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ORIGINAL PAPER

Estimation of nutrient removals in stem-only and whole-tree harvesting of Scots pine, Norway spruce, and birch stands with generalized nutrient equations

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Abstract Whole-tree harvesting (WTH), where logging residues are removed in addition to stems, is widely practised in Fennoscandian boreal forests. WTH increases the export of nutrients from forest ecosystems. The extent of nutrient removals may depend on tree species, harvesting method, and the intensity of harvesting. We developed generalized nutrient equations for Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* Karsten), and birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) stands to be able to calculate the amounts of nitrogen, phosphorus, potassium, and calcium in stems and above-ground biomass (stem and crown) as a function of stand volume. The equations were based on Fennoscandian literature data from 34 pine, 26 spruce, and 5 birch stands, and they explained, depending on the tree species and nutrient, 61–99% and 56–87% of the variation in the nutrient amounts of stems and above-ground biomass, respectively. The calculations based on the equations showed that nutrient removals caused by stem-only harvesting (SOH) and WTH per harvested stem m^3 were smaller in pine than in spruce and birch stands. If the same volume of stem is harvested, nutrient removals are, in general, nearly equal at thinnings and final cuttings in SOH, but larger in thinnings than final cuttings in WTH. If the principal aim is to minimize the nutrient removals per harvested stem m^3, the harvesting should be done at mature pine stands. The effect of biomass removal on overall site nutrient status depends on site-specific factors such as atmospheric deposition, weathering of minerals, and the size of the nutrient pools in the soil.

Keywords Calcium · Clear-cutting · Crown · Nitrogen · Phosphorus · Potassium · Stem wood · Thinning · Whole-tree harvesting

Introduction

The substitution of fossil fuels with renewable energy sources increases the use of forest biomass for energy production (European Commission 1997). Finland and Sweden have become leading countries in Europe regarding the utilization of wood-based energy in 2000s (Asikainen et al. 2008; Röser et al. 2008), and the use of forest energy is expected to further increase in the next decades (Björheden 2006; Hakkila 2006). In Finland, for example, the annual consumption of forest chips has increased from 1 million solid m^3 to 5 million solid m^3 during the past 10 years (Peltola 2009), and the objective of Finland's National Forest Programme 2015 is to increase the annual use of forest chips to 13 million solid m^3 by 2015. Energy wood is harvested at all stages of forest development, in final fellings, thinnings, and tending of seedling stands. Forest chips are produced from logging residues, roundwood, stumps, and small diameter trees. Currently, the logging residues from clear-cut areas are the largest source for forest chips (Peltola 2009).

Intensive biomass harvesting increases the export of nutrients from forests, as a result soil nutrient pools (Olsson et al. 1996a, b; Saarsalmi et al. 2010) and later on also tree

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growth (Jacobson et al. 2000; Egnell and Valinger 2003) may decrease. Particularly whole-tree harvesting (WTH), where all the above-ground biomass (stem and crown) is removed, can substantially increase nutrient losses compared with stem-only harvesting (SOH) where only the stem is removed (Mälkönen 1972; Nykvist 1974; Björkroth and Rosén 1977; Finér et al. 2003). Nutrient balance calculations indicate that in many cases, nutrient removals by WTH exceed the replenishment rate of plant-available nutrient pools in soil by mineral weathering and atmospheric deposition (Olsson et al. 1993; Sverdrup and Rosen 1998; Joki-Heiskala et al. 2003; Akselsson et al. 2007; Raulund-Rasmussen et al. 2008). This contravenes the principles of sustainable forest management where the productive capacity of forest ecosystems has to be maintained (Raulund-Rasmussen et al. 2008). In Fennoscandian boreal forests on upland mineral soils, WTH affects first nitrogen (N) supply and on peatlands, the phosphorus (P) and potassium (K) supply since upland forests are mostly N limited (e.g., Nohrstedt 2001) and those of peatlands P and K limited (e.g., Paarlahti et al. 1971). In addition, nutrient balance calculations also suggest that in many parts of Fennoscandia, WTH can result in net losses of base cations (K and Ca) (Sverdrup and Rosen 1998; Joki-Heiskala et al. 2003; Akselsson et al. 2007).

The magnitude of nutrient removals depends on the harvesting method, the developmental stage of the stand, and the tree species. WTH causes greater nutrient removals than SOH because nutrient concentrations are generally higher in foliage and branches than in stems (Mälkönen 1974; Mälkönen and Saarsalmi 1982; Kubin 1983; Finér 1989). The developmental stage of the stand, in turn, affects biomass allocation and nutrient contents (Mälkönen 1974; Helmisaari 1995; Augusto et al. 2000). The proportion of nutrient-rich crown and bark out of the total biomass decreases as a stand ages (Albrektson 1980; Hakkila 1989; Vanninen et al. 1996) and accordingly also the nutrient amount per unit of stem and total biomass (Augusto et al. 2000). Nutrient concentrations (Finér 1989; Alriksson and Eriksson 1998) and the patterns of biomass production and allocation also differ between tree species (Björkroth and Rosén 1977; Hakkila 1989; Finér et al. 2003). Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* Karsten), and birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) are the dominant tree species in Fennoscandian forests. Birch generally has higher nutrient concentrations than pine or spruce (Finér 1989; Alriksson and Eriksson 1998). Spruce, in turn, allocates a greater proportion of biomass to its crown than pine or birch (Hakkila 1989; Kärkkäinen 2005; Repola 2009).

