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ORIGINAL ARTICLE

Dynamics of soil C, N and Ca in four Swedish forests after removal of tops, branches and stumps as predicted by the Q model

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Abstract
We used the Q model to examine the dynamics of carbon (C), nitrogen (N) and calcium (Ca) in the litter/soil system in different scenarios of harvesting intensities, S (stems only), SSl (stems and slash, i.e. tops, and branches including needles) and SSlSt (stems, slash and stumps including coarse roots). Empirical data from long-term field experiments in Sweden, two sites with Norway spruce and two with Scots pine with different levels of productivity, were used to calibrate the model against the stem-only treatment. The highest initial reduction in soil C, N and Ca stores was predicted for SSlSt, and the reduction was more pronounced at low productive sites than at the high productive ones. Most of the decline in soil C and Ca stocks was offset by the litter production in the following forest stand. N showed an initial phase of immobilisation in stumps and coarse roots, while N was immediately released from tops and branches, which contained N-rich needles. Removal of stumps and coarse roots in combination with slash resulted in a similar load of inorganic soil N as for the S treatment, whereas the SSl treatment with stumps left in the soil initially reduced the inorganic soil N pool.

Keywords: *Bioenergy, forest soil, carbon, nitrogen, calcium, boreal.*

Introduction

Residues from harvesting operations in conventional forestry are used at an increasing rate for energy purposes, particularly in northern Europe (Björheden, 2006). Until recently, mostly the slash (i.e. tops, branches and needles) has been used, but there is also a growing interest in harvesting the stump biomass for energy. These biomass fractions have potentially the same energy value, and tops plus branches and stumps including coarse roots each make up 20–25% of the biomass of conifers (Marklund, 1988; Petersson & Ståhl, 2006). Analyses of carbon (C) and nitrogen (N) mass balances at single sites have indicated that coarse wood decomposes more slowly and are more slowly produced than fine tree fractions, which implies that the removal of slash should have more short-term effects than removal of stumps (Lindholm et al., 2011; Repo et al., 2011; Walmsley & Godbold, 2010).

There is considerable variation in the observed response to harvesting of logging residues in soil and tree C (Johnson & Curtis 2001; Nave et al., 2010; Thiffault et al., 2011). Generally, harvesting reduces soil C, particularly in boreal forests, and discernible effects are more frequently found in the forest floor than in the mineral soil. Nave et al. (2010) suggested that C losses were neither permanent nor unavoidable depending on species composition, time, and sampling depth. A few field studies on effects of stump harvest are published so far, indicating that reductions in the soil C stocks can be discernible for decades in temperate and boreal coniferous forests (Hope, 2007; Strömgren et al., 2012; Zabowski et al., 2008). Temporal changes in soil C through the rotation period and inputs of C from above and below ground litter are suggested to mask effects of slash harvesting (Thiffault et al., 2011). Short- to medium-term field experiments of slash harvesting have often shown negative effects, yet sometimes positive or no effects on soil stores of C and other elements have been observed. A question still to be answered is to what extent the variation in the different responses to intensified harvesting of logging residues can be ascribed to the removal of logging residues or to the changes in litter production of the regenerating forest stand.

Because wood has low nutrient concentrations compared to other tree parts, slash harvesting means a substantially greater increase in the removal of nutrients from forest sites than stem-only harvesting. Thus, slash harvesting may lead to growth reductions in the regenerating stand, not the least in boreal forests that are already N limited (Tamm, 1991). Reduced N and P availability have reduced tree growth in some stands for at least 20 years in some stands (Helmisaari et al., 2011; Thiffault et al., 2011). Many experiments in the Nordic countries have demonstrated reductions in forest growth following slash harvesting after clear-felling and thinning (Egnell, 2011; Egnell & Leijon, 1997; Egnell & Valinger, 2003; Helmisaari et al., 2011; Jacobson et al., 2000), and there is also some experimental evidence of a relatively long-term lowered N mineralisation in the soil following harvesting of slash (Smolander et al., 2008). On the other hand, removal of N in biomass may also have beneficial effects by reducing N load and eutrophication (Akselsson et al., 2008).

Increased removal of base cations in harvested biomass is directly associated with acidification which adds to the acidification from air pollutants. Although sulfate deposition has decreased markedly in Europe and North America over recent decades (Pihl Karlsson et al., 2011), acidification of surface waters is still a concern in areas with low buffer capacity against acidification, and harvesting of residues may offset the recovery from acidification. Calcium (Ca) is the most important base cation in this context due to its abundance. The mass balance calculations by Akselsson et al. (2007) showed net losses of Ca and Mg in almost the whole country after both stem-only and slash harvesting. Ca is also the base cation, which shows the strongest and most long-lasting response to slash harvesting in experi-

mental studies (Brandtberg & Olsson, 2012; Olsson et al., 1996a).

The aim of this study was to compare the effects of slash and stump harvesting at final felling on the dynamics and accumulation of soil C, N and Ca over the rotation period, i.e. 85–100 years, following clear-cut. The Q model was used to describe the dynamics of these elements in trees and soil, and the results were compared with experimental results from two sites with Scots pine (*Pinus sylvestris* (L.) and two sites with Norway spruce (*Picea abies* (L.) Karst.). Each of the tree species had one stand in southern and one in northern Sweden.

Materials and methods

Study sites and experimental data

A first step in our analysis was to examine how well the Q-model (Ågren et al., 2007) described C, N and Ca dynamics in tree biomass and soil in the control plots of four coniferous field experiments in Sweden (Tönnersjöheden and Kosta in the south and Lövliden and Lund in the north; Table I), established between 1974 and 1976 by Björkroth and Rosén (1977). The biomass and nutrient contents of the harvested stands were estimated from allometric functions based on the harvested trees. The allometric functions were unique for each species and site (Björkroth & Rosén, 1977). More details on C, N and cation pools in the soils of these sites are given in Olsson et al. (1996a, 1996b) and Brandtberg and Olsson (2012). Only the measured element pools in the humus layer will be used for comparison with model predictions.

The aim of these experiments was to test the effects of different harvesting regimes of logging residues on soils and forest production.

Table I. Characteristics of the experimental sites.

