



Carbon and nitrogen pools in an old-growth, Norway spruce mixed forest in eastern Finland and changes associated with clear-cutting

Leena Finér^{a,*}, Hannu Mannerkoski^b, Sirpa Piirainen^b, Michael Starr^c

^aFaculty of Forestry, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland

^bFinnish Forest Research Institute, Joensuu Research Centre, P.O. Box 68, FIN-80101 Joensuu, Finland

^cThe Finnish Forest Research Institute, Vantaa Research Centre, P.O. Box 18, FIN-01301 Vantaa, Finland

Received 11 January 2001; received in revised form 19 October 2001; accepted 18 December 2001

Abstract

The amount of carbon (C) and nitrogen (N) removed in stems after clear-cutting a forest in eastern Finland is compared with ecosystem pools (above- and below-ground tree and understorey vegetation biomass + organic layer + 0–60 cm mineral soil layer) and fluxes before clear-cutting. The tree stand was an old-growth mixed coniferous forest dominated by Norway spruce. The ecosystem pools of C and N before clear-cutting were 175 536 and 2848 kg ha⁻¹, respectively. Most (62%) of the C was in living vegetation, mainly trees (60%), whereas most of the N pool was in the soil (80%). C and N pools in understorey vegetation were small (<2% of ecosystem pools) and those in dead tree compartments were somewhat greater (C: 8%; N: 4%). The annual net uptake (defined as net accumulation in tree biomass + aboveground litterfall) of C by trees was 2013 kg ha⁻¹ and that of N was 16.1 kg ha⁻¹. The annual return to the forest floor as aboveground litterfall was 958 kg ha⁻¹ of C and 12 kg ha⁻¹ of N, corresponding to 48 and 75% of annual net uptake, respectively. During clear-cutting, some 239 m³ ha⁻¹ of stemwood (overbark) were removed from the site, corresponding to 32% (C) and 3.0% (N) of the pre-harvest ecosystem pools; branches and foliage were left on site. The pool of C in living vegetation was reduced by 89% and that of N by 81% while the C pool in dead vegetation increased fourfold and that of N somewhat less. Our results indicate that clear-cutting will affect the C and N pools and fluxes of forest ecosystems significantly, even though some living trees are left on site.

© 2002 Elsevier Science B.V. All rights reserved.

Keywords: Biomass; Birch; Harvesting; Nutrient fluxes; Norway spruce; Soil organic matter; Scots pine

1. Introduction

Boreal forest ecosystems in Fennoscandia and elsewhere are known to contain large amounts of carbon (C) and nitrogen (N) (Tamminen, 1991, 2000; Dixon et al., 1994; Kauppi et al., 1997; Liski and Westman,

1997b). However, most studies in Fennoscandia have dealt with forests managed to produce a single species through artificial regeneration and periodic selective felling, and relatively little is known about semi-natural, old-growth forests. Such forests are relatively rare in Finland, with less than 10% of the total forest area having stands older than 140 years and in southern Finland even less, 1.7% (Sevola, 1999). However, the structure and species composition of managed forests throughout Finland is set to change as a result

* Corresponding author. Tel.: +358-13-251-4040;

fax: +358-13-251-4444.

E-mail address: leena.finer@joensuu.fi (L. Finér).

of changes in management practices that took place during the 1990s. More forests will become like old-growth forests, i.e. mixed composition and retaining a significant proportion of dead trees to sustain biodiversity. Old-growth forests contain more biomass than younger managed forests and their nutrient cycling is tight, with minor losses by leaching (e.g. Miller, 1984). In view of increasing awareness about climate change and the role of forests as C sinks, information about the C and N pools and fluxes of such stands is needed (Karjalainen, 1996a; Liski et al., 1998).

Forest ecosystem pools and fluxes of C and N are strongly affected by disturbances, including forest management and fire (Johnson, 1992; Ryan et al., 1992; Bengtsson and Wikström, 1993; Karjalainen, 1996a,b). Nowadays, wild fires in Finland are effectively controlled but the forests will continue to be managed for timber and pulp production. The effects of strong management tend to reduce soil C and N pools while the effects of less intensive management practices have been ambiguous (Johnson, 1992; Olsson et al., 1996). Long-term simulation studies have indicated that the total ecosystem C pools in unmanaged, boreal forests are bigger than in managed forests (Bengtsson and Wikström, 1993; Karjalainen, 1996b). More experimental data are needed to validate the differences in the C and N pools and fluxes between managed and unmanaged forest ecosystems.

Removal of timber obviously results in an immediate loss of C and N from the ecosystem; the greatest reduction resulting from whole-tree harvesting (Morrison and Foster, 1979; Huntington and Ryan, 1990; Olsson et al., 1996). With conventional stem-only harvesting where only the stems with bark are removed from the forest, soil C and N pools are initially increased by the addition of logging residues to the forest floor. Although stem-only harvesting is still the most common practice, recent European legislation promoting the use of biomass for energy production may be expected to lead to increased whole-tree harvesting, especially at final cutting. Besides the loss of C and N associated with timber removals, harvesting also affects a number of soil processes which in turn affect the fluxes of C and N leaving soil.

Litterfall and nutrient uptake by trees decrease and decomposition, denitrification, respiration, leaching and runoff all tend to increase after harvesting, resulting in losses of soil C and N by leaching (Vitousek

et al., 1981; Rosén, 1984; Tiedeman et al., 1988; Reynolds et al., 1995). However, the increase in leaching tends to disappear within a few years and is small compared to the biomass removals at harvesting (Mann et al., 1988; Reynolds et al., 1995). Leaching losses are also small compared to the soil pools and have no detectable effect on the soil C and N pools (McCull and Grigal, 1979; Sollins and McCorison, 1981; Huntington and Ryan, 1990). However, in some studies significant leaching losses of soil C and N have been reported (e.g. Mroz et al., 1985). The C and N pools of forests can also be severely reduced by heavy wild fires and by harvesting combined with intensive soil preparation (Johnson, 1992; Trettin et al., 1992).

The aim of this study is to give a detailed report on the amount of C and N stored in the vegetation biomass and soil of an old-growth, mixed boreal forest ecosystem before and after clear-cutting. Besides calculating C and N removal with harvesting, the changes in the fluxes due to removal of trees are also discussed. The results presented are a part of the VALU-project, the aim of which is to study the effects of clear-cutting on nutrient cycling, soil properties, soil water and stream water quality and yield (Finér et al., 1997).