The amount of nutrients bound in tree biomass has been estimated by calculating the biomass of different tree fractions with biomass equations and multiplying them by the corresponding nutrient concentrations (Nihlgård 1972; Mälkönen 1974; Mälkönen and Saarsalmi 1982; Finér 1991; Brække and Håland 1995). These calculations have first been done on the tree level, and thereafter, the stand-level calculations have been done by summing up the nutrient content of the individual trees. The determination of the amounts of nutrients bound in tree biomass in such a way is time consuming and expensive. An easier and less laborious way to estimate accumulated nutrient amounts is to use nutrient equations, in which nutrient content of trees is predicted by tree height, breast height diameter, or tree biomass (Jokela et al. 1981; Laiho 1997; Ingerslev and Hallbäcken 1999; Augusto et al. 2000; Ponette et al. 2001; Raulund-Rasmussen et al. 2008; Stupak et al. 2008). So far, most of the existing nutrient equations have been developed for temperate forests; they are site specific or applicable only for single trees (Jokela et al. 1981; Ingerslev and Hallbäcken 1999; Ponette et al. 2001; Stupak et al. 2008). Since the utilization of forest biomass is increasing in Fennoscandian boreal forests, there is a need for generalized easy to use stand-level nutrient equations for estimating the nutrient removals in different harvesting operations. Nutrient equations form a base for nutrient balance calculations, and they are useful for forest managers in adjusting forest management strategies to the resiliency of the site concerned and in evaluating the need for fertilization. Nutrient equations based on the relationships between stand volume, which is a commonly estimated stand characteristic, and the nutrient content in stems and the whole above-ground stand biomass would provide a good tool for estimating nutrient removals in SOH or WTH. Data from several individual studies in boreal forests can be utilized for making such nutrient equations (e.g., Holmén 1964; Nihlgård 1972; Mälkönen 1974; Nykvist 1974; Lehtonen 1978; Mälkönen and Saarsalmi 1982; Finér 1991; Brække and Håland 1995; Ukonmaanaho et al. 2008).

The aim of this study was to develop, based on the literature data from Fennoscandian Scots pine, Norway spruce, and birch forests, generalized stand-level equations for the N, P, K, and Ca concentration and content of stems and total above-ground biomass with stand volume as an independent variable. The data and the developed equations were used for evaluating the effects of different tree species and harvesting intensities on nutrient removals.

Materials and methods

Material

We collected literature data of biomass and nutrient content in the above-ground parts of trees from pure Fennoscandian

Scots pine, Norway spruce, and birch forests (Tables 1, 2, 3). Data from fertilized stands were not included. The data consisted of 34 pine, 26 spruce, and 5 birch stands. They covered a wide range of variation in climatic conditions, site types, and stand characteristics. The southernmost pine and spruce stands were situated in southern Sweden (55–57°N) and the northernmost ones near the Arctic Circle (66–67°N). Birch stands were situated at latitudes between 61°N and 64°N. The mean annual temperatures varied between −0.4 and +6°C and the annual precipitation between 480 and 1,040 mm. The stand volumes were in the range of 6–359, 22–802, and 39–169 m^3 ha^{-1} in pine, spruce, and birch stands, respectively. The ages of stands ranged from 15 to 150 years in pine stands, from 18 to 250 years in spruce stands, and from 20 to 60 years in birch stands.

Biomass and N, P, K, and Ca contents in stems (stem wood and stem bark) and the total above-ground biomass (stems, live and dead branches and foliage) of the forest stands were collected from the literature. The studies used sample trees for analyzing the nutrient concentrations and for formulating biomass equations between different stem or crown fractions (dead and living branches and foliage) and easily measurable stem variables (e.g., breast height diameter, height). The sample trees were harvested at the end of the growing season. Nitrogen concentrations were analyzed by the Kjeldahl method. The determinations of P, K, and Ca concentrations were made from wet acid digested samples. In the most recent studies, the concentrations of P, K, and Ca were determined with inductively coupled plasma atomic emission spectrophotometer (ICP), whereas in older studies (before the 1990s), P was usually determined with colorimetric methods, K with flame photometer or atomic absorption spectrophotometer (AAS), and Ca with AAS. The methodologies for analyzing nutrient concentrations varied between studies, but we think that they are well comparable, since different nutrient analysis methods have generally shown good agreement (Handson and Shelley 1993). The biomass equations and the nutrient concentrations were then used to calculate the nutrient content for all trees in the stand.

