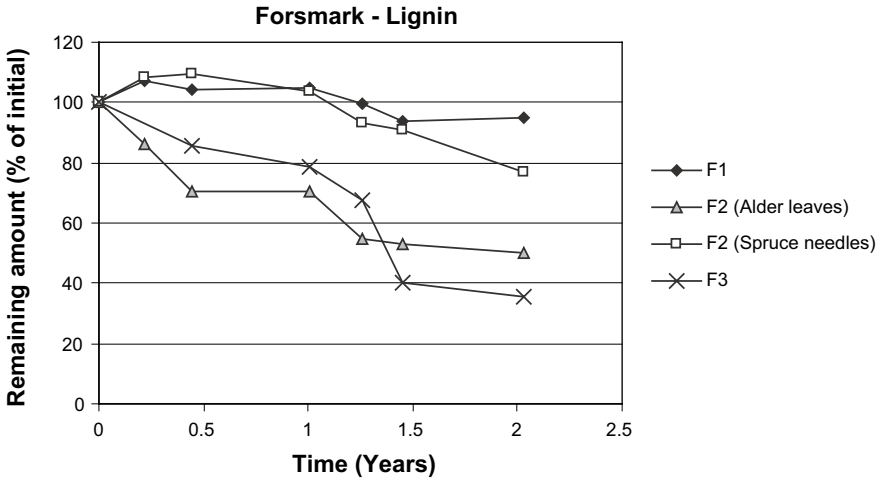

Figure 5-13. *Remaining amount (% of initial) of lignin at sites F1, F2 (alder leaves), F2 (spruce needles) and F3 within the Forsmark investigation area, after different times of decomposition.*

The decomposition proceeded slowly, however, and after two years the amount had decreased from about 300 mg g^{-1} at both sites down to 270 mg g^{-1} and 230 mg g^{-1} at the F1 and the F2 site respectively (Figs. 4-11 and 4-15). This corresponds to a loss of only 5% of the initial lignin amount at the F1 site and a loss of 20% at the F2 site. An increase in the absolute amount of lignin during initial stages is frequently observed in litter decomposition studies and can perhaps be ascribed to the analytical method used for lignin /Berg et al. 1982b, Johansson 1994/. The sulphuric acid lignin (Klason lignin) is the acid-insoluble residue of sulphuric acid hydrolysis and includes both native lignin and recalcitrant compounds formed during decomposition of the litter. Thus the method only shows the net changes taking place in the acid-insoluble substances of the litter. However, lignin degradation may be faster in reality than indicated by the method used /Stott et al. 1983, Johansson et al. 1986/.

In the spruce needle litter and the alder leaf litter decomposing at the F3 site and F2 site, respectively, the lignin fraction showed a consistent pattern and the amount decreased throughout the whole period studied (Fig. 5-13). The decomposition was most rapid during the first five months when the spruce needles lost 15% and the alder leaves 30% of their initial lignin amount. Thereafter, the decrease slowed down but the decomposition rate in the spruce needles increased markedly at the beginning of the second year. After two years only about 40–50% of the initial lignin amount remained in the two litter types (Fig. 5-14).

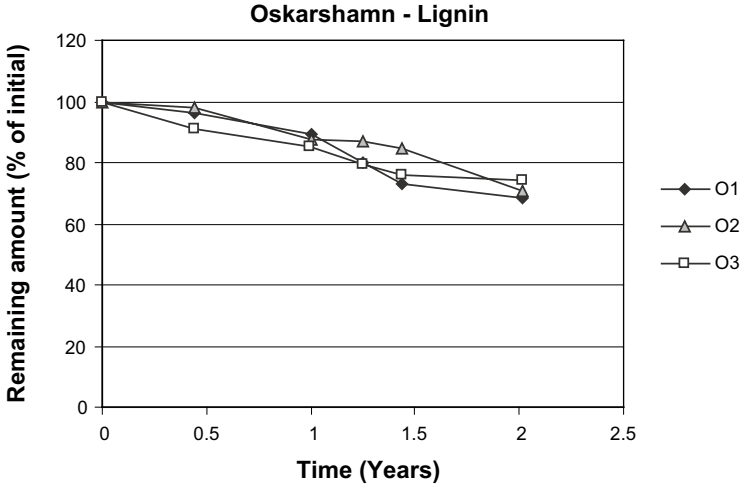

Figure 5-14. *Remaining amount (% of initial) of lignin at sites O1, O2 and O3 within the Oskarshamn investigation area, after different times of decomposition.*

In the Forsmark area, the concentration of lignin increased in all litters as decomposition proceeded (Appendix A2). For the alder leaves (site F2) a steady level of about 50% seemed to have been reached after 531 days of decomposition, whereas for spruce needles at site F1 a steady level was not reached during the two years studied. At site F2 the spruce lignin concentration stabilised at 46% after 458 days. The spruce needles at site F3 reached a steady level (42%) already after one year of decomposition, after which the concentration decreased. This supports the theory that the needles started to decompose on the trees.

In the litters in the Oskarshamn area, the lignin fraction showed a consistent pattern with decreasing absolute amounts during the two first years of decomposition. The decomposition was slow during initial stages and all three litters lost about 10% of their initial amount during the first year. After two years the lignin fraction had decreased by about 30% in all litter types (Fig. 5-14). The concentration of lignin increased in all three litters as decomposition proceeded (Appendix A2). For oak leaves a steady level of about 50% seemed to have been reached after 456 days of decomposition, whereas for spruce needles the increase was slower and reached about the same level (48%) after two years. The increase in the lignin concentration was very slow in the pine needles (site O2) and reached 40% after two years. /Berg et al. 1982b/ reported that this increase in Scots pine needle litter can continue for about five years, up to a lignin concentration of 47%.