2. Material and methods

2.1. Site

The data presented were collected from three 50 m × 50 m permanent sample plots located in the Kangasvaara catchment in eastern Finland (63°51'N, 28°58'E, 220 m a.s.l.) (Finér et al., 1997). The plots were established in an old-growth, mixed coniferous stand dominated by Norway spruce (*Picea abies* Karsten), but with Scots pine (*Pinus sylvestris* L.), white and silver birch (*Betula pubescens* Ehrh. and *B. pendula* Roth) and European aspen (*Populus tremula* L.) also present (Table 1). There were dead trees in the stand, both standing and lying on the ground. The stand was uneven-aged, with the average age being 140 years and the oldest trees being 170 years old. The site type was *Vaccinium–Myrtillus*-type according to the classification of Cajander (1949). The field layer vegetation was dominated by dwarf shrubs (*Vaccinium vitis-idaea* L. and *V. myrtillus* L.) and the bottom layer

Table 1

Tree stand characteristics of the sample plots ($n = 3$) before harvesting in 1996 (standard deviation in parentheses)

Characteristics	Pine	Spruce	Deciduous trees
Living trees			
No. of stems per hectare	123 (94)	1220 (178)	242 (102)
Mean height (m)	20.8 (1.0)	8.1 (1.0)	10.5 (3.1)
Mean breast height diameter (mm)	308 (41)	100 (18)	115 (37)
Stem volume with bark ($\text{m}^3 \text{ha}^{-1}$)	87 (61)	137 (55)	36 (9)
Volume growth with bark ($\text{m}^3 \text{ha}^{-1} \text{a}^{-1}$)	1.0 (0.8)	1.9 (0.3)	0.3 (0.1)
Dead trees			
Standing, volume ($\text{m}^3 \text{ha}^{-1}$)	6 (3)	2 (1)	6 (4)
Fallen, volume ($\text{m}^3 \text{ha}^{-1}$)	13 (34)	4 (3)	6 (0.4)

by feather mosses (*Pleurozium schreberi* Brid. and *Hylocomium splendens* (Hedw.) B. S. & G.).

Clear-cutting with the conventional “stem-only” method was carried out according to the recommended standard practices in August–October 1996. Accordingly, only stands classified as mature for final cutting and not adjacent to the stream draining the catchment were felled. Two of the permanent plots were located in an area (8.3 ha) designated for clear-cutting while the third remained uncut. The total harvested area in five different compartments was 19.4 ha, i.e. 35% of the catchment area. Some living trees and all dead trees were left standing on the harvested area. All trees were removed from the two harvested plots.

The upland soils in the catchment were developed in sandy till with a clay content of <2% and classified as Haplic Podzols (FAO, 1988). The underlying bedrock is granodiorite. The stone content (>20 mm) of the upper 0.3 m layer of soil, determined by the steel rod penetration method of Viro (see Tamminen and Starr, 1994), was $0.28 \text{ m}^3 \text{ m}^{-3}$. The mean annual air temperature was $+1.2 \text{ }^\circ\text{C}$, the effective temperature sum, $922 \text{ }^\circ\text{C}$ (sum of daily mean temperature exceeding $+5 \text{ }^\circ\text{C}$), and the amount of precipitation 709 mm for the period 1992–1995 (for more details about the site, see Finér et al., 1997).

2.2. Stand measurements and estimation of biomass, C and N pools

2.2.1. Aboveground biomass of trees

2.2.1.1. Living trees. Biomass estimations were made using allometric functions. The dbh (mean of two breast height diameter measurements in right-angled

directions, accuracy 1 mm), tree height (accuracy 0.1 m) and crown length (accuracy 0.1 m) of all living trees (height > 1.3 m) on the three permanent plots were measured in September 1992 and again in July–August 1996.

Sample tree harvesting for derivation of biomass functions was carried out in August–September 1996 in connection with the clear-cutting. Using stratified random sampling based on the distribution of dbh values, nine Scots pine, nine Norway spruce and seven birch trees growing on the two harvested plots were selected, and carefully felled. Derivation of the allometric biomass functions and subsequent calculation of biomass components (stemwood, stem bark, foliage, and branches) at the stand-level was carried out as described in detail by Finér (1989). The number of sample branches from each sample tree was 10 and they were taken at regular intervals from along the entire length of the crown.

2.2.1.2. Standing dead trees. The dbh and height were measured from living trees and the degree of decay was determined of all standing dead trees (height > 1.3 m) on the sample plots in August 1996. The following decay classes were used for standing dead stems. (1) Tree recently died, but bark and branches had not yet dropped. (2) Had lost its bark, but some could exist on the base of the stem; deciduous trees had kept their bark but the stemwood had started to decay and most branches had dropped. (3) Stem was largely decayed and soft and only bark kept it standing; usually only deciduous trees were recorded into this class. (4) Stem had lost all branches and was dry; usually only conifers were recorded into this class (Metsäntutkimuslaitos, 1995). The stem

volume of dead trees was calculated using well-established allometric functions (Laasasenaho, 1982) and the stand stem volume per hectare of standing dead trees was calculated. A total of eight dead Scots pine, 11 Norway spruce and eight birch trees, representing different dbh classes and degrees of decay, were sampled for the determination of wood density. The biomass of standing dead stems was calculated by multiplying the stem volume per hectare by the mean density of the sample trees (weighted by dry-weight) of each decay class and summing the values.

2.2.1.3. Fallen dead trees. The diameter (mean of two measurements taken in right-angled directions, accuracy 10 mm) at both ends of all fallen dead stems (>5 m length and >40 mm diameter), length (accuracy 0.1 m) and degree of decay of the stems on the sample plots were determined in August 1996. Five decay classes were distinguished for the fallen dead stems based on the structural integrity, wood texture and the presence of bark, branches and other vegetation. In decay class 1, the stem had recently fallen with no decay whereas in class 5 the stem was soft, powdery and covered totally by epiphytes (Metsäntutkimuslaitos, 1995). The volume of dead fallen stems was calculated assuming a truncated cone form. A disc was cut from the middle of the stem (13 Scots pines, 19 Norway spruces and 14 birches representing different diameters and degrees of decay) for determination of wood density. The stand-level biomass of fallen dead stems was calculated in the same way as described for standing dead trees.

Fallen dead branches were collected in August 1996 from 20 quadrats (each 4 m²) located systematically along the sides of each of the three permanent plots. Logging residues (without foliage) were collected in June 1997 from 30 quadrats (each 4 m²) located on a line crossing the clear-cut area near the plots. The biomass of the dead branches and logging residues were divided by tree species into different diameter classes (<1, 1–3, 3–5 and >5 cm), their dry mass determined and the results were used to calculate stand-level values.

2.2.2. Aboveground biomass of understory vegetation

Aboveground biomass sampling of understory vegetation was carried out in July 1996. The above-

ground parts of the bush layer vegetation were harvested from the same quadrats as fallen dead branches. The zero level for sampling for all layers was taken as the lower level of the living moss layer. The bush layer mainly consisted of young saplings (0.5 < height < 1.3 m). Aboveground parts of the field and bottom layer vegetation were harvested from smaller subplots (each 0.25 m²) located in the bush layer quadrats. The sampled field layer consisted of the aboveground parts of dwarf shrubs, herbs and grasses, and tree seedlings (height < 0.5 m). The bottom layer consisted of bryophytes and litter. The aboveground biomass and N content of the understory vegetation was calculated from dry mass of the harvested biomass samples.

2.2.3. Belowground biomass of trees and understory vegetation

The living stump and coarse root biomass of Scots pine and Norway spruce were calculated using the allometric functions presented by Marklund (1988) and those of birch with functions presented by Finér (1989). The biomass of all living fine (diameter < 2 mm) and small (2–10 mm) roots was determined by the core method. Twenty cylindrical cores of the soil were systematically taken from each permanent plot. The cores were taken from the organic horizon (core diameter 137 mm) and upper 20 cm mineral soil layer (core diameter 35 mm) in August 1996. The living roots were extracted from the cores by hand and divided into living conifer roots, and living roots of deciduous trees and understory vegetation. These fractions were further divided into fine and small roots and their dry mass was determined. These data were then used to calculate the stand-level biomass of stumps and roots.