Statistical analyses

Nutrient concentrations in stems, crowns, and total above-ground biomass were calculated by dividing the nutrient content by the corresponding biomass. Differences in nutrient concentrations between tree species and biomass fractions (stem and crown) were analyzed using one-way ANOVA followed by either Bonferroni (equal variances) or Dunnett T3 (unequal variances) post hoc tests. The homogeneity of variances was tested using the Levene's test. Differences in the nutrient content of stem and total above-ground biomass between tree species were tested with a general linear model by using stand volume as a covariate. All statistical tests were conducted using SPSS software (PASW Statistics 17.0, SPSS Inc., Chicago, USA).

Derivation of equations and calculations

Regression equations were formulated between stem biomass or total above-ground biomass (kg ha^{-1}) and stand volume (m^3 ha^{-1}) and the N, P, K, and Ca content (kg ha^{-1}) in stems or total above-ground biomass and stand volume (m^3 ha^{-1}). The parameters were estimated by the Levenberg–Marquardt algorithm (PASW Statistics 17.0, SPSS Inc., Chicago, USA). The following model was used:

$$\mathrm{Y} = \mathrm{aX^b} \tag{1}$$

where Y is the amount of biomass or nutrient (kg ha^{-1}), X is stand volume (m^3 ha^{-1}), and a and b are parameters. The models were converted to linear form using the natural log transformation:

$$\ln(\mathrm{Y}) = \ln(\mathrm{a}) + \mathrm{b}\ \ln(\mathrm{X})$$

Logarithmically transformed values were used in the analyses. In order to correct the underestimate of the regression estimate caused by this transformation, a condensed form (Madgwick and Satoo 1975) of the correction term (Finney 1941) was used for calculating the results:

$$k = e^{1/2S_e^2} \tag{2}$$

k = correction term, S_e^2 = residual variance.

Since stand age was available from most stands and it has been shown that nutrient concentrations in stand biomass are related to stand age (Augusto et al. 2000), we also attempted to formulate regression equations for N, P, K, and Ca content in stems or above-ground biomass with stand age as an independent variable. In addition, we tried to formulate equations for N, P, K, and Ca concentrations in stems or total above-ground biomass with stand volume as an independent variable, since its has been shown that nutrient concentrations of trees are related to tree size (Augusto et al. 2008). None of these equations were statistically significant ($P > 0.05$), thus they are not presented here. The fact that the nutrient content of stems and above-ground biomass could not be explained by stand age could be related to the correlation between the geographical location and the fertility of the site and stand age. Tree stands of a particular volume are older on infertile or northern sites than the tree stands of the same volume growing on fertile or southern sites (Kärkkäinen 2005). Thus, when the range of site fertilities or geographical locations is large, the correlation between age and tree size is weakened. The age of the stands in this study were also

Table 1 Site and stand characteristics in Scots pine stands

Site	Latitude and longitude	Elevation a.s.l., m	Annual air temperature (°C)	Annual precipitation (mm)	Site type[a]	Soil type	Volume (m^3 ha^{-1})	Volume growth (m^3 ha^{-1} a^{-1})	Stem number, trees (ha^{-1})	Age (years)	Reference
1	N 61°35′–61°52′ E 24°05′–24°25′	105–170	3.0	650	VSR	Peat	6		444		Laiho (1997)
2	N 62°47′ E 30°58′	145	1.4	690	VT	Podzol, Sand	8	1.8	7,425	15	Helmisaari (1995)
3	N 61°35′–61°52′ E 24°05′–24°25′	105–170	3.0	650	VSR, drained	Peat	10		554		Laiho (1997)
4	N 57.5°	200					27	2.0		39	Tamm (1969)
5	N 60°31′ E 23°53′	135	3.7	545	VT	Podzol, Fine sand moraine	30	2.3	2,911	28	Mälkönen (1974)
6	N 61°35′–61°52′ E 24°05′–24°25′	105–170	3.0	650	VSR	Peat	35		1,567		Laiho (1997)
7	N 59°38′ E 11°14′	190	5.0	861	IR, drained	Peat	41	0.9	1,658		Brække and Håland (1995)
8	N 62°51′ E 30°53′	155	2.2	605	VNR, drained	Peat	48	2.7	922	40–50	Finér (1989)
9	N 62°47′ E 30°58′	145	1.4	690	VT	Podzol, Sand	58	5.2	2,660	35	Helmisaari (1995), Helmisaari et al. (2009)
10	N 60°47′ E 24°18′	150	3.3	642	VT	Moraine	60			25	Lehtonen (1978)
11	N 59°20′ E 18°20′	35	5–6	500	Ledum pinetum, drained	Peat	66	3.6	1,282	44	Holmén (1964)
12	N 62°51′ E 30°53′	155	2.2	605	RhNR, drained	Peat	72	2.0	557	40–60	Finér (1989)
13	N 61°49′ E 24°19′				VT	Fine sand	74		848	45	Mälkönen (1972)
14	N 61°40′ E 24°19′	140	2.9	576	VT	Podzol, Coarse sand	76	5.0	845	47	Mälkönen (1974)