The dynamics of N and P in decomposing needles and leaves are shown in Figures 5-15 to 5-18. Alder leaves had the highest initial content of N and P followed by spruce needles, oak leaves and finally pine needles, which was the poorest litter type with respect to these elements. The initial N content was as high as 25 mg g^{-1} in the alder leaf litter and one-sixth of that in the pine needle litter (4 mg g^{-1}). The other litter types had contents varying between 7 and 10 mg g^{-1}. These concentrations are in agreement with those reported for these kinds of litters in other investigations /Johansson and Grälls 1989, Johansson 1994, Johansson 1995/. Mineralisation of N started immediately from alder leaves, and proceeded at a rapid rate during the first five months, after which it slowed down markedly. Due to the fast initial mineralisation, the alder litter lost about half its original amount of N during these first months. There was generally a small loss of N from the other litter types too during the first months but this loss was of a minor extent and never exceeded 10% of the initial N amounts in the litter. This first loss was then generally followed by short irregular periods when N was immobilised. Generally, about 80% to 90% of the initial N amount still remained in the litters after two years of decomposition (100% in the pine needles), whereas alder leaves had lost 60% of their N.

The initial P concentrations followed the same pattern as N, with the highest concentration found in alder leaf litter (0.9 mg g^{-1}), the lowest in pine needle litter (0.3 mg g^{-1}) and the other litter types concentrations intermediate (0.4 to 0.6 mg g^{-1}). These initial concentrations are

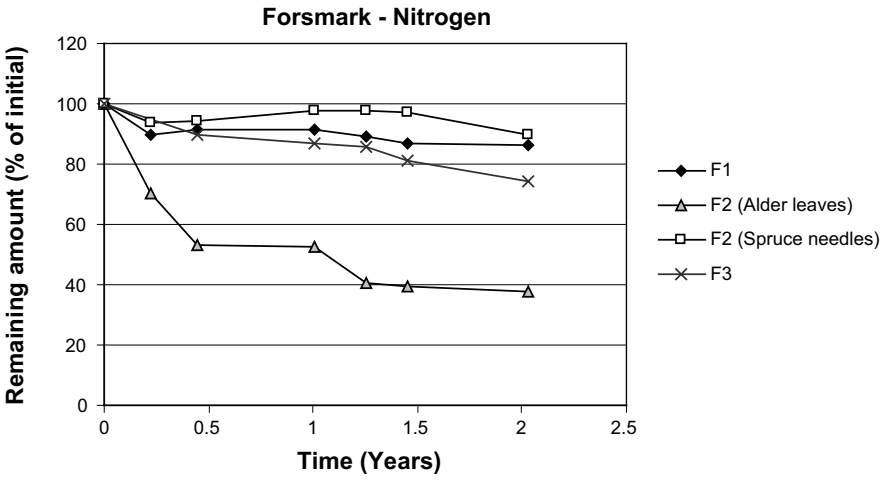

Figure 5-15. *Remaining amount (% of initial) of nitrogen at sites F1, F2 (alder leaves), F2 (spruce needles) and F3 within the Forsmark investigation area, after different times of decomposition.*

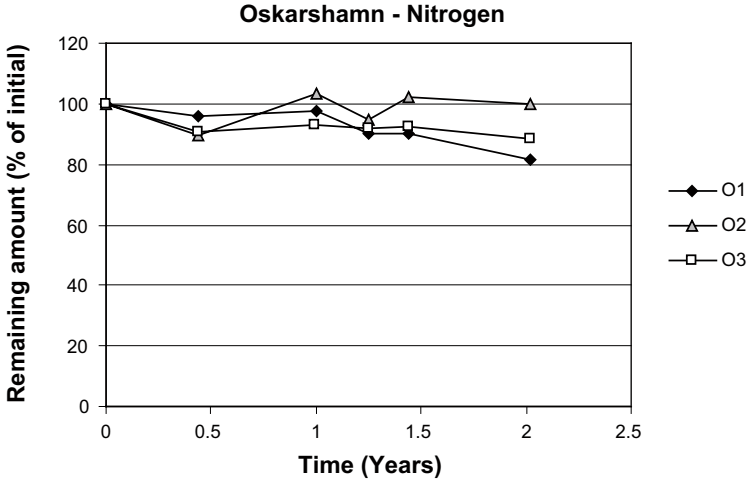

Figure 5-16. *Remaining amount (% of initial) of nitrogen at sites O1, O2 and O3 within the Oskarshamn investigation area, after different times of decomposition.*

