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# Effects of clearfelling, slash removal and prescribed burning on amounts of plant nutrients in biomass and soil

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# Abstract

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Total amounts of plant nutrients in biomass, humus and mineral soil were determined in two old Norway spruce ecosystems in central (Garpenberg) and northern Sweden (Flakaträsk). Measurements were repeated 1, 4, 10 and 16 years after clearfelling on plots on which slash was retained, removed or burnt. Half of each plot was planted with Norway spruce, half with Scots pine. Both total and plant-available nutrient elements were determined in the mineral soil to 50 cm depth. Different analytical methods for plant-available nutrients were used and the relationship between them was calculated. Total amounts of nitrogen in the humus layer and biomass had decreased by *ca.* 840 kg ha$^{-1}$ four years after clearfelling on plots with retained slash at Garpenberg, and by *ca.* 840 kg ha$^{-1}$ on burnt plots. Corresponding losses at Flakaträsk were *ca.* 50 kg and 340 kg N ha$^{-1}$. Losses of total phosphorus at Garpenberg were *ca.* 42 and at Flakaträsk 17 kg ha$^{-1}$ on plots with retained slash, *ca.* 39 and 35 kg ha$^{-1}$ on burnt plots. During the first four years after clearfelling at Garpenberg, losses of potassium were *ca.* 100 kg ha$^{-1}$ both on plots with retained slash and on burnt plots. Corresponding losses at Flakaträsk were *ca.* 60 and 100 kg ha$^{-1}$. More than 70% of potassium was lost from burnt plots during the first year after clearfelling at both sites. Clearfelling significantly increased *p*H (95% confidence) in many humus samples and most samples of mineral soil at both sites. *p*H generally increased less on plots with slash removed than on those with slash retained, but differences were not significant. Time required for litter to lose its structure in the mor layer was estimated as the quotient between amounts of litter ocularly identified in the mor layer, and litterfall. For needle litter this was 1.7 years at Garpenberg and 4.1 years at Flakaträsk. Thus the litter disintegration rate far exceeded that from other investigations of mass loss of spruce litter in litterbags incubated on the forest floor. Residence times of soil organic carbon, estimated as a quotient between total soil carbon to 50 cm depth and carbon in annual above- and belowground litter production, were 9.5–28 years at Garpenberg and 16.5–42 years at Flakaträsk. Belowground litter production was estimated from literature concerning the quotient between below- and aboveground litter production. Other literature estimates of residence times for organic carbon in forest soils were higher than those obtained in the present investigation. Four years after clearfelling, the carbon pool had decreased by *ca.* 18 Mg C ha$^{-1}$ at Garpenberg and 13 Mg C ha$^{-1}$ at Flakaträsk for plots with retained slash. For burnt plots, decreases were *ca.* 20 and 28 Mg C ha$^{-1}$ at Garpenberg and Flakaträsk, respectively.

*Keywords:* Total nutrients, biomass components, mor, mineral soil, carbon turnover, litter decomposition, litter disintegration, plantations, age, nutrient uptake, nutrient loss, *Picea abies*, *Pinus sylvestris*, Sweden.

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# Contents

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# Introduction

Clearfelling is one of the most common methods of forest regeneration throughout the world. However, it drastically changes the entire ecosystem. Once the dominant plants have been removed, other plant species, which earlier were unable to live in the forest owing to a scarcity of light and strong competition for water and nutrients, colonise the clearfelled areas.

A large amount of logging slash is deposited on the soil surface, and many roots and fungal hyphae die in consequence of clearfelling. This organic matter subsequently decomposes, leading to a release of plant nutrients which can be taken up by the plants or lost through leaching. To reduce leaching losses, it is important that tree seedlings are established on the clearfelled area as soon as possible. Prescribed burning was one of the methods still carried out over large areas of northern Sweden when this investigation started more than 30 years ago. However, a discussion had already started about utilisation of the slash for forest energy or as a raw material for the rapidly expanding forest industry, instead of burning it. Therefore, the experiments included plots on which slash had been removed, retained and burnt, respectively.

The aim of this paper is to describe the changes in amounts of plant nutrients in biomass and soil after clearfelling, prescribed burning and slash removal.

# Material and methods

## Site and stand

An initial reconnaissance was conducted to find two old Norway spruce stands in different climatic regions, but closely matched in terms of slope, aspect, soil and bedrock type. Two suitable spruce forests were found, at Garpenberg and at Flakaträsk, which were due to be clearfelled and where the landowner was willing to pay the extra cost of clearfelling and treatment of the experimental areas according to our wishes. The landowner at Garpenberg was the State Forest Service, and at Flakaträsk, Modo AB. Owing to the high cost of sampling and analysis of soil and biomass, funds could be obtained for two experimental areas only. The investigation began in July 1966 in a 100-year-old spruce stand at Garpenberg, in middle Sweden. One year later, a similar investigation was carried out in a 140-year-old spruce stand at Flakaträsk, *ca.* 100 km WNW of Umeå in northern Sweden. The sites and stands are described in Table 1.

The soil texture in the experimental areas was a sandy till, the most common soil-textural type in Swedish forests. To avoid water-logging of the soils after clearfelling, the experimental areas were situated on moderate slopes. In the FAO-UNESCO system (FAO-UNESCO, 1989), the soil type was a Haplic Podzol, which generally had a thicker A2-layer at Flakaträsk than at Garpenberg, where the humus layer was more mixed with mineral soil. The soil in the experimental area at Garpenberg is described in more detail by Lyford & Troedsson (1973).

## Sampling in the old forests

### *Trees*

In the old forests, ten sample trees from breast-height diameter classes 8, 12, 16, 20, 24, 28, 32, 36 and 40 cm were randomised on lines 40 m apart and at different distances along the lines.

When the trees were felled, their roots were cut 50 cm from the centre of the stump, and they were winched down with an autotractor. Each stump-root section was freed from soil and weighed. The stem top was cut at a diameter of 7.5 cm – conventional in Swedish forestry at that time – and weighed. The tree stems, *i.e.* without stump and top, were then cut into eight sections of similar length. The branches and stem from each section were weighed. A stem disc and a sample branch from each section were weighed fresh, then dried and separated into needles, and different diameter classes of branches with the help of calipers. From the dry mass and number of trees by diameter classes, the biomass per hectare of the various components was calculated. The two spruce stands also contained some pines and deciduous trees, which were assumed to be spruces in the biomass calculations (Table 1).

All samples and subsamples were dried as soon as possible, in an oven at 105°C. Stem discs and coarse branches were first dried in a

Table 1. *Description of sites and stands before clearfelling ($m^3sk$=forest cubic metres)*

| Characteristic | *Garpenberg* | *Flakaträsk* |
|---|---|---|
| Situation | 60°16′N, 16°13′E | 64°15′N, 18°30′E |
| Altitude | 200–220 m | 420–450 m |
| Slope | ENE 4% | SSE 7% |
| Area, ha | 3.7 ha | 2.9 ha |
| Bedrock | Granite | Granite |
| Soil texture | Sandy till | Sandy till |
| Soil type[a] | Haplic Podzol | Haplic Podzol |
| Humus layer | Mor | Mor |
| Forest type | Mesic dwarf-shrub | Mesic dwarf-shrub |
| Stand age, years | 100 (45–132) | 139 (128–160) |
| Tree height, m | 22.6 | 17 |
| No. trees $ha^{-1}$ | 544 | 1002 |
| Spruce | 493 | 988 |
| Pine | 40 | 9 |
| Broadleaves | 11 | 5 |
| Basal area at 1.3 m, $m^{-2}$ $ha^{-1}$ | 29.8 | 33.5 |
| Basal-area-weighted mean diameter, cm | 26.4 | 20.6 |
| Form factor | 0.464 | 0.486 |
| Mean volume, $m^3$ sk $ha^{-1}$ | 331 | 278 |
| Site quality class, $m^2$ sk $ha^{-1}$ $yr^{-1}$ | 4.9 | 2.6 |

[a] FAO-UNESCO system.

warm room with good ventilation, then transferred to 105°C.

For the nutrient analyses, samples from the sample trees were combined to form one or two composite samples of the same tree fraction, *i.e.* stemwood, stembark, stump, needles and branches and roots of different diameter classes.

### *Field-layer vegetation*

The aboveground biomass of shrubs, grasses and herbs was determined by total harvesting. Samples (50 × 50 cm) were taken along parallel lines (40 m apart), with a distance of 20 m between samples. If the sampled point coincided with a tree, it was displaced 50 cm along the line away from the centre of the tree. A correction was applied for this 'stump' area when calculating the biomass and amounts of plant nutrients per hectare. Sample points on wet areas were excluded. No other restrictions on sampling, *e.g.* for large boulders, were made. At Garpenberg, 53 samples (50 × 50 cm) were taken from the field-layer vegetation, and at Flakaträsk 31 samples were collected.

### *Humus*

The humus layer, which was of mor type, was sampled on the 50 × 50 cm trial plots used for sampling field-layer vegetation. In coniferous forests, the litter is mostly mixed with mosses, and a real layer of litter without mosses can only be found in very dense stands. The layer consisting of living mosses and litter is called the S-layer (Forsslund, 1944). There is often a 'decomposition zone' beneath the S-layer, which makes it easy to separate this layer from the F-layer (fermentation layer). The boundary between the F-layer and the H-layer (humified layer), as well as that between the H-layer and the mineral soil, was very diffuse. It was therefore not possible to avoid contamination of samples of the H-layer with mineral soil.

Roots in the F- and H-layers were separated into different diameter classes with calipers, then dried and weighed. The humus samples of the two layers were weighed separately in the field, and about one-tenth was weighed and dried, on the basis of which the dry mass of the whole sample was calculated. From the dry mass of the total samples and the size and numbers of samples, the dry mass per hectare was calculated. A correction was made to account for the area occupied by stumps.

The humus layers of the two investigated spruce ecosystems were very heterogeneous, and mean values for humus amounts had large standard deviations. The size and number of samples needed to achieve acceptably accurate estimates of amounts of plant nutrients in the humus layers has been discussed by Troedsson & Tamm (1969), Falck (1973) and Nykvist (1977).

To learn more about the composition of the ground vegetation and the humus layer, 30 samples (10 × 10 cm) at Garpenberg and 28 at

Flakaträsk were taken at random, using a grid system. All constituents of the S, F and H-layers visible to the naked eye were separated, dried, weighed and calculated per hectare.

*Mineral soil*

Samples of the mineral soil were taken from every fourth quadrat on which humus samples were collected. Cylinders with an area of 37.5 cm$^2$ and a height of 5 cm were used. Samples were taken at 5-cm intervals down to 50 cm, from 13 soil pits in the old forests at Garpenberg and 14 at Flakaträsk. The samples were dried, and roots, stones, gravel and fractions smaller than 2 mm were separated and weighed. Composite samples from the same depth and experimental plot were used for chemical analysis.

When sampling mineral soil, it was necessary to avoid boulders and larger stones. Therefore, when calculating the values per hectare, a correction was applied for the volume of boulders and large stones not sampled in the cylinders. Their volume was determined by weighing the stones and estimating the volume of boulders in 50 × 50 cm soil pits to 50 cm depth.

## Treatment of the clearfelled areas

The spruce stands were clearfelled some months after the investigation of the old forest ecosystems in 1966 and 1967 (see Nykvist, 1997). In the following spring, six 50 × 50 m trial plots were laid out in each experimental area. The slash was left on two of them and removed from two others. On the two remaining trial plots, the slash was burnt. After manual soil scarification, half of each 50 × 50 m trial plot was planted with Norway spruce (*Picea abies* (L.) Karst.), the other half with Scots pine (*Pinus sylvestris* L.).

## Sampling

*Field-layer vegetation*

After clearfelling, the biomass of the field-layer vegetation was determined on five 50 × 50 cm sample plots distributed at random using a grid system in each trial plot (25 × 50 m). Small deciduous trees were sampled from five 10 × 10 m sample plots adjacent to the smaller sample plots. No sampling was carried out in the scarified areas which occupied about 100 m$^2$ of each 2500 m$^2$ trial plot.

The dense vegetation of *Deschampsia flexuosa* (L.) was sampled in cylinders with an area of 37.5 cm$^2$. From each trial plot (25 × 50 m), five composite samples were taken, each containing 15–18 subsamples.

*Tree seedlings on the clearfelled plots*

The average dry mass of stems, branches, needles and roots was determined for 50 pine and 50 spruce seedlings before planting. Four and ten years after clearfelling, four pine and four spruce plants were sampled at random from each plot. As the difference in size between tree plants increased with age, two of the largest and two of the smallest plants on each trial plot were sampled from two randomly selected sample points ten years after clearfelling. Sixteen years after clearfelling, the height and diameter of all trees in the plots were measured, and the stem of mean basal area was calculated for each plot. Two trees equal in size to the stem of mean basal area were randomly sampled. All sample trees were separated into stem, branches of different sizes and needles, after which the total biomass per hectare was calculated by multiplying the figures by the number of plants on the plots.

*Humus and mineral soil*

The humus layer was sampled on the 50 × 50 cm sample plots used for sampling field-layer vegetation. The humus layer was separated into the S-, F- and H-layer. The mineral soil beneath the mor layer was sampled with cylinders (area 37.5 cm$^2$, height 5 cm). This type of sampling was done before clearfelling and one and four years thereafter.

Ten and 16 years after clearfelling, five composite samples of the humus layer and the field- and ground-layer vegetation were taken with cylinders to reduce the standard deviation. The plant species, humus and humus mixed with some mineral soil in the cylinder were separated and sampled. Each composite sample contained 15–18 subsamples randomly distributed over the 25 × 50 m trial plots. One of the five composite samples also contained 15–18 subsamples from 0–5 cm, 5–10 cm, 10–15 cm and 15–20 cm soil depth. Fractions of mineral soil larger than 6 mm were removed by sieving before the samples were extracted.

### Sampling times on the clearfelled plots

Sampling was repeated 1, 4, 10 and 16 years after clearfelling. Since the amount of plant biomass varies with season, sampling was always carried out in early July. In 1978, spring was very late in northern Sweden; the biomass of the field vegetation layer was therefore low at Flakaträsk ten years after clearfelling.

### Litterfall and throughfall

Litterfall and throughfall were sampled in the old forests adjacent to the clearfelled areas. The sampling started in 1968 and continued for four years at Garpenberg and for five years at Flakaträsk. The litter was collected in ten 50 × 50 cm litter traps, randomised in the areas and placed *ca.* 30 cm above ground. Thus, only litterfall from the trees and taller shrubs was measured.

Rainfall inside and outside the forest was collected in plastic bottles with plastic funnels of 10 cm diam. A piece of glass wool was placed in the funnel pipe to keep litter from entering the bottles. Ten bottles with funnels were randomly placed on the ground in the forests and on the clearfelled areas, except for the clearfelled area at Flakaträsk, where five bottles only were used. The water was stored in a deep-freeze until 24 h before the samples were chemically analysed.

The litter and water samples were collected every fortnight when the ground was not snow-covered. Composite samples of litter and water were analysed for various elements, and means were calculated for Garpenberg (4 years) and Flakaträsk (5 years).

### Chemical analyses

Samples of biomass and humus layer were analysed to determine total amounts of organic C, N, K, P, Ca, Mg, Na, Mn, Zn and Cu. Organic C was analysed using the wet-combustion method, and N was determined according to the Kjeldahl method. Samples from the old forest ecosystems and the trial plots one year after clearfelling were analysed at the National Laboratory of Agricultural Chemistry. The samples were combusted in an electric furnace and the ash dissolved in HCl, after which the elements were analysed according to standard methods (Karlsson, 1964). Samples collected from the trial plots four years after clearfelling (1971 and 1972) were analysed at the Department of Plant Ecology, University of Lund, and the samples collected subsequently were analysed at the Department of Forest Site Research, SLU, Umeå. In Umeå, ground and dried samples of biomass and humus were subjected to a wet-combustion treatment, utilising a mixture of concentrated nitric and perchloric acids (4:1) for 1–3 days. After filtration and dilution, the analyses were made according to standard methods (Emteryd, 1989).

In dried samples of the mineral soil from the old spruce ecosystems, total elements were analysed after digestion of the soil samples with perchloric and hydrofluoric acids. The only fractions of mineral soil analysed were those with a particle size less than 2 mm. Analyses of plant-available nutrients were also carried out on the dried samples from the mineral soil one and four years after clearfelling. Concentrations of exchangeable cations were determined by ICP-EMS after extraction with 1-N ammonium acetate at *p*H 7, and filtration of the solution. Plant-available P was analysed with the Sibbesen method and the Bray C method. For the determination of available P and K, the ammonium lactate acetate method (AL-method) was also used, whereby soil samples are extracted in a solution of ammonium lactate and acetic acid at *p*H 3.75 for two hours (Egnér, Riehm & Domingo, 1960). The stores of P (P-HCl) and K (K-HCl) were analysed after extraction of the soil samples in 2-M HCl during two hours in boiling water and filtration of the solutions.

To investigate the effects of clearfelling on the amounts of plant-available nutrients, samples were analysed which were deep-frozen on the day of sampling and removed from the deep-freeze one day before analysis. Ammonium-N and nitrate-N were analysed after extraction of soil samples in 2-M KCl, according to standard procedures. For determination of available P and K, the AL-method was used, according to Egnér, Riehm & Domingo (1960).

The *p*H -analysis was carried out in a suspension of soil and water (1 part soil:1 part distilled water, by mass). The suspension was left overnight, and measured on the following day with a glass electrode.

The methods chosen for chemical analysis were those commonly used for analysing soil and biomass in forest ecosystems when the experiments started in 1966. Dried soil samples were later also analysed by other methods, to obtain results more comparable with those from later investigations. A detailed description of the methods can be found in Emteryd (1989).

# Results

## Old forest

The total dry mass of the mineral soil to 50 cm depth, including boulders and stones, was 6300 Mg ha$^{-1}$ for Garpenberg and 6340 for Flakaträsk. The dry mass of the various size classes is shown in Fig. 1. Amounts of soil particles less than 2 mm are shown in Table 2 for 5 cm layers, down to 50 cm depth. This soil fraction was used for chemical analysis. Mineral soil particles larger than 2 mm also contain plant nutrients (except N), but in the present study, these fractions were of little interest, because only small amounts of plant nutrients can be released through their chemical weathering.

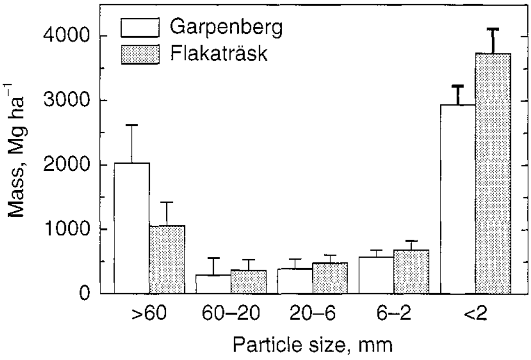


*Fig. 1.* Dry mass of particle size classes in mineral soil to 50 cm depth at Garpenberg and Flakaträsk. For particle sizes >60 mm, the means were based on 13 and 14 samples; for particle sizes <60 mm they were based on 5 composite samples, each containing 4–9 subsamples. Mean values in Mg ha$^{-1}$ ±95% confidence intervals.

Table 2. *Dry mass of mineral soil particles <2 mm at different soil depths (Mg ha$^{-1}$)*

| Soil depth cm | *Garpenberg* | *Flakaträsk* |
|---|---|---|
| 0–5 | 273 ± 34 | 316 ± 56 |
| 5–10 | 271 ± 33 | 357 ± 18 |
| 10–15 | 280 ± 20 | 334 ± 40 |
| 15–20 | 294 ± 17 | 345 ± 18 |
| 20–25 | 299 ± 29 | 373 ± 35 |
| 25–30 | 329 ± 69 | 387 ± 44 |
| 30–35 | 297 ± 40 | 396 ± 42 |
| 35–40 | 371 ± 31 | 424 ± 77 |
| 40–45 | 301 ± 46 | 399 ± 66 |
| 45–50 | 304 ± 46 | 426 ± 92 |
| 0–50 | 2965 ± 271 | 3758 ± 386 |

The sampling of mineral soil excluded boulders and larger stones. Their volume was estimated at 15% at Garpenberg and 8% at Flakaträsk, and was taken into consideration when calculating the amounts of plant nutrients per hectare.

The dry mass and amounts of plant nutrients in above- and belowground biomass components are shown in Table 3. A more detailed description of the biomass of shrubs, herbs, grasses and mosses is given in Nykvist (1997).

The dry mass of the remnants of litter fractions identified with the naked eye in the S-layer was 4753 kg ha$^{-1}$ at Garpenberg and 4066 kg ha$^{-1}$ at Flakaträsk (Table 4). The corresponding figures for the F-layer were 7093 and 16744 kg ha$^{-1}$ at Garpenberg and Flakaträsk, respectively. The total amount of organic C in the humus layer was *ca.* 30 Mg C ha$^{-1}$ at Garpenberg and *ca.* 26 Mg C ha$^{-1}$ at Flakaträsk (Table 4).

The greatest amounts of plant nutrients were found in the unidentified organic matter (Table 4). Among the recognisable litter fractions, most of the plant nutrients in the S-layer at Garpenberg were in needles, except K, which was most abundant in moss remnants. At Flakaträsk, all nutrients except Ca were most abundant in moss remnants, amounts of Ca being greatest in needle remnants. In the F-layer at Garpenberg, cone remnants had the greatest amounts of all plant nutrients except K and Mn, whereas at Flakaträsk, the greatest amounts of all plant nutrients were found in moss remnants.

Total amounts of the most common elements (except Si, $O_2$ and $H_2$), in the mineral soil to 50 cm depth in the soils at Garpenberg and Flakaträsk before clearfelling, are shown in Table 5. Of the analysed elements, Al, K, organic C, Fe, Na and Ca were present in the greatest amounts at Garpenberg, and Al, Fe, K, Na, organic C and Ca were most abundant at Flakaträsk. However, only very small proportions of total plant nutrients in the soil are available to plants.