Table 1 continued

Site	Latitude and longitude	Elevation a.s.l.,m	Annual air temperature (°C)	Annual precipitation (mm)	Site type[a]	Soil type	Volume (m^3 ha^{-1})	Volume growth (m^3 ha^{-1} a^{-1})	Stem number, trees (ha^{-1})	Age (years)	Reference
15	N 61°35′–61°52′ E 24°05′–24°25′	105–170	3.0	650	VSR, drained	Peat	76		4,750		Laiho (1997)
16	N 62°14′ E 29°50′	81		618	IR, drained	Peat	80	5.9	2,219	85	Finér (1991)
17	N 66°37′ E 19°50′	250	−0.4	480		Sand moraine	89	2.1		70	Popović and Burgtorf (1964)
18	N 66.5°	250					89	2.0		75	Tamm (1969)
19	N 58°	240					90	3.0		72	Tamm (1969)
20	N 61°35′–61°52′ E 24°05′–24°25′	105–170	3.0	650	VSR, drained	Peat	102		1,782		Laiho (1997)
21	N 57.5°	200					109	5.0		40	Tamm (1969)
22	N 62°04′ E 24°34′				IR, drained	Peat	116	4.5	688	>65	Paavilainen (1980)
23	N 60° E 16°	185	3.8	607		Podzol, Sand	129		393	120–150	Bringmark (1977)
24	N 60°31′ E 23°51′	125	3.7	545	MT	Fine sand moraine	149	5.9	1,420	45	Mälkönen (1974)
25	N 61°35′–61°52′ E 24°05′–24°25′	105–170	3.0	650	VSR, drained	Peat	150		2,786		Laiho (1997)
26	N 66°21′ E 26°44′	145	0.0	587	EMT	Carbic podzol	167		1,755	60	Ukonmaanaho et al. (2008), Derome et al. (2007)
27	N 60°42′ E 27°50′	48	3.8	600	CT	Ferric podzol	178		415	125	Ukonmaanaho et al. (2008), Derome et al. (2007)
28	N 64°18′ E 19°36′	180	1.0	565	Dry lichen forest	Moraine, sand	185	3.7		90–95	Björkroth and Rosén (1977), Olsson et al. (1996a, b)
29	N 62°01′ E 24°49′				VT	Fine sand	208		492	70	Mälkönen (1972)
30	N 61°52′ E 24°12′	154	3.0	629	VT	Ferric podzol	211		378	85	Ukonmaanaho et al. (2008), Derome et al. (2007)

Table 1 continued

Site	Latitude and longitude	Elevation a.s.l.,m	Annual air temperature (°C)	Annual precipitation (mm)	Site type[a]	Soil type	Volume (m^3 ha^{-1})	Volume growth (m^3 ha^{-1} a^{-1})	Stem number, trees (ha^{-1})	Age (years)	Reference
31	N 60°36′ E 23°50′	120	4.0	619	VT	Haplic podzol	255		604	65	Ukonmaanaho et al. (2008), Derome et al. (2007)
32	N 62°47′ E 30°58′	145	1.4	690	VT	Podzol, Sand	258	3.5	432	100	Helmisaari (1995), Helmisaari et al. (2009)
33	N 63°09′ E 30°42′	168	1.5	580	EVT	Haplic podzol	298		588	135	Ukonmaanaho et al. (2008), Derome et al. (2007)
34	N 61°46′ E 29°20′	99	3.2	526	VT	Ferric podzol	359		959	85	Ukonmaanaho et al. (2008), Derome et al. (2007)

[a] Site types in mineral soil sites: *CT* calluna type, *VT* vaccinium type, *MT* myrtillus type, *EVT* empetrum-vaccinium type, *EMT* Empetrum-Myrtillus type (Cajander 1949). Site types in peatland sites: *VSR* Tall-sedge pine fen, *VNR* Sedge pine mire, *IR* Dwarf-shrub pine bog, *RhNR* Herbrich sedge pine mire (Heikurainen and Pakarinen 1982)

at the range where the relationship between nutrient concentrations of biomass and stand age is stable (Augusto et al. 2000). The weak correlation between stand volume and the nutrient concentrations of stems and above-ground biomass, in turn, may be related to the variation in stand density and accordingly to the mean tree size between the stands of the same volume in this study. Since the nutrient concentrations are related to tree size (Augusto et al. 2008), the relationships between volume and nutrient concentrations were not observed at stand level in this small dataset.

The derived equations were used to evaluate the effects of different harvesting intensities on nutrient removals and to give an example of the amounts of nutrients removed in Scots pine, Norway spruce, and birch stands at thinning and final cutting. In this study, nutrient removals by harvesting were assumed to be equal to the accumulated nutrient amounts. The example calculations were made only for one site type, one region in Finland and one management option (number of seedlings at stand establishment, number of thinnings, thinning regime, and rotation age) that was based on current Finnish forest management practices. We used the MOTTI stand simulator (Hynynen et al. 2005; Salminen et al. 2005) to simulate the stand volume development over the whole rotation on medium-rich Myrtillus type (MT) forest in Central Finland (Table 4). The MT site type was chosen because it is the most common site type in Finland, and all these three tree species are grown on MT sites. The stand development was started by planting (2,000 seedlings ha^{-1}), and the stands were thinned two times before the end of the rotation. The total yield of stem wood during the whole rotation was 425, 430, and 358 m^3 ha^{-1} in the pine, spruce, and birch stands, respectively.