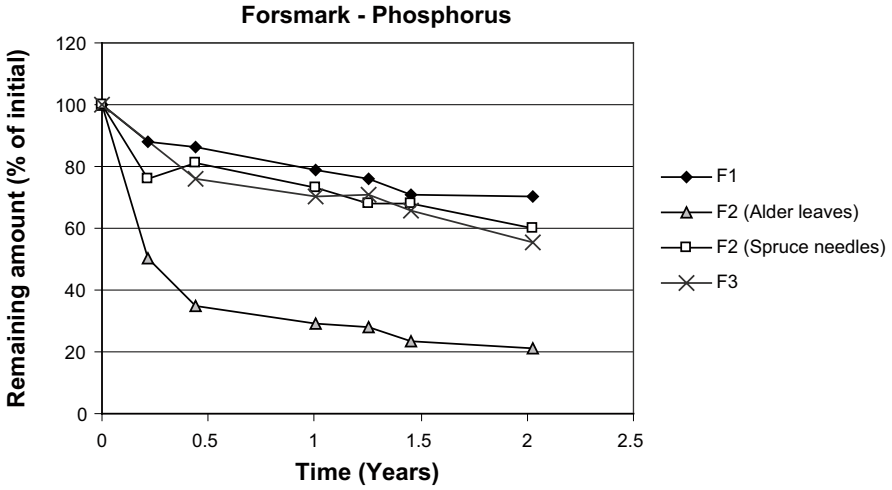

Figure 5-17. *Remaining amount (% of initial) of phosphorus at sites F1, F2 (alder leaves), F2 (spruce needles) and F3 within the Forsmark investigation area, after different times of decomposition.*

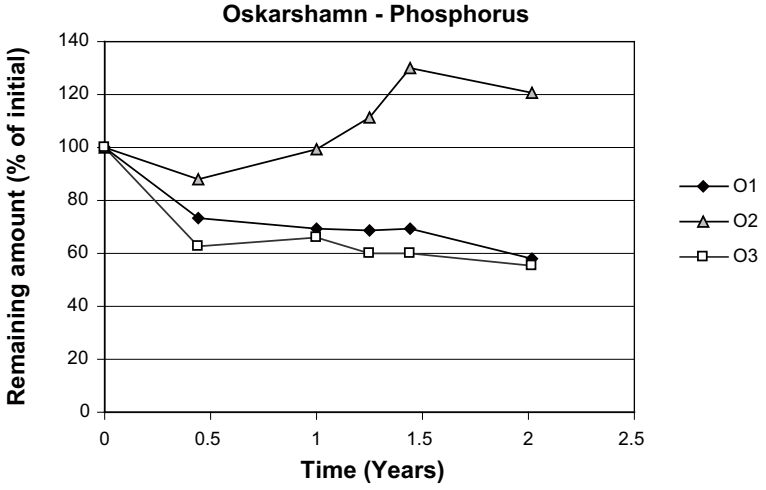

Figure 5-18. *Remaining amount (% of initial) of phosphorus at sites O1, O2 and O3 within the Oskarshamn investigation area, after different times of decomposition.*

also in agreement with the figures reported from other litter chemical investigations (see above) except for the initial P content in alder leaves, which was higher in this investigation. The release of P started immediately from all litter types and was most rapid from the alder leaf litter, which lost about 60% of its initial amount during the first five months. The losses of P from the other litter types were generally around 10–20% within the same time period, but both the oak leaves and the spruce needles at sites O1 and O3, respectively, in the Oskarshamn area showed a higher loss (30–40% of initial amount). After this initial phase the release rate slowed down and generally about 60–70% of the initial P amount remained in the different litters (except for the alder leaves and the pine needles) after two years of decomposition. In the alder leaves only 20% of the original P amount remained, whereas the pine needle litter had increased its original amount of P by about 20%. The fact that P (as well as N) is released very slowly from Scots pine needle litter during decomposition or is even immobilised is well known from other studies /i.e. Berg and Staaf 1982b, Johansson 1992/. Element accumulation in litters is generally linked to low initial element content, while a marked release of elements is typical for litters with high initial element content /Ågren and Bosatta 1998/.

The differences in N and P dynamics in the decaying litters can be attributed to differences in physical and chemical properties of the litter. The physical properties determine the leachability of the litter, which is higher for leaf litters than for needle litters. The chemical properties seem to be species-specific rather than site-specific /Leyton 1948, Staaf 1982, Johansson 1995/ due to the growth demand of the tree species, which is not fulfilled at all sites. The fact that both N and P were released faster from the alder leaves can thus be explained by both the physical properties of the alder leaves (high ability for leaching) and by their chemical properties. Alder is one of the few tree species that can fix N from the atmosphere, and therefore does not have to translocate and save N before shedding of its litter. In the case of Scots pine the concentration of N may decrease to about 33% of that in green needles before the needles are shed in the autumn /Berg and Laskowski 2006/.

The slow release or even immobilisation of P and N from litters initially poor in these elements in this study is due to the requirements of the microbial biomass decomposing the organic material /Haynes 1986/. The small decrease taking place in the coniferous needles during initial stages is partly probably due to leaching.

Phosphorus is indispensable for all forms of life because of its role in genetics as ribonucleic acid and its function in energy transfers via adenosine triphosphate. In natural ecosystems P is usually the life-limiting element due to its low availability. Within the soil P can be considered to be in three fractions – the organic matter, which may hold up to 50% of the total soil P, the insoluble inorganic fraction and a small, very variable part that is soluble and can be absorbed by plants /Ozanne 1980/. Trees absorb most of their P in their early years. When trees are 20–40 years old, the uptake of P decreases because of internal P circulation /Ballard 1980/. Microbial processes strongly influence the supply of available phosphorus /Wallbridge 1991/.