Concentrations of the common nutrients K,

Table 3. *Dry mass and amounts of organic C, N, P, K, Ca, Mg, Mn, Na, Zn and Cu at Garpenberg (G) and Flakaträsk (F). Dead roots included in root fraction. Dry mass and organic C in Mg ha$^{-1}$. Others in kg ha$^{-1}$*

| | Site | Stemwood | Stem bark | Needles | Branches | Stump | Field-layer | Mosses | Roots in mor layer | | | Roots in mineral soil | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | >20 mm | 20–2 mm | <2 mm | | |
| Dry mass | G | 127.3 | 11.1 | 14.9 | 28 | 20 | 0.2 | 0.5 | 4.5 | 3.5 | 1.3 | 1.9 | 213 |
| | F | 103.6 | 12.4 | 9.4 | 23.5 | 26 | 0.5 | 1.1 | 14.2 | 5.2 | 2.6 | 5.8 | 205 |
| C | G | 59.8 | 5.2 | 6.7 | 13.2 | 9.5 | 0.1 | 0.2 | 2.1 | 1.7 | 0.6 | 0.4 | 100 |
| | F | 48.7 | 5.8 | 4.2 | 11.2 | 12.4 | 0.2 | 0.5 | 6.9 | 2.4 | 1.2 | 1.2 | 95 |
| N | G | 74 | 38 | 155 | 101 | 16 | 3 | 8 | 10 | 17 | 10 | 5 | 437 |
| | F | 86 | 48 | 76 | 86 | 27 | 5 | 11 | 20 | 20 | 15 | 14 | 408 |
| P | G | 5.2 | 4.6 | 14.4 | 10.6 | 1.2 | 0.3 | 1.2 | 1.2 | 1.7 | 0.9 | 0.6 | 41.9 |
| | F | 5.2 | 7.3 | 12.2 | 10.5 | 5.7 | 0.7 | 1.8 | 1.9 | 2.5 | 2.0 | 1.9 | 51.7 |
| K | G | 37.1 | 20.8 | 64.6 | 37 | 13 | 3 | 6.7 | 5.9 | 6.6 | 2.7 | 2.3 | 200 |
| | F | 49.8 | 33.7 | 41.2 | 35 | 19.8 | 2.5 | 6.5 | 11.4 | 9.1 | 5.1 | 7 | 221 |
| Ca | G | 93 | 119 | 119 | 125 | 25 | 1 | 1 | 13 | 10 | 3.0 | 5 | 514 |
| | F | 85 | 100 | 69 | 121 | 58 | 2 | 4 | 44 | 14 | 5.2 | 16 | 518 |
| Mg | G | 10.2 | 6.6 | 14.9 | 15.9 | 2.8 | 0.3 | 0.5 | 1.6 | 1.8 | 0.8 | 0.6 | 56.0 |
| | F | 19.7 | 8.7 | 9.6 | 10.9 | 7.3 | 0.4 | 0.9 | 3.1 | 1.6 | 1.2 | 1.9 | 65.3 |
| Mn | G | 22.5 | 12.5 | 35.7 | 16.9 | 3.8 | 0.7 | 0.4 | 1.3 | 2.0 | 1.1 | 0.5 | 97.4 |
| | F | 15.1 | 9.7 | 14.6 | 10.9 | 5.6 | 1.3 | 1.1 | 3.1 | 2.1 | 1.8 | 1.4 | 66.7 |
| Na | G | 1.27 | 1.33 | 1.2 | 1.92 | 0.34 | 0.01 | 0.08 | 0.26 | 0.30 | 0.18 | 0.14 | 7.03 |
| | F | 2.07 | 1.25 | 0.7 | 1.83 | 0.96 | 0.03 | 0.12 | 0.39 | 0.21 | 0.13 | 0.41 | 8.11 |
| Zn | G | 2.12 | 2.83 | 0.96 | 2.22 | 0.27 | 0.01 | 0.06 | 0.24 | 0.32 | 0.15 | 0.10 | 10.68 |
| | F | 1.91 | 2.02 | 0.57 | 2.11 | 0.86 | 0.02 | 0.09 | 0.42 | 0.30 | 0.12 | 0.30 | 8.72 |
| Cu | G | 0.53 | 0.07 | 0.06 | 0.28 | 0.13 | 0.003 | 0.007 | 0.010 | 0.017 | 0.009 | 0.008 | 1.115 |
| | F | 0.19 | 0.06 | 0.02 | 0.11 | 0.08 | 0.004 | 0.008 | 0.024 | 0.016 | 0.015 | 0.025 | 0.551 |

Table 4. *Dry mass and amounts of organic C, N, P, K, Ca, Mg, Mn, Na, Zn and Cu in branches on the soil surface and in the mor layer (kg ha$^{-1}$)*

| | | | S-layer | | | | | | | | F-Layer | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Site | Surface branches | Needles | Bark | Cones | Grasses | Shrubs | Herbs Ferns | Mosses | Others | Branches | Needles | Bark | Cones | Shrubs Grasses | Mosses | Others | S + F + H Layer unidentified organic matter | Total |
| Dry mass | G | 1575 | 2450 | 120 | 822 | 246 | 23 | 54 | 1038 | 0 | 2163 | 810 | 390 | 2631 | 11 | 1075 | 13 | 90834 | 104255 |
| | F | 951 | 1556 | 24 | 299 | 58 | 213 | 6 | 1817 | 93 | 2420 | 1727 | 939 | 3547 | 0 | 7972 | 139 | 38109 | 59870 |
| C | G | 809 | 1225 | 63 | 428 | 117 | 11 | 25 | 476 | 0 | 1140 | 397 | 190 | 1281 | 5 | 422 | 7 | 23490 | 30086 |
| | F | 475 | 771 | 13 | 163 | 27 | 99 | 3 | 851 | 47 | 1167 | 806 | 401 | 1515 | 0 | 3453 | 70 | 16008 | 25869 |
| N | G | 13.06 | 28.49 | 0.83 | 5.69 | 2.91 | 0.34 | 0.92 | 13.20 | 0 | 20.91 | 11.18 | 4.09 | 27.87 | 0.11 | 16.07 | 0 | 998.23 | 1144 |
| | F | 8.11 | 14.42 | 0.19 | 2.42 | 0.82 | 2.98 | 0.09 | 18.48 | 1.35 | 24.48 | 20.91 | 8.26 | 31.87 | 0 | 103.73 | 1.88 | 288.54 | 529 |
| P | G | 1.06 | 2.18 | 0.07 | 0.49 | 0.30 | 0.03 | 0.08 | 1.62 | 0 | 1.40 | 0.74 | 0.28 | 1.49 | 0.01 | 1.39 | 0 | 51.89 | 63.0 |
| | F | 0.68 | 1.34 | 0.02 | 0.20 | 0.07 | 0.27 | 0.01 | 2.38 | 0.11 | 2.40 | 1.73 | 0.67 | 2.44 | 0 | 9.61 | 0.15 | 23.34 | 45.4 |
| K | G | 0.97 | 2.22 | 0.16 | 1.07 | 2.95 | 0.08 | 0.12 | 6.50 | 0 | 1.40 | 0.58 | 0.20 | 1.05 | 0 | 1.81 | 0 | 60.50 | 79.6 |
| | F | 0.96 | 1.59 | 0.04 | 0.54 | 0.14 | 0.51 | 0.02 | 8.32 | 0.18 | 3.49 | 1.70 | 0.68 | 2.24 | 0 | 11.47 | 0.24 | 22.74 | 54.9 |
| Ca | G | 4.48 | 21.29 | 0.23 | 1.56 | 0.52 | 0.17 | 0.52 | 4.17 | 0 | 6.27 | 4.10 | 1.39 | 9.29 | 0.04 | 4.06 | 0 | 203.57 | 261.7 |
| | F | 5.22 | 20.84 | 0.04 | 0.51 | 0.39 | 1.40 | 0.04 | 10.20 | 0.74 | 10.46 | 18.19 | 2.93 | 15.65 | 0 | 34.24 | 1.07 | 77.72 | 199.6 |
| Mg | G | 0.37 | 0.97 | 0.05 | 0.33 | 0.12 | 0.03 | 0.07 | 0.81 | 0 | 0.87 | 0.33 | 0.18 | 1.04 | 0 | 0.74 | 0 | 66.62 | 72.5 |
| | F | 0.42 | 0.75 | 0.02 | 0.22 | 0.03 | 0.11 | 0 | 1.24 | 0.07 | 0.92 | 0.83 | 0.20 | 1.14 | 0 | 3.60 | 0.10 | 13.81 | 23.5 |
| Mn | G | 0.93 | 3.66 | 0.04 | 0.25 | 0.25 | 0.04 | 0.18 | 1.15 | 0 | 1.38 | 1.04 | 0.26 | 1.24 | 0.01 | 1.39 | 0 | 59.25 | 71.1 |
| | F | 0.91 | 2.67 | 0.01 | 0.12 | 0.1 | 0.37 | 0.01 | 3.15 | 0.27 | 3.28 | 4.08 | 0.81 | 2.38 | 0 | 11.11 | 0.39 | 12.56 | 42.2 |
| Na | G | 0.100 | 0.245 | 0.008 | 0.058 | 0.017 | 0.003 | 0.008 | 0.153 | 0 | 0.160 | 0.062 | 0.022 | 0.170 | 0.001 | 0.091 | 0 | 11.045 | 12.14 |
| | F | 0.076 | 0.218 | 0.001 | 0.009 | 0.005 | 0.017 | 0.001 | 0.241 | 0.004 | 0.190 | 0.220 | 0.060 | 0.290 | 0 | 0.910 | 0.006 | 2.782 | 5.03 |
| Zn | G | 0.127 | 0.222 | 0.009 | 0.062 | 0.019 | 0.002 | 0.014 | 0.141 | 0 | 0.170 | 0.102 | 0.060 | 0.230 | 0.001 | 0.146 | 0 | 9.050 | 10.36 |
| | F | 0.098 | 0.128 | 0.001 | 0.018 | 0.006 | 0.021 | 0.001 | 0.159 | 0.012 | 0.220 | 0.160 | 0.070 | 0.210 | 0 | 0.560 | 0.022 | 12.632 | 14.32 |
| Cu | G | 0.016 | 0.016 | 0.001 | 0.007 | 0.002 | 0 | 0.001 | 0.014 | 0 | 0.016 | 0.013 | 0.006 | 0.019 | 0 | 0.018 | 0 | 1.262 | 1.389 |
| | F | 0.008 | 0.009 | 0 | 0.001 | 0 | 0.001 | 0 | 0.014 | 0.001 | 0.022 | 0.013 | 0.007 | 0.015 | 0 | 0.119 | 0.002 | 0.138 | 0.350 |

Table 5. *Amounts of the most common elements in dried mineral soil (particle size <2 mm) to 50 cm depth at Garpenberg and Flakaträsk before clearfelling. Averaged figures for two composite samples containing 8 and 5 subsamples, respectively (kg ha$^{-1}$)*

| Element | Method | *Garpenberg* | *Flakaträsk* |
|---|---|---|---|
| C | Organic C | 67852 | 59039 |
| N | N-tot | 2731 | 1629 |
| P | P-tot | 994 | 1739 |
| | P-HCl | 790 | 1735 |
| | P-Sibb. | 17.27 | 30.55 |
| | P-Bray C. | 15.50 | 46.34 |
| | P-AL | 5.81 | 13.02 |
| | P-$NH_4$Ac, *p*H7 | 9.80 | 22.89 |
| K | K-tot | 79296 | 87564 |
| | K-HCl | 1345 | 1954 |
| | K-AL | 58.39 | 78.40 |
| | K-$NH_4$Ac, *p*H7 | 43.48 | 72.82 |
| Ca | Ca-tot | 33920 | 46117 |
| | Ca-HCl | 6421 | 5152 |
| | Ca-AL | 106.84 | 170.03 |
| | Ca-$NH_4$Ac, *p*H7 | 76.22 | 142.76 |
| Mg | Mg-tot | 16145 | 19666 |
| | Mg-HCl | 8049 | 8132 |
| | Mg-AL | 19.81 | 32.62 |
| | Mg-$NH_4$Ac, *p*H7 | 13.92 | 32.19 |
| Mn | Mn-tot | 1321 | 1491 |
| | Mn-$NH_4$Ac, *p*H7 | 14.60 | 13.33 |
| Na | Na-tot | 58106 | 68826 |
| | Na-$NH_4$Ac, *p*H7 | 19.34 | 23.85 |
| Zn | Zn-tot | 123 | 155 |
| | Zn-$NH_4$Ac, *p*H7 | 2.26 | 4.02 |
| Cu | Cu-tot | 40 | 62 |
| | Cu-$NH_4$Ac, *p*H7 | 1.85 | 3.97 |
| Fe | Fe-tot | 67155 | 91357 |
| | Fe-$NH_4$Ac, *p*H7 | 37.28 | 27.88 |
| Al | Al-tot | 194253 | 234690 |
| | Al-$NH_4$Ac, *p*H7 | 159 | 111 |

Ca, Mg and P at different depths in the soil, as determined by different analytical methods, are shown in Fig. 2–4. Amounts of plant-available nutrients in the mineral soil to 50 cm depth are shown in Table 5.

The most common method used at present for determining contents of plant-available cations in soil is the extraction of exchangeable cations, whereas in Sweden the method formerly most common was the AL-method. The results in Table 5 and Fig. 2 show that the difference between the two methods is rather small. Most of the investigated cations were in the top layers. The relationship between K-AL and K-exchangeable was K-AL = 1.18(K-exch.), $r^2$ = 0.79. The corresponding relationship for Ca was Ca-AL = 1.01(Ca-exch.), $r^2$ = 0.80 and that for Mg, Mg-AL = 1.05(Mg-exch.), $r^2$ = 0.83.

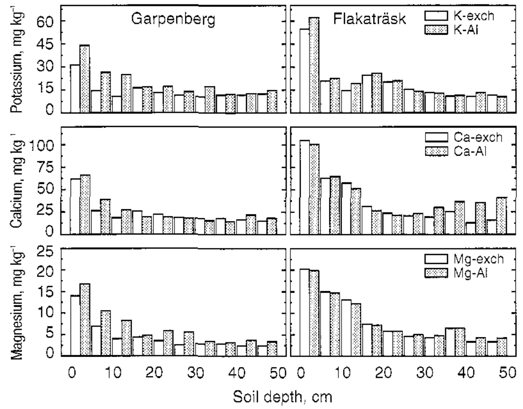


*Fig. 2.* Concentrations of K, Ca and Mg in dried soil samples extracted in ammonium acetate at *p*H 7 (exchangeable) and AL-solution.

The relationship between P-tot and P-HCl ('phosphorus store') was P-HCl = 0.89(P-tot.), $r^2 = 0.34$. Table 5 and Fig. 3 show that most of the total P in the soil was extracted by treating the soil samples with 2-M HCl.

The results obtained with some of the most common extraction methods used for determining plant-available P are shown in Table 5 and Fig. 4. According to the Sibbesen method, concentrations of P were greatest in the uppermost 5-cm soil layer, whereas according to the Bray C method, they dominated in the deeper soil layers, owing to the complex formation of fluoride in the extraction solution and the presence of Al and Fe compounds in the soil, thus making P more soluble. In the present study, concentrations of P obtained after extraction in ammonium acetate at *p*H 7, *i.e.* the method used for extracting exchangeable cations, were also investigated. Concentrations were about the same as for P-AL, although the relationship was not as good (P-$NH_4$Ac = 1.02(P-AL), $r^2 = 0.12$). The method is, however, of great interest, because the cost of chemical soil analyses could be reduced considerably if the method used for extracting exchangeable cations could also be used for extracting plant-available P.

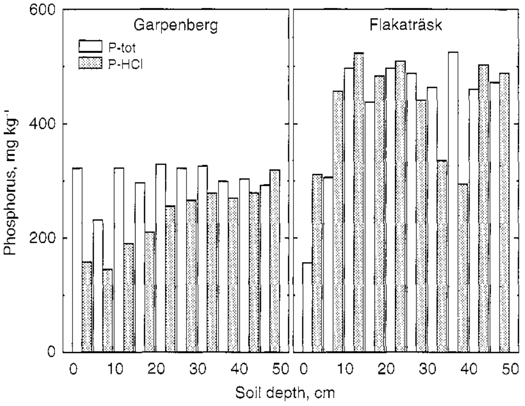


*Fig. 3.* Concentrations of total P and HCl-extracted P in dried soil samples.

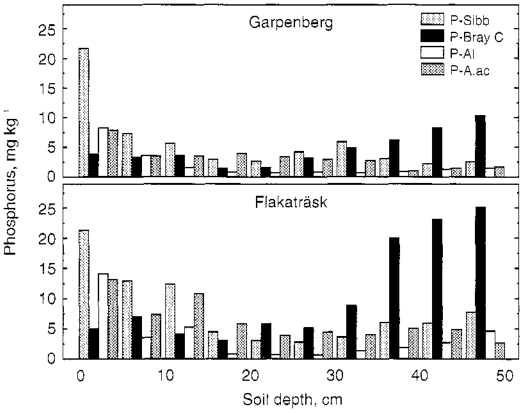


*Fig. 4.* Concentrations of P in dried soil samples from different depths in the soil, extracted according to the methods of Sibbesen (P-Sibb.), and Bray and Kurtz (P-Bray C), Egnér's AL-method (P-AL) and the method for extracting exchangeable cations (P-$A_{ac}$).

Two of the most common elements in the soils of Garpenberg and Flakaträsk were Al and Fe (Table 5). Downwards through the soil profile, there was a gradual increase in the Al-concentration to *ca.* 20 cm depth, and in the Fe-concentration to *ca.* 15 cm depth, at both Garpenberg and Flakaträsk (Fig. 5). When a separate podzol profile is analysed, a great difference in low and high contents of Al and Fe is mostly found at a certain depth, indicating the boundary between the A- and the B-horizons. When composite samples are analysed, a gradual increase in Al and Fe contents is more common, because the thickness of the A-horizon varies considerably in different subsamples, especially in till soils.

For the determination of exchangeable cations, soil samples are generally extracted with ammonium acetate at *p*H 7. The reason for extraction at *p*H 7 was originally that hydrogen ions were released from the soil when Al and Fe-hydroxides were formed during extraction,

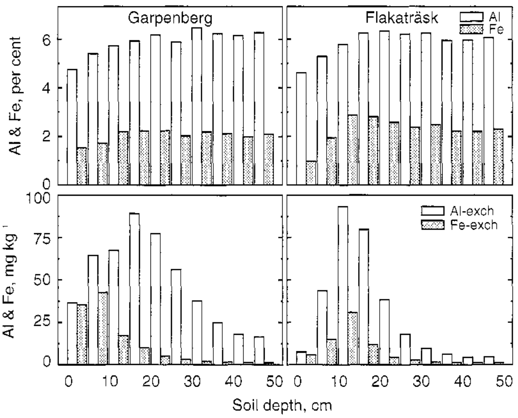


*Fig. 5.* Concentrations of total Al and Fe in dried soil samples (above) and concentrations of Al and Fe in dried soil samples extracted in ammonium acetate at *p*H 7 (below).

and could be titrated. However, owing to the occurrence, and perhaps also the formation, of water-soluble complexes with organic ligands, Al- and Fe-compounds were also extracted with ammonium acetate at *p*H 7. For Al, the extracted amount was of about the same magnitude as for Ca (Table 5). The highest concentrations were found at 5–25 cm soil depth (Fig. 5).

## Effects of clearfelling

### *Amounts of plant nutrients in the humus layer*

The dry mass of branches on the soil surface, and the plant remains recognisable with the naked eye in the mor layer in the old forests and in the plots one and four years after clearfelling, are shown in Table 6 for Garpenberg and in Table 7 for Flakaträsk. Amounts of branches on the soil surface and needles in the mor layer were greater one year after clearfelling than in the old forest ecosystems, because slash was left after clearfelling. The amounts left could be calculated from the biomass figures for the old forests (Table 3). Since litterfall from the small tree seedlings was negligible one and four years after clearfelling, decomposition of the tree components in the mor layer and in the slash after clearfelling could be calculated.

Losses of plant nutrients from the decomposition of recognisable needles in the mor layer, calculated in per cent of the amounts in the mor layers of the old forests, and, for plots with slash left on-site, added as slash after clearfelling, are shown in Table 8. Decreases greater than those for dry mass were found for K, Na, Mg and P in samples from plots with retained slash, indicating a decrease in concentrations of these nutrients during decomposition. Plant nutrients for which the decreases were lower in relation to the dry mass of the needles, were N, Mn, Zn and Cu. One year after clearfelling, the amounts of Zn and Cu at Garpenberg were even larger than the sum of the amounts in the slash and mor layer of the old forests, probably because

Table 6. *Dry mass of remnant plant biomass fractions on the soil surface and in the S-, F- and H-layers in the old forest at Garpenberg, and one and four years after clearfelling. a = slash retained, b = slash removed and c = burnt (kg ha$^{-1}$)*

| | Plant remnants | Old forest | One year after clearfelling | | | Four years after clearfelling | | |
|---|---|---|---|---|---|---|---|---|
| | | | a | b | c | a | b | c |
| Soil surface | Branches, >20 mm | 0 | 13366 | 391 | 5380 | 16668 | 0 | 17386 |
| | Branches, 5–20 mm | 58 | 9903 | 664 | 3037 | 3904 | 555 | 3233 |
| | Branches, <5 mm | 1517 | 6340 | 616 | 671 | 4357 | 330 | 241 |
| | **Total** | **1575** | **29609** | **1671** | **9088** | **24929** | **885** | **20860** |
| S-layer | Branches | 0 | 70 | 259 | 231 | 7 | 82 | 200 |
| | Spruce needles | 2298 | 4926 | 1354 | 1287 | 35 | 32 | 10 |
| | Pine needles | 152 | 137 | 27 | 71 | 13 | 0 | 0 |
| | Bark | 120 | 288 | 839 | 163 | 137 | 22 | 78 |
| | Cones | 822 | 55 | 628 | 249 | 316 | 302 | 894 |
| | *Deschampsia flexuosa* | 246 | 408 | 328 | 70 | 3702 | 3481 | 560 |
| | *Luzula pilosa* | 0 | 112 | 38 | 164 | 41 | 82 | 149 |
| | *Vaccinium myrtillus* | 23 | 12 | 6 | 2 | 0 | 0 | 0 |
| | Herbs and ferns | 54 | 0 | 0 | 0 | 43 | 40 | 182 |
| | *Pleurozium schreberi* | 602 | 460 | 623 | 641 | 675 | 64 | 0 |
| | *Dicranum* spp. | 270 | 257 | 401 | 88 | 63 | 29 | 0 |
| | *Ptilium crista castrensis* | 59 | 8 | 367 | 3 | 0 | 1 | 126 |
| | *Hylocomium splendens* | 107 | 17 | 96 | 261 | 0 | 26 | 12 |
| | Mosses, unidentified | 0 | 0 | 9 | 0 | 41 | 82 | 270 |
| | Sawdust | 0 | 43 | 587 | 8 | 0 | 0 | 0 |
| | **Total** | **4753** | **6793** | **5553** | **3238** | **5073** | **4243** | **2481** |
| F-layer | Branches | 2163 | 2170 | 897 | 1044 | 1559 | 298 | 982 |
| | Spruce needles | 810 | 4383 | 2104 | 2112 | 1065 | 527 | 769 |
| | Bark | 390 | 1212 | 1219 | 1457 | 687 | 797 | 731 |
| | Cones | 2631 | 1281 | 843 | 1766 | 355 | 844 | 637 |
| | Herbs and ferns | 11 | 0 | 0 | 0 | 5 | 13 | 17 |
| | Mosses, unidentified | 1075 | 11118 | 9434 | 8809 | 418 | 1104 | 1542 |
| | Others | 13 | 0 | 0 | 0 | 340 | 23 | 11 |
| | **Total** | **7093** | **20164** | **14497** | **15188** | **4429** | **3606** | **4687** |
| S + F + H layer | Unidentified organic matter | 90834 | 74780 | 57095 | 60864 | 48619 | 60982 | 60494 |