Results

Nutrient concentrations and contents

The concentrations of all studied nutrients were lower in stems than in the crowns of pine, spruce, and birch (Table 5). Nitrogen concentrations did not differ in the stems (stem wood and stem bark combined) of the three tree species. Phosphorus concentrations were higher in birch stems than in pine stems. Potassium concentrations were higher in spruce stems than in pine stems, and Ca concentrations were higher in spruce stems than in the stems of pine and birch. In the crowns (including branches and foliage), N concentrations were highest in birch crowns. Phosphorus and Ca concentrations were lowest in pine crowns. The K concentrations of crowns did not differ significantly between the tree species. Nitrogen, P, and K

Table 2 Site and stand characteristics in Norway spruce stands

Site	Latitude and longitude	Elevation a.s.l., m	Annual air temperature (°C)	Annual precipitation (mm)	Site type[a]	Soil type	Volume (m^3 ha^{-1})	Volume growth (m^3 ha^{-1} a^{-1})	Stem number, trees (ha^{-1})	Age (years)	Reference
1	N 59.5°	130					22	12.0		18	Tamm (1969)
2	N 67°59′ E 24°14′	300	−1.8	545	HMT	Ferric podzol	73		1,104	145	Ukonmaanaho et al. (2008), Derome et al. (2007)
3	N 60°55′ E 16°01′	350	3.2	740		Podzol, sandy-silty moraine	81			35	Eriksson et al. (1996)
4	N 64°28′ E 27°33′	200–210	2.1	545	VMT	Fine sandy moraine	116			137	Kubin (1977)
5	N 66°22′ E 29°15′	270		500	HMT	Sand moraine	125		550	250	Kubin (1983)
6	N 66°19′ E 26°38′	252	−0.5	585	HMT	Ferric podzol	133		1,663	75	Ukonmaanaho et al. (2008), Derome et al. (2007)
7	N 62°51′ E 30°53′	155	2.2	605	MK, drained	Peat	162	4.0	565	>100	Finér (1989)
8					OMT		192			30	Helmisaari et al. (2009)
9	N 59.5°	65					215	8.0		59	Tamm (1969)
10	N 62°02′ E 16°32′	360	4.0	657		Podzol	230	5.0			Rosén (1982)
11	N 63°51′ E 28°58′	220	1.2	709	MT	Podzol, sandy till	260	3.2	1,585	140	Finér et al. (2003), Finér et al. unpublished
12	N 64°25′ E 18°52′						278	2.6	1,002	139	Nykvist (1974)
13	N 57°	150					287	13.0		53	Tamm (1969)
14	N 64°16′ E 19°31′	260	1.0	565	Mesic-wet dwarf-shrub forest type	Moraine	290	3.8		155	Björkroth and Rosén (1977), Olsson et al. (1996a, b)
15	N 59°20′ E 18°20′	35	5–6	500	Bilberry-spruce, drained	Peat	312	15.0	987	60–70	Holmén (1964)
16	N 56°42′ E 13°50′	100	6.4	1,040	Mesic dwarf-shrub forest type	Moraine	325	10.1		70	Björkroth and Rosén (1977), Olsson et al. (1996a, b)
17	N 60°16′ E 16°13′	200–220			Mesic dwarf-shrub type	Sandy till	331	4.5	544	100	Nykvist (1971)
18					OMT		342			62	Helmisaari et al. (2009)
19	N 55.8°	100					351	18.0		50	Tamm (1969)

Table 2 continued

Site	Latitude and longitude	Elevation a.s.l., m	Annual air temperature (°C)	Annual precipitation (mm)	Site type[a]	Soil type	Volume (m^3 ha^{-1})	Volume growth (m^3 ha^{-1} a^{-1})	Stem number, trees (ha^{-1})	Age (years)	Reference
20	N 61°51′ E 24°18′	177	2.9	629	OMT	Dystric cambizol	376		852	85	Ukonmaanaho et al. (2008), Derome et al. (2007)
21	N 61°48′ E 29°19′	88	3.2	526	OMT	Cambic arenosol	387		374	75	Ukonmaanaho et al. (2008), Derome et al. (2007)
22	N 63°33′ E 22°29′	3	2.9	462	OMT	Cambic podzol	387		963	60	Ukonmaanaho et al. (2008), Derome et al. (2007)
23	N 55.9°	150					393	15.0		85	Tamm (1969)
24	N 55.8°	100					528	21.0		50	Tamm (1969)
25	N 55.9°	150					791	21.0		85	Tamm (1969)
26	N 55°59′ E 13°10′		6–7	800	Former beech forest	Moraine	802	26.6	880	55	Nihlgård (1972)

[a] Site types in mineral soil sites: *VMT* vaccinium myrtillus type, *HMT* hylocomium-myrtillus type, *MT* myrtillus type, *OMT* oxalis-myrtillus type (Cajander 1949). Site types in peatland sites: MK = *Vaccinium myrtillus* spruce mire (Heikurainen and Pakarinen 1982)

concentrations in the total above-ground biomass did not differ between the tree species, and Ca concentrations were lowest in pine.