	Tönnersjöheden (T103)	Kosta	Lövliden	Lund
Latitude	56°42′N	56°52′N	64°16′N	64°18′N
Longitude	13°50′E	15°23′E	19°31′E	19°36′E
Mean ann. air temp (°C)	6.4	6.2	1.0	1.0
Precipitation (mm yr^{-1})	1040	595	565	565
Forest type	Mesic dwarf-shrub	Mesic dwarf-shrub	Mesic-wet dwarf-shrub	Dry lichen
Soil type	Orthic podzol	Orthic podzol	Orthic podzol	Orthic podzol
Old stand (at harvest)				
Tree species	*Picea abies*	*Pinus sylvestris* (50%) *Picea abies* (50%)	*Picea abies* (70%) *Pinus sylvestris* (30%)	*Pinus sylvestris*
Stand age, years	70	100	155–175	90–95
Stem volume (m^3 ha^{-1})	325	305	290	185
Site productivity (m^3 ha^{-1} yr^{-1})	10.1	5.9	3.8	3.7
Time of harvest	Spring 1975	Autumn 1975	Autumn 1976	Autumn 1974
New stand				
Tree species	*Picea abies*	*Pinus sylvestris*	*Picea abies*	*Pinus sylvestris*
Time of planting	Spring 1976	Autumn 1976	Spring 1977	Spring 1975

The treatments included: (1) complete removal of stems and logging residues; (2) stems and the woody fractions of the logging residues being harvested but needles were left on site; whereas (3) conventional stem-only harvesting meant that all logging residues were left on the ground as a control. In the present study, only the four control plots at each site were used for model calibration.

Modelling of stand development

The development of tree biomass is described in detail in Ågren and Hyvönen (2003). Briefly, height development of pine and spruce trees was calculated from site indices using empirical growth functions (pine: Elfving & Kiviste (1997), spruce: Hägglund (1972, 1973)). The height growth was then fed into empirical stand basal area development functions (pine: Elfving & Norgren (1993), spruce: Eriksson (1976)). At harvests, both stand density and basal area were reduced in the same proportion. The stand density and mean diameters of the trees were combined with the allometric functions given by Marklund (1988) to calculate the standing biomass of different tree parts for each year during a rotation period. In our experience, these functions over-estimate the biomass of branches and needles in dense stands as those in our study sites. The biomass of each of these fractions was therefore reduced by

branches was lost as litter each year according to Ågren et al. (2007).

Modelling soil C, N and Ca dynamics

The part of the produced litter that is not lost during decomposition builds up the store of soil organic matter. In this study, the soil C, N and Ca stores are built up from litter produced by the forest stand following clear-felling and harvesting residues from the initial clear-felling and thinnings; the stores from the previous stand (in other studies labelled "old soil") was disregarded here. The decomposition rates of different litter fractions are estimated by the functions by Hyvönen and Ågren (2001); see also Ågren and Hyvönen (2003). The parameters used for defining these functions are initial litter quality (q_0), a constant decomposer carbon use efficiency (e_0), a basal temperature (latitude) dependent decomposer growth rate (u_0), a constant rate of decrease in litter quality (η_{11}), and a parameter β describing the relation between decomposer growth rate and substrate quality. Decomposers are also described by their nitrogen:carbon ratio (r_d). The substrate is not immediately accessible, but it takes a certain time (t_{max}) for the decomposers to invade a substrate completely. The fraction of a litter cohort remaining after a time t is then:

$$G_1(t, t_{max}, z) = \left[\frac{2}{t_{max}}\frac{1}{\alpha(1-z)}\left[(1+\alpha t)^{1-z} - \left(1 - \frac{t}{t_{max}}\right)\right]\right] + \left[\frac{2}{t_{max}^2}\frac{1}{\alpha^2(1-z)(2-z)}\left[1 - (1+\alpha t)^{2-z}\right]\right]$$
$$+ \left(1 - \frac{t}{t_{max}}\right)^2 t < t_{max} \tag{1}$$

$$G_2(t, t_{max}, z) = \frac{2}{t_{max}}\frac{1}{\alpha(1-z)}\left[(1+\alpha t)^{1-z}\right] + \left[\frac{2}{t_{max}^2}\frac{1}{\alpha^2(1-z)(2-z)}\left[[1+\alpha(t-t_{max})]^{2-z} - (1+\alpha t)^{2-z}\right]\right] t \geq t_{max} \tag{2}$$

50%. Björkroth and Rosén (1977) did not include stumps and coarse roots in their investigations although these tree parts contribute significantly to the total C, N and Ca content of trees. The amount of C in different tree parts was estimated by assuming that the content of C is 50% of biomass dry weight. Contents of N and Ca in above-ground tree parts were estimated by using information on element concentrations reported by Björkroth and Rosén (1977). The concentrations of N and Ca in coarse roots and stumps were adopted from Hellsten et al. (2009). In the model predictions, stumps were assumed to have the same concentrations of N and Ca as stem–wood. In the model, a certain fraction of the standing biomass of needles, fine roots and

where

$$z = \frac{1 - e_0}{\beta\eta_{11}e_0} \tag{3}$$

and

$$\alpha = \beta\eta_{11}u_0 q_0^\beta$$

For needles and fine roots, where $t_{max} = 0$, these expressions simplify considerably.

The dynamics of Ca and N are strongly linked to carbon during decomposition. Low nutrient availability in the litter leads to a lack of that nutrient and results in immobilisation. When the nutrient concentration in the litter exceeds a critical concentration,

the nutrient will be mineralised. Following Ågren and Bosatta (1998), the amount of a nutrient remaining per unit initial litter biomass can be estimated as

$$H_1(t, r_0, f_n, t_{max}) = \left[r_0 \left(1 - \frac{t}{t_{max}}\right)^2 + r_d G_1(t, t_{max}, z) \right] \\ - (r_d - r_0) G_1(t, t_{max}, z_2) \quad t < t_{max}$$

(4)

$$H_2(t, r_0, r_d, t_{max}) = r_d G_2(t, t_{max}, z) \\ - (r_d - r_0) G_1(t, t_{max}, z_2) \quad t \geq t_{max}$$

(5)

where r_0 is the initial litter nutrient to carbon ratio and

$$z_2 = \frac{1}{\beta \eta_{11} e_0}$$

(6)

Since Ca is in large excess in fresh litters in relation to the decomposers' need, we simplify the Ca dynamics during decomposition by assuming that the amount of Ca remaining in a litter cohort is simply its initial concentration (Ca_0) multiplied by the amount of remaining litter biomass.

The calculations of remaining carbon and nutrients are made by year for each litter component and each litter cohort separately such that the total soil carbon consists of the sum of remaining C and nutrients in litter cohorts of different ages and from different tree components. The list of the parameters used in the models is shown in Tables II and III.

Values for the initial nutrient concentrations in fresh needles, branches and stems were adopted from Björkroth and Rosén (1977). Fresh stumps were assumed to have the same concentrations as stems. The initial nutrient concentrations in fresh coarse roots at the southern sites (Tönnersjöheden and Kosta) were set to those observed in Asa (Hellsten et al., 2009) and for the stands in northern Sweden (Lund and Lövliden) to those observed at Svartberget by Hellsten et al. (2009) (Tables II and III).