Table 7. *Dry mass of remnant plant biomass fractions on the soil surface and in the S-, F- and H-layers in the old forest at Flakaträsk, and one and four years after clearfelling. a = slash retained, b = slash removed and c = burnt (kg ha$^{-1}$)*

| | Plant remnants | Old forest | One year after clearfelling | | | Four years after clearfelling | | |
|---|---|---|---|---|---|---|---|---|
| | | | a | b | c | a | b | c |
| Soil surface | Branches, >20 mm | 0 | 8563 | 475 | 1121 | 8812 | 100 | 1456 |
| | Branches, 5–20 mm | 35 | 10987 | 894 | 484 | 14163 | 679 | 1559 |
| | Branches, <5 mm | 916 | 6418 | 891 | 162 | 6888 | 529 | 431 |
| | **Total** | **951** | **25968** | **2260** | **1767** | **29863** | **1308** | **3446** |
| S-layer | Branches | 0 | 39 | 546 | 674 | 0 | 129 | 576 |
| | Spruce needles | 1537 | 4302 | 2669 | 75 | 295 | 160 | 93 |
| | Pine needles | 19 | 53 | 2 | 0 | 21 | 0 | 0 |
| | Bark | 24 | 395 | 364 | 13 | 17 | 73 | 106 |
| | Cones | 299 | 899 | 168 | 0 | 378 | 468 | 0 |
| | *Deschampsia flexuosa* | 57 | 6 | 5 | 0 | 718 | 1028 | 163 |
| | *Luzula pilosa* | 1 | 2 | 0 | 0 | 0 | 45 | 0 |
| | *Vaccinium myrtillus* | 213 | 102 | 174 | 0 | 235 | 47 | 12 |
| | Herbs and ferns | 6 | 0 | 0 | 0 | 98 | 110 | 126 |
| | *Pleurozium schreberi* | 525 | 219 | 523 | 0 | 12 | 237 | 6 |
| | *Dicranum* spp. | 412 | 109 | 1113 | 0 | 52 | 16 | 0 |
| | *Ptilium crista castrensis* | 117 | 87 | 187 | 0 | 40 | 0 | 0 |
| | *Hylocomium splendens* | 633 | 702 | 594 | 0 | 125 | 32 | 18 |
| | *Barbilophozia lycopodiodes* | 130 | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Polytrichum commune* | 0 | 114 | 64 | 0 | 0 | 0 | 0 |
| | Mosses, unidentified | 0 | 417 | 134 | 0 | 182 | 85 | 0 |
| | Others | 93 | 6 | 305 | 0 | 0 | 0 | 17 |
| | **Total** | **4066** | **7452** | **6848** | **762** | **2173** | **2430** | **1117** |
| F-layer | Branches | 2420 | 352 | 542 | 0 | 719 | 205 | 47 |
| | Spruce needles | 1727 | 738 | 1097 | 210 | 1959 | 602 | 521 |
| | Bark | 939 | 2673 | 668 | 1028 | 1165 | 1565 | 820 |
| | Cones | 3547 | 905 | 553 | 222 | 402 | 501 | 675 |
| | Herbs and ferns | 0 | 10 | 15 | 1 | 27 | 18 | 2 |
| | Mosses, unidentified | 7972 | 1874 | 2247 | 437 | 4157 | 2511 | 4771 |
| | Others | 139 | 1 | 18 | 0 | 3 | 53 | 586 |
| | **Total** | **16744** | **6553** | **5140** | **1898** | **8432** | **5455** | **7422** |
| S + F + H layer | Unidentified organic matter | 38109 | 43332 | 40882 | 29705 | 35725 | 43686 | 31025 |

Table 8. *Decreases ( − ) or increases ( + ) in dry mass and amounts of plant nutrients during the decomposition of recognisable needles in the mor layer, in per cent of the amounts of needle remnants in the mor layer of the old forests and amounts added with the slash for plots with slash retained on site. a = slash retained, b = slash removed*

| | *Garpenberg* | | | | *Flakaträsk* | | | |
|---|---|---|---|---|---|---|---|---|
| | Year 1 | | Year 4 | | Year 1 | | Year 4 | |
| | a | b | a | b | a | b | a | b |
| Dry mass | −48 | +7 | −94 | −83 | −60 | +15 | −82 | −77 |
| N | −30 | +29 | −89 | −76 | −44 | +29 | −67 | −65 |
| P | −52 | −1 | −93 | −80 | −67 | +19 | −82 | −71 |
| K | −82 | +9 | −98 | −83 | −86 | +9 | −94 | −74 |
| Ca | −61 | −32 | −94 | −91 | −36 | +0 | −75 | −77 |
| Mg | −56 | −7 | −94 | −72 | −64 | +34 | −86 | −67 |
| Mn | −46 | −58 | −92 | −86 | −41 | +8 | −68 | −71 |
| Na | −79 | −24 | −96 | −91 | −87 | −64 | −77 | −83 |
| Zn | +2 | +54 | −82 | −76 | −27 | +15 | −63 | −64 |
| Cu | +22 | +100 | −82 | −52 | −45 | +19 | −50 | −57 |

the number of samples collected was too low in relation to the great spatial variation of these elements.

One year after clearfelling, the amounts of most plant nutrients in needles recognisable in the mor layer from the plots with slash removed were higher than the corresponding amounts in the old forests. This difference is due to the contribution of needles falling off the branches before or during the removal of slash from the plots. Three years later, however, decreases in plant nutrients in the mor layer on plots from which slash had been removed, were only slightly lower than those on plots where the slash had been left on-site after clearfelling (*cf.* Table 8).

Some of the nutrients released during decomposition are taken up by the plants that invade the clearfelled areas. Therefore, when investigating the effect of clearfelling on the amounts of plant nutrients in the soil, the amounts added to the soil surface with slash and those taken up by the vegetation, must also be included.

The amounts of plant nutrients in the mor layer, roots, slash and biomass at clearfelling and one and four years thereafter, are shown in Fig. 6. Most plant nutrients were found in the mor layer, which decreased in mass with time after clearfelling, except on burnt plots and plots with slash removed at Flakaträsk one to four years after clearfelling (Fig. 7). The spatial variation was great, and statistical significance at the 95% level was found only between the mor layers of the old forests and those of plots with slash retained and slash removed at Garpenberg four years after clearfelling, and for the burnt plots at Flakaträsk.

At Garpenberg, the loss of N was *ca.* 600 kg N ha$^{-1}$ one year after clearfelling and burning of the slash. Over the next three years, a further 240 kg ha$^{-1}$ was lost (Fig. 6). On plots with retained slash, the corresponding losses were *ca.* 430 and 410 kg ha$^{-1}$. Thus, during the four years following clearfelling, the amount of N lost was about the same for the burnt plots and the plots with retained slash, *ca.* 840 kg N ha$^{-1}$.

During the first four years after clearfelling at Flakträsk, the loss of N amounted to *ca.* 340 kg N ha$^{-1}$ on burnt plots and 50 kg N ha$^{-1}$ on plots with retained slash. The N-conserving mechanism of the ecosystem at Flakaträsk seems to be well developed, as indicated also by the fact that N reaching the ground with rain was lower inside the forest than outside it, thus reflecting an uptake of N by the canopy (*cf.* Tab. 18).

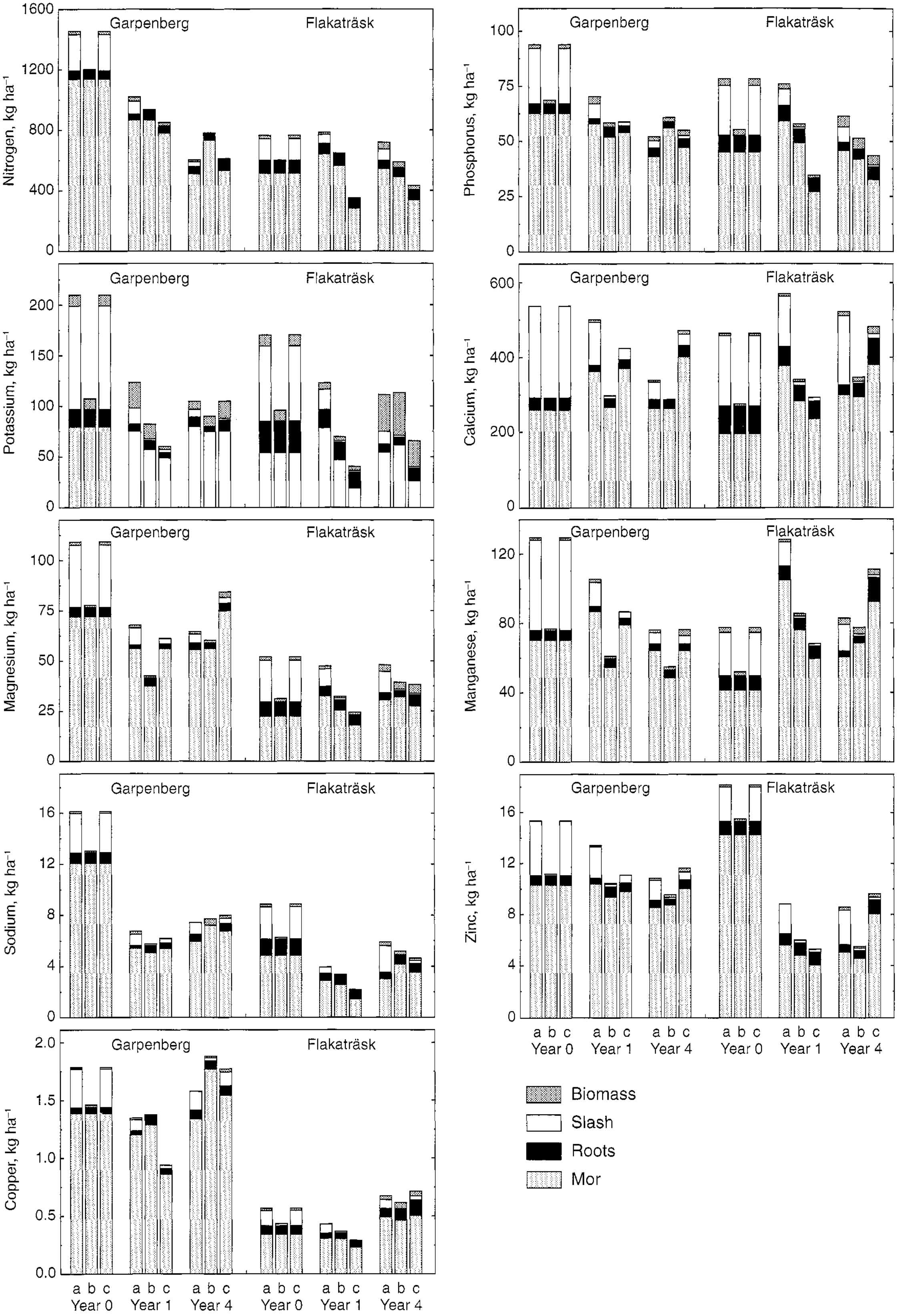
The loss of P during a four-year period following clearfelling was *ca.* 39 and 35 kg P ha$^{-1}$ on burnt plots at Garpenberg and Flakaträsk, and *ca.* 42 and 17 kg P ha$^{-1}$ on plots with retained slash (Fig. 6).

Amounts of K in the mor layer, roots, slash and biomass at clearfelling were 209 and 170 kg K ha$^{-1}$ at Garpenberg and Flakaträsk, respectively. Four years after clearfelling, *ca.* 100 kg K ha$^{-1}$ was lost from plots with retained slash and from burnt plots at Garpenberg. The same amount was lost from burnt plots at Flakaträsk (Fig. 6).

In plots with slash removed, part of the needles fell off the branches while they were being removed from the plots. The dry mass of branches one year after clearfelling was, however, only slightly greater than the biomass of branches in the old forests, indicating that most of the branches from the clearfelling had been removed from the plots. The concentrations of plant nutrients in needles are high; it is therefore not possible to estimate the loss of plant nutrients from the mor layer resulting from clearfelling followed by slash removal. However, it was possible to calculate differences between the amounts of plant nutrients present one year after clearfelling and the amounts present three years later.

The loss of N from biomass, slash, roots and the mor layer between the first and the fourth year after clearfelling was 154 kg N ha$^{-1}$ at Garpenberg and 56 kg N ha$^{-1}$ at Flakaträsk on plots with slash removed (Fig. 6). The amount of P increased by 2.9 kg P ha$^{-1}$ at Garpenberg, but decreased by 6.2 kg P ha$^{-1}$ at Flakaträsk. The amount of K increased by 8 kg K ha$^{-1}$ at Garpenberg and by 44 kg K ha$^{-1}$ at Flakaträsk. During the same period, the amount of K in the aboveground biomass of the field vegetation layer decreased at Garpenberg from *ca.* 14 to 7 kg K ha$^{-1}$, and increased at Flakaträsk from *ca.* 4 to 41 kg K ha$^{-1}$ (Fig. 6). The difference between the two sites was mainly due to very rapid colonisation by *D. flexuosa* during the first year at Garpenberg, followed by a decrease in biomass. Colonisation occurred later at Flakaträsk.

Changes in the amount of organic C, N, P, K, Ca, Mg, Mn, Na, Zn and Cu in the mor layer, roots, slash and biomass of the field-layer vegetation, and mosses after clearfelling, are


Nitrogen, kg ha$^{-1}$
0
400
800
1200
1600
Phosphorus, kg ha$^{-1}$
0
25
50
75
100
Potassium, kg ha$^{-1}$
0
50
100
150
200
Calcium, kg ha$^{-1}$
0
200
400
600
Magnesium, kg ha$^{-1}$
0
25
50
75
100
Manganese, kg ha$^{-1}$
0
40
80
120
Sodium, kg ha$^{-1}$
0
4
8
12
16
Zinc, kg ha$^{-1}$
0
4
8
12
16
Copper, kg ha$^{-1}$
0.0
0.5
1.0
1.5
2.0
Garpenberg
Flakaträsk
a b c
Year 0
a b c
Year 1
a b c
Year 4
a b c
Year 0
a b c
Year 1
a b c
Year 4
Biomass
Slash
Roots
Mor

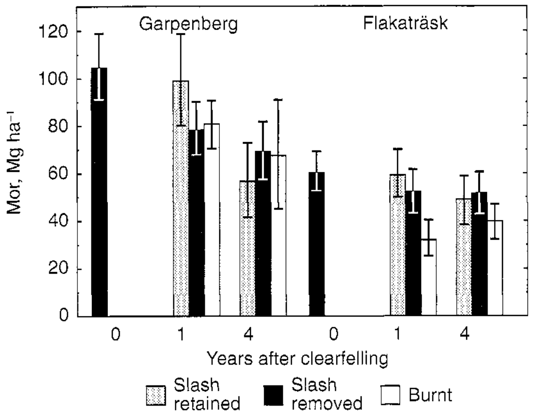


*Fig. 7.* The dry mass of mor layers before, and one and four years after, clearfelling. Means with 95% confidence intervals. The number of samples before clearfelling was 44 at Garpenberg and 31 at Flakaträsk. After clearfelling, the sample number was 20, except for plots with retained slash at Flakaträsk, where the number was 16.

shown in Table 9 as a percentage of the corresponding amounts in the old forest, and amounts added with the slash for plots where slash was retained, and for burnt plots.

Burning resulted in the greatest losses of elements, owing to the formation of gaseous C, N and S oxides, particle transport of nutrients as smoke and the high surface runoff of ash particles and soluble plant nutrients. More than 70% of K was lost from the burnt plots at Garpenberg and Flakaträsk within the first year after clearfelling. The figures for the decrease of plant nutrients during the first year after clearfelling seem to be rather accurate for the burnt plots, as indicated by the statistically significant differences at the 95% level between the mass of mor layers before clearfelling and the mass one year later (*cf.* Fig. 7).

Four years after clearfelling, the dry mass of branches on the burnt plots was higher than that found three years earlier. This was a consequence of there being too few samples relative to the great spatial variation in branches on the plots (*cf.* Tables 6 and 7). At Flakaträsk, a higher mass was also found for mor on burnt plots four years after clearfelling, compared with three years earlier. The calculated losses of plant nutrients one year after clearfelling were therefore higher than the total losses on the burnt plots three years later.

Table 9. *Decreases ( – ) or increases ( + ) in the amounts of elements in biomass, slash, roots and mor layer after clearfelling, in per cent of the corresponding amounts in biomass and mor layer of the old forests and amounts added with the slash for plots with slash retained and burnt plots. a = slash retained, b = slash removed and c = burnt plots*

| | Year 1 | | | Year 4 | | |
|---|---|---|---|---|---|---|
| | a | b | c | a | b | c |
| *Garpenberg* | | | | | | |
| Organic C | −9 | −14 | −40 | −33 | −23 | −36 |
| N | −30 | −21 | −41 | −58 | −34 | −58 |
| P | −26 | −16 | −37 | −45 | −12 | −41 |
| K | −41 | −23 | −71 | −50 | −16 | −50 |
| Ca | −7 | +2 | −21 | −37 | −2 | −12 |
| Mg | −38 | −45 | −44 | −40 | −23 | −23 |
| Mn | −18 | −21 | −33 | −41 | −29 | −40 |
| Na | −58 | −55 | −62 | −54 | −40 | −51 |
| Zn | −13 | −6 | −27 | −29 | −14 | −24 |
| Cu | −25 | −6 | −48 | −12 | +30 | −1 |
| *Flakaträsk* | | | | | | |
| Organic C | −15 | −18 | −62 | −23 | −21 | −53 |
| N | +2 | +6 | −55 | −7 | −3 | −44 |
| P | −3 | −4 | −56 | −22 | −7 | −44 |
| K | −28 | −26 | −76 | −34 | +20 | −61 |
| Ca | +22 | +23 | −37 | +12 | +26 | +3 |
| Mg | −9 | +3 | −52 | −8 | +25 | −26 |
| Mn | +65 | +64 | −12 | +7 | +50 | +43 |
| Na | −54 | −46 | −75 | −33 | −18 | −47 |
| Zn | −51 | −60 | −71 | −52 | −64 | −47 |
| Cu | −24 | −15 | −50 | +19 | +42 | +27 |

For plots with slash retained and slash removed, the amounts of organic C decreased with time after clearfelling, owing to decomposition (Table 9). At Garpenberg, amounts of most plant nutrients also decreased with time. Increases were found only on plots from which slash had been removed, and were limited to Ca one year after clearfelling and Cu three years later. At Flakaträsk, however, the amounts of many plant nutrients on plots with slash removed appeared to be greater after clearfelling than before, probably because needles had fallen from branches when they were removed from the plots. The increases cannot be explained by

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*Fig. 6* (opposite). Amounts of N, P, K, Ca, Mg, Mn, Na, Zn and Cu in biomass, slash, roots (living and dead) and mor layer after slash removal but before burning the clearfelled plots (Year 0) and one and four years thereafter (kg ha$^{-1}$). a = slash retained, b = slash removed and c = burnt plots.

uptake by plants of nutrients from the mineral soil.

Decreases or increases in the amounts of plant nutrients varied considerably between elements. By comparing the percentage decrease in organic C with the percentage decrease in specific plant nutrients, differences among plant nutrients, in terms of their patterns of loss from the mor layer, could be identified (*cf.* Table 9). Thus, all measurements – except those made on plots where slash had been removed four years after clearfelling at Garpenberg and Flakaträsk – indicated that K was lost more easily than organic C. Percentage decreases in Na were higher than those for organic C on all plots and measurement occasions, except at Flakaträsk four years after clearfelling on burnt plots and on slash-free plots. At Garpenberg, percentage decreases were greater for N than for organic C, indicating a loss of N. The percentage decrease for N was much lower at Flakaträsk. One year after clearfelling, there was even an increase in plots with retained slash and slash removed. For Ca, on the other hand, the only occasion on which its percentage decrease was found to be greater than that of organic C, was on plots with retained slash four years after clearfelling at Garpenberg.

### *Amounts of plant-available nutrients in the soil before and after clearfelling*

Clearfelling caused an increase in exchangeable Ca, Mg and Mn on plots with retained slash, and a decrease in exchangeable Na during the first four years (Tables 10, 11). Exchangeable K increased with time at Garpenberg, but decreased at Flakaträsk. A decrease in exchangeable hydrogen ions over time was observed at Flakaträsk, which was expected, since *p*H increased after clearfelling. However, at Garpenberg a decrease was only apparent one year after clearfelling on unburnt plots and three years later on burnt plots.

Amounts of exchangeable Ca, Mg and Mn in mineral soil to 20 cm depth at Garpenberg and Flakaträsk also increased on plots from which slash was removed. Exchangeable K increased at Garpenberg, but decreased at Flakaträsk (Tables 10, 11).

Amounts of ammonium-N on spruce plots increased during the first year after clearfelling in all treatments, but subsequently decreased (Fig. 10). The amounts in the humus layer were significantly greater 10 years after clearfelling compared with 16 years, for all treatments on pine and spruce plots at Garpenberg (Fig. 8). About the same amounts were present in the mineral soil when it was sampled to 20 cm depth. At Flakaträsk, significant differences in ammonium amounts were found between 10 and 16 years after clearfelling on pine and spruce plots with slash removed, and on pine plots with slash burnt. For amounts of nitrate-N in the humus layer, a significant difference was found only between pine plots with slash retained and slash burnt, 10 years after clearfelling at Garpenberg (Fig. 8).

Amounts of plant-available P were smaller at Garpenberg than at Flakaträsk, where amounts increased with time after clearfelling (Fig. 10). The amounts in the humus layer were considerably greater 10 years after clearfelling than after 16 years, for all treatments on pine and spruce plots at Garpenberg (Fig. 8).

The amounts of plant-available K increased at Flakaträsk during the first year after clearfelling. At Garpenberg, however, the amounts decreased during the first four years after clearfelling, in spite of the addition of *ca.* 102 kg K $\text{ha}^{-1}$ to the soil surface in the form of branches and needles, on plots with slash retained at clearfelling (Fig. 10). In pine plots at Garpenberg, the amounts of plant-available K in the humus layer were greater 10 years after clearfelling in plots with slash retained and slash removed, compared with those 16 years after clearfelling (Fig. 8).

No significant difference could be found between pine and spruce plots in amounts of ammonium-N, nitrate-N, P-AL and K-AL in the soil.