The N and P content of stems were higher in birch than in pine (Table 6). The K content of stems did not differ significantly between the tree species. The Ca content of stems was higher in spruce than in pine. The N, P, K, and Ca content of total above-ground biomass were higher in spruce than in pine. Spruce also had higher Ca content in total above-ground biomass than birch.

Nutrient equations

There was a clear relationship both between stem or total above-ground biomass and stem volume and the content of different nutrients in stem or total above-ground biomass and stand volume (Figs. 1, 2, 3, 4, 5). All of the equations for pine and spruce were statistically highly significant ($P < 0.001$), whereas the significance levels of birch equations were generally somewhat lower (Table 7). The equations explained, depending on the nutrient, 61–89, 60–87, and 78–99% of the variation in stem nutrient content in pine, spruce, and birch stands, respectively. The equations also accounted for most of the variation in the nutrient content of total above-ground biomass, the R^2 values ranging from 0.58 to 0.80 in pine stands, from 0.56 to 0.84 in spruce stands, and from 0.56 to 0.87 in birch stands. The crown represented a small proportion of the total above-ground biomass, but its nutrient content was high. The relative proportion of the crown out of total above-ground biomass was considerably larger in spruce than in pine (Fig. 1). The form of the curves indicated that the proportion of crown out of the total above-ground nutrient content generally decreases with the increasing stand volume. WTH thus removes more nutrients per harvested stem m^3 in small volume stands.

The results indicate that WTH substantially increases nutrient removals compared with SOH, and the relative increase in nutrient removals are generally greater the smaller the stand volume is. On average, WTH increased the removals of N, P, K, and Ca by 2.9 (range 1.7–5.1), 3.9 (range 2.4–11.2), 2.7 (range 1.8–5.3), and 1.9 (range 1.3–3.3) times, respectively, compared with SOH in pine stands. In spruce stands, WTH removed on average 3.7 (range 2.1–8.2), 5.0 (range 2.4–11.7), 2.9 (range 1.8–5.9), and 2.5 (range 1.4–9.8) times more N, P, K, and Ca, respectively, than did SOH. Corresponding values for birch stands were 2.4 (range 1.9–2.9), 2.7 (range 1.9–3.1), 2.2 (range 1.6–2.9), and 2.1 (range 1.6–3.0).

According to the equations, about two times more N and P are removed in birch than in pine and spruce stands with equal stand volumes in SOH. According to the equations, the amounts of K and Ca in stems are the highest in spruce

Table 3 Site and stand characteristics in birch stands

Site	Latitude and longitude	Elevation a.s.l., m	Annual air temperature (°C)	Annual precipitation (mm)	Site type[a]	Soil type	Volume (m^3 ha^{-1})	Volume growth (m^3 ha^{-1} a^{-1})	Stem number, trees (ha^{-1})	Age (years)	Reference
1	N 62°51′ E 30°53′	155	2.2	605	RhNR, drained	Peat	39	2.0	443	40–60	Finér (1989)
2	N 63°7′ E 27°45′	115			OMT	Fine sand	50	7.4	4,422	20	Mälkönen and Saarsalmi (1982)
3	N 64°	90			Drained	Peat	79	7.0		26	Tamm (1969)
4	N 61°37′ E 24°9′	160			OMT	Fine sand moraine	155	6.1	1,012	40	Mälkönen (1977)
5	N 61°25′ E 21°38′	45			OMT	Sand moraine	169	7.9	3,948	40	Mälkönen and Saarsalmi (1982)

[a] Site types in mineral soil sites: *OMT* oxalis-myrtillus type (Cajander 1949). Site types in peatland sites: *RhNR* herbrich sedge pine mire (Heikurainen and Pakarinen 1982)

Table 4 Stand age, stem numbers, mean height, basal area, mean breast height diameter, stand volume, stem and above-ground biomass and removed stand volume in thinnings and final cutting in simulated pine, spruce and birch stands growing on Myrtillus site types in Central Finland

Tree species	Management	Age (years)	Stems (ha^{-1})	Height (m)	Basal area (m^2 ha^{-1})	Diameter (cm)	Volume (m^3 ha^{-1})	Stem biomass (kg ha^{-1})	Above-ground biomass (kg ha^{-1})	Removal (m^3 ha^{-1})
Pine	1st thinning									
	Before	31	2,082	10.8	23.43	13.4	133	55,557	71,434	
	After	31	1,161	11.1	15.23	14.2	88	37,049	50,682	45
	2nd thinning									
	Before	44	1,152	14.9	26.99	18.6	200	82,899	100,263	
	After	44	677	15.2	17.99	19.5	136	56,786	72,770	64
	Final cutting	69	676	20.4	33.13	26.0	316	129,847	146,631	316
Spruce	1st thinning									
	Before	38	1,846	12.5	25.36	14.3	158	66,941	103,458	
	After	38	1,090	12.9	16.73	15.0	107	45,903	77,234	51
	2nd thinning									
	Before	50	1,072	16.6	28.86	20.0	234	97,903	138,894	
	After	50	617	17.2	18.93	21.2	157	66,531	102,966	77
	Final cutting	65	607	21.0	30.52	27.1	302	125,326	168,180	302
Birch	1st thinning									
	Before	36	2,402	16.2	22.57	13.7	169	92,782	107,212	
	After	36	1,386	16.8	15.05	14.7	118	64,969	77,123	51
	2nd thinning									
	Before	49	1,234	20.8	22.39	18.9	214	117,265	133,125	
	After	49	714	21.6	15.05	20.0	149	81,884	95,517	65
	Final cutting	64	680	24.9	21.47	23.9	242	132,478	149,015	242