Nutrient concentrations in needle litter have only been measured for spruce at Tönnersjöheden (B. Olsson, unpublished data). Nutrient concentrations tend to be lower in dead needles than in living needles due to translocation before abscission (Aerts, 1996). Nutrient concentrations in dead needles at the other sites were calculated from values in living needles by assuming that the same proportion of nutrients has been translocated before abscission as at Tönnersjöheden. Nutrient concentrations in living and dead fine roots (<2 mm) were set as for living and dead needles. The measured exchangeable stocks of Ca were assumed to be 50% of the total soil Ca stock.

The value of decomposer r_d for decomposing living and dead needles and woody parts, respectively, was set as for decomposing needles and branches as suggested by Hyvönen et al. (2000). The values of r_d are shown in Table III.

Treatments to be compared

The model will analyse the following treatments:

- S: stem-only harvest
- SSl: stem and slash (tops, branches and needles) harvest
- SSt: stem and stump (including coarse roots) harvest
- SSlSt: stem, slash and stump harvest

Results

Comparisons between predicted and measured stores of C, N and Ca in trees and soil

The amounts of C, N and Ca in different tree parts of the four stands were well predicted by the model (Figure 1). According to the model, stems including bark had the highest biomass, making 60–70% of the total biomass followed by the stump–root system (20%). Needles and living branches comprised 14–

Table II. List of parameters used in the model simulations.

Parameter	Meaning	Value
q_0	Initial quality of a substrate	1
e_0	Decomposer carbon use efficiency	0.25 for northern sites, 0.30 for southern sites
u_0	Basic decomposer growth rate	Depends on latitude
r_d	Concentration: C ratio in decomposers	
r_{0n}	Initial element-to-C ratio of a substrate	Substrate specific, n =N, Ca. See Table III
t_{max}	Time (years) required to invade the substrate	Needles/fine roots = 0 year, branches = 13 years, stems = 34 years, roots <5 cm = 13 years, roots >5 cm = 20 years, stumps = 34 years
η_{11}	Rate of decrease in quality	0.36
β	Shape of decomposer-quality response	7

Table III. Values of r_{0n} and r_d (mg nutrient/g C) for different decomposing tree part at the southern and northern sites (see Table I). Data on "live" biomass are from biomass investigations and "dead" is from litterfall studies.

		Needles	Fine roots	Branches	[d]Coarse roots >5 mm	[d]Coarse roots < 5 mm	Stem–wood	Stem–bark
Tönnersjöheden	r_d^a	105	105	40	40	40	40	40
Tönnersjöheden	r_{0N} live[b]	22.9	22.9	9.0	2.7	11.0	1.2	8.2
Tönnersjöheden	r_{0N} dead[c]	19.0	19.0	7.4	2.7	11.0	1.2	8.2
Tönnersjöheden	r_{0Ca} live[b]	8.3	8.3	5.6	3.0	4.5	1.1	5.3
Tönnersjöheden	r_{0Ca} dead[c]	13.0	13.0	3.4	3.0	4.5	1.1	5.3
Kosta	r_d^a	105	105	40	40	40	40	40
Kosta	r_{0N} live[b]	18.8	18.8	8.2	2.7	11.0	1.0	6.8
Kosta	r_{0N} dead[c]	17.0	17.0	5.4	2.7	11.0	1.0	6.8
Kosta	r_{0Ca} live[b]	6.4	6.4	7.2	3.0	4.5	1.4	14.4
Kosta	r_{0Ca} dead[c]	10.0	10.0	2.2	3.0	4.5	1.4	14.4
Lövliden and Lund	r_d^a	126	126	40	40	40	40	40
Lövliden and Lund	r_{0N} live[b]	18.0	18.0	6.4	2.6	7.4	1.2	6.4
Lövliden and Lund	r_{0N} dead[c]	14.0	14.0	3.4	2.6	7.4	1.2	6.4
Lövliden and Lund	r_{0Ca} live[b]	21.4	21.4	11.8	3.1	3.2	1.7	22.3
Lövliden and Lund	r_{0Ca} dead[c]	34.0	34.0	11.8	3.1	3.2	1.7	22.3

[a]Hyvönen et al. (2000).
[b]B. Olsson (pers. comm.).
[c]B. Olsson (pers. comm.).
[d]Hellsten et al. (2009).

24% of the total tree biomass and fine roots about 1% of the total biomass of the trees (Table IV).

The distribution of N and Ca in different tree parts differed from that of the biomass (C) as these elements were more equally allocated to stems, canopy structures and below-ground biomass than C. Of the total N stock of the trees, 35–37% was allocated in needles and branches, 19–35% was allocated in the stump–root system and 22–41% in stem–wood and stem–bark. Stems and bark had the
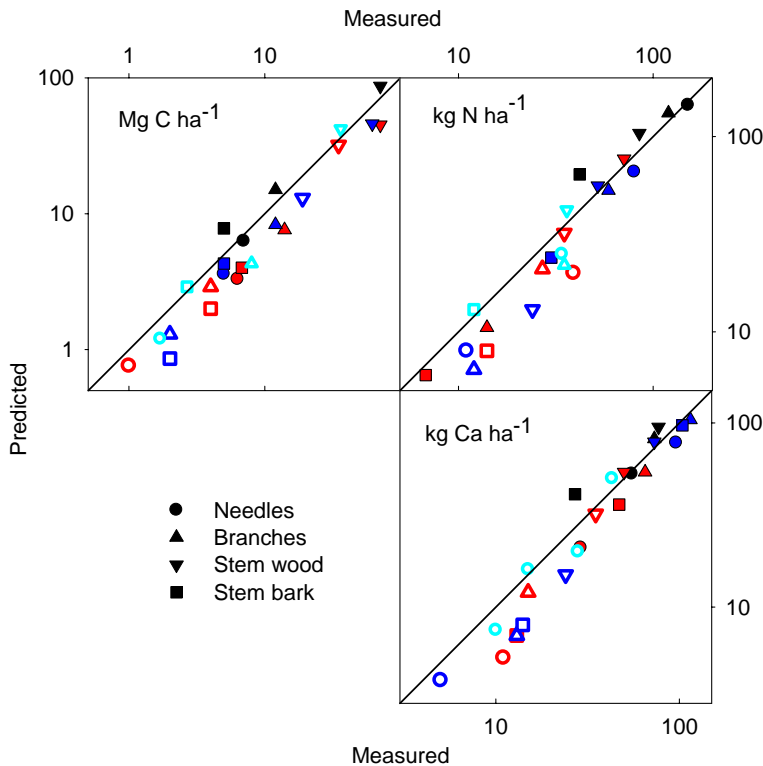

Figure 1. Measured vs. predicted amounts of C, N and Ca in different tree parts at clear-felling. Tree parts from Tönnersjöheden, Kosta, Lövliden and Lund are denoted by black, red, dark blue and light blue symbols, respectively.