5.3 Modelling of decomposition and N and P dynamics

The model simulations showed that the relative order observed for the litters during the two-year measurement period was maintained during the following eight years of decomposition. The model predicted that about 80% of the initial mass was decomposed from needle litters and oak leaves after 10 years but over 90% the initial mass of alder leaves (Fig. 4-48). According to the theory applied in the decomposition model, the initial quality q_0 is the most important biotic determinant of initial decomposition rate /Ågren and Bosatta 1998/. It is difficult to draw any general correlations between q_0 and initial element concentration /Hyvönen et al. 1996/. Since water-solubles constitute a large fraction of litters with high initial mass loss rate (Figs. 5-9 and 5-10), and since this fraction is lost rapidly, a relationship between water-solubles and early mass loss (q_0) makes sense. There was a tendency for a positive correlation between water-solubles and the values of q_0 in the present study. In the long-term decomposers, efficiency of utilising

organic matter as an energy source is a more significant biotic determinant of decomposition and soil C storage. The most important factors regulating decomposition rate at advanced stages of decomposition are the rate of decrease in quality and the interaction between organic matter and soil physical properties such as soil texture /Hyvönen and Ågren 1998/. The interaction between soil organic matter and soil physical properties contributes to a very slow approach to complete decomposition of litter. The model predicted that 6–7% of the initial amount of spruce, pine and oak litter was found after 20 years, but the amount of alder litter was lower, only 2%. These residual amounts are slightly lower than that reported for barley straw after 10 years of field incubation by /Jenkinson and Rayner 1977/ and after 10 and 20 years (16% and 9.3%, respectively) by /Sörensen 1987/.

The model parameters used for nutrient dynamics were the initial N and P concentration in litter, which was obtained from chemical analyses, and decomposer N/C and P/C ratios, which were obtained by fitting equation (3) to the measured amounts of N and P in litter. The initial N/C ratios in the present litters varied between 0.015–0.05 and were thus lower than those found by /Hyvönen et al. 2000/ (0.023–0.0303). The decomposer N/C ratios obtained (0.06–0.11) were also slightly lower than those (0.105–0.126) obtained by /Hyvönen et al. 2000/. The initial P/C ratio in the present litters varied between 0.0005–0.002, again slightly lower compared with the ratios (0.0021–0.0029) in Hyvönen et al. (2000). However, the decomposer P/C ratios for the litters at Forsmark and Oskarshamn (0.006–0.24) were higher than the corresponding ratios (0.0014–0.0051) obtained by /Hyvönen et al. 2000/. Fumigation studies indicate that the decomposer N/C ratio is affected by total soil C and N contents, and thus there is no universal decomposer N/C ratio /Andersson and Domsch 1989, Smith and Paul 1990, Wardle 1992/. This is probably also the case for the P/C ratios.

The initial content of N varied between 4-10 mg g^{-1} for coniferous needles and oak leaves, but it was considerably higher for alder leaves, 25 mg g^{-1}. Nitrogen was rapidly released from alder leaves, while a short phase of immobilisation was predicted for the other litters studied. The model predicted that the initial differences in N content would slowly disappear and after 10 years the N content was around 4–5 mg g^{-1} in all litters. A similar pattern was predicted for P. After the initial differences, the P content levelled off at 0.1–0.2 mg g^{-1}. Although nutrient content in decomposing litter decreases with time, the nutrient/C ratio increases. Thus after 10 years the N/C ratio varied between 0.03–0.07 and the P/C ratio between 0.001–0.002, approaching very slowly the nutrient/C ratio of decomposers. The predicted values for N/C ratio of 0.03 for pine needles and 0.04–0.07 for spruce needles are comparable with those found by /Berg et al. 1991/, and /Hyvönen et al. 2000/. Thus, there is a tendency for higher N content in spruce needles compared with pine needles. The ratio for P/C seems to be more similar for the different litters as also found by /Berg et al. 1991/.

6 Acknowledgements

This investigation was financed by the Nuclear Fuel and Waste Management Co (SKB). We are grateful to Anita Sundberg and Anna-Stina Nilsson who provided invaluable assistance during the field work and who performed the laborious work with the litter in the laboratory (cleaning of litter, litter bag preparation and milling of samples). Furthermore, Kjell Larsson and Kent Andersson are thanked for technical assistance during the chemical analysis and Mary Mc Afee for linguistic revision. The authors are also most thankful to Sara Karlsson, Erik Wijnbladh and Anders Löfgren (SKB) for great support and valuable comments on the manuscript.

7 References

Ågren G I, Hyvönen R, Nilsson T. (In press). Are Swedish forest soils sinks or sources for CO_2 – model analyses based on forest inventory data. Biogeochemistry.

Ågren G I, Bosatta E, 1996. Quality: A bridge between theory and experiment in soil organic matter studies. Oikos 76, 522–528.

Ågren G I, Bosatta E, 1998. Theoretical Ecosystem Ecology – Understanding Element Cycles. Cambridge University Press, Cambridge.

Albrektson A, 1988. Needle litterfall in stands of *Pinus sylvestris* L. in Sweden, in relation to site quality, stand age, and latitude. Scand. J. For. Res. 3: 333–342.

Alexander M, 1977. Introduction to Soil Microbiology. John Wiley and Son, New York. 467 pp.

Andersson T H, Domsch K H, 1989. Ratios of microbial biomass carbon to total organic carbon in arable soils. Soil Biol. Biochem. 21: 471–479.

Archibald F, Roy B, 1992. Production and of manganic chelates by laccase from the lignin-degrading fungus *Trametes (Coriolus) versicolor*. Appl. Environ. Microbiol. 58: 1496–1499.