at small stand volumes but after stand volume exceeds 98 m^3 ha^{-1}, the amounts of K are the highest in birch stands (Fig. 4). The amount of Ca in birch stems becomes higher than in spruce stems when stand volume exceeds 154 m^3 ha^{-1} (Fig. 5). Nutrient removal in WTH is smallest in pine stands. Pine has about half the amount of nutrients in above-ground biomass as spruce. The equations predict that the removals of N, P, and K are greatest in the WTH

Table 5 The mean and the range of N, P, K and Ca concentrations (mg g^{-1}) in pine, spruce and birch stems (stem wood and stem bark), crown (branches and foliage) and total above-ground biomass

Nutrient	Tree species	Stem			Crown			Above-ground biomass			*F*-value fractions	*P*-value fractions
		Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*		
N	Pine	1.17a*	0.62–2.01	28	6.08a*	3.67–7.96	28	2.39a	1.23–4.62	31	446.5	<0.001
	Spruce	1.12a*	0.68–2.22	22	6.90a*	2.73–9.47	21	2.73a	1.47–6.49	22	223.4	<0.001
	Birch	1.51a*	1.18–1.88	5	9.70b*	8.46–12.00	5	2.94a	2.38–3.93	5	172.0	<0.001
	F-value species	1.818			13.640			1.431				
	P-value species	0.173			<0.001			0.248				
P	Pine	0.08a*	0.02–0.28	28	0.63a*	0.24–1.35	28	0.23a	0.09–0.48	31	222.2	<0.001
	Spruce	0.09ab*	0.04–0.33	22	0.81b*	0.47–1.37	21	0.30a	0.15–1.00	22	94.1	<0.001
	Birch	0.15b*	0.07–0.23	5	0.86ab*	0.54–1.30	5	0.29a	0.15–0.52	5	31.8	<0.001
	F-value species	3.591			5.698			1.739				
	P-value species	0.035			0.006			0.185				
K	Pine	0.45a*	0.19–0.70	28	2.29a*	1.12–3.21	28	0.93a	0.32–1.79	31	221.5	<0.001
	Spruce	0.64b*	0.29–2.00	22	2.81a*	1.41–5.47	21	1.29a	0.61–4.22	22	43.4	<0.001
	Birch	0.58ab*	0.32–0.88	5	3.08a*	2.09–3.65	5	1.01a	0.62–1.27	5	77.1	<0.001
	F-value species	3.847			3.926			2.985				
	P-value species	0.028			0.026			0.059				
Ca	Pine	0.98a*	0.57–1.58	28	2.48a*	1.43–3.86	28	1.38a	0.75–2.35	31	136.4	<0.001
	Spruce	1.53b*	0.69–2.38	22	4.83b*	2.80–8.76	21	2.51b	1.21–6.25	22	25.8	<0.001
	Birch	1.15a*	0.89–1.37	5	5.39b*	4.30–6.02	5	1.91ab	1.46–2.45	5	164.0	<0.001
	F-value species	12.711			34.408			12.824				
	P-value species	<0.001			<0.001			<0.001				

F- and *P*-values are presented for the ANOVA performed to compare the differences in nutrient concentrations between fractions (i.e. stem and crown) and tree species. Pair-wise comparisons were made by using Bonferroni or Dunnett test. Significant differences ($P < 0.05$) between stem and crown are indicated with * and those between tree species are labeled with a different letter

of spruce stands if stand volume is ≤256, ≤220, and ≤228 m^3 ha^{-1}, respectively (Figs. 2, 3, 4). For stand volumes greater than that, the removals of N, P, and K were largest in birch stands. The removal of Ca in WTH would always be greatest in spruce stands (Fig. 5).