Table IV. Predicted stores of C, N and Ca in different tree parts in the control plots (S) at the experimental sites (see Table I) at harvesting.

	Needles	Fine roots <2mm	Branches	Coarse roots >5mm	Coarse roots 2–5mm	Stump	Stem–wood	Stem–bark	Total
				C (Mg ha^{-1})					
Tönnersjöheden	6	2	15	21	6	10	87	8	155
Kosta	4	1	11	17	5	9	76	6	129
Lövliden	4	1	10	14	4	7	59	5	104
Lund	1	0.4	4	8	3	5	42	3	66.4
				N (kg ha^{-1})					
Tönnersjöheden	145	48	132	192	54	12	104	64	751
Kosta	82	27	83	103	30	9	77	36	447
Lövliden	74	25	59	79	25	8	68	32	370
Lund	25	8	22	14	6	5	42	13	135
				Ca (kg ha^{-1})					
Tönnersjöheden	53	17	82	64	27	11	95	41	390
Kosta	25	8	65	39	17	11	94	66	325
Lövliden	82	27	105	41	13	11	94	105	478
Lund	8	2	20	11	4	6	50	16	117

highest Ca stocks in the trees (35–56%), followed by needles and branches (24–39%) and stumps and roots (14–26%). The distribution of C, N and Ca was also different between Norway spruce and Scots pine, as the needle biomass was higher in spruce than pine. Consequently, pine trees had a larger proportion of the biomass in stems than spruce (Table IV).

The predicted stocks of soil C at Kosta, Lövliden and Lund at the time of harvesting were lower than the measured stocks of humus layer C, but at Tönnersjöheden the predicted C stock was fairly similar to the measured amount of C (Table V). The predicted soil N stocks were slightly higher than those measured at all sites. The soil pool of Ca was not measured at the clear-felling in 1974 (Figure 2, Table V).

The predicted soil C and N stocks 16 years after clear-felling were higher than the measured stocks in the humus layer at three sites (with Kosta as an exception). There was no clear trend in similarities or differences between the predicted and measured
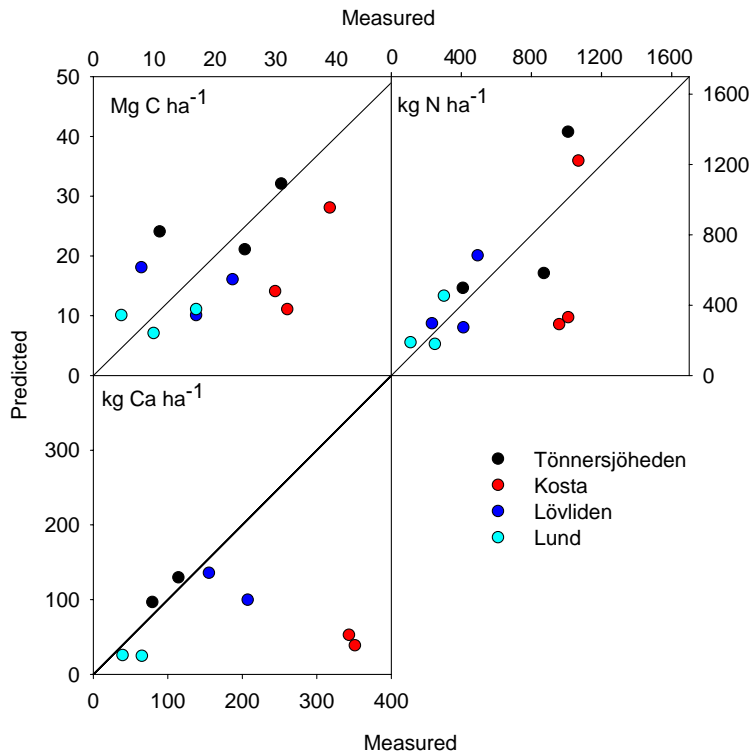

Figure 2. Measured vs. predicted amounts of C and N in the humus layer at clear-felling and at 16 and 27 years after clear-felling. Ca was estimated only after 16 and 27 years (two values per site).

Table V. Predicted (P) and measured (M) amounts (only humus layer) of C, N and Ca in soil at clear-felling and after 16 and 27 years within the regenerating stand in the control plots.

	At clear-felling			16 years after clear-felling			27 years after clear-felling		
	Predicted	Measured	P/M	Predicted	Measured	P/M	Predicted	Measured	P/M
				C (Mg ha^{-1})					
Tönnersjöheden	32	31	1.03	24	11	2.18	21	25	0.84
Kosta	28	39	0.72	14	30	0.47	11	32	0.34
Lövliden	16	23	0.70	18	8	2.25	10	17	0.59
Lund	11	17	0.65	10	5	2.00	7	10	0.70
				N (kg ha^{-1})					
Tönnersjöheden	1383	1012	1.37	495	412	1.20	579	874	0.66
Kosta	1219	1017	1.20	288	962	0.30	328	1013	0.32
Lövliden	680	496	1.37	293	236	1.24	270	415	0.65
Lund	450	304	1.48	185	113	1.64	176	252	0.70
				Ca (kg ha^{-1})					
Tönnersjöheden	305			96	80	1.20	129	115	1.12
Kosta	214			38	352	0.11	52	344	0.15
Lövliden	372			135	156	0.87	99	208	0.48
Lund	65			25	40	0.63	24	66	0.36

stores of Ca. Twenty-seven years after the clear-felling, the predicted humus layer stores of all elements were lower than the measured ones at all sites except Tönnersjöheden. The difference between the measured and predicted humus stores of all elements was highest at Kosta. Sixteen and 27 years after clear-felling, the predicted stocks of all elements were considerably lower than measured at Kosta.

Predicted effect of harvesting slash and stumps

The model predicted that 27 years after clear-felling, the highest reduction in soil C, N and Ca stocks as compared with the stem-only harvesting (S) would be observed when both stumps and slash (SSlSt) were removed (Table VI). Furthermore, the relative reduction was higher at sites of low productivity (Lund and Lövliden) than at high productivity sites (Kosta and Tönnersjöheden). In comparison with S, harvesting of stumps (SSt) reduced soil C stores more than harvesting of slash (SSl). The effects of harvesting of slash and stumps on soil N and Ca stores were different in the Scots pine and Norway spruce stands. Soil N and Ca stocks were on the same level after harvesting of slash (SSl) and after stump harvesting (SSt) in the Scots pine stands. In the Norway spruce stand, harvesting of slash (SSl) resulted in lower stores of N and Ca in soil than after harvesting of stumps (SSt).