### *Concentrations and amounts of inorganic nutrients in field-layer vegetation aboveground*

The aboveground biomass of various plant species in the field-layer vegetation, before and after the clearfelling of two old spruce forests at Garpenberg and Flakaträsk, was described by Nykvist (1997). The biomass figures are summarised by species of herbs, grasses, dwarf shrubs and small deciduous plants (Fig. 9). The biomass of herbs, grasses and dwarf shrubs in-

Table 10. *Amounts of exchangeable cations in dried mineral soil samples from Garpenberg before clearfelling (0) and one year (1) and four years (4) thereafter. a = slash retained, b = slash removed and c = burnt plots. Means ±95% confidence intervals (kg ha$^{-1}$). Number of composite samples (subsamples in brackets) were as follows: Year 0, 2 (4–6); Year 1, 2 (2–3); Year 4a, 8 (2–3); Year 4b, 4 (5) and Year 4c, 4 (4–5)*

| Element | Year | 0–5 cm | 5–10 cm | 10–15 cm | 15–20 cm | **Total** |
|---|---|---|---|---|---|---|
| Ca | 0 | 19 | 8 | 8 | 7 | **42** |
| | 1a | 31 | 17 | 17 | 14 | **79** |
| | 4a | 76 ± 33 | 40 ± 24 | 19 ± 12 | 19 ± 12 | **154** |
| | 4b | 54 ± 20 | 21 ± 12 | 11 ± 5 | 11 ± 5 | **97** |
| | 4c | 97 ± 26 | 31 ± 27 | 25 ± 24 | 20 ± 24 | **173** |
| Mg | 0 | 6.8 | 2.3 | 1.6 | 1.1 | **11.8** |
| | 1a | 5.3 | 3.2 | 2.5 | 2.1 | **13.1** |
| | 4a | 10.8 ± 3.8 | 6.3 ± 3.6 | 3.9 ± 2.7 | 2.4 ± 1.1 | **23.4** |
| | 4b | 10.6 ± 2.7 | 4.9 ± 3.0 | 2.7 ± 2.5 | 2.1 ± 1.5 | **20.3** |
| | 4c | 14.0 ± 10.3 | 7.9 ± 14.0 | 4.5 ± 5.8 | 3.7 ± 5.0 | **30.1** |
| Mn | 0 | 10.5 | 6.0 | 2.6 | 1.1 | **20.2** |
| | 1a | 5.3 | 4.0 | 5.1 | 5.5 | **19.9** |
| | 4a | 23.4 ± 11.5 | 18.1 ± 14.2 | 15.7 ± 11.3 | 12.9 ± 10.1 | **70.1** |
| | 4b | 8.3 ± 5.6 | 5.7 ± 3.4 | 3.4 ± 2.0 | 3.5 ± 3.1 | **20.9** |
| | 4c | 14.6 ± 16.4 | 10.7 ± 12.1 | 10.1 ± 5.3 | 6.8 ± 6.1 | **42.2** |
| K | 0 | 12.9 | 6.8 | 5.9 | 4.8 | **30.4** |
| | 1a | 13.1 | 8.4 | 7.4 | 6.9 | **35.8** |
| | 4a | 17.0 ± 5.4 | 9.3 ± 2.6 | 7.4 ± 2.1 | 7.5 ± 2.2 | **41.2** |
| | 4b | 16.2 ± 1.9 | 8.8 ± 3.4 | 5.6 ± 1.5 | 7.0 ± 6.1 | **37.6** |
| | 4c | 18.3 ± 8.6 | 9.7 ± 6.1 | 7.0 ± 3.3 | 8.7 ± 4.5 | **43.7** |
| Na | 0 | 2.4 | 1.8 | 1.4 | 1.2 | **6.8** |
| | 1a | 1.8 | 1.3 | 1.2 | 1.2 | **5.5** |
| | 4a | 1.4 ± 0.2 | 1.3 ± 0.2 | 1.2 ± 0.2 | 1.2 ± 0.3 | **5.1** |
| | 4b | 1.9 ± 0.8 | 1.5 ± 0.6 | 1.3 ± 0.3 | 1.2 ± 0.2 | **5.9** |
| | 4c | 1.4 ± 0.3 | 1.1 ± 0.6 | 1.1 ± 0.4 | 1.1 ± 0.3 | **4.7** |
| H | 0 | 39 | 28 | 26 | 21 | **114** |
| | 1a | 32 | 26 | 25 | 24 | **107** |
| | 4a | 36 ± 4 | 31 ± 4 | 27 ± 5 | 24 ± 3 | **118** |
| | 4b | 48 ± 6 | 33 ± 8 | 26 ± 6 | 23 ± 3 | **130** |
| | 4c | 34 ± 17 | 27 ± 14 | 23 ± 9 | 22 ± 4 | **107** |

creased after clearfelling at both Garpenberg and Flakaträsk. No deciduous plants were found in the old Garpenberg forest, and only a few shrubs (*Sorbus aucuparia* L.) were present in the Flakaträsk forest. The large biomass of deciduous plants found on burnt plots at Flakaträsk resulted from the coppicing of small trees developing from one large aspen (*Populus tremula* L.) after clearfelling. On plots from which slash had been removed at Flakaträsk, birches (*Betula verrucosa* Ehrh.) accounted for the greatest amount of biomass 16 years after clearfelling.

No significant differences were found in the concentrations of plant nutrients in the biomass, before or after clearfelling, between the treatments on the clearfelled areas, or between pine and spruce. Differences in the amounts of plant nutrients in biomass between treatments and years after clearfelling were therefore rather similar to the biomass differences given in Fig. 9.

### *Amounts of inorganic nutrients in planted trees on the clearfelled plots*

The aboveground biomass of trees before and after clearfelling, and the amounts of plant nutrients present, are shown in Table 12. The largest biomass in the 16-year-old pine and spruce plantations was found on plots from which slash had been removed at Garpenberg and on plots where slash had been retained at Flakaträsk. The result for Garpenberg was unexpected, because large amounts of plant nutrients had been removed with slash from these plots. One explanation could be that, when treatments were randomly assigned to the plots, those in which slash was retained happened to be placed on the highest part of the slope, near the watershed.

Table 11. *Amounts of exchangeable cations in dried mineral soil samples from Flakaträsk before clearfelling (0) and one year (1) and four years (4) thereafter. a = slash retained, b = slash removed and c = burnt plots. Means ±95% confidence limits (kg ha$^{-1}$). Number of composite samples (subsamples in brackets) were as follows: Year 0, 2 (5); Year 1, 2 (1-3); Year 4a, 6 (4–5); Year 4b, 4 (4–5) and Year 4c, 4 (4–5)*

| Element | Year | 0–5 cm | 5–10 cm | 10–15 cm | 15–20 cm | **Total** |
|---|---|---|---|---|---|---|
| Ca | 0 | 33 | 21 | 19 | 12 | **85** |
| | 1a | 51 | 19 | 19 | 12 | **101** |
| | 4a | 67±11 | 29±23 | 27±26 | 21±18 | **144** |
| | 4b | 80±26 | 39±45 | 26±24 | 30±43 | **175** |
| | 4c | 110±42 | 44±16 | 43±63 | 31±39 | **228** |
| Mg | 0 | 7.8 | 5.3 | 4.3 | 2.2 | **19.6** |
| | 1a | 9.9 | 3.6 | 3.6 | 1.9 | **19.0** |
| | 4a | 13.5 ± 9.6 | 8.1 ± 6.1 | 6.2 ± 3.8 | 4.3 ± 3.4 | **32.1** |
| | 4b | 10.2 ± 1.9 | 6.5 ± 3.7 | 4.4 ± 2.2 | 3.5 ± 3.3 | **24.6** |
| | 4c | 12.9 ± 5.9 | 6.1 ± 4.2 | 5.6 ± 7.4 | 5.0 ± 5.1 | **29.6** |
| Mn | 0 | 3.5 | 1.9 | 5.3 | 2.3 | **13** |
| | 1a | 4.6 | 3.9 | 11.2 | 4.5 | **24.2** |
| | 4a | 7.9 ± 6.4 | 4.6 ± 2.9 | 9.6 ± 9.0 | 5.4 ± 5.3 | **27.5** |
| | 4b | 8.1 ± 5.5 | 14.3 ± 30.1 | 12.1 ± 17.5 | 7.3 ± 7.9 | **41.8** |
| | 4c | 6.8 ± 5.0 | 8.0 ± 12.4 | 7.5 ± 8.4 | 6.5 ± 6.5 | **28.8** |
| K | 0 | 20.3 | 9.8 | 8.9 | 10.8 | **49.8** |
| | 1a | 18.9 | 7.0 | 6.3 | 5.0 | **37.2** |
| | 4a | 12.1 ± 3.9 | 9.5 ± 4.2 | 6.5 ± 1.2 | 6.1 ± 0.9 | **34.2** |
| | 4b | 11.5 ± 4.7 | 6.4 ± 4.0 | 4.6 ± 1.6 | 5.1 ± 2.3 | **27.6** |
| | 4c | 17.4 ± 6.2 | 6.5 ± 1.9 | 6.4 ± 2.3 | 7.5 ± 5.5 | **37.8** |
| Na | 0 | 2.3 | 2.0 | 1.7 | 1.6 | **7.6** |
| | 1a | 1.7 | 1.5 | 1.2 | 1.1 | **5.5** |
| | 4a | 1.2 ± 0.2 | 1.2 ± 0.2 | 1.1 ± 0.1 | 1.0 ± 0.2 | **4.5** |
| | 4b | 1.5 ± 0.2 | 1.5 ± 0.2 | 1.2 ± 0.2 | 1.1 ± 0.2 | **5.3** |
| | 4c | 1.2 ± 0.1 | 1.3 ± 0.2 | 1.3 ± 0.3 | 1.3 ± 0.4 | **5.1** |
| H | 0 | 26 | 30 | 35 | 26 | **117** |
| | 1a | 26 | 29 | 32 | 24 | **111** |
| | 4a | 22±7 | 33±18 | 28±5 | 27±3 | **110** |
| | 4b | 22±5 | 29±8 | 27±10 | 28±4 | **106** |
| | 4c | 17±3 | 25±6 | 28±4 | 27±7 | **97** |

Laterally moving water, containing plant nutrients released from the slash after clearfelling, could therefore have improved growth conditions on plots farther downslope.

There were no significant differences in concentrations of plant nutrients in tree biomass between treatments or tree ages. Thus, differences in amounts of plant nutrients in tree biomass between plots generally follow the pattern in the data for tree biomass in Table 12. There were, however, some interesting differences between pine and spruce, owing to higher concentrations of Ca, Mn and Zn in some biomass fractions of spruce. Spruce contained more of these nutrients than pine, in all treatments at Garpenberg and Flakaträsk (*cf.* Table 13).

Trees take up some plant nutrients faster than others. After 16 years, the tree seedlings at Garpenberg had taken up and stored in their aboveground biomass 33–50% of the N found in the aboveground biomass of the old spruce forest (Table 13). Corresponding figures were 34–48% for P, 44–65% for K and 13–40% for Ca. At Flakaträsk, the figures were far lower, owing to slower growth in the colder climate.

### *Amounts of N, P and K in aboveground plant biomass in relation to available amounts in the soil*

Amounts of N in the aboveground biomass of spruce and field-layer vegetation and as ammonium-N in the soil to 20 cm depth, are shown in Fig. 10. Only during the first few years after clearfelling were amounts of ammonium-N higher than the amounts of N in biomass. In the 10- and 16-year-old plantations, most ammonium-N was found on spruce and pine plots on which slash had been retained (Fig. 10). At Flakaträsk, most N was present in the bio-

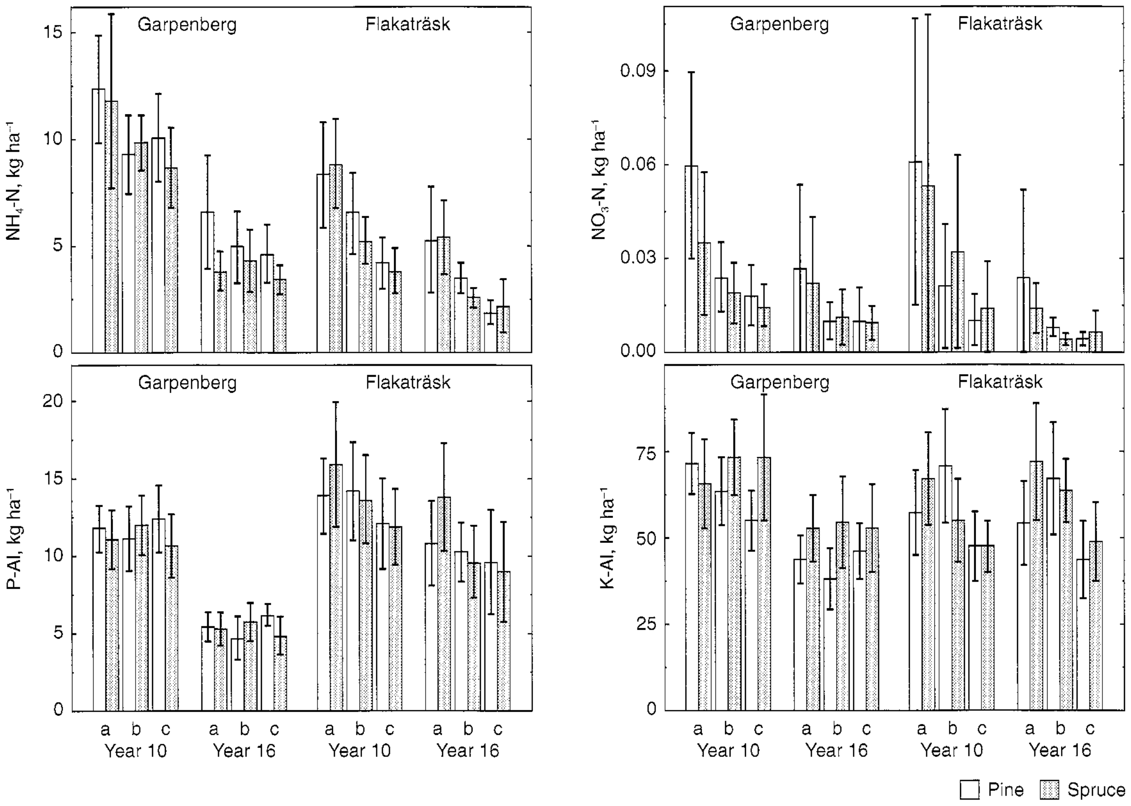

*Fig. 8.* Amounts of ammonium-N, nitrate-N, P-AL and K-AL in the humus layer of pine and spruce plots 10 and 16 years after clearfelling. Means with 95% confidence intervals. a = slash retained, b = slash removed and c = burnt plots (kg $ha^{-1}$). For number of samples, see Table 15.

mass on these plots, suggesting that uptake and storage in biomass did not appear to have decreased amounts of ammonium in the soil.

In the old forests at Flakaträsk, the amounts of plant-available P, determined as P-AL, were about 50% of those in the biomass, whereas at Garpenberg, the proportion was somewhat lower (Fig. 10). After clearfelling, the P-AL content was considerably greater than the P content of biomass. Not until 16 years after clearfelling did the amounts in the biomass at Garpenberg exceed the P-AL content in the soil (Fig. 10). Amounts of P-AL at Flakaträsk, which were greater than those at Garpenberg, increased after clearfelling, and 10 and 16 years after clearfelling they were surprisingly high on plots with retained slash and on burnt plots.

Results obtained with the P-AL method for determining plant-available P indicated that the plants were well supplied with P during the first 10 years at Garpenberg, and for more than 16 years at Flakaträsk. Compared with other methods of determining plant-available P, the P-AL method gave the lowest amounts of P when soil samples from Garpenberg and Flakaträsk were extracted (*cf.* Table 5).

The amounts of plant-available K, determined as K-AL, were higher than K contents in biomass, except in the old forests and 16 years after clearfelling on pine plots at Garpenberg from which slash had been removed (Fig. 10).

### *Effect of clearfelling on soil pH*

Clearfelling caused an increase in *p*H which was statistically significant ($p<0.05$) for many humus samples and most samples of mineral soil from different treatments at Garpenberg and Flakaträsk (Fig. 11). At Garpenberg, the increase had ceased at all investigated soil depths by 16 years after clearfelling, probably owing to the uptake of cations by the tree seedlings.

For most samples, the increase in *p*H was smaller for plots where slash had been removed than for plots where it had been retained, al-

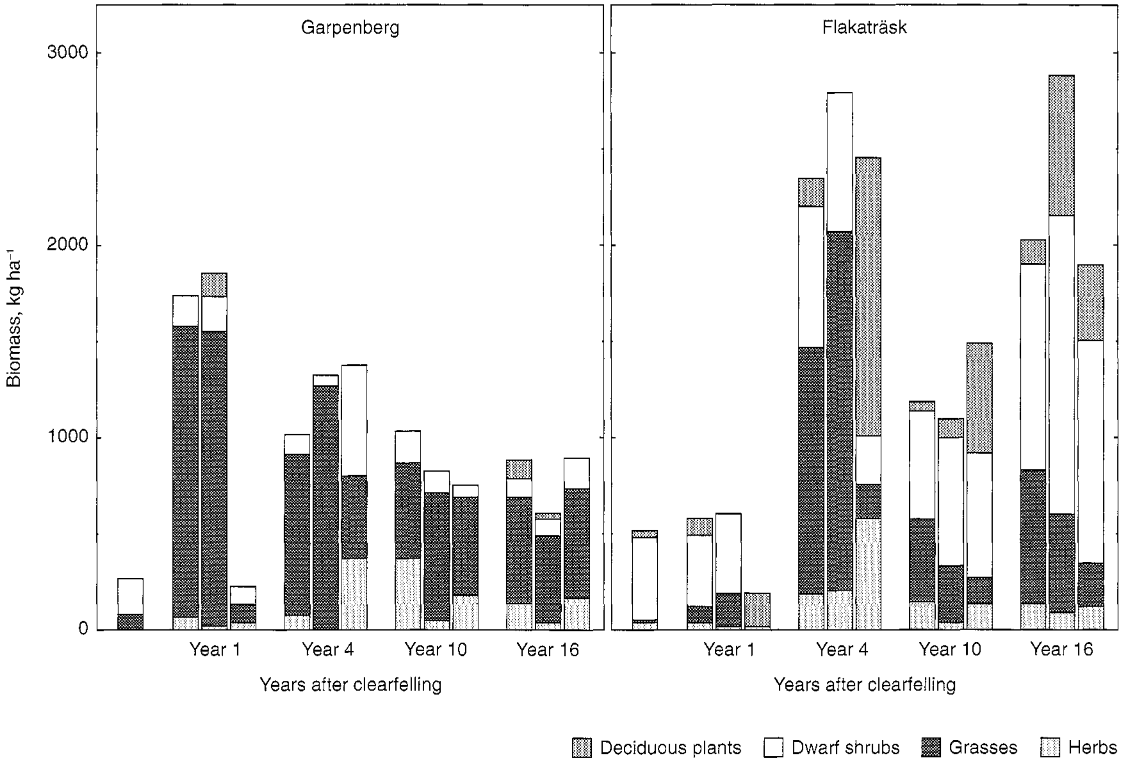

*Fig. 9.* Biomass of aboveground field-layer vegetation before, and 1, 4, 10 and 16 years after, clearfelling. The first column in each series of three for the clearfelled plots refers to plots with slash retained, the second to plots with slash removed and the third to burnt plots. Means of pine and spruce plots, kg $ha^{-1}$ (from Nykvist, 1997).

though the differences were not statistically significant ($p > 0.05$).

There was a positive correlation between the soil *p*H of spruce plantations and that of pine plantations 10 and 16 years after clearfelling at Garpenberg and Flakaträsk (Table 14). However, significant differences ($p < 0.05$) in soil *p*H between pine and spruce 10 and 16 years after clearfelling were found in only a few cases, and the relationship was not consistent. Thus pine plots had a higher *p*H in some comparisons but a lower *p*H in others, compared with spruce plots. The uptake and storage of K, Ca and Mg in the aboveground tree biomass ($kmol_c\ ha^{-1}$), could not explain these differences. The number of samples for the determination of *p*H is given in Table 15.

## Litterfall, throughfall and residence times of organic carbon

### *Annual litterfall and throughfall in the old spruce ecosystems*

Spruce needle litter was the dominating fraction in litterfall in the old spruce ecosystems. Its elemental concentrations were higher in the samples from Garpenberg than in those from Flakaträsk, with the exception of Ca and Zn (Table 16). For comparison, concentrations of the same elements in biomass are also given in Table 16. Concentrations of N, P, K and Mg were higher in biomass than in litter, whereas concentrations of ash, Ca, Mn and Cu were lower. Many investigations have shown that compounds containing N, P, K and Mg are translocated from leaves into other parts of the tree before the leaves are shed. Calcium, however, appears to be enriched in leaves as they grow older.

The amounts of various elements reaching the forest floor as litter can be calculated from the dry mass of the litter fractions and their element concentrations. These amounts were far greater at Garpenberg than at Flakaträsk, owing to the greater litterfall and the higher concentrations of elements in the Garpenberg litter (Table 17).