Ballard R, 1980. Phosphorus nutrition and fertilization in forest trees. In: Khasaweneh F E, Sample E C, and Kamprath W J, (eds): The Role of Phosphorus in Agriculture. American Soc. of Agronomy. pp: 763–804.

Berg B, 1986. Nutrient release from litter and humus in coniferous soils – a mini review. Scand. J. For. Res. 1: 359–370.

Berg B, Staaf H, 1980a. Decomposition rate and chemical changes of Scots pine needle litter. I. Influence of stand age. In: T. Persson (ed). Structure and Function of Northern Coniferous Forest – An Ecosystem Study. Ecol. Bull (Stockholm) 32. pp 363–372.

Berg B, Staaf H, 1980b. Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. In: T. Persson (ed). Structure and Function of Northern Coniferous Forest – An Ecosystem Study. Ecol. Bull (Stockholm) 32. pp 373–390.

Berg B, Hannus K, Popoff T, Theander O, 1982a. Changes in organic-chemical components during decomposition. Long-term decomposition in a Scots pine forest. I. Can. J. Bot. 60: 1310–1319.

Berg B, Wessén B, Ekbohm G, 1982b. Nitrogen level and decomposition in Scots pine needle litter. Oikos 38: 291–296.

Berg B, Wessén B, 1983. Changes in organic-chemical components and in growth of fungal mycelium in decomposing birch leaf litter as compared with pine needles. In: Wessen (ed.). Decomposition of Some Leaf Litters and Barley Straw – Some Rate-determining Factors. Report 19. Department of Microbiology, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Berg B, Booltink H, Breymeyer A, Ewertsson A, Gallardo A, Holm B, Johansson M B, Koivuoja S, Meentemeyer V, Nyman P, Olofsson J, Pettersson A S, Reurslag A, Staaf H, Staaf I, Uba L, 1991. Data on needle litter decomposition and soil climate as well as site characteristics for some coniferous forest sites. Part 2. decomposition data. Swedish University of Agricultural Sciences. Department of Ecology and Environmental Research. Report 42. Second edition.

Berg B, Tamm C O, 1991. Decomposition and nutrient dynamics of litter components at Ivantjärnsheden – Data from the decomposition studies. Swed. Con. For. Proj. Internal Report 104, 17 pp.

Berg B, Berg M P, Bottner P, Box E, Breymeyer A, Calvo de Anta R, Couteaux M M, Gallardo A, Escudero A, Kratz W, Madeira M, Mälkönen E, Meentemeyer V, Munoz F, Piussi P, Remacle J, Virzo De Santo A, 1993. Litter mass loss in pine forests of Europe and eastern United States as compared with actual evapotranspiration on a European scale. Biogeochemistry, 20: 127–153.

Berg B, Johansson M B, Calvo de Anta R, Escudero A, Gärdenäs A, Laskowski R, Madeira M, Mälkönen E, McClaugherty C, Meentemeyer V, Virzo De Santo A, 1995. The chemical composition of newly shed needle litter of different pine species and Scots pine in a climatic transect. Long-term decomposition in a Scots pine forest. Can. J. Bot. 73: 1423–1435.

Berg B, Ekbohm G, Johansson M B, McClaugherty C, Rutigliano F, Virzo De Santo A, 1996. Maximum decomposition limits of forest litter types: A synthesis. Can. J. of Botany 74(5):659–672.

Berg B, Albrektsson A, Berg M, Cortina J, Johansson M B, Gallardo A, Madeira M, Pausas J, Kratz W, Vallejo R, McClaugherty C, 1999a. Amounts of litterfall in some pine forests in a European transect, in particular Scots pine. Annals of Forest Science 56, 625–639.

Berg B, Johansson M B, Tjarve I, Gaitniekes T, Rokjanis B, Beier C, Rothe A, Bolger T, Göttlein A, Gertsberger P, 1999b. Needle Litterfall in a North European Spruce Forest Transect. Report 80. Reports in Forest Ecology and Forest Soils. Department of Forest Soils, Swedish University of Agricultural Sciences.

Berg B, Johansson M B, Meentemeyer V, 2000. Litter decomposition in a transect of Norway spruce forests: substrate quality and climate control. Can. J. For. Res. 30: 1136–1147.

Berg B, Laskowski R, 2006. Advances in Ecological Research, volume 38. Elsevier Amsterdam. ISBN 0-12-013938-3

Bethge P O, Rådeström R, Theander O, 1971. Kvantitativ kolhydratbestämning – en detaljstudie. Swedish Forest Product Research Laboratory, Stockholm. Commun. 63B.

Bocock K L, Gilbert O, Capstick C K, Twinn D C, Waid J S, Woodman M J, 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. I. Losses in dry weight of oak and ash leaf litter. J. Soil Sci. 11: 1–9.

Bonnevie-Svendsen C, Gjems O, 1957. Amount and chemical composition of the litter from larch, beech, Norway spruce and Scots pine stands and its effect on the soil. Meddelelser fra det Norske skogs-försöksvesen 14: 115–168.

Bornebusch C H, 1937. Iakttagelser over rodgranens nalefald. Forstl. Forsoksv. Danm. 14: 173–176.

Bosatta E, Ågren G I, 1997. Theoretical analyses of soil texture effects on organic matter dynamics. Soil Biology and Biochemistry 29, 1633–1638.