2.2.4. Soil C and N pools

Volumetric samples of the organic layer and mineral soil were taken in August 1993 for calculating the soil C and N pools. On each permanent plot from nine systematically located points, five samples were taken from the organic and 0–20 cm mineral soil layers and pooled by sampling point and layer. These samples were used to determine bulk density. C and N were analysed from three samples pooled from the nine samples on each plot. The size of individual samples from the organic layer was 10 cm × 10 cm and the samples were extracted with a knife. For the mineral

soil, samples were taken with a stainless steel corer (diameter 35 mm). For the 20–40 and 40–60 cm mineral soil layers, four pits were excavated close to the permanent sample plots and from each pit two samples were taken horizontally with a corer (diameter 72 mm and height 50 mm) in the middle of the respective layer and pooled to make one sample per layer for analysis. The stone content (>20 mm) of the soil was determined by the steel rod penetration method of Viro (see Tamminen and Starr, 1994) at 30 systematically located points on each plot. The average thickness of the organic layer was 31 mm and the stone content was $28 \text{ m}^3 \text{ m}^{-3}$.

2.2.5. Laboratory analyses

The biomass and soil samples were dried to constant mass at 60°C . Mineral soil samples were sieved through a 2 mm sieve and the mass of the 2–20 and <2 mm fractions were recorded. Subsamples of biomass and soil samples were taken for dry mass determination at 105°C . Total N concentrations (% of dry-weight) were determined by the Kjeldahl method (Halonen et al., 1983) in biomass and organic soil samples. Carbon concentrations in organic soil samples and also N concentrations in mineral soil (<2 mm fraction) samples were determined using a LECO CHN-600 analyser. Since the soils have no carbonate, the total C concentrations correspond to organic C concentrations.

2.2.6. Calculation of biomass C and N pools, litterfall fluxes and removals at clear-cutting

The pools of C and N in all biomass compartments in 1996 (before clear-cutting) were calculated from the biomass determined as described above. For the C pool, all biomass compartments were assumed to have a C content of 52%. For the N pool, the samples taken for biomass and wood density determination were also analysed for total N concentrations. The N concentration (% dry-weight) value for each compartment was multiplied by the corresponding biomass value to calculate N pools. In calculating the ecosystem N pools in different aboveground tree compartments, the dry-weight weighted mean N concentration of the respective compartments of the sample trees was used. For Scots pine and Norway spruce, we used the stemwood N concentrations to calculate the N content of the stumps and the N concentration of small

roots (diameter 2–10 mm) to calculate the N content of coarse roots since we did not sample these compartments for N concentration analyses. For birch, the N contents of all belowground compartments were calculated using the N concentration values for stemwood since we did not have data for birch root N concentrations. Our procedures probably somewhat underestimated the N pool in roots for birch since the N concentrations of roots are known to be higher than those in stemwood and increase with the decrease in root diameter (Helmisaari, 1991; Finér, 1992). The biomass C and N pools of aspen were calculated using the biomass functions and N concentrations for birch.

The biomass C and N pools of the trees in 1992 were also calculated in order to obtain values for annual C and N net accumulation in tree biomass. The stand measurements made in 1992 were used to calculate the C pool in the same way as described above. For N, the biomass values from 1992 were multiplied by the N concentrations determined in 1996. The mean annual C and N net accumulation in trees were calculated as the difference between 1992 and 1996 values divided by the number of intervening years. The current net annual uptake of C and N was calculated by summing the current annual net accumulation in biomass (aboveground and belowground) and the current annual aboveground litterfall values described below.

Tree canopy litterfall was collected from September 1992 to 1996 using 16 funnels during summer (June–September) and eight funnels during winter (collecting area 0.5 m^2 , collecting height 1.3 m) in each plot. The funnels were emptied once a week during summer and once a month during winter. Litterfall was separated into branches and twigs, foliage, and the rest and their dry mass and N concentrations were determined.

The amount of C and N removed in stem harvesting, retained in the living and dead trees, and left in logging residues on the harvested area on and around two of the permanent sample plots were calculated for each tree species. Only trees with dbh > 8 cm were harvested and they were cut as close to the ground as possible and the removed volume was recorded by the harvester with an error of <4%. The species, dbh and height of trees (dbh > 8 cm) left on the site were measured after harvesting. The biomass of stumps, roots, branches and foliage stripped from the stems and left on site were estimated using the relationships established between these biomass fractions and stemwood from

the 1996 data described above. Estimation of the proportion of fine (diameter < 1 cm) branches out of the total branch biomass was based on the logging residue data collected from the site. The mean content of C and N in stumps, roots, stems (over bark), branches and foliage were then used to calculate C and N removals and logging residue inputs to the forest floor.

The C and N pools in the soil compartment (organic layer + 0–60 cm mineral soil layer) were calculated from the C and N concentrations (of the <2 mm fraction in the case of the mineral soil), bulk density and the layer thickness values on each plot. The subsequent values for the mineral soil were also corrected for gravel (2–20 mm) and stone (>20 mm) contents as described by Tamminen (1991). The C and N pools fixed in living roots were subtracted from the soil C and N pools.

3. Results

3.1. Ecosystem C and N pools

Ecosystem (i.e. total biomass + soil) C and N pools for the old-growth Norway spruce-dominated stand were 175 536 and 2848 kg ha⁻¹, respectively (Fig. 1, Table 2). Most of the C pool (62%) was in living

Table 2

Carbon and nitrogen pools (kg ha⁻¹) in living and dead vegetation and soil before harvesting (standard deviation in parentheses ($n = 3$))

Compartment	C	N
Vegetation aboveground		
Living trees	80068 (8213)	276.0 (21.0)
Bush layer	677 (362)	6.6 (3.1)
Field layer	436 (112)	10.9 (2.7)
Moss layer	751 (135)	18.1 (3.7)
Standing dead stems	2636 (412)	6.0 (1.5)
Fallen dead stems	2720 (314)	11.7 (1.3)
Fallen dead branches	6422 (3890)	50.5 (29.3)
Litter in moss layer	1673 (462)	45.7 (13.9)
Vegetation belowground		
Stumps and coarse roots	21875 (2046)	94.5 (8.1)
Fine and small roots of conifers	3345 (487)	44.9 (7.7)
Fine and small roots of other species	2075 (385)	25.1 (2.6)
Soil		
Organic layer	21244 (4256)	551.0 (65.7)
Mineral soil (0–0.6 m)	31614 (1024)	1707.0 (99.0)

vegetation, mainly the trees (60%), whereas most of the N was in the soil pool (80%), with only 15% in the living trees. The mineral soil C and N pools were larger than the pools associated with the organic layer.