Chemical elements also reach the forest floor in the form of precipitation and leaf leachate. The amounts of some plant nutrients were deter-

Table 12. *Biomass and amounts of N, P, K, Ca, Mg, Mn and Zn in trees above stump level. SL=slash left, SR=slash removed and B=burnt (kg ha$^{-1}$)*

| | | Biomass | | N | | P | | K | | Ca | | Mg | | Mn | | Zn | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Treat. | Pine | Spruce | Pine | Spruce | Pine | Spruce | Pine | Spruce | Pine | Spruce | Pine | Spruce | Pine | Spruce | Pine | Spruce |
| *Garpenberg* | | | | | | | | | | | | | | | | | |
| 0 | | | 181300 | | 368 | | 34.8 | | 160 | | 456 | | 47.6 | | 87.6 | | 9.13 |
| 1 | SL | 11 | 33 | 0.13 | 0.37 | 0.014 | 0.042 | 0.06 | 0.18 | 0.04 | 0.21 | 0.008 | 0.022 | 0.013 | 0.045 | 0.001 | 0.005 |
| | SR | 17 | 43 | 0.20 | 0.45 | 0.021 | 0.055 | 0.09 | 0.21 | 0.06 | 0.29 | 0.014 | 0.031 | 0.021 | 0.073 | 0.001 | 0.006 |
| | B | 24 | 33 | 0.22 | 0.32 | 0.024 | 0.042 | 0.13 | 0.18 | 0.11 | 0.24 | 0.015 | 0.024 | 0.027 | 0.046 | 0.002 | 0.005 |
| 4 | SL | 112 | 235 | 1.36 | 2.84 | 0.152 | 0.345 | 0.62 | 1.39 | 0.30 | 1.32 | 0.093 | 0.181 | 0.090 | 0.297 | 0.008 | 0.034 |
| | SR | 342 | 334 | 3.81 | 3.70 | 0.423 | 0.476 | 1.76 | 1.79 | 0.93 | 2.06 | 0.290 | 0.256 | 0.278 | 0.481 | 0.023 | 0.043 |
| | B | 402 | 340 | 3.71 | 3.63 | 0.452 | 0.513 | 2.22 | 2.06 | 1.53 | 2.13 | 0.285 | 0.271 | 0.361 | 0.421 | 0.025 | 0.049 |
| 10 | SL | 6964 | 4793 | 48.6 | 30.8 | 5.34 | 3.48 | 23.0 | 18.8 | 14.7 | 23.7 | 3.49 | 2.23 | 3.27 | 5.63 | 0.295 | 0.424 |
| | SR | 6372 | 6855 | 43.5 | 42.1 | 3.91 | 4.23 | 19.8 | 23.8 | 12.0 | 33.5 | 3.12 | 3.64 | 3.46 | 10.09 | 0.270 | 0.598 |
| | B | 14420 | 9315 | 93.1 | 55.9 | 10.4 | 6.02 | 50.3 | 33.4 | 29.7 | 46.6 | 7.52 | 5.25 | 6.21 | 10.80 | 0.642 | 0.829 |
| 16 | SL | 28279 | 31698 | 120 | 149 | 12.0 | 14.1 | 70 | 85 | 57.7 | 124 | 11.0 | 14.5 | 11.7 | 32.3 | 1.00 | 2.22 |
| | SR | 51011 | 34014 | 179 | 183 | 16.7 | 15.0 | 104 | 91 | 82.5 | 180 | 15.0 | 19.3 | 18.0 | 40.6 | 1.05 | 2.17 |
| | B | 33664 | 28254 | 129 | 139 | 14.4 | 14.6 | 75 | 81 | 74.3 | 155 | 13.8 | 11.6 | 14.1 | 39.0 | 0.92 | 2.17 |
| *Flakaträsk* | | | | | | | | | | | | | | | | | |
| 0 | | | 148900 | | 296 | | 35.2 | | 160 | | 375 | | 48.9 | | 50.3 | | 6.61 |
| 1 | SL | 22 | 40 | 0.19 | 0.28 | 0.024 | 0.045 | 0.10 | 0.14 | 0.05 | 0.21 | 0.011 | 0.027 | 0.020 | 0.054 | 0.001 | 0.004 |
| | SR | 28 | 50 | 0.24 | 0.43 | 0.024 | 0.055 | 0.11 | 0.23 | 0.10 | 0.28 | 0.019 | 0.036 | 0.032 | 0.058 | 0.002 | 0.004 |
| | B | 39 | 51 | 0.31 | 0.40 | 0.037 | 0.060 | 0.17 | 0.22 | 0.13 | 0.24 | 0.022 | 0.029 | 0.039 | 0.057 | 0.002 | 0.005 |
| 4 | SL | 331 | 183 | 2.48 | 1.39 | 0.331 | 0.235 | 1.48 | 0.72 | 0.56 | 0.81 | 0.214 | 0.145 | 0.169 | 0.201 | 0.019 | 0.020 |
| | SR | 296 | 226 | 2.17 | 1.92 | 0.267 | 0.288 | 1.14 | 1.09 | 0.69 | 1.07 | 0.211 | 0.180 | 0.181 | 0.231 | 0.017 | 0.022 |
| | B | 380 | 267 | 2.66 | 2.12 | 0.280 | 0.295 | 1.64 | 1.23 | 0.88 | 1.14 | 0.245 | 0.178 | 0.197 | 0.261 | 0.020 | 0.026 |
| 10 | SL | 4573 | 2884 | 31.1 | 19.9 | 3.21 | 2.85 | 13.0 | 11.9 | 11.73 | 11.80 | 2.68 | 1.93 | 1.96 | 3.18 | 0.149 | 0.201 |
| | SR | 2059 | 3256 | 14.2 | 19.6 | 1.64 | 2.96 | 5.9 | 12.3 | 4.56 | 17.28 | 1.42 | 2.38 | 1.12 | 3.27 | 0.087 | 0.311 |
| | B | 2949 | 2173 | 16.5 | 11.2 | 1.98 | 2.11 | 8.2 | 7.7 | 4.96 | 11.40 | 1.68 | 1.31 | 1.26 | 1.38 | 0.134 | 0.165 |
| 16 | SL | 16806 | 11494 | 65 | 49 | 9.55 | 8.99 | 40 | 41 | 33.9 | 45.1 | 7.7 | 5.1 | 7.4 | 12.2 | 0.46 | 0.78 |
| | SR | 11972 | 6180 | 51 | 26 | 6.91 | 4.74 | 30 | 19 | 21.3 | 37.0 | 5.2 | 3.1 | 5.1 | 6.9 | 0.34 | 0.48 |
| | B | 12588 | 7982 | 52 | 34 | 6.79 | 7.10 | 27 | 30 | 32.2 | 42.1 | 5.9 | 3.9 | 4.9 | 7.0 | 0.40 | 0.69 |

Table 13. *Aboveground biomass and amounts of plant nutrients in the biomass of 16-year-old trees in per cent of the amounts in the aboveground biomass of the old forests at Garpenberg and Flakaträsk*

| | *Garpenberg* | | *Flakaträsk* | |
|---|---|---|---|---|
| | Pine | Spruce | Pine | Spruce |
| Biomass | 16–28 | 16–19 | 8–11 | 4–8 |
| N | 33–49 | 38–50 | 17–22 | 9–17 |
| P | 34–48 | 40–43 | 19–27 | 14–26 |
| K | 44–65 | 51–57 | 17–25 | 12–25 |
| Ca | 13–18 | 27–40 | 6–9 | 10–12 |
| Mg | 23–32 | 24–41 | 11–16 | 6–10 |
| Mn | 13–20 | 37–46 | 10–15 | 14–24 |
| Na | 5–8 | 6–7 | 6–9 | 3–5 |
| Zn | 10–11 | 24–24 | 5–7 | 7–12 |
| Cu | 10–13 | 9–13 | 6–9 | 3–9 |

mined by collecting rainfall inside and outside the forest, and analysing the rainwater (Table 18). Interception by the canopy decreased the amount of rain, but the amounts of the investigated plant nutrients increased, with the exception of N compounds at Flakaträsk, where a decrease occurred. Among the plant nutrients, the amount of K in leaf leachate was especially high, being even higher than the supply of this element to the forest floor in litter.

The *p*H of rainwater was far lower at Garpenberg than in the more northerly situation at Flakaträsk, probably owing to the greater amount of acid rain in the southern part of the country (Table 18).

### *Disintegration of litter in the old spruce ecosystems*

To demonstrate the first gradual decomposition of spruce needle litter, 100 needles from various depths in the mor layer were sampled, dried and weighed. The loss of mass was *ca.* 29% at Garpenberg (Fig. 12). Needles at the top of the

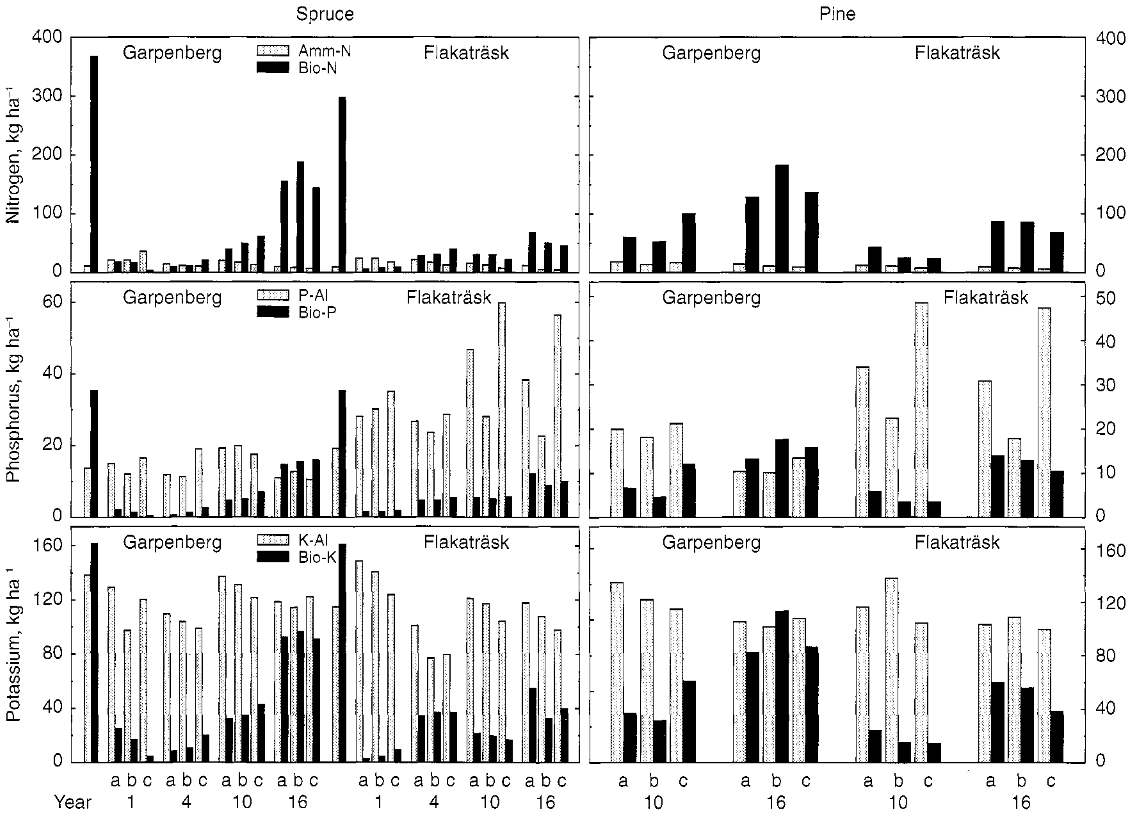

*Fig. 10.* Amounts of N, P and K in aboveground biomass of trees and field-layer vegetation and as ammonium-nitrogen, P-AL and K-AL in humus and mineral soil to 20 cm depth. One and four years after clearfelling, the figures for plant-available nutrients are based on 50 × 50 m plots with pine and spruce, whereas 10 and 16 years after clearfelling they are based on spruce and pine plots 25 × 50 m. a = slash retained, b = slash removed and c = burnt plots (kg $ha^{-1}$). Note the small difference in the scale maximum for P between pine and spruce.

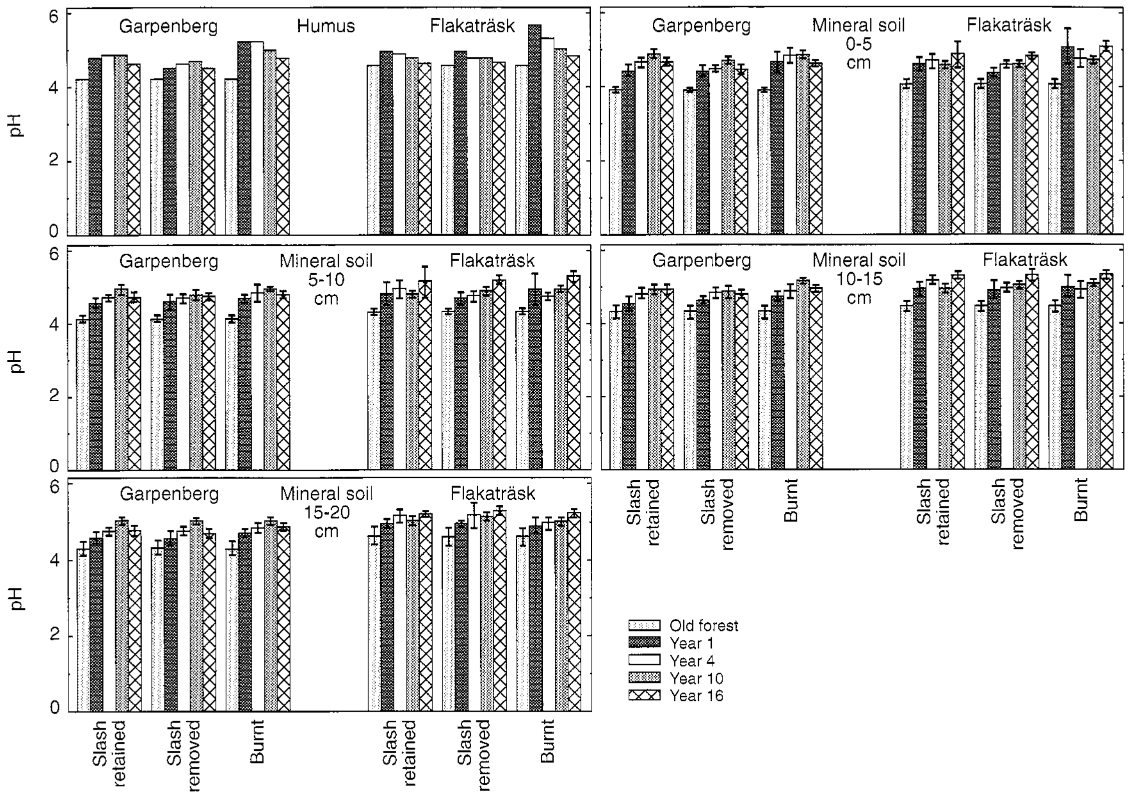

*Fig. 11.* The *p*H of humus, 0–5 cm, 5–10 cm, 10–15 cm and 15–20 cm soil layer before clearfelling and 1, 4, 10 and 16 years thereafter, for the differently treated spruce plots. Numbers of samples are shown in Table 15.

Table 14. *Linear regression relationships and coefficients of determination ($r^2$) for soil pH-values of spruce plantations (y), plotted against those of pine plantations (x), 10 and 16 years after clearfelling at Garpenberg and Flakaträsk*

| Soil depth | Equation | $r^2$ |
|---|---|---|
| Humus | $y = 0.6358x + 1.6685$ | 0.5224 |
| 0–5 cm | $y = 0.9843x + 0.0407$ | 0.7839 |
| 5–10 cm | $y = 0.6917x + 1.4635$ | 0.6942 |
| 10–15 cm | $y = 0.7462x + 1.2308$ | 0.7011 |
| 15–20 cm | $y = 0.8619x + 0.7132$ | 0.7412 |

Table 15. *Number of samples for determination of pH and amounts of plant-available nutrients in the soil. Number of subsamples in brackets*

| | Humus layer | Mineral soil |
|---|---|---|
| *Old forests* | | |
| Garpenberg | 5–6 (9–11) | 3 (4–6) |
| Flakaträsk | 14 (2–5) | 7 (5) |
| *One year after clearfelling* | | |
| Garpenberg | 19–20 | 4 (3–5) |
| Flakaträsk | 16–19 | 4 (5) |
| *Four years after clearfelling* | | |
| Garpenberg | 14–20 | 4 (4–5) |
| Flakaträsk | 8–13 | 4 (4–5) |
| *10 & 16 years after clearfelling* | | |
| Garpenberg | 10 (15–18) | 28–35 |
| Flakaträsk | 10 (15–18) | 27–36 |

S-layer at Flakaträsk were lying on the surface, indicating that they were newly shed. Needles from the bottom of the F-layer at Flakaträsk weighed about 50% less than these needles, mainly as a result of the decomposition of the needle interior.

The number of years required for litter to lose its structure to the extent that it was no longer recognisable to the naked eye, was obtained by calculating the quotient between the amount of recognisable litter remnants in the humus layer and the corresponding amount in litterfall (Table 19). It took longer for needle litter to lose its structure at Flakaträsk (4.1 years) than at Garpenberg (1.7 years), probably owing to the lower organism activity in the colder climate at Flakaträsk. Branches, bark and cones took longer to disintegrate than needles, although

Table 16. *Amounts of spruce needle litter and its concentration of some elements. Mean values for four (Garpenberg) and five (Flakaträsk) years, with least significant differences at the 95% level. For comparison, the corresponding values for biomass are given*

| | *Garpenberg* | | *Flakaträsk* | |
|---|---|---|---|---|
| | Biomass | Litter | Biomass | Litter |
| Dry mass kg ha$^{-1}$ | 14930 | 1942±1303 | 9370 | 792±296 |
| Ash, % | 4.5±0.3 | 5.9 | 4.3±0.4 | 5.2±0.6 |
| N% | 1.02±0.03 | 0.85±0.21 | 0.84±0.03 | 0.60±0.06 |
| P% | 0.104±0.006 | 0.080±0.028 | 0.126±0.009 | 0.066±0.005 |
| K% | 0.46±0.05 | 0.29±0.05 | 0.40±0.02 | 0.14±0.01 |
| Ca% | 0.63±0.06 | 0.76±0.05 | 0.78±0.10 | 1.14±0.05 |
| Mg% | 0.117±0.011 | 0.090±0.008 | 0.113±0.016 | 0.068±0.006 |
| Mn% | 0.18±0.02 | 0.25 | 0.14±0.01 | 0.16±0.02 |
| Al% | | 0.018 | | 0.016±0.003 |
| Fe% | | 0.019 | | 0.009±0.005 |
| Na, ppm | 90±20 | 110±30 | 80±10 | 100±10 |
| Zn, ppm | 70±10 | 80 | 60±10 | 110±30 |
| Cu, ppm | 3.4±0.6 | 7.0 | 2.2±0.4 | 6.0±2.0 |

Table 17. *Annual litterfall and its content of some elements in (kg ha$^{-1}$ yr$^{-1}$) for the old spruce forests at Garpenberg (G) and Flakaträsk (F). Mean values for four (Garpenberg) and five years (Flakaträsk), with least significant differences at the 95% level*

| | Site | Needle litter | Branches | Bark | Cones | Others | Total |
|---|---|---|---|---|---|---|---|
| Dry mass | G | 1942±1303 | 644±710 | 104±93 | 640±420 | 186±163 | 3516±2146 |
| | F | 792±296 | 285±134 | 75±30 | 179±285 | 135±116 | 1466±410 |
| Ash | G | 114 | 11 | 4 | 6 | 8 | 143 |
| | F | 41±18 | 5 | 2 | 14 | 5 | 67 |
| C | G | 864±1102 | 300 | 51 | 286 | 76 | 1577 |
| | F | 356±133 | 128 | 34 | 81 | 61 | 660 |
| N | G | 16.4±11.8 | 5.3 | 1.1 | 2.5 | 2.1 | 27.4 |
| | F | 4.7±1.5 | 1.9 | 0.7 | 0.9 | 1.3 | 9.5 |
| P | G | 1.55±1.20 | 0.41 | 0.11 | 0.27 | 0.22 | 2.56 |
| | F | 0.52±0.18 | 0.16 | 0.08 | 0.07 | 0.16 | 0.99 |
| K | G | 5.53±3.60 | 0.74 | 0.20 | 2.32 | 0.56 | 9.35 |
| | F | 1.09±0.34 | 0.24 | 0.17 | 0.38 | 0.41 | 2.29 |
| Ca | G | 14.80±9.88 | 2.11 | 0.42 | 1.80 | 0.79 | 19.92 |
| | F | 9.09±3.59 | 1.16 | 0.36 | 1.00 | 1.09 | 12.70 |
| Mg | G | 1.74±1.21 | 0.22 | 0.06 | 0.35 | 0.29 | 2.66 |
| | F | 0.54±0.22 | 0.08 | 0.03 | 0.11 | 0.29 | 1.05 |
| Mn | G | 4.89 | 0.20 | 0.03 | 0.04 | 0.19 | 5.35 |
| | F | 1.27±0.61 | 0.10 | 0.03 | 0.02 | 0.17 | 1.59 |
| Na | G | 0.20±0.13 | 0.03 | 0.01 | 0.01 | 0.01 | 0.26 |
| | F | 0.08±0.03 | 0.02 | 0.01 | 0.01 | 0.01 | 0.13 |
| Zn | G | 0.16 | 0.06 | 0.02 | 0.02 | 0.03 | 0.29 |
| | F | 0.08±0.04 | 0.03 | 0.01 | 0.01 | 0.03 | 0.16 |
| Cu | G | 0.014 | 0.007 | 0.002 | 0.003 | 0.003 | 0.029 |
| | F | 0.005 | 0.002 | 0.001 | 0.001 | 0.001 | 0.010 |
| Al | G | 0.36 | 0.11 | 0.10 | 0.04 | 0.09 | 0.70 |
| | F | 0.13±0.07 | 0.09 | 0.05 | 0.01 | 0.04 | 0.32 |
| Fe | G | 0.38 | 0.44 | 0.27 | 0.05 | 0.37 | 1.51 |
| | F | 0.08±0.06 | 0.09 | 0.04 | 0.01 | 0.04 | 0.26 |

these figures are less accurate because of the great year-to-year variation in these fractions.

Losses of certain plant nutrients during litter decomposition were estimated by calculating the quotient between the amount of nutrients in recognisable litter remnants and those in fresh

Table 18. *Amount of rainfall and certain plant nutrients in rainwater collected during the growing season beneath the trees in the forest and on clearfelled areas. Mean values for four years, with least significant differences at the 95% level*

| | Forest | | Clearfelled area | | (Forest minus Clearfelled area) | |
|---|---|---|---|---|---|---|
| | *Garpenberg* | *Flakaträsk* | *Garpenberg* | *Flakaträsk* | *Garpenberg* | *Flakaträsk* |
| Rainfall mm | 300±54 | 270±95 | 483±72 | 332±43 | −183 | −62 |
| Ash, kg ha$^{-1}$ | 107±27 | 55±37 | 40±14 | 28±21 | 67 | 27 |
| Ignition loss, kg ha$^{-1}$ | 479±980 | 106±91 | 62±40 | 36±10 | 417 | 70 |
| $NH_4$-N, kg ha$^{-1}$ | 2.2±2.2 | 0.7 | 1.2±2.1 | 1.4 | 1.0 | −0.7 |
| $NO_3$-N, kg ha$^{-1}$ | 1.0±2.2 | 0.2 | 0.6±0.5 | 0.35 | 0.43 | −0.15 |
| N-tot, kg ha$^{-1}$ | 5.9 | 2.0 | 2.9 | 3.3 | 3.0 | −1.3 |
| P-tot, kg ha$^{-1}$ | 0.7±1.3 | 0.2±0.1 | 0.2±0.1 | 0.1±0.1 | 0.48 | 0.03 |
| K-tot, kg ha$^{-1}$ | 15.7±1.5 | 6.1±3.1 | 2.9±1.3 | 1.6±0.6 | 12.8 | 4.5 |
| Ca-tot, kg ha$^{-1}$ | 12.1±4.9 | 5.4±2.3 | 3.3±1.5 | 2.6±2.1 | 8.8 | 2.8 |
| Mg-tot, kg ha$^{-1}$ | 2.7±0.4 | 1.2±1.3 | 0.6±0.4 | 0.5±0.3 | 2.1 | 0.7 |
| Na-tot, kg ha$^{-1}$ | 7.5±4.9 | 3.7±2.1 | 3.8±2.2 | 2.7±0.7 | 3.7 | 1.0 |
| *p*H | 4.0 | 5.3 | 4.9 | 5.7 | −0.9 | −0.4 |

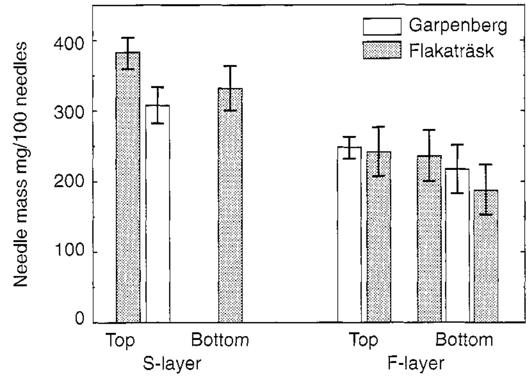

*Fig. 12.* The dry mass of 100 more or less decomposed spruce needles sampled from different depths of the mor layer. Mean ±95% confidence intervals (mg) for 11–15 samples from Garpenberg and 8–14 samples from Flakaträsk.

litter, and comparing it with the corresponding dry mass. With the exception of branches at Flakaträsk, the quotients for K and Mg were lower than those for dry mass. This indicates a loss of those nutrients during the disintegration of litter (Table 20).