The dynamics of soil C derived from the decomposing logging residues and litter from the growing forest is shown in Figure 3. In general, the soil C

Table VI. Predicted soil C, N and Ca stores in relation to the stores in the stem-only harvesting scenario (S) 27 years after clear-cutting.

	Lund Fraction of S	Kosta Fraction of S	Lövliden Fraction of S	Tönnersjöheden Fraction of S
		Soil C		
S	1	1	1	1
SSl	0.86	0.91	0.75	0.9
SSt	0.71	0.73	0.58	0.81
SSlSt	0.57	0.64	0.42	0.67
		Soil N		
S	1	1	1	1
SSl	0.83	0.88	0.62	0.77
SSt	0.80	0.80	0.78	0.84
SSlSt	0.63	0.71	0.40	0.60
		Soil Ca		
S	1	1	1	1
SSl	0.83	0.91	0.62	0.85
SSt	0.88	0.92	0.89	0.91
SSlSt	0.71	0.85	0.52	0.76

SSl: removal of stems and slash; SSt: removal of stems, stumps and coarse roots; SSlSt: removal of stems, slash, stumps and coarse roots.
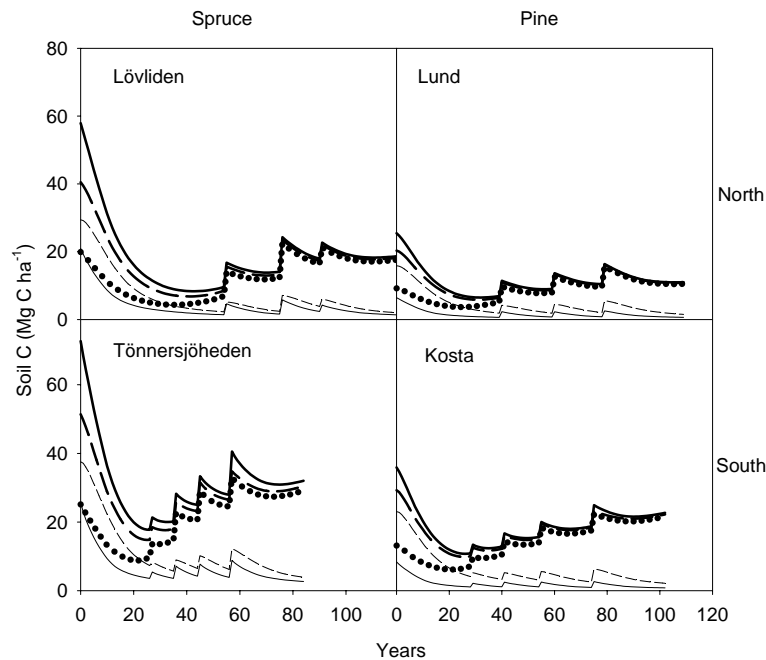
Figure 3. Predicted soil C (Mg ha^{-1}) development at Norway spruce and Scots pine sites in southern and northern Sweden at different harvesting scenarios. Thick lines show total soil C stores: (1) stem only harvesting (S, solid line); (2) harvest of stems, tops, branches and needles (SSl, broken line); (3) harvest of all logging residues including stumps and coarse roots (SSlSt, dotted line). Thin lines show soil C stores in separate fractions of harvesting residues when left at site; (4) slash only (thin solid line); and (5) stumps and coarse roots only (thin broken line).

storage was lower in the Scots pine stands than in the Norway spruce stands, but all stands showed a significant initial decrease in soil C stocks with increasing biomass harvesting. The differences were more long-lasting at the low productive sites than at the high productive sites. In addition, the differences decreased markedly after the first thinning for both tree species irrespective of stand productivity level and levelled off with time. The harvesting of stumps and coarse roots decreased the soil C storage more than harvesting of needles and branches, because the mass of stumps and coarse roots was higher than the mass of needles and branches at clear-cutting.

In contrast to C, where decomposition caused a gradual decrease, the dynamics of N in the residues and litters showed both strong immobilisation as well as rapid net mineralisation. In particular, the N dynamics in needles and branches differed markedly from the dynamics in stumps and coarse roots (Figure 4). There was initially a phase of immobilisation in stumps and coarse roots, while the net release of N started immediately from needles and branches. The immobilisation of N in stumps and coarse roots almost balanced the net N mineralisation from needles and branches.

The model predicted a higher rate of net N mineralisation under a longer period for Norway spruce than for Scots pine, and this was due to the larger biomass of needles and branches in Norway spruce. Moreover, the N dynamics differed markedly depending on which tree parts were harvested. In the stem-only harvesting scenario, when all logging residues and stumps were left on site, the net mineralisation of N increased slowly initially but culminated about 10 years after clear-cutting in all stands (Figure 4), probably because parts of the N mineralised from the needles will be immobilised in the coarse wood from stumps and roots, which initially led to lower net N release. If, on the other hand, stumps and roots were harvested but slash remained on site (SSt), a pronounced net N release from the residues started immediately. The lowest net N release during the first years following clear-felling occurred when tops and branches but not stumps were harvested (SSl). With time, these differences in release dynamics between C and N disappeared and the dynamics of C and N showed similar trends.

The release of Ca from needles and branches was more pronounced than from stumps and coarse roots (Figure 5). There was also a difference between tree species as the rate of Ca release from harvesting residues of Norway spruce was considerable higher than of Scots pine. The increasing intensity of harvesting of logging residues decreased the rate of Ca release, but the difference between the harvesting scenarios was considerably lower than for N.
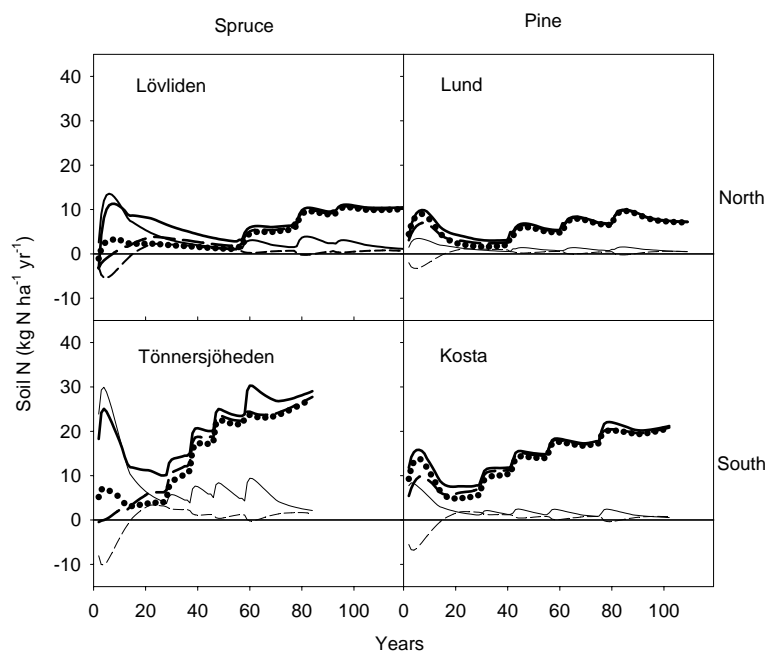
Figure 4. Predicted soil net N mineralisation (kg N ha^{-1} yr^{-1}) at Norway spruce and Scots pine sites in southern and northern Sweden at different harvesting scenarios. For explanation of thick and thin lines, see Figure 3.