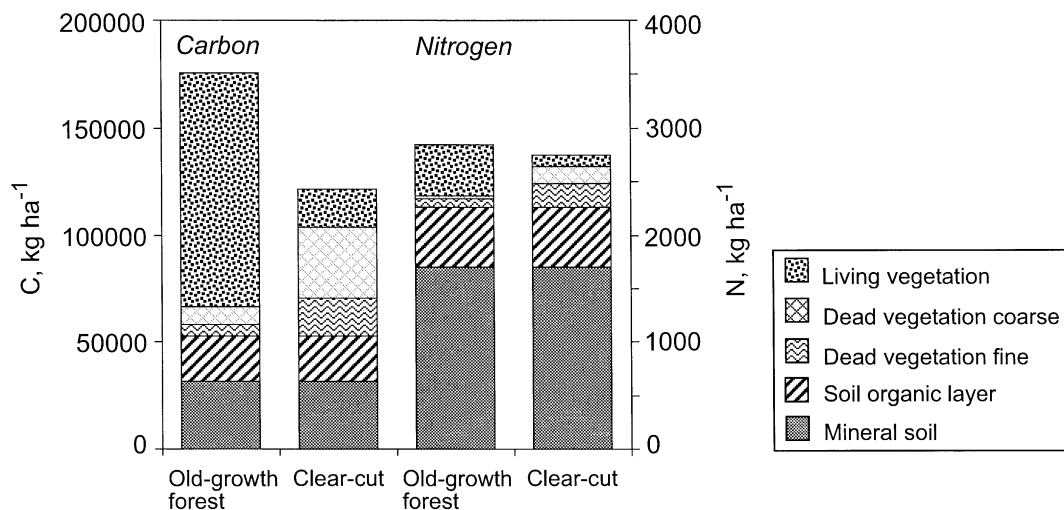


Fig. 1. Distribution of C and N pools into the living and dead vegetation (dead stems, roots, leaves, branches and litter) and soil in the old-growth forest before and after clear-cutting. Fine dead vegetation fraction includes leaves, branches diameter <1 cm and fine roots diameter <2 mm.

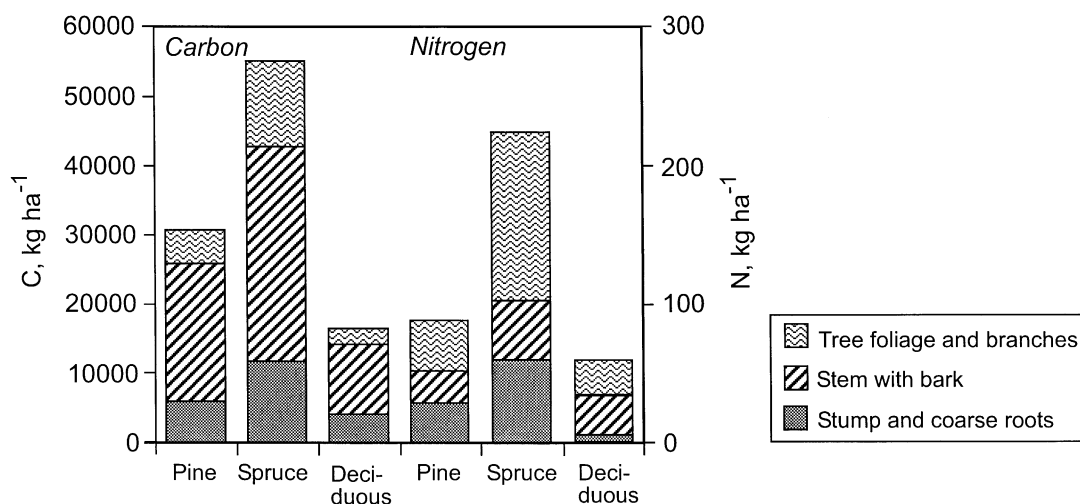


Fig. 2. Distribution of C and N in the different tree compartments of the living Scots pines, Norway spruces and deciduous trees in the old-growth forest.

The pools of C and N in the aboveground understorey vegetation compartment were very small (<2%), and those in dead tree compartments and litter only somewhat larger (8 and 4% of ecosystem C and N pools).

Norway spruce accounted for 53% of the total stem volume of living trees, Scots pine 33% and deciduous tree species 14% (Table 1). The distribution of stem C pools among species was very similar to that of their volumes, but that of N was two times greater in deciduous tree species (30%) than their share of the stand stem volume (Fig. 2). Norway spruces had

relatively more N in their foliage and branches compared to Scots pine and deciduous trees (Fig. 2). The stem volume of the dead trees was 12% of the total (living + dead) stem volume. Scots pine and deciduous tree species accounted for most of the stem volume of dead trees as well as for the C and N pools (Fig. 3). The C and N pool in dead branch compartment consisted mainly of the spruce branches.

The current mean annual stem volume growth of the stand was $3.2 \text{ m}^3 \text{ ha}^{-1}$ (Table 1). Norway spruce accounted for 60% of the growth, Scots pine 31%

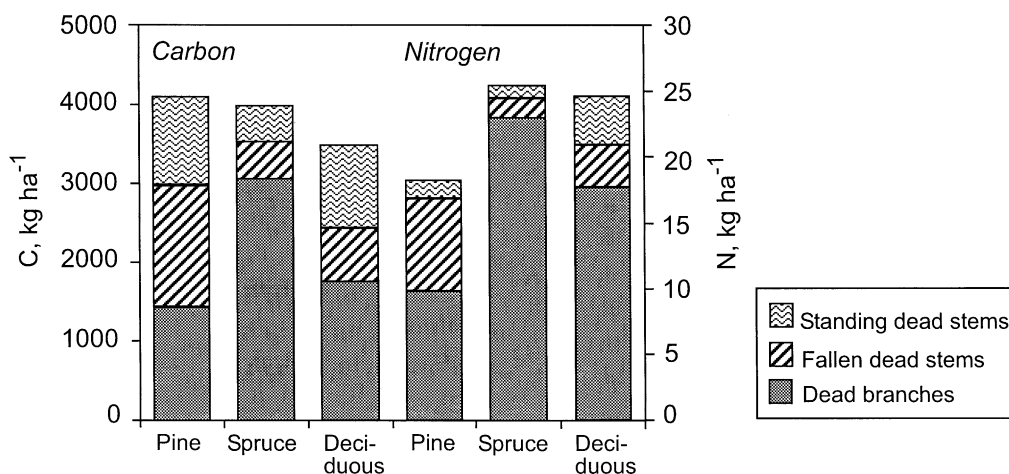


Fig. 3. Distribution of C and N in the different dead tree compartments by tree species in the old-growth forest.

Table 3

Annual accumulation of C and N in above- and belowground tree biomass compartments and aboveground litterfall ($\text{kg ha}^{-1} \text{a}^{-1}$) by species (values are means calculated from three plots; standard deviation in parentheses; total represents the annual uptake)

	C	N
Pine		
Aboveground	166.4 (267.1)	0.32 (0.70)
Belowground	45.8 (36.9)	0.21 (0.17)
Needle litterfall	79.1 (47.0)	0.86 (0.56)
Other litterfall	130.6 (98.5)	1.19 (0.88)
Total	421.9	2.58
Spruce		
Aboveground	562.6 (170.5)	2.02 (1.73)
Belowground	112.4 (48.3)	0.50 (0.29)
Needle litterfall	142.9 (81.6)	1.86 (0.82)
Other litterfall	389.4 (76.8)	4.71 (1.00)
Total	1207.3	9.09
Deciduous		
Aboveground	133.1 (33.4)	0.98 (0.29)
Belowground	34.4 (10.4)	0.05 (0.02)
Leaf litterfall	69.5 (35.6)	1.17 (0.54)
Other litterfall	146.4 (17.7)	2.21 (0.22)
Total	383.4	4.41
Stand total	2012.6	16.08

and deciduous trees 9%. The mean annual net uptake of C was 2013 kg ha^{-1} and that of N 16.1 kg ha^{-1} (Table 3). Norway spruce took up almost the same proportion of C and N as their share of stem volume growth, whereas Scots pine took up relatively less and

deciduous trees relatively more. The return of C and N to the forest floor as aboveground litterfall was 48 and 75% of the net annual uptake.