*Residence times of organic C in the soil profile of the old spruce forest ecosystem*

On the assumption that a steady state had been attained in the old spruce ecosystems and that annual belowground litter production could be estimated from annual litterfall, the mean residence time of soil organic C was calculated from figures of C pools in soil down to 50 cm depth, and annual litter production. The residence time was 9.5–28 years at Garpenberg and 16.5–42 years at Flakaträsk (Table 21).

Table 19. *Dry mass of recognisable remnants from the plant biomass in the mor layer, litterfall in (kg ha$^{-1}$) and the quotient between them. Means ±95% confidence intervals for litterfall from Tables 4 and 17*

| | Component | *Garpenberg* | *Flakaträsk* |
|---|---|---|---|
| *a* Recognisable litter remnants, kg ha$^{-1}$ | Needles | 3260 | 3283 |
| | Branches | 3738 | 3371 |
| | Bark | 510 | 963 |
| | Cones | 3453 | 3846 |
| *b* Litterfall | Needles | 1942±1303 | 792±296 |
| | Branches | 644±710 | 285±134 |
| | Bark | 104±93 | 75±30 |
| | Cones | 640±420 | 179±285 |
| *a/b* | Needles | 1.7 | 4.1 |
| | Branches | 5.8 | 11.8 |
| | Bark | 4.9 | 12.8 |
| | Cones | 5.4 | 21.5 |

Table 20. *Quotients obtained by dividing dry mass of recognisable litter remnants in the mor layer by the dry mass of the litterfall at Garpenberg and Flakaträsk, and corresponding values for plant nutrients. From Tables 4 and 17*

| | Needles | | Branches | | Bark | | Cones | |
|---|---|---|---|---|---|---|---|---|
| | *Garpenberg* | *Flakaträsk* | *Garpenberg* | *Flakaträsk* | *Garpenberg* | *Flakaträsk* | *Garpenberg* | *Flakaträsk* |
| Dry mass | 1.7 | 4.1 | 5.8 | 11.8 | 4.9 | 12.8 | 5.4 | 21.5 |
| C | 1.9 | 4.4 | 6.5 | 12.8 | 5.0 | 12.2 | 6.0 | 20.7 |
| N | 2.4 | 7.5 | 6.4 | 17.2 | 4.5 | 12.1 | 13.4 | 38.1 |
| P | 1.9 | 5.9 | 6.0 | 19.3 | 3.2 | 8.6 | 7.3 | 37.7 |
| K | 0.5 | 3.0 | 3.2 | 18.5 | 1.8 | 4.2 | 0.9 | 7.3 |
| Ca | 1.7 | 4.3 | 5.1 | 13.5 | 3.9 | 8.3 | 6.0 | 16.2 |
| Mg | 0.8 | 2.9 | 5.6 | 16.8 | 3.8 | 7.3 | 3.9 | 12.4 |
| Mn | 1.0 | 5.3 | 11.6 | 41.9 | 10.0 | 27.3 | 37.3 | 125.0 |
| Na | 1.5 | 5.5 | 8.7 | 13.3 | 3.0 | 6.1 | 22.8 | 29.9 |
| Zn | 2.0 | 3.6 | 5.0 | 10.6 | 3.5 | 7.1 | 14.6 | 22.8 |
| Cu | 2.1 | 4.3 | 4.5 | 15.0 | 3.4 | 6.6 | 8.5 | 16.6 |

*Effect of clearfelling on amounts of organic C*

The amounts of organic C in the mor layer, roots, slash and biomass before clearfelling and one and four years thereafter, are shown in Fig. 13. The amount of organic matter was measured as organic C, because it was difficult completely to separate the unidentified organic matter from mineral soil.

The loss of organic C four years after burning of the slash was *ca.* 20 Mg C ha$^{-1}$ at Garpenberg and 28 Mg C ha$^{-1}$ at Flakaträsk. On plots with retained slash, the amount of organic C had decreased after four years by *ca.* 18 Mg C ha$^{-1}$ at Garpenberg and by 13 Mg C ha$^{-1}$ at Flakaträsk. On plots from which slash had been removed, corresponding to *ca.* 20 Mg C ha$^{-1}$ at Garpenberg and 15 Mg C ha$^{-1}$ at Flakaträsk, the loss four years after clearfelling was *ca.* 8 Mg C ha$^{-1}$ at both Garpenberg and Flakaträsk.

# Discussion

## The old forest

*Particle size distribution*

Mineral soil was sampled between boulders and large stones. The importance of taking boulders and stones into consideration when amounts of plant nutrients are calculated on an areal basis is illustrated by the following example: The estimated amount of total N in mineral soil to 50 cm depth was 2731 kg ha$^{-1}$ at Garpenberg, when boulders and large stones were included in the total soil volume, whereas it was 3213 kg ha$^{-1}$ when based on the volume of sampled soil calculated per hectare to 50 cm depth. Corresponding figures for Flakaträsk were 1629 and 1771 kg ha$^{-1}$, respectively. In the present investigation, all amounts were calculated on the basis of the total volume per hectare, including boulders and stones.

Compared with the amounts of fine soil (<2 mm) in a spruce ecosystem with a sandy till soil at Farabol in S Sweden (Andersson, Bergholm, Hallbäcken, Möller, Pettersson & Popovic, 1995), the amounts at Garpenberg and Flakaträsk were somewhat lower, except for Flakaträsk at 30–40 cm depth, where they were somewhat higher.

*Amounts of plant nutrients in the old spruce forest ecosystems*

Several reviews of the literature concerning plant nutrients in different parts of the above-

Table 21. *Amounts of organic C in the soil, and in annual aboveground and estimated belowground litter production, and the mean residence time of soil organic C, calculated as the quotient between the amount of organic C in the soil and the annual litter production, assuming that a steady state obtains*

| | | *Garpenberg* | *Flakaträsk* |
|---|---|---|---|
| Organic C in the soil, kg $ha^{-1}$ | | | |
| Mor layer | | 30086 | 25869 |
| Mineral soil 0–50 cm depth | | 67852 | 59039 |
| **Total** | *a* | **97938** | **84908** |
| Organic C in annual aboveground litter production, kg $ha^{-1}$ $yr^{-1}$ | | | |
| Trees | | 1577 | 660 |
| Field-layer vegetation[a] | | 55 | 85 |
| Ground-layer vegetation (estimated)[b] | | 260 | 538 |
| **Total** | *b* | **1892** | **1283** |
| Estimated amount of organic C in annual belowground litter production, based on the quotient between belowground litter production and litterfall, kg $ha^{-1}$ $yr^{-1}$. | | | |
| Figures from | *c* | | |
| Raich & Nadelhoffer (1989)[c] | | 2366 | 1254 |
| Nadelhoffer, Aber & Melillo (1985)[d] | | 1632 | 745 |
| Grier, Vogt, Keyes & Edmonds (1981)[e] | | 8438 | 3852 |
| Mean residence time of soil organic C, years, based on figures for belowground litter production divided by litterfall from | *a*/*b*+*c* | | |
| Raich & Nadelhoffer | | 23 | 33.5 |
| Nadelhoffer, Aber & Melillo (1985) | | 28 | 42 |
| Grier, Vogt, Keyes & Edmonds (1981) | | 9.5 | 16.5 |

[a] Mainly leaves of dwarf shrubs. From Nykvist (1997).

[b] The annual production is estimated to be half the biomass of moses. Biomass figures from Nykvist (1997).

[c] Estimation based on a large number of published data on soil respiration and litterfall.

[d] Investigation of annual allocations of N to leaf litter, perennial tissues and fine roots for nine stands in Wisconsin.

[e] Investigation of the biomass distribution and above- and belowground net primary production in a 180-year-old *Abies amabilis* stand in the western Washington Cascade range.

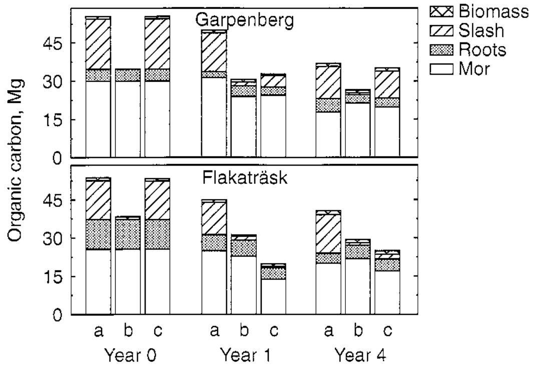

*Fig. 13.* Amounts of organic C in biomass, slash, roots and mor layer after slash removal but before burning the clearfelled plots, and one and four years after clearfelling. a = slash retained, b = slash removed and c = burnt plots (Mg $ha^{-1}$).

ground biomass of forest stands have been published (*e.g.* Ovington, 1962; Rodin & Basilevich, 1967; Weetman & Webber, 1972). In Sweden, the first quantitative studies on plant nutrients in pine and spruce forests were carried out by C.O. Tamm (1963, 1969), and in pine forest on drained peatland by Holmen (1964). A summary of Swedish investigations in coniferous stands made before 1973 shows that the old forests at Garpenberg and Flakaträsk did not differ from other investigated stands more than could be expected with regard to age and site factors (Nykvist, 1974).

The dry mass of the unidentified organic matter in the humus layer was considerably greater at Garpenberg than at Flakaträsk, probably owing to the greater activity of soil animals in the more southerly situation at Garpenberg. The activity of ants and earthworms in the soil of the experimental area at Garpenberg was investigated by Troedsson & Lyford (1973).

Total amounts of organic C in the mor layer were *ca.* 30 Mg C $ha^{-1}$ at Garpenberg and 26 Mg C $ha^{-1}$ at Flakaträsk (Table 4). These figures, when converted to ash-free organic matter, correspond fairly well with the average amounts of 40.2 Mg (standard deviation (SD) ±21.3) of ash-free soil organic matter per hectare in the forest floor, found by Gärdenäs (1998) when summarising results for 15 stands of Norway spruce in Europe.

The total N content in the humus layer was 1144 kg N ha$^{-1}$ at Garpenberg and 529 kg N ha$^{-1}$ at Flakaträsk. From the same area at Garpenberg, Troedsson & Tamm (1969) found 1149 mg total N dm$^{-2}$ (SD ±506), when they investigated small-scale spatial variation on the basis of 20 humus samples. This figure corresponds to 1149 kg N ha$^{-1}$, with a 95% confidence interval of ±237 kg N ha$^{-1}$.

Total amounts of plant nutrients in the humus layer at Garpenberg and Flakaträsk were of about the same magnitude as those reported by Rosén (1982) and Eriksson, Berdén, Rosén & Nilsson (1996) from spruce ecosystems in central Sweden.

The total N content of the humus layer and mineral soil to 50 cm depth was 3875 kg N ha$^{-1}$ at Garpenberg and 2158 kg N ha$^{-1}$ at Flakaträsk. In the investigation by Troedsson & Tamm (1969) from the same area at Garpenberg, the total amount in the humus and mineral soil to 50 cm depth was 4.13 g N dm$^{-2}$ (SD ±0.96). This figure, which corresponds to 4130 ± 449 kg N ha$^{-1}$ (95% confidence interval), is based on samples from a small area (9 × 11 m), whereas in the present investigation, the samples were taken from an area of *ca.* 1 ha, which might explain the difference.

Rosén (1982) investigated the total amounts of N, P, K, Ca, Mg and Na in the mineral soil of spruce stands on till soils about 200 km north of Garpenberg and 260 km south of Flakaträsk. At Rosén's site, the amount of total Ca was about the same, whereas amounts of total K and P were somewhat greater, and the amounts of total Mg lower, compared with figures for Garpenberg calculated for the same depth, *viz.* 20 cm.

Andersson *et al.* (1995) investigated the amounts of exchangeable Ca, Mg, K and Na in soil samples from a spruce ecosystem on a sandy till at Farabol in southern Sweden, by means of the extraction method employed in the present investigation. Amounts of K and Na lay between those for Garpenberg and Flakaträsk, whereas the amount of Ca was only 28 kg ha$^{-1}$ to 40 cm depth, compared with 76 and 143 kg ha$^{-1}$ for Garpenberg and Flakaträsk to 50 cm depth. The amount of exchangeable Mg was *ca.* 10 kg Mg ha$^{-1}$ at Farabol, 14 kg Mg ha$^{-1}$ at Garpenberg and 32 kg Mg ha$^{-1}$ at Flakaträsk.

## Effects of clearfelling, slash removal and prescribed burning

Olsson, Staaf, Lundkvist, Bengtsson & Rosén (1996) compared the amount of N in humus and mineral soil to 20 cm depth before clearfelling of a spruce forest at Tönnersjöheden in southern Sweden, with the corresponding amount 15 years after clearfelling. On trial plots with retained slash, their results indicated that *ca.* 580 kg N ha$^{-1}$ was lost from the humus layer between the measurement dates. The corresponding figure for a spruce ecosystem at Lövliden, Vindeln, about 60 km ENE of Flakaträsk in northern Sweden, was *ca.* 200 kg N ha$^{-1}$. On plots with retained slash at Garpenberg, the loss of N from the humus layer and slash remaining on the soil surface was *ca.* 840 kg N ha$^{-1}$ four years after clearfelling. The corresponding figure for Flakaträsk was *ca.* 70 kg N ha$^{-1}$. In whole-tree harvesting, about 480 kg N ha$^{-1}$ was lost at Tönnersjöheden and about 260 kg N ha$^{-1}$ was lost at Vindeln. According to calculations which assumed that all needles had been removed from the plots, the loss from the humus layer four years after clearfelling was 408 kg N ha$^{-1}$ at Garpenberg and 20 kg N ha$^{-1}$ at Flakaträsk.

Nitrogen losses following whole-tree harvesting of three northern hardwood forest stands of low, medium and high site quality in Michigan, USA, were investigated by Mroz, Jurgensen & Frederick (1985). Losses of N from the forest floor in the first 1.5 years after harvesting were 87 kg N ha$^{-1}$ on the low-quality site, 424 kg N ha$^{-1}$ on the medium-quality site and 846 kg N ha$^{-1}$ on the high-quality site. The total losses of N from the forest floor and from the mineral soil to 1 m depth were 1342, 1287 and 1330 kg N ha$^{-1}$, respectively.

Mroz *et al.* (1985) suggested that the sandy soil, and the mixing of the forest floor with the surface mineral soil by tree skidding, might explain the comparatively high figures. In the Swedish investigations, the experiments were carried out on till soils, which are generally subject to less leaching of plant nutrients than are sandy soils.

Using ceramic cup lysimeters installed at 50 cm depth, Berdén, Nilsson & Nyman (1997) investigated the leaching of different ions before and after clearfelling of unfertilised and fertilised spruce stands at Stråsan, about 50 km N of Garpenberg. During the first five years after clearfelling of the unfertilised plots at Stråsan, the leaching losses were *ca.* 1 kg N ($NO_3$-N and $NH_4$-N), 8 kg K, 30 kg Ca, 10 kg Mg, 0.5 kg Mn and 21 kg Na $ha^{-1}$. The leaching losses of $NO_3$-N and $NH_4$-N were *ca.* 0.1% of the N losses from humus and slash minus uptake by plants during the first four years after clearfelling plots with retained slash at Garpenberg, and *ca.* 2% compared with losses at Flakaträsk. Corresponding figures for K were *ca.* 8 and 13%. At Garpenberg, the corresponding figures were *ca.* 15% for Ca, 22% for Mg and 1% for Mn, whereas leaching losses at Stråsan were greater than nutrient losses at Flakaträsk. For Na, leaching losses at Stråsan were greater than losses of this element at Garpenberg and Flakaträsk.

The investigation of mor layers before and after clearfelling at Garpenberg and Flakaträsk showed that the loss of plant nutrients after clearfelling can be considerable, although statistically significant differences between treatments were difficult to obtain, because too few samples of the mor layer and slash were taken in relation to the great spatial variation. The large losses of plant nutrients and organic C from the humus layer emphasise the importance of rapid regeneration after clearfelling.

Plants also take up nutrients from the mineral soil. However, the very large total amounts of plant nutrients in the mineral soil (Table 5) made it impossible to detect any changes caused by clearfelling, slash removal or burning. Nevertheless, from general knowledge of the solubility and fixation of different plant nutrients in mineral soils, the following conclusions can be drawn:

Most of the N reaching the mineral soil from the humus layer is in the form of nitrate ions, which are rather rapidly leached downwards in the humid climate of Garpenberg and Flakaträsk, and thus lost from the site. Phosphate ions, on the other hand, are precipitated as Al and Fe phosphates in the B-horizon. These compounds can, however, be utilised by plants through the formation of soluble organic ligands with Al and Fe compounds, thus making P compounds more available. Potassium is very easily leached from soil organic matter if it is not taken up by plants. However, it is fixed to clay minerals further down the soil profile. The divalent Ca and Mg ions are adsorbed more strongly to soil colloids compared with the monovalent K ion, and are therefore not as easily leached out from the humus layer. In addition, the output of K, Ca and Mg in stream water from Swedish till soils is much higher than the input from the atmosphere, indicating that the supply of these elements through chemical weathering is comparatively large (Rosén, 1982).

### *Amounts of plant-available nutrients in the mineral soil before and after clearfelling*

Amounts of exchangeable Ca, Mg and Mn to 20 cm depth increased during the first four years after clearfelling on all investigated plots at Garpenberg and Flakaträsk (see Tables 10, 11). Exchangeable K increased at Garpenberg but decreased at Flakaträsk. On sandy soils in Michigan, the amounts of exchangeable Ca, Mg and K in mineral soil to 1 m depth decreased during the first 1.5 years after whole-tree harvesting of northern hardwood forests (Mroz *et al.*, 1985).

Olsson, Bengtsson & Lundkvist (1996) determined the amounts of exchangeable cations in humus and mineral soil samples from four coniferous stands in southern and northern Sweden 15–16 years after clearfelling. At the northern spruce forest site (Lövliden, Vindeln), the amounts of Ca, Mg, K and Na in the mineral soil to 20 cm depth were 15.2 $kmol_c$ $ha^{-1}$ for conventional stem-only harvesting, and 10 $kmol_c$ $ha^{-1}$ for whole-tree harvesting in which all above-stump biomass was removed. At the southern spruce site (Tönnersjöheden), the corresponding figures were 5.2 $kmol_c$ $ha^{-1}$ and 4.5 $kmol_c$ $ha^{-1}$. Statistically significant differences were found in comparatively few cases. At Garpenberg, the amounts of exchangeable Ca, Mg, K and Na in mineral soil to 20 cm depth four years after clearfelling were 10.9 $kmol_c$ $ha^{-1}$ on plots with retained slash, and 7.8 $kmol_c$ $ha^{-1}$ on plots from which slash was removed. At Flakaträsk, amounts were smaller on plots with retained slash (11 $kmol_c$ $ha^{-1}$) than on those from which slash was removed (11.7 $kmol_c$ $ha^{-1}$).

Staaf & Olsson (1994) investigated the effects of slash removal on soil-water chemistry in a clearfelling at Tönnersjöheden in SW Sweden. When slash was left after clearfelling and evenly spread on the ground, there was an initial flush of ammonium, nitrate and K ions through the topsoil to 30 cm depth. For K, this phase lasted for about one year, but there was a strong second peak during the third year. The loss was estimated to be *ca.* 70 kg K $ha^{-1}$ over a four-year period (Olsson, Bengtsson & Lundkvist, 1996). The loss of plant-available K (K-AL) from humus and mineral soil to 20 cm depth on plots where slash had been retained, was 29 kg K $ha^{-1}$ at Garpenberg and 13 kg K $ha^{-1}$ at Flakaträsk over a four-year period (Fig. 10).

Hendrickson, Chatarpaul & Burgess (1989) noted that leaching of ammonium and nitrate was higher from areas with retained slash than from areas where slash was removed during the second year after clearfelling of a northern mixed forest in Canada; but the opposite was found for K, Ca and Mg.

### *Concentrations and amounts of inorganic nutrients in planted trees on the clearfelled plots*

Concentrations of Ca, Mn and Zn in the biomass of needles, stem bark and branches (diameter classes 5–10 and 10–20 cm) were statistically higher for spruce plants compared with pine plants at Garpenberg and Flakaträsk. Alriksson & Eriksson (1998) found that concentrations of Ca in foliage, branches, stems and litter plus the soil organic horizon, were significantly higher in 27-year-old stands of Norway spruce than in Scots pine of similar age in a field experiment about 100 km ESE of Flakaträsk. The trees were planted on former farmland, with an average clay content of 7–18% in the A-horizon.

No differences in N concentration between plots where slash had been retained and plots from which it had been removed, were found by Björkroth (1983) in an investigation of 18-year-old spruce plantations at Tönnersjöheden in southern Sweden and at Kulbäcksliden in northern Sweden. Amounts of N were, however, greater in plots where slash had been retained, owing to the greater biomass on these plots. At Kulbäcksliden, about 60 km ENE of Flakaträsk, there was *ca.* 20 kg N $ha^{-1}$ on plots with retained slash and *ca.* 13 kg N $ha^{-1}$ on plots from which slash had been removed. Corresponding figures for 16-year-old spruce plantations at Flakaträsk were 49 and 26 kg N $ha^{-1}$, respectively.

By comparing the amounts of plant nutrients in the biomass of planted trees with those in the biomass of the old forest before clearfelling, the uptake of different plant nutrients could be calculated. After 16 years, the tree plants at Garpenberg had stored in the aboveground biomass 33–50% N, 34–48% P, 44–65% K and 13–40% Ca (*cf.* Table 13).

Crow, Mroz & Gale (1991) measured annual uptake rates of macronutrients 1, 2 and 4 years after whole-tree harvesting of a maple-oak forest in Michigan, USA. Four years after clearfelling, the annual rate of N uptake was 80% of that measured before clearfelling. Corresponding figures were 64% for P, 86% for K, 55% for Ca and 87% for Mg.

In fast-growing plantations of *Acacia mangium* in Sabah, Malaysia, the amount of P in aboveground biomass, calculated in per cent of the corresponding figure for the rainforest before clearfelling, was 32 and 80% in the 1.6-year-old and 3.8-year-old plantations, respectively. Corresponding figures were 35 and 72% for K, 21 and 68% for N and 7 and 24% for Ca (Sim & Nykvist, 1991; Nykvist, Sim & Malmer, 1996). The very rapid accumulation of P, K and N illustrates the fact that growth in even-aged stands is concentrated primarily in leaves and fine roots (Miller, 1995). In the belowground biomass of the 3.8-year-old stand in Sabah, however, the amounts of P, K and N were only 11, 12 and 11% of the corresponding amounts in the old rainforest.

### *Amounts of N, P and K in aboveground plant biomass relative to available amounts in the soil*

Large amounts of plant-available nutrients enter the soil when trees are cut down and plant remains on the soil surface and in the soil decompose. The rapidly growing field-layer vegetation after clearfelling takes up some of these plant nutrients, and has often been cited as an important factor in conserving nutrients, especially K. Compared with the losses from the humus layer, the amount taken up and stored in the aboveground biomass four years after clearfelling in the plots with retained slash at Garpenberg was about 1% for N, *ca.* 3% for P, *ca.* 9% for K and *ca.* 2% for Ca. At Flakaträsk, the corresponding figures were 67% for N, 27% for P and 64% for K. The amount of Ca increased in the humus layer and biomass after clearfelling at Flakaträsk (*cf.* Fig. 6). The difference between Garpenberg and Flakaträsk was mainly due to the slower mineralisation rates in the colder climate at Flakaträsk and differences in the degree of colonisation by grasses and herbs four years after clearfelling. (*cf.* Fig. 9).