Discussion

Measured vs. predicted C and N stocks

The test of the model's ability to predict stocks of C and N in agreement with measured stocks showed greater deviations for the soil sub-model than the stand sub-model. An explanation of the greater deviations in the soil sub-model is at least partly a result of differences between what was included in measured and predicted stores. One cause of the lower C stocks according to predictions than found by observations by Björkroth and Rosén (1977) at the time of clear-felling is that the model did not include litter produced by the understorey vegetation. This effect should have been less marked at Tönnersjöheden, as understorey vegetation is typically less developed in the dense spruce forests in southern Sweden than in pine forests and in sparse spruce forests in the boreal zone. This explanation is also supported by the fact that the deviation between predicted and measured stocks was the least at Tönnersjöheden. Another explanation is that the measured soil pools contained C and N older than the stand itself, which were by definition not included in the model. This explanation may be of particular significance at the Kosta site, which not only showed the greatest difference between predicted and measured soil stocks for all elements, but also had the greatest C, N and Ca stocks in the humus layer of all sites.

In contrast to the situation at the time of clear-felling, the predicted soil C and N stocks 16 years after clear-felling were higher than the measured stocks at three sites, with Kosta as an exception. Coarse woody litter was not included in the field samplings, but remaining logging residues are a part of the model soil C stock. This discrepancy in definition of compartments is the likely explanation to the difference between predicted and measured stocks. For Ca, there was no clear trend between the predicted and measured stocks, and for soil N stocks, the predicted and measured stocks were closer than for the soil C stores at this time.

In the latest soil sampling, 27 years after clear-felling, predicted soil C and N stores were again lower than the measured ones. At this time, most of the slash material remaining was most likely included in the soil sampling. However, input of litter from the field-layer vegetation was not included in the model simulations.

The predicted soil Ca store was consistently lower than the measured store both at 16 and 27 years after clear-felling, with Tönnersjöheden being the exception. This result is difficult to explain because of the lack of clear trends between the sites or investigation occasions. A systematic underestimation of soil Ca stocks was perhaps introduced because we have assumed for the calculation of the soil Ca stocks that the measured,
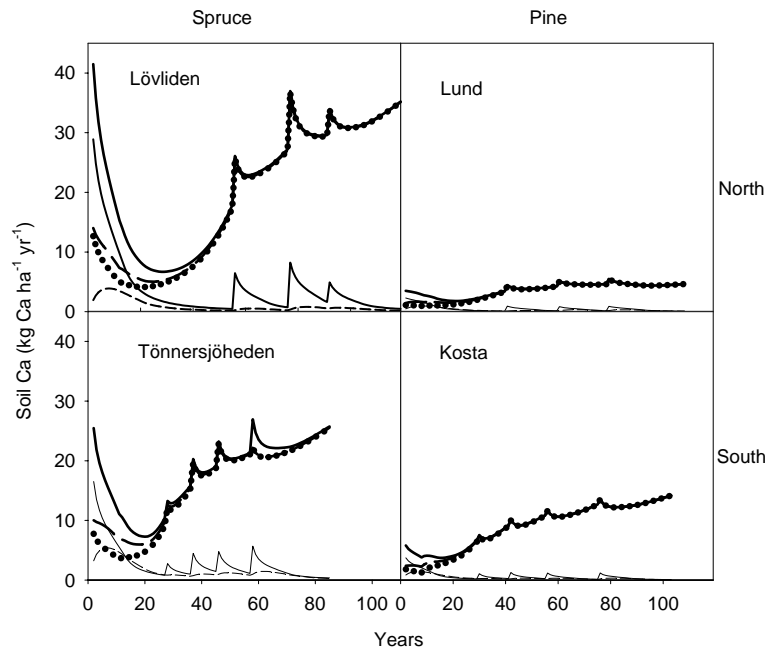
Figure 5. Predicted soil Ca release (kg Ca ha^{-1} yr^{-1}) at Norway spruce and Scots pine sites in southern and northern Sweden at different harvesting scenarios. For explanation of thick and thin lines, see Figure 3.

exchangeable stocks of Ca represents 50% of the total Ca stock.

Carbon dynamics

In the present study, soil C stocks were predicted to decrease rapidly following clear-felling as a consequence of decomposition of logging residues. The C stocks reached its lowest values at stand ages of 20–30 years and increased thereafter. This general pattern is similar to Covington's (1981) chronosequence study of forest floor dynamics of hardwood forests in north-eastern United States. The predicted decrease in C stocks following clear-felling also agree with measured changes in C stock of the humus layer at the four study sites during the first 16 years (Olsson et al., 1996b). Furthermore, Brandtberg and Olsson (2012) observed increasing humus C stocks over the following stand age period, 16–27 years. However, this increase was probably overestimated, because the later sampling of the humus layer included the uppermost mineral soil. The difficulty to correctly separate the organic horizon from the mineral soil is a well-known problem in longitudinal studies (e.g. Yanai et al., 2003). It should also be remembered that the predicted and the measured soil C stocks did not include the same soil compartments.

Inevitable, an increasing intensity of harvesting biomass leads to an instant decrease in the C stock of soil organic matter and litter. However, a relevant question is in what time perspective such effects

persist and if there are negative or positive feedback mechanisms between soil processes and tree growth. In the present study, harvesting of slash was predicted to cause moderately lower soil C stocks at the time of soil C minimum (stand age 20–30 years), and the additional extraction of stumps caused an even more substantial loss in soil C. However, no general effect of slash harvesting on soil C stocks have been measured at the study sites (Brandtberg & Olsson, 2012; Olsson et al., 1996b), and there is little evidence from other empirical studies that slash harvesting significantly reduces soil C stocks (e.g. Johnson & Curtis, 2001; Thiffault et al., 2011). On the other hand, Strömgren et al. (2012) examined four coniferous forest sites in Sweden 25 years after clear-felling and found that the combination of slash harvesting and stump extraction had caused a 12% reduction of the soil C stock.