3.2. Removal at clear-cutting

The stem removal at harvesting amounted to $239 \text{ m}^3 \text{ ha}^{-1}$, of which 33% was Scots pine, 54% Norway spruce, and the rest (13%) deciduous trees. In terms of C and N, $56\,402 \text{ kg ha}^{-1}$ C and 84.8 kg ha^{-1} N were removed from the site (Fig. 4). These removals corresponded to 32 and 3% of the ecosystem C and N pools (Fig. 1). The pool of C in living vegetation was reduced by 89% and that of N by 81%. The C pool in dead vegetation increased fourfold while that of N was somewhat less. The proportion of C in fine fractions of dead vegetation (leaves, fine branches and fine roots) decreased from 40 to 35% and that of N from 72 to 59%, respectively. Some $21 \text{ m}^3 \text{ ha}^{-1}$ of living trees were left on the clear-cut area, of which $8 \text{ m}^3 \text{ ha}^{-1}$ was Scots pine, $7 \text{ m}^3 \text{ ha}^{-1}$ Norway spruce and $6 \text{ m}^3 \text{ ha}^{-1}$ deciduous trees. More C was removed with the stems than was left on the site in the form of logging residues. For N, three times more was left in the logging residues than removed in the harvested stems. The amounts of C (8376 kg ha^{-1}) and N (29.3 kg ha^{-1}) in the living trees left after clear-cutting were 15 and 35% of the amounts removed in stems and, respectively, greater and smaller than the pools in living understorey vegetation (aboveground). After clear-cutting, most of the ecosystem C was in dead vegetation while the soil remained the largest pool of ecosystem N.

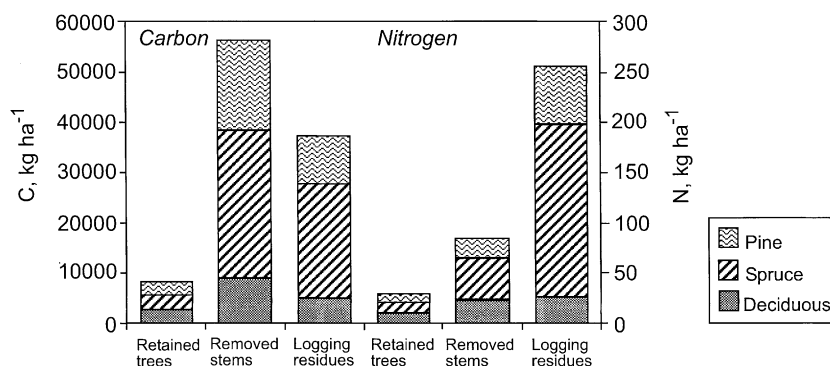


Fig. 4. The C and N amounts fixed at the clear-cutting in the retained and in the removed Scots pines, Norway spruces and deciduous trees and those left in the logging residues.

4. Discussion

4.1. C and N pools and fluxes before clear-cutting

The living vegetation, especially the trees, was the main pool of C, and the soil, was the main pool of N in our old-growth forest ecosystem. Earlier studies concerned with boreal forest biomass, and N pools and fluxes in Fennoscandia are relatively few and have mainly been carried out in managed stands of either pure Scots pine (Mälkönen, 1975; Paavilainen, 1980; Finér, 1989, 1991; Helmisaari, 1995), Norway spruce (Nykqvist, 1971; Nihlgård, 1972; Finér, 1989) or birch (Mälkönen, 1978; Mälkönen and Saarsalmi, 1982). The standing volume, biomass and amounts of N fixed in trees in our old-growth forest were at the upper end of the range reported in these studies. Only Havas and Kubin (1983) and Kubin (1983) have published results on biomass and nutrients fixed in an old-growth Norway spruce-dominated forest in Finland. In their studies, the total tree biomass and its N content were smaller than in ours, even though their forest had grown unmanaged for 250 years. The more northern location of their site probably explains this difference.

Dead trees and litter constituted significant pools of C and N in our old-growth forest ecosystem (Table 2). Russian studies in an old-growth forest south from our site, found even more in coarse dead wood $17\,000\text{ kg C ha}^{-1}$, corresponding to 20% of the total aboveground tree biomass (Krankina and Harmon, 1995). The amount of coarse dead wood in our forest was somewhat underestimated because we did not include stumps and coarse roots of dead trees. Biomass, C and N pools in dead trees have seldom been reported for managed boreal forests. This is presumably because dead trees are removed at thinning and the fraction is not considered important. Most of the C and N in standing and fallen dead trees were associated with Scots pines and deciduous trees, which would be compatible with the successional change away from pioneer birch and pine forest to spruce forest.

The current mean annual stem volume growth of the forest, $3.2\text{ m}^3\text{ ha}^{-1}$, was somewhat less than the average growth of forests in Finland ($3.8\text{ m}^3\text{ ha}^{-1}\text{ a}^{-1}$, Sevola, 1999) but more than that reported for 120-year-old unmanaged *Myrtillus*-type forests in Finland ($2.5\text{--}2.7\text{ m}^3\text{ ha}^{-1}\text{ a}^{-1}$) (Koivisto, 1959). The annual net uptake of $2013\text{ kg ha}^{-1}\text{ C}$ and $16.1\text{ kg ha}^{-1}\text{ N}$ by the

trees was within the range reported for boreal coniferous forests (Mälkönen, 1975; Finér, 1991; Helmisaari, 1995), whereas the N uptake was much smaller than that in a birch-dominated boreal forest studied by Mälkönen (1978). Our results support the finding that birch binds more N per unit of biomass than conifers (Mälkönen, 1978; Finér, 1989). However, all such values are likely to be underestimates of uptake since they do not include accumulation in fine root biomass, belowground litterfall, dying of trees or canopy exchange.

Throughfall at Kangasvaara has been monitored (Piirainen et al., 1998, 2000). Calculations indicate that some $58\text{ kg ha}^{-1}\text{ a}^{-1}$ of organic C was leached from the canopy while $1.2\text{ kg ha}^{-1}\text{ a}^{-1}$ inorganic N was taken up by the foliage. Adding the canopy leaching of organic C to the current annual net uptake value increases the value for uptake by 3.1% to 2074 kg ha^{-1} . The canopy uptake of N is already accounted for in the net uptake estimate. The annual atmospheric deposition of organic C to the forest was 12.1 kg ha^{-1} and that of total N was 3.8 kg ha^{-1} . We have estimated the annual leaching flux of C and N from below the illuvial B-horizon in the permanent plots is 2.8 and 0.2 kg ha^{-1} , respectively (Piirainen et al., 1998, 2000). There is thus net accumulation of atmospheric inputs of organic C and total N within the ecosystem.

Belowground litterfall, especially that of fine roots, may account for more than half of the annual biomass production (Axelsson and Axelsson, 1986; Helmisaari et al., 2000). However, the net accumulation of C and N in fine and small roots is probably insignificant since fine root biomass has been found to be relatively constant in forests after canopy closure (e.g. Vogt et al., 1983; Laiho and Finér, 1996). The forest at our site was monitored for 4 years before the clear-cutting, but no estimates of tree death were made.

The understorey vegetation represented an insignificant pool of C and N compared to total ecosystem pools, and even to the tree biomass pool. However, element pools in understorey vegetation can be expected to be rather variable since they depend on species composition and abundance, which in turn will depend on many factors, including location, site type, tree species composition and shading. Nevertheless, the understorey vegetation pools of C and N at our site were within the range reported for the few studies carried out in *Myrtillus*- or *Vaccinium*-type forests dominated by Norway spruce or Scots pine (Nykqvist,

1971; Mälikönen, 1975; Havas and Kubin, 1983; Kubin, 1983; Helmisaari, 1995; Mäkipää, 1995).