Bringmark L, Bringmark E, 1991. Large-scale patterns of mor layer degradability in Sweden measured as standard respiration. – In: Allard B, Borén H, and Grimwall A, (eds). Humic Substances in the Aquatic and Terrestrial Environment. Lecture Notes in Earth Sciences 33:255–259. Springer Verlag.

Edmonds R L, 1979. Decomposition and nutrient release in Douglas-fir needle litter in relation to stand development. Can. J. For. Res. 9: 132–140.

Fogel R, Cromack K Jr., 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Can. J. Bot. 55: 1632–1640.

Fox J F, van Cleve K, 1984. Relationships between cellulose decomposition, Jenny`s *k*, forest floor nitrogen, and soil temperature in Alaskan taiga forests. Can. J. For. Res.13: 789–794.

Haynes R J, 1986. Mineral nitrogen in the plant-soil system. Physiological ecology. A series of Monographs, Texts and Treaties. Academic Press, Inc.

Hyvönen R, Ågren G I, Andrén O, 1996. Modelling long-term carbon and nitrogen dynamics in an arable soil receiving organic matter. Ecological Applications 6, 1345–1354.

Hyvönen R, Ågren G I, 1998. Predicting long-term soil carbon storage from short-term information. Soil Science Society of America Journal 62: 1000–1005.

Hyvönen R, Olsson B A, Lundkvist H, Staaf H, 2000. Decomposition and nutrient release from *Picea abies* (L.) Karst. and *Pinus sylvestris* L. logging residues. Forest Ecology and Management 126**:** 97–112.

Jenkinson D S, Rayner J H, 1977. The turnover of soil organic matter in some Rothamsted classical experiments. Soil Science 123: 298–305.

Johansson M B, 1986. Chemical composition and decomposition pattern of leaves litters from forest trees in Sweden with special reference to methodological aspects and site properties. Report 56. Reports in Forest Ecology and Forest Soils. Department of Forest Soils, Swedish University of Agricultural Sciences, Uppsala.

Johansson M B, 1992. The influence of disc trenching on the turn-over rate of soil organic matter and nutrient release. Report 66. Reports in Forest Ecology and Forest Soils. Department of Forest Soils, Swedish University of Agricultural Sciences, Uppsala.

Johansson M B, 1994. Decomposition rates of Scots pine needle litter related to site properties, litter quality, and climate. Can. J. For. Res. 9: 1771–1781.

Johansson M B, 1995. The chemical composition of needle and leaf litter from Scots pine, Norway spruce and white birch in Scandinavian forests. Forestry vol. 68, No.1: 49–62.

Johansson M B, Grälls C, 1989. Quantity, decomposition and nutrient dynamics of litterfall in some forest stands at Hålebäck, southern Sweden. Report 62. Reports in Forest Ecology and Forest Soils. Department of Forest Soils, Swedish University of Agricultural Sciences, Uppsala.

Johansson M B, Kögel I, Zech W, 1986. Changes in the lignin fraction of spruce and pine needle litter during decomposition as studied by some chemical methods. Soil Biol. Biochem. 18: 611–619.

Johansson M B, Lundmark J E, 1986. Markmiljön i gran- och björkbestånd. Skogsvårds-förbundets tidskrift. SST 2/86: 31–37.

Johansson M B, Berg B, Meentemeyer V, 1995. Litter mass-loss rates in late stages of decomposition in a climatic transect of pine forests. Long-term decomposition in a Scots pine forest. IX. Can. J. Bot. 73: 1509–1521.

Karlsson P, 2000. Carbon mineralization in litter and soil organic matter in forests with different nitrogen status. Licentiate thesis No. 2, Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, Uppsala, ISSN 1403-770X.

Leyton L, 1948. Mineral nutrient relationships of forest trees. For. Abstr. 9: 399–408.

Löfgren A, 2005. Oskarshamn/Forsmark site investigation. Estimation of biomass and net primary production in field and ground layer, and biomass in litter layer of different vegetation types in Forsmark and Oskarshamn. SKB P-05-80, Svensk Kärnbränslehantering AB. 37 pp.

Lundin L, Lode E, Stendahl J, Melkerud P A, Björkvald L, Thorstensson A, 2004. Soils and site types in the Forsmark area. SKB R-04-08, Svensk Kärnbränslehantering AB. 102 pp.

Lundin L, Lode E, Stendahl J, Björkvald L, Hansson J, 2005. Soils and site types in the Oskarshamn area. SKB R-05-15, Svensk Kärnbränslehantering AB. 96 pp.

Lundmark J E, Berg B, Nilsson Å, 1982. Contortatallens inflytande på mark och markvegetation i jämförelse med sylvestristallens. Sveriges Skogsvårdsförbunds Tidskrift, Nr 1–2: 43–48.

Lundmark J E, 1988. Skogsmarkens ekologi. Ståndortsanpassat skogsbruk. Del 2 – Tillämpning. Skogsstyrelsen, Jönköping. 319 pp.

Mälkönen E, 1974. Annual primary production and nutrient cycle in some Scots pine stands. Commun. Inst. Forest. Fenn. 84.5.

Marshner H, 1995. Mineral Nutrition of Higher Plants. Second Edition. Academic Press. 889 pp. Inc. Ltd, London.

McClaugherty C A, Pastor J, Aber J D, Melillo J M, 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66:266–275.