In a 40-year-old Scots pine plantation at Norrliden, about 50 km NNE of Flakaträsk, Tamm, Aronsson & Popovic (1995) found *ca.* 70 kg K $ha^{-1}$ in the aboveground biomass of trees and *ca.* 40 kg $ha^{-1}$ of exchangeable K in mineral soil to 20 cm depth. The K content in biomass of pine 16 years after clearfelling at Flakaträsk was *ca.* 40 kg K $ha^{-1}$ on the plot with retained slash (*cf.* Table 12). The amount of exchangeable K was *ca.* 34 kg K $ha^{-1}$ in the mineral soil to 20 cm depth, four years after clearfelling (*cf.* Table 11).

The amount of Ca in the tree biomass of the 16-year-old pine plots where slash had been retained, was 34 kg Ca $ha^{-1}$ at Flakaträsk (*cf.* Table 12), whereas it was *ca.* 80 kg Ca $ha^{-1}$ at Norrliden. Corresponding figures for exchangeable Ca in the mineral soil to 20 cm depth were 144 kg Ca $ha^{-1}$ at Flakaträsk four years after clearfelling (*cf.* Table 11) and *ca.* 110 kg Ca $ha^{-1}$ at Norrliden. For Mg, the corresponding figures for tree biomass were 7.7 kg Mg $ha^{-1}$ at Flakaträsk and *ca.* 18 kg Mg $ha^{-1}$ at Norrliden. For amounts of exchangeable Mg in soil to 20 cm depth, the values were 32 kg Mg $ha^{-1}$ at Flakaträsk and *ca.* 9 kg Mg $ha^{-1}$ at Norrliden.

### *Effect of clearfelling on soil pH*

Clearfelling causes an increase in soil *p*H (Hesselman, 1926). At Garpenberg and Flakaträsk, this increase was smaller for plots where slash had been removed than for plots where it had been retained, although the differences were not statistically significant (*cf.* Fig. 11). In some cases the *p*H-values were even lower on plots where slash had been retained than on plots where it had been removed. This unexpected result could not be explained by more cations having been taken up by tree seedlings, which would have made the soil more acid on plots where slash had been retained. For the 10- and 16-year old plantations of pine and spruce at Garpenberg and Flakaträsk, amounts of K, Ca and Mg in aboveground tree biomass ($kmol_c$ $ha^{-1}$), were higher on plots where slash had been retained in only about half of the cases where the *p*H of these plots was lower than that on plots where slash had been removed.

Studies of soil *p*H on plots where slash was retained or removed at Garpenberg and Flakaträsk were earlier described by Nykvist & Rosén (1985). At four of nine other sites in Sweden investigated 6–21 years after clearfelling, they found that *p*H-values were significantly higher for humus sampled from plots where slash had been retained, than for humus sampled from plots where it had been removed.

On four of these nine plots, soil acidity was investigated 6–9 years after clearfelling by Staaf & Olsson (1991). In the spruce forest sites of southern Sweden (Tönnersjöheden) and northern Sweden (Lövliden, Vindeln), *p*H in the humus layer and mineral soil to 5 cm depth was higher in stands where slash had been retained than in those from which it had been removed. Statistically significant differences were found, however, only for the humus layer at Lövliden. The same sites were investigated 7–8 years later by Olsson, Bengtsson & Lundkvist (1996). Differences in the soil *p*H of humus samples and samples from most depths down to 20 cm in the mineral soil at the northern spruce site Lövliden still existed between plots with slash and those without slash, although the differences were not significant. In the southern spruce ecosystem, differences in *p*H were non-existent or very small.

In most cases, the greatest increases in *p*H after clearfelling were found for samples from burnt areas. The *p*H-values were, however, significantly higher ($p < 0.05$) for only three of 40 investigated burnt plots from different depths and years after clearfelling, compared with paired unburnt plots containing slash. In eight of the 40 plots, *p*H was lower on the burnt plots than on plots with retained slash, although the differences were not significant ($p > 0.05$).

No statistically significant difference in soil *p*H between pine and spruce plots was found at Garpenberg and Flakaträsk. Pine plots had higher *p*H in some comparisons but a lower *p*H in others, compared with spruce plots.

In a field experiment on former farmland near Umeå, about 100 km ESE of Flakaträsk, *p*H in the mor layer was 5.0 in the spruce plots and 4.9 in the pine plots (Alriksson & Eriksson, 1998). At a soil depth of 0–2 cm and 2–5 cm,

$p$H tended to be slightly lower on spruce plots (4.6 and 4.7) than on pine plots (5.0 and 5.1).

Bergholm (1995) calculated potential acidification, based on excess uptake of base cations in pine and spruce stands along three transects across Sweden. The forest stands were 30–50 years old, and had previously been used for monitoring forest yield. He found that 'The release of $H^+$ to the soil due to the excess uptake of cations was higher in spruce ($0.89 \pm 0.35$ kmol$_c$ ha$^{-1}$ yr$^{-1}$) than in pine ($0.22 \pm 0.10$ kmol$_c$ ha$^{-1}$ yr$^{-1}$).' However, in the much younger forest stands at Garpenberg and Flakaträsk, where the even-aged pine and spruce stands were growing adjacent to each other on the same soil type, no consistent statistically significant difference in $p$H of pine and spruce stands was found.

Troedsson (1980), Nilsson, Miller & Miller (1982), Bergholm, Andersson & Ekman (1985) and Bergholm (1995) have stressed the strong influence of the age and biomass of forest stands on the $p$H of forest soils. However, neither biomass nor uptake and storage of K, Ca and Mg in the aboveground biomass in 10- and 16-year-old plantations of pine and spruce at Garpenberg and Flakaträsk, could explain why soil $p$H was, unexpectedly, lower on some plots where slash had been retained than on with plots where it had been removed.

Spatial variation in $p$H of the mor layer from some coniferous stands in northern Sweden has been investigated by Nykvist & Skyllberg (1989). The difference between the highest and lowest $p$H values in a spruce forest near Umeå, northern Sweden, was about 0.6 $p$H-units in a 2 m$^2$ sample plot. The same magnitude of variation was found in a 200 m$^2$ plot in a spruce forest at Kulbäcksliden, about 55 km NW of Umeå and about 60 km E of Flakaträsk. The two spruce stands were comparable in age (80–100 yr), field-layer vegetation, soil type (podzol) and bedrock type (gneiss). The results indicate that the great variation in mor layer $p$H is mainly due to differences between microsites.

## Litterfall, throughfall and residence times of organic C

The total litterfall was *ca.* 3500 kg ha$^{-1}$ at Garpenberg and *ca.* 1500 kg ha$^{-1}$ at Flakaträsk. Litterfall in spruce forests of different ages in south Norway was 1500–3300 kg ha$^{-1}$ (Mork, 1942). Near Stockholm, the litterfall in a spruce forest was 3400 kg ha$^{-1}$ (Lindberg & Norming, 1943). Evidently, the total litterfall at Garpenberg and Flakaträsk did not differ much from that reported in other investigations.

The needle litterfall was *ca.* 1900 kg ha$^{-1}$ yr$^{-1}$ at Garpenberg and *ca.* 800 kg ha$^{-1}$ yr$^{-1}$ at Flakaträsk. These amounts are within the range of what may be expected for sites of these types, considering the age of the trees. In a 60-year-old spruce forest in SE Sweden, needle litterfall was $1752 \pm 398$ kg ha$^{-1}$ yr$^{-1}$ (Johansson, 1995).

Amounts of plant nutrients in rainwater reaching the ground inside and outside the forest are somewhat higher than corresponding figures from other investigations (*e.g.* Rosén, 1982). One reason probably is that the rainwater was collected in bottles standing on the ground, where nutrients can also be leached from shrubs and tall herbs.

### *Spruce litter disintegration in the old spruce ecosystems*

The original structure of the litter is destroyed by a myriad of different organisms in the soil. This structural disintegration occurs very fast in soils where earthworms are abundant, but is much slower in humus layers where earthworms are few, and mites and collembola are more common soil animals.

The cuticule surrounding spruce needles is less decomposable than the more nutritious internal parts which, therefore, are the first to be decomposed by micro-organisms and soil animals. The original shape of the needle is therefore preserved, despite a high degree of decomposition (Grosskopf, 1928).

At Garpenberg and Flakaträsk, as in most other Swedish spruce forests, the litter is mixed with living and dead mosses, forming a separate layer, called the S-layer. In the upper part of the S-layer, the physical conditions are mostly too dry for most soil organisms, compared with conditions further down in the humus layer. A 'decomposition zone' is therefore usually formed between the S-layer and the F-layer, which is often seen as a greyish-white zone rich in hyphae (Oksbjerg, 1957). The various litter types are mostly still recognisable in the S-layer and in the upper part of the F-layer. In addition to the more or less decomposed remnants of the aboveground biomass, the F- and H-layers also contain living and dead roots.

Numerous investigations of litter decomposition, using the litter-bag technique, have been carried out in Sweden. Berg (1986*a*) found that the accumulated mass loss of pine needle litter in bags was about 60% after three years' incubation in the mor layer of a spruce forest at Garpenberg. The pine needle litter was collected at Jädraås, about 60 km N of Garpenberg. Spruce needle litter collected from Jädraås and incubated in a 65–70-year-old spruce forest at Fäxboda, about 90 km east of Garpenberg, showed about the same accumulated mass loss over a three-year period (Berg, 1986*b*).

In an almost 40-year-old spruce plantation at Stråsan, the accumulated mass loss in litter bags was *ca.* 50% after four years (Berg & Tamm, 1991; Fig. 3). After seven years' incubation in litter bags on the forest floor of a 60-year-old spruce forest in SE Sweden, the accumulated mass loss of spruce needle litter was 74%. (Johansson, 1995).

In the Garpenberg and Flakaträsk investigations, where the quotient between the dry mass of recognisable remnants of needle litter in the mor layer and the annual production of needle litter was used as an indicator of litter disintegration, the needles had lost their structure and could no longer be identified with the naked eye after 1.7 years at Garpenberg and after 4.1 years at Flakaträsk (Table 19).

Evidently, great differences exist between the two methods of measuring the disintegration of needle litter in the mor layer. Disadvantages of the litter-bag technique include the ingrowth of small roots, adsorption of organic matter, losses of small particles and the fact that many soil animals cannot contribute to litter disintegration. With the mesh size used in the litter bags, relatively few groups of soil animals had access to the litter, according to Berg (1986*b*). Referring to Persson, Bååth, Clarholm, Lundkvist, Söderström & Sohlenius (1980), he concludes that 'As compared to other systems, the soil fauna is normally sparse in northern coniferous forests and we could thus expect that the decomposition in this type of system is predominantly due to microbial activity'. In the old spruce forest ecosystem at Garpenberg, Troedsson & Lyford (1973) found that small ants, one to two millimetres in length, transported mineral soil particles from the B-horizon up into the mor layer. There were 2–5 concealed ant mounds per square metre, 5–7 cm in diameter and 1–2 cm in height. Small earthworms (*Allolobophora caliginosa, Dendrobaena octaedra* and *Lumbricus rubellus*) also occurred in several places within the experimental area. Thus the activities of ants and earthworms appear to be of importance to the decomposition of the needle litter, at least at Garpenberg.

The disadvantage of the method used at Garpenberg and Flakaträsk is that it is difficult to separate very small particles of the litter in the mor layer, which also could be lost with the litter-bag technique. The identification of small litter fragments is much easier for spruce needle litter than for many leaves, since the decomposition of needle litter starts in the most nutritious, internal part of the needles.

The quotients between the amounts of K and Mg in recognisable litter and those in litterfall was lower than those for dry mass at Garpenberg and Flakaträsk, which indicated a loss of these nutrients during decomposition. It has been shown in many investigations that K, in particular, is rapidly lost from organic matter. In leaching experiments with leaf litter of *Fraxinus excelsior*, more than 80% of the K content of the litter was leached out during one day (Nykvist, 1959). Johansson (1995) found that the K content of spruce needle litter had decreased by about 50% after six months in litter-bags incubated on the forest floor in a spruce forest in SE Sweden. After four years' decomposition in litter bags, less than 25% of the initial contents of K, Ca, Mg and Mn remained in most bags, whereas N and P increased during the same period.

With the exception of bark, the quotients for N were slightly higher than those for dry mass. This outcome could be expected in the light of the results of many experiments showing that the C/N quotient decreases during the decomposition of litter until a critical C/N ratio is reached in the substrate (Waksman, 1932). Berg & Tamm (1991) reported that K and Mg were released during the decomposition of spruce needles in litter-bags used in the Stråsan experiments, while the content of N and P increased.

### *Litter decomposition in the old spruce ecosystems*

Jenny, Gessel & Bingham (1949) estimated the turnover and build-up of dead organic matter in the soil by comparing the ignition loss of annual litterfall with that of forest floor. The idea was, in fact, not new in principle, having already been mentioned in Kostychev's work in 1885, according to Jenny *et al.* (1949).

Olson (1963), working further along these lines, developed mathematical models for 'litter production and decay in idealised evergreen and deciduous forests'. Although litterfall in the old spruce forests of Garpenberg and Flakaträsk was not continuous during the year, it might be of interest to calculate 'the decomposition parameter $k$' according to Olson with figures for Garpenberg and Flakaträsk, using the simplest equation $k = L/x_\infty$, where $L$ is the annual litter production calculated as organic C and $x_\infty$ the amount of organic C in a steady state in the forest floor. For the old forests of Garpenberg and Flakaträsk, Olson's decomposition parameter was 0.05 and 0.03, respectively. These figures were low to very low in Olson's index and about the same as the figures from Jenny *et al.* (1949) for *Pinus ponderosa* and *Pinus contorta* at various elevations above sealevel in the Sierra Nevada and *Abies amabilis* zone ecosystems of the Washington Cascades (Grier *et al.*, 1981).

Instead of estimating Olson's decomposition parameter $k$, Vogt, Grier & Vogt (1986) estimated the residence times for dry matter in the forest floor using the formula $T = H/L$, where $T$ is mean residence time of organic matter in the forest floor (years), $H$ is the mass of the forest floor and $L$ is the mass of annual litterfall. When this formula was used for organic C instead of dry matter, the residence time of aboveground tree litter in the mor layer was about 19 years at Garpenberg and about 39 years at Flakaträsk (*cf.* Table 21). The mean residence times for 'boreal needleleaf evergreen' forests, most of them spruce forests from Karelia in Russia, summarised by Vogt *et al.* (1986), was about 60 years. If the annual litter production of field-layer and ground-layer vegetation was also included, the residence time was about 16 years at Garpenberg and about 20 years at Flakaträsk.

The figures for Garpenberg and Flakaträsk were calculated on the basis of C amounts, which perhaps can explain the lower figures compared with those given by Vogt *et al.* (1986), because it is usually very difficult to avoid mineral soil particles when sampling the forest floor.

Morrison, Foster & Hazlett (1993) estimated the residence time of organic C in the forest floor to be approximately six years for a sugar maple stand in Ontario, Canada. The figure was based on the annual input of organic C, the decay of roots in the forest floor, throughfall and the total mass of the forest floor. The corresponding figure for a Jack pine stand on a sandy outwash soil in northern Ontario was 17 years.

The main reason for the great differences in residence times of organic C in the forest floor is that the activities of burrowing animals vary considerably in the same climatic region, owing to litter type and differences in soil properties, especially *p*H (Darwin, 1840, 1881; Müller, 1978). Litter cannot be considered to be decomposed merely because it has been dragged down into the mineral soil by earthworms, thus disappearing from the forest floor. When discussing the complete turnover of organic matter, it is therefore necessary also to consider the organic matter in the mineral soil (Romell, 1932, 1934, 1935).

### *Residence times of organic C in the soil profile of the old spruce forest ecosystems*

The estimate of the residence time of soil organic carbon, based on the formula $T = H/L$ (where $T$ is the time in years, $H$ the mass of the forest floor and $L$ the annual litter production), used by Vogt *et al.* (1986) for the forest floor, has not, to my knowledge, been used for the whole soil profile. The reason for this probably is that belowground litter production is difficult to measure, owing to the short life span of root hairs and fine roots.

However, studies of C allocation to roots in forest ecosystems in relation to litterfall (Raich & Nadelhoffer, 1989), annual allocation of N to leaf litter, perennial tissues and fine roots (Nadelhoffer, Aber & Melillo, 1985; Nadelhoffer & Raich, 1992), and figures for 'below-ground and aboveground detritus production' (Grier, Vogt, Keyes & Edmonds, 1981) make it possible to estimate belowground litter production when annual litterfall is known. On the basis of these investigations, figures for annual aboveground litter production and figures for C pools in soil down to 50 cm depth in the old spruce ecosystems at Garpenberg and Flakaträsk, the mean residence time of soil organic C was calculated at 9.5–28 years at Garpenberg and 16.5–42 years at Flakaträsk, on the assumption that a steady state had been attained (Table 21).

The figures for the mean residence times of soil organic C at Garpenberg and Flakaträsk are lower than literature values. Using conventional radiocarbon dating, Tamm & Holmen (1967) found that the formal age of soil organic matter from the B-horizon in coniferous forest ecosystems in middle Sweden varied from 330 ± 65 to 465 ± 65 years and from 460 ± 65 to 1260 ± 60 years for samples from the B-horizon in northern Sweden. In a spruce forest at Garpenberg, the formal age was 370 ± 100 years for the B-horizon (Tamm & Östlund, 1960).

Organic matter younger than 150 years cannot be dated by conventional radiocarbon dating. However, the testing of nuclear weapons in the late 1950s and early 1960s increased the $^{14}C$ in the atmosphere; this can now be used for studying the age of younger soil organic matter. Using this method, Harrison & Harkness (1993) found that the estimated mean residence times of soil organic C in a deciduous woodland in England increased from two years for the humus layer to 18, 40, 100, 500 and 600 years for the soil depths 0–5, 5–10, 10–15, 15–25 and 25–50 cm, respectively.

In an old-growth southern beech (*Nothofagus*) forest in New Zealand, Tate, Ross, O'Brien & Kelliher (1993) found that the mean turnover time of organic C in the litter layer was 12 years, while in the upper 23 cm of two soil profiles representing the morphological range in soil development, it was 76 and 207 years. These figures were estimated from the distribution of $^{14}C$ using a 'bomb' radiocarbon model, in combination with other measurements.

Harrison, Post & Richter (1995) made 'bomb' radiocarbon measurements and model predictions for native temperate and grassland soils in South Carolina. They found that a 'mixture of 82% soil C having a 25-year turnover time (active) and 18% soil C having a 4700-year turnover time (passive) produced the best visual fit through the observations'. These figures refer to surface soil. In deep soil, they assumed that only the passive component was present.

The 'bomb' radiocarbon method was also used by Bird, Chivas & Head (1996) to estimate C turnover times for particulate organic C in forest soils from different parts of the world. For the high-latitude soil samples, the residence time for C in the 63–500 µm fraction of the surface soils was 10–50 years. According to the authors, this represented 'a minimum value for the average time required to transfer additional particulate C through the SOC pool'.

The comparatively few publications about residence times of organic C in forest soils are based on simulations, in which most of the models rely on the concept of a small, active pool which has a short turnover time, and one or more pools which are larger and turn over more slowly. Nabuurs & Mohren (1995) used the model CO2FIX to quantify the C-sequestration potential of the forest, forest soil and forest products in ten selected forest types. The input parameters were derived from literature sources. Two of the selected forest types were old Norway spruce stands, one in montane central Europe and the other in the Boreonemoral zone of Russia. For the soil compartments, the model CO2FIX uses a litter residence time, a litter humification factor, and a stable humus residence time. For the central European spruce ecosystem, the litter residence times were 2–3.5 years, and the stable humus residence times were 320–350 years for three site classes. Corresponding figures for the Russian spruce ecosystem were 5–8 and 550–600 years. From the histogram showing the stocks of carbon in each compartment of the ecosystem (Nabuurs & Mohren, 1995), the C pool in stable humus was estimated to be about 85% of the total C pool in the soil from the spruce ecosystem in central Europe, which indicates that the residence time of organic C must be more than 200 years for the whole soil profile.

Most figures of mean residence times of soil organic C found in the literature refer to some compartments within the soil, mainly humus or litter layer and 'stable humus' in mineral soils. However, mean residence times cannot be based on average figures for a few compartments, since the turnover time of total soil organic C is the average over many compartments, with turnover times ranging in a single soil from less than one year to thousands of years. Mean residence time, based on total C pools in the whole soil profile divided by annual inputs of organic C, is therefore a better method of estimating residence times.

The input of organic substances occurs through litter production and output through decomposition and leaching. Needle litter of spruce contained 12.5% of water-soluble substances, which were easily decomposed under aerobic conditions during the first months of decomposition, and were therefore not lost from the topsoil through leaching (Nykvist, 1961, 1963). Edwards & Harris (1977) found that the 'total carbon loss below the rooting zone amounted to 2.9 g $m^{-2}$ $yr^{-1}$ (29 kg $ha^{-1}$ $yr^{-1}$) or less than 0.3% of the total carbon (as $CO_2$) efflux to the atmosphere'. The annual leaching from coniferous forest soils into stream water was 26–46 kg organic C per ha from three catchments on till soils in central Sweden (Rosén, 1982). This loss of organic substances from the soil was 2–5% of the annual aboveground litter production at Garpenberg and Flakaträsk, and has been omitted from the calculation of the residence times of soil organic carbon.

With the exception of belowground litter production, which had to be estimated, the other factors for calculating the mean residence time of soil organic C, *i.e.* the soil C pool and annual aboveground litter production, were what could be expected for spruce ecosystems on till soils in Sweden.

Amounts of organic C in humus and mineral soil to 50 cm depth were 98 Mg C $ha^{-1}$ at Garpenberg and 85 Mg C $ha^{-1}$ at Flakaträsk. Andersson *et al.* (1995) found 83 Mg C $ha^{-1}$ in humus and mineral soil to 40 cm depth in a spruce ecosystem on till soils at Farabol in SE Sweden. The amount of organic C in three spruce ecosystems on till soils in central Sweden was *ca.* 35 Mg C $ha^{-1}$ in humus and in mineral soil to 20 cm depth (Rosén, 1982). Liski & Westman (1995) investigated the amounts of soil organic C to 50 cm depth in 30 mature coniferous forests in southern Finland. For the *Myrtillus* and *Oxalis-Myrtillus* types of forest, which were most similar to the spruce stands at Garpenberg and Flakaträsk, the average amounts of organic C were 65 and 75 Mg C $ha^{-1}$, which was somewhat lower than those for Garpenberg and Flakaträsk. According to Liski and Westman, the figures to 100 cm depth were lower than the mean value of 116 Mg C $ha^{-1}$ used by Post, Emanuel, Zinke & Stangenbauer (1982) for moist boreal forests, in their study of world-wide C reserves.