The annual uptake of C and N by the understorey vegetation was not estimated in our study. Mälikönen (1975) reported aboveground biomass production and nutrient uptake of understorey vegetation in three *Myrtillus*- or *Vaccinium*-type Scots pine-dominated forests. He found that the annual aboveground biomass production of understorey vegetation was, on average, 32% of the aboveground total biomass. The corresponding value reported by Helmisaari (1995) for three *Vaccinium*-type Scots pine-dominated forests was 17%. If we assume that the aboveground biomass production of the understorey vegetation at our site was 25% of the total standing biomass and its N content was the same as in the standing biomass, the annual uptake by the understorey vegetation at our site would be $466 \text{ kg ha}^{-1} \text{ C}$ and $8.9 \text{ kg ha}^{-1} \text{ N}$. These values would correspond to as much as 22% of the annual net uptake of C and 56% of that of N by trees. The relative importance of understorey vegetation in fixing C has been shown to decrease with increasing stand age whereas its role in fixing N remains high, even in old forests (Mälikönen, 1975; Helmisaari, 1995).

The pools of C and N in the organic layer were close to the average reported for *Myrtillus*-type forests in Finland (Tamminen, 1991, 2000; Liski and Westman, 1995, 1997a). However, the organic matter and N pools were at the lower end of the ranges reported by Tamminen (1991, 2000) for the 0–30 cm mineral soil layer. According to Liski and Westman (1995), mineral soil below 1 m depth to the groundwater level may contain 18–28% of the total pool of C in the soil. However, the organic matter at this depth is probably much more stable and beyond forest management effects than that in the upper soil layer. Sampling to this depth would also be prohibitive for most studies.

4.2. Effects of clear-cutting

We estimated the C and N content of logging residues from the total pools in trees before harvesting and the measured stem volume of harvested trees and their C and N content. We also harvested all logging residues from 30 squares (each 4 m^2) after harvesting (data not shown). The logging residues were distributed very irregularly on the site and the coefficient of variation for the logging residue biomass was large

(>100%). Thus, we should have carried out a much more intensive sampling to get an accurate estimate of the logging residue C and N pools.

Most of the studies on the effects of forest harvesting in boreal forests have focussed on the possible nutrient losses from the soil and reductions in subsequent forest growth (Mälikönen, 1976; Mälikönen and Saarsalmi, 1982; Jacobson et al., 1996; Rolff and Ågren, 1999). Since forest growth is limited by N availability, most attention has been paid to N (e.g. Mälikönen et al., 1990; Jacobson et al., 2000). Stemwood removals at clear-cutting significantly reduced the ecosystem C pool at our site and the loss was relatively less for N. The annual uptake of C (124 kg ha^{-1}) and N (0.6 kg ha^{-1}) by the trees remaining after harvesting, assuming that their uptake was not affected by the harvesting, was insignificant compared to what it had been by the whole stand prior to clear-cutting. More living trees were left on our site than for the average Finnish clear-cut areas ($3.8 \text{ m}^3 \text{ ha}^{-1}$, Eeronheimo et al., 1997). If all the trees had been cut and harvested at our site, as would have been the practice earlier, it would have increased the biomass losses of C by 6% and that of N by 11%, resulting in total losses from the forest of 35 and 3.5%, respectively. If the proportion of deciduous trees left on site had been higher, the losses, of N in particular, would have been lower. If whole-tree harvesting, in which the foliage and branches are also removed from site, had been practised at our site the C and N losses would have increased to 46 and 9.7% of the total ecosystem pools, respectively.

In addition to the immediate losses of C and N associated with the removal of stemwood, clear-cutting affects many biogeochemical processes that bring about further changes in the C and N pools and fluxes. Once the trees are removed there is no longer a regular supply of litterfall, but there is a large, single flux of logging residues to the forest floor. The average C/N ratio, a factor known to control the initiation of net N mineralisation, was 80 in annual litterfall (Table 3). Before harvesting the average C/N ratio of the fine dead vegetation fraction was 65 and that of the coarse fraction was 256 and in the logging residues the respective ratios were 84 and 199 (calculated from the data presented in Fig. 1). A threshold C/N ratio of 60–110 for the initiation of net N mineralisation of Scots pine needle litter has been reported in Swedish

studies (Berg and Staaf, 1980; Berg and Ekbohm, 1983). The high C/N ratios at our site, especially in the coarse dead vegetation fractions, therefore would indicate low N mineralisation, and even immobilisation in logging residues (Berg and Staaf, 1980; Berg and Ekbohm, 1983; Titus and Malcolm, 1999; Hyvönen et al., 2000). However, the C/N ratio of different biomass compartments varies, being much lower in foliage than in branches and some net mineralisation may therefore, have occurred, as indicated by a small increase in mineral N leaching we observed after the clear-cutting (Piirainen et al., 2000).

The removal of trees at clear-cutting represents a sudden decrease in nutrient uptake from the soil, which when combined with a greater amount of water reaching the forest floor, increases the risk for mineral N leaching. In boreal coniferous forests, mineral N is growth limiting and is largely immobilised in the soil. The understorey vegetation is also affected by changes in light conditions (Kellomäki et al., 1977), nutrient availability, mechanical disturbance, and covering by logging residues at the time of cutting (Olsson and Staaf, 1995), and subsequently changes due to succession. A strong flush in the growth of ground vegetation immediately after clear-felling would help immobilise mineral N. Furthermore, much of the available N in the soil may also become rapidly immobilised, at least temporarily, in soil microbes or dead organic matter after clear-cutting, leaving little for leaching.

We consider the soil C and N pools at Kangasvaara unchanged immediately after harvesting. This is confirmed by our initial analysis of soil water fluxes of dissolved organic carbon (DOC) and N. Up to 3 years after clear-cutting there was only a small increase in the leaching flux of DOC and total N, dominated by organic N, from below the illuvial B-horizon (Piirainen et al., 2000). There are only a few studies on the long-term changes in soil C or N pools after clear-cutting of boreal forest. The results of Olsson et al. (1996), 15–16 years after clear-cutting, show that soil C pools decreased 17–22% and those of N 13–22% on sites with Norway spruce. A modelling study by Liski et al. (1998) indicated that clear-cutting of unmanaged *Myrtillus*-type forest decreases soil C pool by 14% and that by Karjalainen (1996b) suggests that the total C pool of forest would decrease by 3% within 100 years after clear-cutting. The soil pools can further be decreased by intensifying the harvesting method

(Bengtsson and Wikström, 1993), by repeated cuttings (Bengtsson and Wikström, 1993; Karjalainen, 1996b; Liski et al., 1998) or by shortening the rotation length (Aber et al., 1978; Karjalainen, 1996b). In temperate forests observed decreases in forest floor mass and N content level-off after 50–60 years (Covington, 1981; Federer, 1984) or no clear decrease after clear-cutting has been observed (Yanai et al., 2000). In the future we intend to evaluate the long-term effects of harvesting on soil C and N pools and leaching losses from the stand on the stream water draining the catchment.