Melillo J M, Aber J D, Muratore J F, 1982. Nitrogen and lignin control of hardwood leaf litter dynamics in forest ecosystems. Ecology 63: 621–626.

Mork E, 1942. Om strofallet i våre skoger. Medel. Norske Skogsforsoksv. 29: 297–365.

Olson J, 1964. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322–331.

Ozanne P G, 1980. Phosphate nutrition of plants – a general treatise. In: Khasaweneh F.E, Sample F.C & Kamprath E.J (eds.): The Role of Phosphorus in Agriculture. pp 559–589.

Perez J, Jeffries T W, 1992. Roles of manganese and organic acid chelates in regulating lignin degradation and biosynthesis of peroxidases by *Phanerochaete chrysosporium*. Appl. Environ. Microbiol. 58: 2402–2409.

SAS Institute Inc., 2004. SAS/STAT®.9.1 User's Guide. Cary, North Carolina.

Smith J L, Paul E A, 1990. The significance of soil microbial biomass estimations. In: JM Pollag and G. Stotzky (eds) Soil Biochemistry 6, pp. 357–396.

Staaf H, 1982. Plant nutrient changes in beech leaves during senescence as influenced by site characteristics. Acta Oecol. Plant 3: 161–170.

Stott D E, Kassim G, Jarrel W M, Martin J P, Haider K, 1983. Stabilization and incorporation into biomass of specific plant carbons during biodegradation in soil. Plant Soil 70: 15–26.

Sörensen L H, 1987. Organic matter and microbial biomass in soil incubated in the field for 20 years with 14C-labelled barley straw. Soil Biol. Biochem. 19: 39–42.

Tenney F G, Waksman S A, 1929. Composition of natural organic materials and their decomposition in the soil. IV. The nature and rapidity of decomposition in various organic complexes in different plant soil materials, under aerobic conditions. Soil Sci. 28: 55–84.

Viro P J, 1956. Investigations of forest litter. Commun. Inst. For. Fenn. 45 (6), 65 pp.

Wallbridge M R, 1991. Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. Ecology 72(6): 2083–2100

Wardle D, 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biological Review 67: 321–358.

Yamaya K, Branch T, 1968. On the influence of alder (*Alnus inkumae*) on soil properties in northern Japan. In: Trappe J M, Franklin J F, Tarrant R F and Hausen, G M (eds). Biology of Alder. Proceedings from a symposium held at Northwest Scientific Association Fortieth Annual Meeting, Pullman, Washington, April 14–15, 1967.

Appendix A1

Annual amounts (± S.D, N = 30) of aboveground tree litterfall (gdw m^{-2} yr^{-1}) in stands F1, F2 and F3 in the Forsmark investigation area and stands O1, O2 and O3 in the Oskarshamn investigation area. Measurement periods: June 2004 – June 2005, June 2005 – June 2006 and June 2004 – June 2006.

Site	Year	Needles	Leaves	Other	Total
F1	2004/05	70.8 ± 29.2	60.5 ± 28.8	57.4 ± 30.4	188.7 ± 43.5
	2005/06	89.7 ± 37.1	61.7 ± 28.8	50.6 ± 21.1	202.1 ± 35.8
	2004/06[1]	80.4 ± 33.1	61.1 ± 28.6	54.0 ± 24.2	195.5 ± 38.3
F2	2004/05	68.2 ± 39.7	94.4 ± 69.3	56.0 ± 19.5	218.6 ± 65.5
	2005/06	90.1 ± 52.5	80.6 ± 63.2	72.0 ± 42.1	242.7 ± 71.4
	2004/06[1]	79.3 ± 45.1	87.4 ± 65.8	64.1 ± 28.7	230.8 ± 63.9
F3	2004/05	92.4 ± 35.2	1.4 ± 1.7	30.7 ± 16.6	124.5 ± 48.5
	2005/06	110.0 ± 45.1	1.4 ± 1.1	36.1 ± 21.4	147.5 ± 62.5
	2004/06[1]	101.3 ± 40.0	1.4 ± 1.4	33.4 ± 18.7	136.1 ± 55.3
O1	2004/05	2.9 ± 4.0	167.6 ± 19.2	93.9 ± 40.2	264.5 ± 58.0
	2005/06	2.8 ± 3.2	204.8 ± 44.1	110.2 ± 40.1	317.7 ± 81.1
	2004/06[1]	2.9 ± 3.4	186.4 ± 26.8	102.1 ± 37.3	291.3 ± 63.3
O2	2004/05	110.1 ± 40.3	0 ± 0	42.1 ± 35.4	152.2 ± 68.6
	2005/06	85.3 ± 33.2	0.1 ± 0.2	38.2 ± 25.1	123.6 ± 48.8
	2004/06[1]	97.6 ± 34.6	0.1 ± 0.1	40.1 ± 26.4	137.8 ± 55.7
O3	2004/05	316.7 ± 124.4	0 ± 0	161.9 ± 106.9	478.6 ± 220.4
	2005/06	231.0 ± 39.3	0 ± 0	76.4 ± 33.0	307.4 ± 56.3
	2004/06[1]	273.4 ± 79.5	0 ± 0	118.7 ± 61.4	392.1 ± 133.2

[1] N = 60

Appendix A2

Cumulative litter mass loss in different time periods at different sites and chemical composition for the litter types studied at different decomposition stages.