At the end of the rotation period, the effect of slash or stump harvesting was predicted to have caused only small differences in soil C stocks. The effects also seemed fairly small compared with other model predictions, spanning over longer periods. Peng et al. (2002) compared the effects of slash harvest over several rotation periods in the boreal zone by running the Century model and estimated carbon losses in the order of 32% over 500 years. Bengtsson and Wikström (1993) predicted <10% C losses in total soil organic matter due to slash harvesting, over 300 years. Ågren and Hyvönen (2003) predicted effects of slash harvesting for the

national C stocks of Sweden and found a decrease in soil C of ca. 10% after 150 years.

One reason as to why the predicted effects of slash and stump harvesting diminish at the end of the rotation period is that the model had no feedback link between nutrient supply and tree growth. Empirical studies indicate that this is a simplification that may lead to an underestimating of the long-term effects on soil C stocks. A number of studies have shown that harvesting of slash at thinnings or at clear-fellings reduce forest growth, and this was also shown for the study sites of the present studies (Egnell, 2011; Egnell & Leijon, 1997; Egnell & Valinger, 2003; Jacobson et al., 2000). At Lövliden, this reduction in relative growth rates levelled off after ca. 20 years and Egnell (2011) therefore concluded that the growth reduction was not permanent. However, the effect of stump harvesting on tree growth is less clear (e.g. Strömgren et al., 2012).

Nitrogen dynamics

The dynamics of N in plant litters depended to a large extent on the initial N concentrations in combination with the decomposition rate. The nutrient-rich slash and the nutrient-poor stump biomass differ markedly with respect to these characteristics. As a consequence, the predicted N dynamics in the stumps was characterised by a substantial initial N immobilisation followed by a long-term mineralisation phase of N, in marked contrast to the N dynamics of the slash. This result may have important implications for the ambitions to reduce nitrogen leaching following clear-felling in practical forestry, indicating that the dynamics of N in stump biomass in conventional forestry should not be overlooked. We thus expect the lowest levels of leaching after clear-felling when slash and stems are harvested but stumps are left on site. In contrast, N leaching following clear-felling or disturbance is expected to be large if slash remains on site but stumps are harvested. This alternative is not a common practice today in Sweden or Finland. However, severe storm damages have the potential to result in similar situations if trees are uprooted and the slash is left for, e.g. practical reasons. Staaf and Olsson (1994) also observed low inorganic N concentrations in soil water following clear-felling in the SSl treatment, but peaks of high nitrate concentrations when slash was left on site or in spots disturbed by stump extraction.

Calcium dynamics

The theory on decomposition by Ågren and Bosatta (1998) has previously only been applied for the elements C, N, P and S, based on the binding properties in organic matter and their key role in organism growth. The metal cations, albeit essential to organisms, show more varying binding properties, and their release upon decomposition may not be strictly associated with microbial degradation and turnover. However, the Ca ion is an exception, since major parts of Ca in plant biomass are complex—bound in plant cell walls or excreted as insoluble, organic Ca-oxalate. Microbial consumption of cell walls or oxalate is therefore the most likely agent of Ca release, although the term mineralisation is not strictly applicable.

The predicted dynamics of Ca indicated that slash is a more important source of Ca release following clear-felling than stumps. Harvesting of slash will thus cause a substantial reduction in the release of Ca after harvesting, and additional stump harvesting will have fairly little effect. The Ca stocks in the harvested stand vary greatly, but in the present study site productivity was little reflected in Ca stocks. The large Ca amounts in the biomass at Lövliden were due to a relatively high Ca saturation in the soil, slow growth rate in combination with old age. The uptake of Ca is passive, determined by transpiration, typically in excess of physiological needs and therefore trapped in extracellular structures.

The predicted Ca dynamics indicated that the litter production of the new stand will gradually diminish the differences between the harvesting regimes. However, this was basically as a result of both Ca concentrations in biomass and the tree growth rate not being affected by harvesting treatments. Experimental evidence from the study sites indicate that this is not the case, at least not in the short-term perspective of ca. 20–25 years, as both tree growth rate (Egnell 2011; Egnell & Leijon 1997; Egnell & Valinger 2003) and Ca concentration in foliage and other biomass components in the following stand are reduced after slash harvesting (Olsson et al., 2000).

Conclusions

Most of the decline in soil C stocks after harvesting of logging residues was offset by the litter production of the following forest stands by the time of first thinning in the low productive stands, while in the high productive stands slightly lower stores were observed during the entire rotation period, given that no decline in biomass production has occurred.

Stumps and coarse roots are important to N retention after final felling due to their high capacity to immobilise N. Harvesting of stumps and coarse roots increase the risk of N leaching as long vegetation is absent after final felling.

Needles and branches are important to Ca release, and the initial differences after harvesting of logging residues are compensated by the litter production of the growing forest stand, given that no decline in biomass production or concentration in litter has occurred.

Acknowledgements

References

Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology, 84,* 597–608.

Ågren, G. I. & Bosatta, E. (1998). *Theoretical ecosystem ecology— Understanding element cycles.* Cambridge: Cambridge University Press.

Ågren, G. I. & Hyvönen, R. (2003). Changes in carbon stores in Swedish forest soils due to increased biomass harvest increased temperatures analyzed with a semi-empirical model. *Forest Ecology and Management, 174,* 25–37.

Ågren, G. I., Hyvönen, R. & Nilsson, T. (2007). Are Swedish forest soils sinks or sources for CO_2—Model analyses based on forest inventory data. *Biogeochemistry, 82,* 217–227.

Akselsson, C., Westling, O., Alveteg, M., Thelin, G., Fransson, A.-M. & Hellsten, S. (2008). The influence of N load and harvest intensity on the risk of P limitation in Swedish forest soils. *Science of the Total Environment, 404,* 284–289.

Akselsson, C., Westling, O., Sverdrup, H., Holmqvist, J., Thelin, G., Uggla, E., et al. (2007). Impact of harvest intensity on long-term base cation budgets in Swedish forest soils. *Water Air Soil Pollution Focus, 7,* 201–210.

Bengtsson, J. & Wikström, F. (1993). Effects of whole-tree harvesting on the amount of soil carbon: Model results. *New Zealand Journal of Forestry Science, 23,* 380–389.

Björheden, R. (2006). Drivers behind the development of forest energy in Sweden. *Biomass Bioenergy, 30,* 289–295.

Björkroth, G. & Rosén, K. (1977). Biomass and amounts of nutrients in four sites. Projekt Helträdsutnyttjande, Stockholm. Rapport 5 No. 49. 20 pp. Umeå: Swedish University of Agricultural Sciences (in Swedish).

Brandtberg, P.-O. & Olsson, B. A. (2012). Changes in the effects of whole tree harvesting on forest floor and soil chemistry during early stand development in Norway spruce and Scots pine stands in Sweden. *Forest Ecology and Management, 277,* 150–162.

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

Egnell, G. (2011). Is the productivity decline in Norway spruce following whole-tree harvesting in the final felling in boreal Sweden permanent or temporary? *Forest Ecology and Management, 261,* 148–153.