5. Conclusions

We made a detailed study of the ecosystem C and N pools in an old-growth forest and showed that the vegetation is the major pool of C, whereas soil is the major pool of N. The understorey vegetation pools were very small (<2%). Stem removals after clear-cutting reduced the ecosystem pool of C by one-third while the reduction for N was only 3%. It will be necessary to continue monitoring in order to determine the long-term effect of clear-cutting on the pools of C and N in the soil and vegetation as the regenerating stand develops.

Acknowledgements

We thank the motivated and skilful staff of the Finnish Forest Research Institute, Joensuu Research Centre and the Laboratory of Vantaa Research Centre for technical help in carrying out the field work and laboratory analyses. We also thank the Ministry of Agriculture and Forestry for partially funding the project and Finnish Forest and Park Service for providing access to the study site and carrying out the harvesting operations.

References

- Aber, J.D., Botkin, D.B., Melillo, J.M., 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res.* 8, 306–315.
- Axelsson, E., Axelsson, B., 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. *Tree Physiol.* 2, 189–204.

- Bengtsson, J., Wikström, F., 1993. Effects of whole-tree harvesting on the amount of soil carbon: model results. *NZ J. For. Sci.* 23, 380–389.
- Berg, B., Ekbohm, G., 1983. Nitrogen immobilization in decomposing needle litter at variable carbon: nitrogen ratios. *Ecology* 64, 63–67.
- Berg, B., Staaf, H., 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. *Ecol. Bull.* 32, 373–390.
- Cajander, A.K., 1949. Forest types and their significance. *Acta For. Fenn.* 56, 72.
- Covington, W.W., 1981. Changes in forest floor organic matter and nutrient content following clear-cutting in northern hardwoods. *Ecology* 62, 41–48.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–190.
- Eeronheimo, O., Ahti, A., Sahlberg, S. (Eds.), 1997. Suomen kestävän metsätalouden kriteerit ja indikaattorit metsätalouden tilan kuvaajina. Maa- ja Metsätalousministeriö, Helsinki (in Finnish).
- FAO, 1988. FAO/UNESCO 'Soil map of the World', Revised Legend. World Resources Report 60, Rome. Reprinted as Technical Paper 20. ISRIC, Wageningen, 1989.
- Federer, C.A., 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Can. J. For. Res.* 14, 763–767.
- Finér, L., 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. *Acta For. Fenn.* 208, 63.
- Finér, L., 1991. Effect of fertilization on dry mass accumulation and nutrient cycling in Scots pine on an ombrotrophic bog. *Acta For. Fenn.* 223, 42.
- Finér, L., 1992. Nutrient concentrations in *Pinus sylvestris* growing on an ombrotrophic pine bog, and the effects of P and NPK fertilization. *Scand. J. For. Res.* 7, 205–218.
- Finér, L., Ahtiainen, M., Mannerkoski, H., Möttönen, V., Piirainen, S., Seuna, P., Starr, M., 1997. Effects of harvesting and scarification on water and nutrient fluxes. A description of catchments and methods, and results from the pretreatment calibration period. Research Paper 648. Finnish Forest Research Institute, 38 pp.
- Halonen, O., Tulkki, H., Derome, J., 1983. Nutrient analysis methods. Research Paper 121. Finnish Forest Research Institute, 28 pp.
- Havas, P., Kubin, E., 1983. Structure, growth and organic matter content in the vegetation cover of an old spruce forest in northern Finland. *Ann. Bot. Fenn.* 20, 115–149.
- Helmisaari, H.-S., 1991. Variation in nutrient concentrations of *Pinus sylvestris* roots. In: McMichael, B.L., Persson, H. (Eds.), *Plant Roots and Their Environment*. Elsevier Science, Amsterdam, pp. 204–212.
- Helmisaari, H.-S., 1995. Nutrient cycling in *Pinus sylvestris* stands in eastern Finland. *Plant Soil* 168–169, 327–336.
- Helmisaari, H.-S., Lehto, T., Makkonen, K., 2000. Fine roots and soil properties. In: Mälkönen, E. (Ed.), *Forest Condition in a Changing Environment—The Finnish Case*. Kluwer Academic Publishers, Dordrecht, pp. 203–217.
- Huntington, T.G., Ryan, D.F., 1990. Whole-tree-harvesting effects on soil nitrogen and carbon. *For. Ecol. Mgmt.* 31, 193–204.
- Hyvönen, R., Olsson, B.A., Lundkvist, H., Staaf, H., 2000. Decomposition and nutrient release from *Picea abies* (L.) Karst. and *Pinus sylvestris* L. logging residues. *For. Ecol. Mgmt.* 126, 97–112.
- Jacobson, S., Kukkola, M., Mälkönen, E., Tveite, B., Möller, G., 1996. Growth response of coniferous stands to whole-tree harvesting in early thinnings. *Scand. J. For. Res.* 11, 50–59.
- Jacobson, S., Kukkola, M., Mälkönen, E., Tveite, B., 2000. Impact of whole-tree harvesting and compensatory fertilization on growth of coniferous thinning stands. *For. Ecol. Mgmt.* 129, 41–51.
- Johnson, D.W., 1992. Effects of forest management on soil carbon storage. *Water Air Soil Pollut.* 64, 83–120.
- Karjalainen, T., 1996a. Dynamics and potentials of carbon sequestration in managed stands and wood products in Finland under changing climatic conditions. *For. Ecol. Mgmt.* 80, 113–132.
- Karjalainen, T., 1996b. Model computations on sequestration of carbon in managed forests and wood products under changing climatic conditions in Finland. *J. Environ. Mgmt.* 47, 311–328.
- Kauppi, P.E., Posch, M., Hänninen, P., Henttonen, H.M., Ihala, A., Lappalainen, E., Starr, M., Tamminen, P., 1997. Carbon reservoirs in peatlands and forests in the boreal regions of Finland. *Silva Fenn.* 31, 13–25.
- Kellomäki, S., Hari, P., Väisänen, E., 1977. Annual production of some forest mosses as a function of light available for photosynthesis. *Silva Fenn.* 11, 81–86.
- Koivisto, P., 1959. Kasvu- ja tuottotaulukoita. *Commun. Inst. For. Fenn.* 51 (8), 1–49.
- Krankina, O.N., Harmon, M.E., 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. *Water Air Soil Pollut.* 85, 227–238.
- Kubin, E., 1983. Nutrients in the soil, ground vegetation and tree layer in an old spruce forest in northern Finland. *Ann. Bot. Fenn.* 20, 361–390.
- Laasasenaho, J., 1982. Taper curve and volume functions for pine, spruce and birch. *Commun. Inst. For. Fenn.* 108, 74.
- Laiho, R., Finér, L., 1996. Changes in root biomass after water-level drawdown on pine mires in southern Finland. *Scand. J. For. Res.* 11, 251–260.
- Liski, J., Westman, C.J., 1995. Density of organic carbon in soil at coniferous forest sites in southern Finland. *Biogeochemistry* 29, 183–197.
- Liski, J., Westman, C.J., 1997a. Carbon storage in forest soil of Finland. 1. Effect of thermoclimate. *Biogeochemistry* 36, 239–260.
- Liski, J., Westman, C.J., 1997b. Carbon storage in forest soil of Finland. 2. Size and regional patterns. *Biogeochemistry* 36, 261–274.
- Liski, J., Ilvesniemi, H., Mäkelä, A., Starr, M., 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. *Eur. J. Soil Sci.* 49, 407–416.
- Mäkipää, R., 1995. Effect of nitrogen input on carbon accumulation of boreal forest soils and ground vegetation. *For. Ecol. Mgmt.* 79, 217–226.
- Mälkönen, E., 1975. Annual primary production and nutrient cycle in some Scots pine stands. *Commun. Inst. For. Fenn.* 84, 1–87.