Site	SKB ID-code	Substrate	Set no	Date	Days	Mass loss %	S. D.	No of observations	C %	N %	P mg/g	Water-solubles %	Ethanol-solubles %	Lignin %
F1	AFM001068	Norway spruce needles	0	20040601	0				46.1	0.75	0.381	16.6	4.2	28.5
			1	20040820	80	21.9	2.6	25	46.2	0.86	0.428	6.1	2.5	39.2
			2	20041110	162	29.0	3.3	25	46.6	0.97	0.464	5.6	2.4	41.9
			3	20050602	366	33.4	2.4	25	45.8	1.03	0.450	5.1	1.8	45.0
			4	20050902	458	39.8	2.3	25	45.6	1.10	0.476	5.4	1.7	46.6
			5	20051114	531	42.9	4.6	25	45.2	1.14	0.473	5.4	1.8	47.0
			6	20060612	741	44.6	4.6	25	45.5	1.17	0.485	5.2	1.7	48.9
F2	AFM001076	Alder leaves	0	20040601	0				47.0	2.51	0.858	21.0	4.6	27.5
			1	20040820	80	46.9	11.9	25	49.3	3.33	0.811	7.5	2.5	44.7
			2	20041110	162	59.2	12.0	25	48.6	3.28	0.732	5.3	1.7	47.5
			3	20050602	366	60.1	8.7	25	48.2	3.33	0.630	4.9	2.6	48.9
			4	20050902	458	68.8	9.4	25	46.6	3.27	0.766	3.9	2.0	48.3
			5	20051114	531	71.2	12.6	25	48.2	3.44	0.695	4.1	2.1	50.5
			6	20060612	741	72.7	12.5	24	47.9	3.48	0.664	4.3	1.8	50.4
F2	AFM001076	Norway spruce needles	0	20040601	0				47.2	0.73	0.416	19.9	5.2	29.5
			1	20040820	80	22.2	1.5	25	47.6	0.88	0.406	4.3	3.8	41.2
			2	20041110	162	28.2	2.0	25	47.8	0.97	0.471	5.2	3.5	45.0
			3	20050602	366	32.6	2.9	25	47.3	1.06	0.453	5.2	2.7	45.3
			4	20050902	458	40.4	5.0	25	47.6	1.20	0.474	6.0	2.3	46.1
			5	20051114	531	42.7	5.9	25	47.5	1.24	0.491	6.5	2.5	46.7
			6	20060612	741	50.7	8.0	24	46.6	1.33	0.506	7.3	2.5	46.1

Site	SKB ID-code	Substrate	Set no	Date	Days	Mass loss %	S. D.	No of observations	C %	N %	P mg/g	Water-solubles %	Ethanol-solubles %	Lignin %
F3	AFM001247	Norway spruce needles	0	20040601	0				47.1	0.91	0.572	6.4	3.3	36.2
			1	20040820	80	18.8	2.2	25						
			2	20041110	162	27.1	3.6	25	48.3	1.12	0.596	5.5	2.2	42.6
			3	20050602	366	32.3	4.1	25	46.9	1.17	0.596	7.5	2.1	42.0
			4	20050902	458	41.8	7.7	25	46.8	1.34	0.696	7.8	1.9	42.0
			5	20051114	531	49.1	7.8	25	47.3	1.45	0.740	9.4	2.7	28.8
			6	20060612	741	55.6	8.5	25	46.8	1.53	0.714	8.4	2.1	29.1
O1	ASM001426	Oak leaves	0	20040608	0				47.2	1.05	0.580	18.4	2.3	34.6
			1	20040824	77	17.6	4.4	25						
			2	20041116	161	29.5	5.3	24	46.4	1.43	0.601	5.2	2.8	47.3
			3	20050608	365	34.3	6.1	25	46.4	1.56	0.614	5.4	2.9	47.1
			4	20050907	456	44.2	8.1	25	47.0	1.70	0.712	4.4	3.2	49.7
			5	20051116	526	47.6	8.6	25	46.0	1.80	0.769	4.7	3.3	48.1
			6	20060616	736	51.3	9.6	24	46.3	1.82	0.718	5.0	2.5	50.5
O2	ASM001428	Scots pine needles	0	20040608	0				50.7	0.43	0.251	14.5	10.0	26.8
			1	20040824	77	15.5	1.6	25						
			2	20041116	161	24.2	4.0	25	50.7	0.51	0.291	4.9	8.9	34.5
			3	20050607	365	29.3	4.3	25	50.7	0.63	0.353	4.6	9.3	33.2
			4	20050906	455	39.6	7.2	25	51.0	0.68	0.463	5.1	8.9	38.6
			5	20051116	526	43.4	8.3	25	51.0	0.78	0.575	5.0	6.9	40.0
			6	20060614	736	52.4	7.2	25	50.9	0.91	0.639	5.5	6.5	39.8
O3	ASM001440	Norway spruce needles	0	20040608	0				46.1	0.79	0.593	10.4	4.1	35.0
			1	20040824	77	18.1	2.0	25						
			2	20041116	161	24.1	2.7	25	46.4	0.94	0.491	6.4	2.7	42.1
			3	20050607	364	30.9	4.8	25	46.0	1.06	0.566	6.7	2.9	43.1
			4	20050906	455	36.4	7.1	25	44.9	1.14	0.561	7.2	2.9	43.6
			5	20051116	526	39.3	8.4	25	45.4	1.20	0.588	7.3	2.8	43.9
			6	20060614	736	45.6	9.2	25	45.4	1.28	0.604	6.3	2.9	47.9