Egnell, G. & Leijon, B. (1997). Effects of different levels of biomass removal in thinning on short-term production of *Pinus sylvestris* and *Picea abies* stands. *Scandinavian Journal of Forest Research, 12,* 17–26.

Egnell, G. & Valinger, E. (2003). Survival, growth, and growth allocation of planted Scots pine trees after different levels of biomass removal in clear-felling. *Forest Ecology and Management, 177,* 65–74.

Elfving, B. & Kiviste, A. (1997). Construction of site index equations for *Pinus sylvestris* L. using permanent plot data in Sweden. *Forest Ecology and Management, 98,* 125–134.

Elfving, B. & Norgren, O. (1993). Volume yield superiority of lodgepole pine compared to Scots pine in Sweden. In: D. Lindgren (Ed.), *Pinus contorta—From untamed forest to domesticated crop,* pp. 69–80. Umeå: Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, Report 11.

Eriksson, H. (1976). *Yield of Norway spruce in Sweden.* Report No. 41. Stockholm: Department of Forest Yield Research, Royal College of Forestry (in Swedish, summary in English).

Hägglund, B. (1972). *Site index curves for Norway spruce in northern Sweden.* Report No. 21. Stockholm: Department of Forest Yield Research, Royal College of Forestry (in Swedish, summary in English).

Hägglund, B. (1973). *Site index curves for Norway spruce in southern Sweden. Report No. 24.* Stockholm: Department of Forest Yield Research, Royal College of Forestry (in Swedish, summary in English).

Hellsten, S., Helmisaari, H.-S., Melin, Y., Skovsgaard, J. P., Wängberg, I., Kaakinen, S., et al. (2009). *Halter av baskatjoner, fosfor och kväve i stubbar i Sverige, Danmark och Finland.* Rapport B 1855. Stockholm: IVL (in Swedish, English summary).

Helmisaari, H.-S., Holt Hanssen, K., Jacobson, S., Kukkola, M., Luiro, J., Saarsalmi, A., et al. (2011). Logging residue removal after thinning in Nordic boreal forests: Long-term impact on tree growth. *Forest Ecology and Management, 261,* 1919–1927.

Hope, G. D. (2007). Changes in soil properties, tree growth, and nutrition over a period of 10 years after stump removal and scarification on moderately coarse soils in interior British Columbia. *Forest Ecology and Management, 242,* 625–635.

Hyvönen, R. & Ågren, G. I. (2001). Decomposer invasion rate, decomposer growth rate, and substrate chemical quality: How they influence soil organic matter turnover. *Canadian Journal of Forest Research, 31,* 1594–1601.

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

Jacobson, S., Kukkola, M., Mälkönen, E. & Tveite, B. (2000). Impact of whole-tree harvesting and compensatory fertilization on growth of coniferous thinning stands. *Forest Ecology and Management, 129,* 41–51.

Johnson, D. W. & Curtis, P. S. (2001). Effects of forest management on soil C and N storage: Meta analysis. *Forest Ecology and Management, 140,* 227–238.

Lindholm, E.-L., Berg, S. & Hansson, P.-A. (2011). Greenhouse gas balance of harvesting stumps and logging residues for energy in Sweden. *Scandinavian Journal of Forest Research, 26,* 586–594.

Marklund, L. G. (1988). *Biomassafunktioner för tall, gran och björk i Sverige* (Biomass functions for pine, spruce and birch in Sweden). Report 45. Umeå: Department of Forest Survey. Swedish University of Agricultural Sciences (in Swedish), ISBN 91-576-3524-2.

Nave, L. E., Vance, E. D., Swanston, C. W. & Curtis, P. S. (2010). Harvest impacts on soil carbon storage in temperate forests. *Forest Ecology and Management, 259,* 857–866.

Olsson, B. A., Bengtsson, J. & Lundkvist, H. (1996a). Effects of different forest harvest intensities on the pools of

exchangeable cations in coniferous forest soils. *Forest Ecology and Management*, 84, 135–147.

Olsson, B. A., Lundkvist, H. & Staaf, H. (2000). Nutrient status in needles of Norway spruce and Scots pine following harvesting of logging residues. *Plant and Soil*, 223, 161–173.

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

Peng, C., Jiang, H., Apps, M. J. & Zhang, Y. (2002). Effects of harvesting regimes on carbon and nitrogen dynamics of boreal forests in central Canada: A process model simulation. *Ecological Modelling*, 155, 177–189.

Petersson, H. & Ståhl, G. (2006). Functions for below-ground biomass of *Pinus sylvestris, Picea abies. Betula pendula* and *Betula publescens* in Sweden *Scandinavian Journal of Forest Research*, 21, 84–93.

Pihl Karlsson, G., Akselsson, C., Hellsten, S. & Karlsson, P. E. (2011). Reduced European emissions of S and N—Effects on air concentrations, deposition and soil water chemistry in Swedish forests. *Environmental Pollution*, 159, 3571–3582.

Repo, A., Tuomi, M. & Liski, J. (2011). Indirect carbon dioxide emissions from producing bioenergy from forest harvest residues. *Global Change Biology Bioenergy*, 3, 107–115.

Smolander, A., Levula, T. & Kitunen, V. (2008). Response of litter decomposition and soil C and N transformations in a

Norway spruce thinning stand to removal of logging residue. *Forest Ecology and Management*, 256, 1080–1086.

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

Strömgren, M., Egnell, G. & Olsson, B. A. (2012). Carbon stocks in four forest stands in Sweden 25 years after harvesting of slash and stumps. *Forest Ecology and Management*. doi: 10.1016/j.foreco.2012.06.052.

Tamm, C. O. (1991). *Nitrogen in terrestrial ecosystems. Ecological Studies*, vol. 81, p. 115. Berlin: Springer-Verlag.

Thiffault, E., Hannam, K. D., Paré, D., Titus, B. D., Hazlett, P. W., Maynard, D. G., et al. (2011). Effects of forest biomass harvesting on soil productivity in boreal and temperate forests — A review. *Environmental Reviews*, 19, 278–309.

Walmsley, J. D. & Godbold, D. L. (2010). Stump harvesting for bioenergy – A review of the environmental impacts. *Forestry*, 83, 17–38.

Yanai, R. D., Currie, W. S. & Goodale, C. L. (2003). Soil carbon dynamics after forest harvest: An ecosystem paradigm reconsidered. *Ecosystems*, 6, 197–212.

Zabowski, D., Chambreau, D., Rotramel, N. & Thies, W. G. (2008). Long-term effects of stump removal to control root rot on forest soil bulk density, soil carbon and nitrogen content. *Forest Ecology and Management*, 255, 720–727.