Liski & Westman (1995) stressed the importance of the C content in soil layers deeper than 50 cm when calculating C balances in forest soils. According to calculations which assume that the percentage changes in the soil C pool at Garpenberg and Flakaträsk were the same as those obtained by Liski & Westman (1995) when the soil depth at the *Myrtillus* forest type increased from 50 cm to 100, 200 and 250 cm, the mean residence time for Garpenberg increased from 23 (Table 21) to 28, 35 and 36 years, respectively. Corresponding figures for Flakaträsk were from 33.5–41, 52 and 53 years.

All figures for soil C pools in the present investigation refer to well-aerated soils. In water-saturated soils containing organic matter, where a lack of oxygen often occurs, the humus layer can reach many metres in thickness. Plants able to grow under such conditions produce litter faster than it can be decomposed, which results in an accumulation of soil organic matter. Accumulation continues until the humus layer has risen so high that it is no longer saturated with water. At this point, atmospheric oxygen speeds up decomposition, and a steady state between litter production and decomposition can be attained.

On forest slopes, areas where the humus layer is thicker than normal can often be found, even though the soil is not water-saturated at that time and does not contain more or less decomposed old logs or large roots. This phenomenon can often be attributed to the water-saturation of the soil in small depressions of the bedrock during certain times of the year, which results in oxygen deficiency. This deficiency can become even more pronounced when water consumption by plants decreases after clearfelling. At Flakaträsk, the slope levelled out slightly on one of the plots. No differences in humus thickness could be seen in the old forest between this area and the surrounding areas. After clearfelling, however, part of the plot had to be excluded, because the increase in soil water resulted in a thicker humus layer and lower survival of the tree seedlings.

### *Effects of clearfelling, slash removal and burning on C pools in the biomass and humus layer*

It is important to emphasise that the decrease in the C pool after clearfelling at Garpenberg and Flakaträsk is not necessarily associated with an increase in $CO_2$-output from the soil, because felling of the trees also results in a decrease in root respiration (Toland & Zak, 1994; Mattson & Swank, 1989; Edwards & Ross-Todd, 1983). Root respiration accounts for approximately half of total soil respiration in forests (Nakane, Tsubota & Yamamoto, 1983; Ewel, Cropper & Gholz, 1987). Because of the great changes in vegetation and soil after clearfelling, the mean residence time of soil organic C cannot be estimated.

The decrease in the C pool after clearfelling at Garpenberg and Flakaträsk is underestimated somewhat, because leaching and decomposition of organic substances in the mineral soil were not investigated. This decrease is, however, expected to be small during the first four years after clearfelling, owing to the usually low decomposition rate of organic matter in mineral soil.

The effects of clearfelling and slash removal on the C pool in the humus layer and mineral soil to 20 cm depth in two Norway spruce and two Scots pine ecosystems were investigated by Olsson, Staaf, Lundkvist, Bengtsson & Rosén (1996) in southern and northern Sweden. The logging residues after conventional stem harvesting were 20.1 Mg C $ha^{-1}$ at the southern spruce site and 17.2 Mg C $ha^{-1}$ at the northern site. These figures accord with the corresponding figures of 19.9 and 15.3 Mg C $ha^{-1}$ for Garpenberg and Flakaträsk. The initial amounts of organic C in the humus layer were *ca.* 31 at the southern spruce site and *ca.* 23 Mg C $ha^{-1}$ at the northern site. The corresponding figures were 34.5 at Garpenberg and 36.4 Mg C $ha^{-1}$ at Flakaträsk.

Over a 15–16-year period after clearfelling, Olsson *et al.* (1996) found that the total C pool in the humus layer where slash was retained had decreased by *ca.* 26% at the southern spruce site and by *ca.* 28% at the northern site. They found no significant difference in the decrease of soil organic C between plots harvested by whole-tree aboveground biomass removal, and plots subjected to conventional stem-harvesting. At the southern spruce site, the decrease was greatest for the conventional stem-harvested plots, whereas at the northern site, the opposite was true. Four years after clearfelling at Garpenberg, the amount of organic C in the humus layer had decreased by *ca.* 33%, and at Flakaträsk by *ca.* 24% in plots where slash was retained.

Most soil organic C is lost during the first years after clearfelling. However, the decomposition rates gradually decrease, and new plants established or planted on the clearfellings cause an increase in litter production. After some time, soil organic C starts to increase.

Covington (1981) studied the changes in forest-floor organic matter in a secondary succession sequence of 14 northern hardwood stands in the USA. During the first 15 years following clearfelling, the forest floor decreased by 30.7 Mg $ha^{-1}$, corresponding to 13.8 Mg C $ha^{-1}$, if $C = 0.45$ SOM. During the next 50 years, the forest floor increased by 28.0 Mg $ha^{-1}$ (= 12.6 Mg C $ha^{-1}$). After about 60 years, the forest-floor organic matter was only slightly lower than that for a 200-year-old stand.

Houghton, Hobbie, Melillo, Moore, Peterson, Shaver & Woodwell (1983) used the following data in the Terrestrial Carbon Model to define C changes in vegetation and soils during harvesting and regrowth of boreal forests:

*(a)* Time required for soil C to reach minimum following harvest, 15 years.

*(b)* Time required for soil C to go from minimum to level of secondary forest, 35 years.

Johnson (1992) reviewed the literature on forest management, giving special attention to effects on soil C. When the results of 13 studies dealing with the C pools in soils before and after clearfelling were compared, an increase was found in several of them after clearfelling. Such an increase is difficult to understand without being aware that in these investigations, the soil samples from the clearfelled areas were compared with those from the uncut forests; thus the supply of slash at clearfelling was not taken into account.

The effects of burning on C pools in the humus layer are very dependent on fire intensity. At Garpenberg, where the fire was less intense than at Flakaträsk, the C pool four years after clearfelling had decreased by 36%, whereas the decrease at Flakaträsk was 52%. The figures given by Johnson (1992), in his literature review of 15 investigations, including both prescribed burning and wildfire, vary considerably, owing to differences in fire intensity and time elapsed since the burn. A literature review on the environmental effects of burns in forest ecosystems, focussed on the Nordic countries, has been made by Ring (1997).

## Conclusions

One lesson learnt from this investigation has been that a very large number of samples is necessary to obtain statistically significant differences in the average amounts of plant nutrients, when investigating different silvicultural treatments on till soils. The main reason for this is the great variation in humus amounts. When sampling the old spruce ecosystems, the number of samples 50 × 50 cm from the humus layer was 53 at Garpenberg and 31 at Flakaträsk. One and four years after clearfelling, the number of humus samples from each plot (50 × 50 m) was ten, *i.e.* 20 from each treatment. In spite of the large area sampled from each plot, the sampling method was not good enough (*cf.* Fig. 7). No effort has therefore been made to describe the 95% confidence levels for the average amounts of plant nutrients in humus from the old ecosystem and for different treatments one and four years after clearfelling.

Great differences were found in humus mass within sample plots of size 50 × 50 cm. The sampling procedure was therefore changed at the samplings 10 and 16 years after clearfelling, to five composite samples, each containing 15–18 subsamples collected at random within the plots. Thus, from each treatment, 20 composite samples (*i.e.* 300–360 subsamples) were taken, half of them from the pine plantations, half from the spruce plantations. However, even with this great number of samples from each plot, statistically significant differences between treatments, sampling years and tree species were found only in a few cases, for amounts of $NH_4$-N, $NO_3$-N, P-AL and K-AL in the humus layer (*cf.* Fig. 8).

## References

Alriksson, A., & Eriksson, H. 1998. Variations in mineral nutrient and C distribution in the soil and vegetation compartments of five temperate tree species in NE Sweden. *Forest Ecology and Management 108,* 261–273.

Andersson, F., Bergholm, J., Hallbäcken, L., Möller, G., Pettersson, F. & Popovic, B. 1995. Farabolförsöket. Försurning, kalkning och kvävegödsling av en sydöstsvensk granskog. *Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Report 70,* 1–136.

Berdén, M., Nilsson, S.I. & Nyman, P. 1997. Ion leaching before and after clear-cutting in a Norway spruce stand. – Effects of long-term application of ammonium nitrate and superphosphate. *Water, Air and Soil Pollution 93,* 1–26.

Berg, B. 1986*a*. The influence of experimental acidification on nutrient release and decomposition rates of needle and roots litter in the forest floor. *Forest Ecology and Management, 15,* 195–213.

Berg, B. 1986*b*. The influence of experimental acidification on needle litter decomposition in a *Picea abies* L. forest. *Scandinavian Journal of Forest Research 1,* 317–322.

Berg, B. & Tamm, C.O. 1991. Decomposition and nutrient dynamics of Norway spruce needle litter in a long-term optimum nutrition experiment. *Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Report 39,* 7–23.

Bergholm, J., Andersson, R. & Ekman, F. 1985. Markkemiska effekter av biologisk försurning i skogsbestånd av olika ålder. *SNV PM 1989,* 1–55. ISSN 0346-7309.

Bergholm, J. 1995. Biological acidification. In: E. Karltun (Ed) Acidification of forest soils on glacial till in Sweden. p. 51–58. *Swedish Environmental Protection Agency Report 4427.*

Bird, M.I., Chivas, A.R. & Head, J. 1996. A latitudinal gradient in carbon turnover times in forest soils. *Nature 381,* 143–146.

Björkroth, G. 1983. Inverkan av hyggesavfall på kvävet och den organiska substansen i några 14–18 år gamla försöksplanteringar med gran. *Sveriges Lantbruksuniversitet, Institutionen för skogsskötsel. Rapport 9,* 1–38.

Covington, W.W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology 62,* 41–48.

Crow, T.R., Mroz, G.D. & Gale, M.R. 1991. Regrowth and nutrient accumulations following whole-tree harvesting of a maple-oak forest. *Canadian Journal of Forest Research 21,* 1305–1315.

Darwin, C. 1840. On the formation of mould. *Transactions of the Geological Society 2, Ser. 5:3.*

Darwin, C. 1881. *The formation of vegetable mould through the action of worms.* J. Murray, London. 1888 Edition.

Edwards, N.T. & Harris, W.F. 1977. Carbon cycling in a mixed deciduous forest floor. *Ecology 58,* 431–437.

Edwards, N.T. & Ross-Todd, B.M. 1983. Soil carbon dynamics in a mixed deciduous forest following clear-cutting with and without residue removal. *Soil Science Society of America Journal 47*, 1014–1021.

Egnér, H., Riehm, H. & Domingo, W.R. 1960. Untersuchungen über die chemische Boden-Analyse als grundlage für die Beurteilung des Nährzustandes der Boden. *Kungl. Lantbrukshögskolans Annaler 26*, 199–215.

Emteryd, O. 1989. Chemical and physical analysis of inorganic nutrients in plant, soil, water and air. *Swedish University of Agricultural Sciences, Department of Forest Site Research, Mimeo 10, Umeå, Sweden.* ISSN 0280-9168.

Eriksson, H.M., Berdén, M., Rosén, K. & Nilsson, S.I. 1996. Nutrient distribution in a Norway spruce stand after long-term application of ammonium nitrate and superphosphate. *Water, Air and Soil Pollution 92*, 451–467.

Ewel, K.C., Cropper, W.P. & Gholz, H.L. 1987. Soil $CO_2$ evolution in Florida slash pine plantations. II. Importance of root respiration. *Canadian Journal of Forest Research 17*, 330–333.

Falck, J. 1973. A sampling method for quantitative determination of plant nutrient content of the forest floor. *Dept. of Silviculture, Royal College of Forestry, Research Notes 1.* Stockholm.

FAO-Unesco 1989. Soil map of the world, revised legend. *Technical Paper 20. ISRIC*, Washington.

Forsslund, K.-H. 1944. Studien über die Tierwelt des nordschwedischen Waldbodens. *Meddelanden från Statens skogsförsöksanstalt 34*, 1–283.

Gärdenäs, A.I. 1998. Soil organic matter in European forest floors in relation to stand characteristics and environmental factors. *Scandinavian Journal of Forest Research 13*, 274–283.

Grier, C.C., Vogt, K.A., Keyes, M.R. & Edmonds, R.L. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research 11*, 155–167.

Grosskopf, W. 1928. Wie verändern sich stofflich und morphologisch die Fichtennadeln bei der Bildung von Auflagehumus in geschlossenen Fichtenreinbeständen? *Tharandter forstliches Jahrbuch 79*, 343–362.

Harrison, A.F. & Harkness D.D. 1993. Potential for estimating carbon fluxes in forest soils using $^{14}C$ techniques. *New Zealand Journal of Forestry Science 23*, 367–379.

Harrison, K.G., Post, W.M. & Richter, D.D. 1995. Soil carbon turnover in a recovering temperate forest. *Global Biogeochemical Cycles 9*, 449–454.

Hendrickson, O.Q., Chatarpaul, L. & Burgess, D. 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. *Canadian Journal of Forest Research 19*, 725–735.

Hesselman, H. 1926. Studier över barrskogens humustäcke, dess egenskaper och beroende av skogsvården. *Meddelanden från Statens skogsförsöksanstalt 22:5*, 169–378. (Swe., Ger. summary).

Holmen, H. 1964. Forest ecological studies on drained peat land in the province of Uppland, Sweden. *Studia Forestalia Suecica 16*, 1–236.

Houghton, R.A., Hobbie, J.E., Melillo, J.M., Moore, B., Peterson, B.J., Shaver, G.R. & Woodwell, G.M. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: A net release of $CO_2$ to the atmosphere. *Ecological Monographs 53*, 235–262.

Jenny, H., Gessel, S.P. & Bingham, F.T. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Science 68*, 419–432.

Johansson, M.-B. 1995. Fallförna- och förnanedbrytningsstudier på kontrollytor. Appendix 3.1 in Andersson, F., Bergholm, J., Hallbäcken, L., Möller, G., Pettersson. F. & Popovic, B. 1995. Farabolförsöket. Försurning, kalkning och kvävegödsling av en sydöstsvensk granskog. p. 129-132. *Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Report 70.*

Johnson, D.W. 1992. Effects of forest management on soil carbon storage. *Water, Air and Soil Pollution 64*, 83–120.

Karlsson, N. 1964. Undersökning av trädgårdsjord. *Statens Lantbrukskemiska Kontrollanstalt. SLK-MI-7*, 1–24.

Lindberg, S. & Norming, H. 1943. Om produktionen av barrförna och dennas sammansättning i ett granbestånd invid Stockholm. *Svenska Skogsvårdsföreningens tidskrift 41*, 353–357.

Liski, J. & Westman, C.J. 1995. Density of organic carbon in soil at coniferous forest sites in southern Finland. *Biogeochemistry 29*, 183–197.

Lyford, W.H. & Troedsson, T. 1973. Fragipan horizons in soils on moraines near Garpenberg, Sweden. *Studia Forestalia Suecica 108*, 1–21.

Mattson, K.G. & Swank, W.T. 1989. Soil and detrital carbon dynamics following forest cutting in the southern Appalachians. *Biology and Fertility of Soils 7*, 247–253.

Miller, H.G. 1995. The influence of stand development on nutrient demand, growth and allocation. *Plant and Soil 168–169*, 225–232.

Mork, E. 1942. Om ströfallet i våre skoger. *Meddelelser fra det norske skogsforsöksvesen 29*, 299–358.

Morrison, I.K., Foster, N.W. & Hazlett, P.W. 1993. Carbon reserves, carbon cycling, and harvesting effects in three mature forest types in Canada. *New Zealand Journal of Forestry Science 23*, 403–412.

Mroz, G.D., Jurgensen, M.F. & Frederick, D.J. 1985. Soil nutrient changes following whole tree harvesting on three northern hardwood sites. *Soil Science Society of America Journal 49*, 1552–1557.

Müller, P.E. 1978. Studier over skovjord som bidrag till skovdyrkningens theori. I. Om bogemuld og bogemor paa sand og ler. *Tidsskrift for Skovbrug 3*, 1–124.

Nabuurs, G.J. and Mohren, G.M.J. 1995. Modelling analysis of potential carbon sequestration in selected forest types. *Canadian Journal of Forest Research 25*, 1157–1172.

Nadelhoffer, K.J., Aber, J.D. & Melillo, J.M. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. *Ecology 66*, 1377–1390.

Nadelhoffer, K.J. & Raich, J.W. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology 73*, 1139–1147.

Nakane, K., Tsubota, H. & Yamamoto, M. 1983. Estimation of root respiration rate in a mature forest ecosystem. *Japanese Journal of Ecology 33*, 397–408.

Nilsson, S., Miller, M.G. & Miller, J.D. 1982. Forest growth as a possible change of soil and water acidification: an examination of the concepts. *Oikos 39*, 40–49.

Nykvist, N. 1959. Leaching and decomposition of litter. I. Experiments on leaf litter of *Fraxinus excelsior*. *Oikos 10:2*, 190–211.

Nykvist, N. 1961. Leaching and decomposition of litter. IV. Experiments on needle litter of *Picea abies*. *Oikos 12*, 264–279.

Nykvist, N. 1963. Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. *Studia Forestalia Suecica 3*, 1–31.

Nykvist, N. 1974. The loss of plant nutrients at whole-tree utilisation. *Royal College of Forestry, Department of Operational Efficiency, Research Notes 76E*, 76–95.

Nykvist, N. 1977. Changes in the amounts of inorganic nutrients in the soil after clear-felling. *Silva Fennica 11:3*, 224–229.

Nykvist, N. 1997. Changes in species occurrence and phytomass after clear-felling, prescribed burning and slash removal in two Swedish spruce forests. *Studia Forestalia Suecica 201*, 1–33.

Nykvist, N. & Rosén, K. 1985. Effect of clear-felling and slash removal on the acidity of Northern coniferous soils. *Forest Ecology and Management 11*, 157–169.

Nykvist, N. & Skyllberg, U. 1989. The spatial variation of pH in the mor layer of some coniferous forest stands in northern Sweden. *Scandinavian Journal of Forest Research 4*, 3–11.

Nykvist, N., Sim, B.L. & Malmer, A. 1996. Effects of tractor logging and burning on biomass production and nutrient accumulation in *Acacia mangium* plantations in Sabah, Malaysia. *Journal of Tropical Forest Science 9*, 161–183.

Oksbjerg, E. 1957. Rodgranens og nogle andre nåletraers jordbundsdannelse på fattig jord. *Det forstlige forsøksvæsen i Danmark XXIII*, 129–263.

Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J. & Rosén, K. 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. *Forest Ecology & Management 82*, 19–32.

Olsson, B.A., Bengtsson, J. & Lundkvist, H. 1996. Effects of different forest harvest intensities on the pools of exchangeable cations in coniferous forest soils. *Forest Ecology & Management 84*, 135–147.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology 44*, 322–331.

Ovington, J.D. 1962. Quantitative ecology and the woodland ecosystem concept. *Advances in Ecological Research 1*, 103–192.

Persson, T., Bååth, E., Clarholm, M., Lundkvist, H., Söderström, B. & Sohlenius, B. 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a Scots pine forest. *Ecological Bulletins 32*, 419–462.

Post, W.M., Emanuel, W.R., Zinke, P.J. & Stangenbauer, A.G. 1982. Soil carbon pools and world life zones. *Nature 298*, 156–159.

Raich J.W. & Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: Global trends. *Ecology 70*, 1346–1354.

Ring, E. 1997. Environmental impact of fires in forest ecosystems – a study of the literature with the focus on Scandinavia. *SkogForsk 2*. 58 pp. (Swe., Eng. summary.)

Rodin, L.E. & Basilevich, N.T. 1967. *Production and mineral cycling in terrestrial vegetation.* (Eng. translation). Oliver & Boyd, Edinburgh & London, 1–276.

Romell, L.G. 1932. Mull and duff as biotic equilibria. *Soil Science 34*, 161–188.

Romell, L.G. 1934. *En biologisk teori för mårbildning och måraktivering.* (Privately published.). Stockholm. 1–29.

Romell, L.G. 1935. Ecological problems of the humus layer in the forest. *Cornell University, Agricultural Experiment Station Memoir 170*, 1–28.

Rosén, K. 1982. Supply, loss and distribution of nutrients in three coniferous forest watersheds in Central Sweden. *Swedish University of Agricultural Sciences. Reports in Forest Ecology and Forest Soils 41*, 1–70.

Sim, B.L. & Nykvist, N. 1991. Impact of forest harvesting and replanting. *Journal of Tropical Forest Science 3*, 251–284.

Staaf, H. & Olsson, B.A. 1991. Acidity in four coniferous forest soils after different harvesting regimes of logging slash. *Scandinavian Journal of Forest Research 6*, 19–29.

Staaf, H. & Olsson, B.A. 1994. Effects of slash removal and stump harvesting on soil water chemistry in a clearcutting in SW Sweden. *Scandinavian Journal of Forest Research 9*, 305–310.

Tamm, C.O. 1963. Uptake of nutrients after fertilization in spruce and pine stands. *Royal College of Forestry, Dept. of Forest Ecology. Research Notes 1*. 1-17. (Swe., Eng. summary).

Tamm, C.O. 1969. Site damages by thinning due to removal of organic matter and plant nutrients. In: Thinning and mechanization *Proceedings IUFRO Meeting, Royal College of Forestry, Stockholm.* 175–179.

Tamm, C.O., Aronsson, A. & Popovic, B. 1995. Nitrogen saturation in a long-term forest experiment with annual additions of nitrogen. *Water, Air and Soil Pollution 85*, 1683–1688.

Tamm, C.O. & Holmen, H. 1967. Some remarks on soil organic matter turn-over in Swedish podzol profiles. *Meddelelser fra det norske skogsforsøksvesen 23*, 67–88.

Tamm, C.O. & Östlund, G. 1960. Radiocarbon dating of soil humus. *Nature 185*, 706–707.

Tate, K.R., Ross, D.J., O'Brian, B.J. & Kelliher, F.M. 1993. Carbon storage and turnover, and respiratory activity, in the litter and soil of an old-growth southern beech (*Nothofagus*) forest. *Soil Biology & Biochemistry 25*, 1601–1612.

Toland, D.E. & Zak, D.R. 1994. Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. *Canadian Journal of Forest Research 24*, 1711–1716.

Troedsson, T. & Tamm, C.O. 1969. Small-scale spatial variation in forest soil properties and its implications for sampling procedures. *Studia Forestalia Suecica 74*, 1–30.

Troedsson, T. & Lyford, W.H. 1973. Biological disturbance and small-scale spatial variations in a forested soil near Garpenberg, Sweden. *Studia Forestalia Suecica 109*, 1–23.

Troedsson, T. 1980. Long-term changes in forest soils. *Annales Agriculturae Fenniae 19*, 81–84.

Vogt, K.A. Grier, C.C. & Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Advances in Ecological Research 15*, 303–377.

Waksman, S.A. 1932. *Principles of soil microbiology*. 2nd edition. Williams & Wilkins, Baltimore. 1–244.

Weetman, G.F. & Webber, B. 1972. The influence of wood harvesting on the nutrient status of two spruce stands. *Canadian Journal of Forest Research 2:3*, 351–369.

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