- Mälikönen, E., 1976. Effect of whole-tree harvesting on soil fertility. *Silva Fenn.* 10, 157–164.
- Mälikönen, E., 1978. Annual primary production and nutrient cycle in a birch stand. *Commun. Inst. For. Fenn.* 91, 1–35.
- Mälikönen, E., Saarsalmi, A., 1982. Hieskoivikon biomassatuotos ja ravinteiden menetys kokopuun korjuussa (Biomass production and nutrient removal in whole-tree harvesting of birch stands). *Folia For.* 534, 17.
- Mälikönen, E., Derome, J., Kukkola, M., 1990. Effects of nitrogen inputs on forest ecosystems estimation based on long-term fertilization experiments. In: Kauppi, P., Anttila, P., Kenttämies, K. (Eds.), *Acidification in Finland*. Springer, Berlin, pp. 325–347.
- Mann, L.K., Johnson, D.W., West, D.C., Cole, D.W., Hornbeck, J.W., Martin, C.W., Riekerk, H., Smith, C.T., Swank, W.T., Tritton, L.M., van Lear, D.H., 1988. Effects of whole-tree and stem-only clear-cutting on post-harvest hydrologic losses, nutrient capital, and regrowth. *For. Sci.* 34, 412–428.
- Marklund, L.G., 1988. Biomassfunktioner för tall, gran och björk i Sverige. Sveriges Lantbruksuniversitet. Rapport—Skog Rapport 45, 73 pp. (in Swedish).
- McCull, J.G., Grigal, D.F., 1979. Nutrient losses in leaching and erosion by intensive forest harvesting. In: *Proceedings of the Impact of Intensive Harvesting on Forest Nutrient Cycling*. Sponsored by USDA Forest Service, and USDOE, Fuels from Biomass Systems, New York. College of Environmental Science and Forestry, State University of New York, Syracuse, 421 pp.
- Metsäntutkimuslaitos, 1995. Valtakunnan metsien inventointi. Pysyvien koalojen 3. Mittaus 1995. Maastotyön Ohjeet. Finnish Forest Research Institute, Helsinki, 104 pp. (in Finnish).
- Miller, H.G., 1984. Dynamics of nutrient cycling in plantation ecosystems. In: Bowen, G.D., Nambiar, E.K.S. (Eds.), *Nutrition of Plantation Forests*. Academic Press, London.
- Morrison, I.K., Foster, N.W., 1979. Biomass and element removal by complete-tree harvesting of medium rotation forest stands. In: *Proceedings of the Impact of Intensive Harvesting on Forest Nutrient Cycling*. Sponsored by USDA Forest Service, and USDOE, Fuels from Biomass Systems, New York. College of Environmental Science and Forestry, State University of New York, Syracuse, 421 pp.
- Mroz, G.D., Jurgensen, M.F., Frederick, D.J., 1985. Soil nutrient changes following whole-tree harvesting on three northern hardwood sites. *Soil Sci. Soc. Am. J.* 49, 1552–1557.
- Nihlgård, B., 1972. Plant biomass, primary production and distribution of chemical elements in a beech and a planted spruce forest in South Sweden. *Oikos* 23, 69–81.
- Nykvist, N., 1971. The effect of clear felling on the distribution of biomass and nutrients. *Ecol. Bull.* 14, 166–178.
- Olsson, B.A., Staaf, H., 1995. Influence of harvesting intensity of logging residues on ground vegetation in coniferous forests. *J. Appl. Ecol.* 32, 640–654.
- Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., Rosen, K., 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. *For. Ecol. Mgmt.* 82, 19–32.
- Paavilainen, E., 1980. Effect of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. *Commun. Inst. For. Fenn.* 98, 71.
- Piirainen, S., Finér, L., Starr, M., 1998. Canopy and soil retention of nitrogen deposition in a mixed boreal forest in eastern Finland. *Water Air Soil Pollut.* 105, 165–174.
- Piirainen, S., Finér, L., Mannerkoski, H., Starr, M., 2000. Carbon and nitrogen leaching from a podzolic soil following forest clear-cutting. *Pro Terra* 4/2000, pp. 95–97.
- Reynolds, B., Roberston, W.H., Hornung, M., Stevens, P.A., 1995. Forest manipulation and solute production: modelling the nitrogen response to clear-cutting. In: Trudgill, S.T. (Ed.), *Solute Modelling in Catchment Systems*. Wiley, London, pp. 211–233.
- Rolf, C., Ågren, G.I., 1999. Predicting effects of different harvesting intensities with a model of nitrogen limited forest growth. *Ecol. Model.* 118, 193–211.
- Rosén, K., 1984. Effect of clear-felling on runoff in two small watersheds in central Sweden. *For. Ecol. Mgmt.* 9, 267–281.
- Ryan, D.F., Huntington, T.G., Martin, C.W., 1992. Redistribution of soil nitrogen, carbon and organic matter by mechanical disturbance during whole-tree harvesting in northern hardwoods. *For. Ecol. Mgmt.* 49, 87–99.
- Sevola, Y. (Ed.), 1999. Finnish Statistical Yearbook of Forestry, Vol. 6. Finnish Forest Research Institute, Helsinki.
- Sollins, P., McCorison, F.M., 1981. Nitrogen and carbon solution chemistry of an old-growth coniferous forest watershed before and after cutting. *Water Resour. Res.* 17, 1409–1418.
- Tamminen, P., 1991. Kangasmaan ravinnetunnusten ilmaiseminen ja viljavuuden alueellinen vaihtelu Etelä-Suomessa (Expression of soil nutrient status and regional variation in soil fertility of forested sites in southern Finland). *Folia For.* 777, 40.
- Tamminen, P., 2000. Soil factors. In: Mälikönen, E. (Ed.), *Forest Condition in a Changing Environment—The Finnish Case*. Kluwer Academic Publishers, Dordrecht, pp. 72–86.
- Tamminen, P., Starr, M., 1994. Bulk density of forested mineral soils. *Silva Fenn.* 28, 53–60.
- Tiedeman, A.R., Quinley, T.M., Anderson, T.D., 1988. Effects of timber harvest on stream chemistry and dissolved nutrient losses in northeast Oregon. *For. Sci.* 34, 344–358.
- Titus, B.D., Malcolm, D.C., 1999. The long-term decomposition of Sitka spruce needles in brush. *Forestry* 72, 207–221.
- Trettin, C.C., Gale, M.R., Jurgensen, M.F., McLaughlin, J.W., 1992. Carbon storage response to harvesting and site preparation in a forested mire in northern Michigan. *USA Suo* 43, 281–284.
- Vitousek, P.M., Reiners, W.A., Melillo, J.M., Crier, C.C., Gosz, J.R., 1981. Nitrogen cycling and loss following forest perturbation: the components of response. *Stress Effects Nat. Ecosyst.* 1981, 115–127.
- Vogt, K.A., Moore, E.E., Vogt, D.J., Redlin, M.J., Edmonds, R.L., 1983. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. *Can. J. For. Res.* 13, 429–437.
- Yanai, R.D., Arthus, M.A., Siccama, T.G., Federer, C.A., 2000. Challenges of measuring forest floor organic matter dynamics: repeated measures from a chronosequence. *For. Ecol. Mgmt.* 138, 273–283.