Example calculation over the whole rotation period

The amounts of nutrients removed during the whole rotation of typical pine, spruce, and birch stands growing in southern Finland were calculated for SOH and WTH intensities by using the developed nutrient equations (Fig. 6). During the rotation period almost equal amounts, 425, 430, and 358 m^3 ha^{-1} of stems were harvested in pine, spruce, and birch stands, respectively, corresponding to 174,468, 177,736, and 195,672 kg ha^{-1} of biomass in SOH and 194,876, 230,332, and 216,712 kg ha^{-1} in WTH in pine, spruce, and birch stands, respectively (Table 4). Results show that WTH increases nutrient removals by 2- to 3-fold in pine stands and by 2- to 4-fold in spruce stands as compared to SOH. In birch stands, the increase was 2-fold. During the rotation period, the nutrient removals in SOH were the largest in birch stands and the smallest in pine stands. In WTH, the nutrient removals were the lowest in pine stands and somewhat higher in spruce than in birch stands. When considered per unit volume of harvested stem, nutrient removals in SOH were the largest in birch stands and the smallest in pine stands. In WTH, nutrient removals per m^3 of harvested stem were the lowest in pine stands. The most N, P, and K per harvested stem m^3, in turn, were removed in the harvesting of birch stands, and the removals of Ca were largest in spruce stands.

We also calculated the amounts of nutrients removed at the first thinning and final cutting when the same amount of stem (100 m^3) is harvested. The calculations show that almost equal amounts of nutrients are removed at first thinning and final cutting per unit of harvested stem in pine, spruce, and birch stands in SOH, whereas in WTH, nutrient removals at first thinning are considerably greater than at final cutting especially in pine and spruce stands (Fig. 7). In SOH, both at first thinning and final cutting nutrient removals are the largest from birch stands and the smallest from pine stands. When harvesting the stem wood in WTH at first thinning, the nutrient removals are the smallest from pine and the largest from spruce stands. Likewise at final cutting, the nutrient removals are the

Table 6 The results of statistical tests for differences in the nutrient amounts of stems and total above-ground biomass between tree species

Nutrient	Test	Stem		Above-ground biomass	
		F-value	*P*-value	*F*-value	*P*-value
N	The effect of species	3.699	0.031	15.401	<0.001
	Pine vs. spruce		0.896		<0.001
	Birch vs. pine		0.030		0.196
	Spruce vs. birch		0.224		0.376
P	The effect of species	7.413	0.001	13.617	<0.001
	Pine vs. spruce		0.231		<0.001
	Birch vs. pine		0.002		0.415
	Spruce vs. birch		0.085		0.241
K	The effect of species	2.803	0.069	12.577	<0.001
	Pine vs. spruce		0.175		<0.001
	Birch vs. pine		0.280		0.552
	Spruce vs. birch		1.000		0.227
Ca	The effect of species	21.569	<0.001	66.891	<0.001
	Pine vs. spruce		<0.001		<0.001
	Birch vs. pine		0.097		0.109
	Spruce vs. birch		0.153		<0.001

The *F*- and *P*-values of the general linear model and *P*-values of pairwise comparisons are indicated. Stand volume was used as a covariate in the analyses

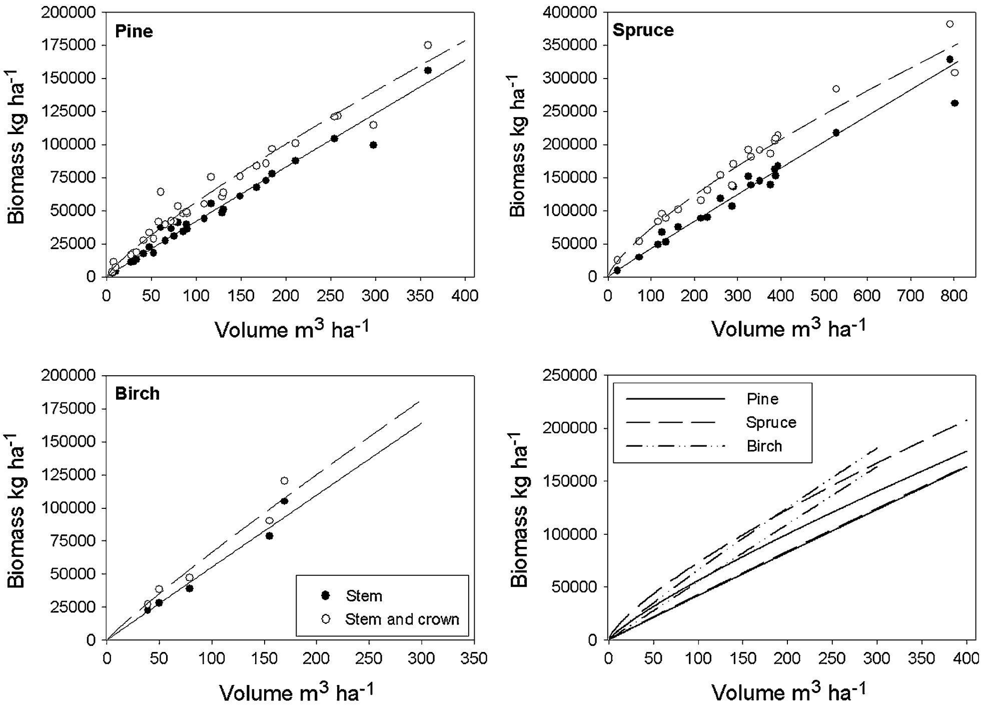

Fig. 1 Stem (stem wood and stem bark) and total above-ground (stem and crown) biomass (kg ha^{-1}) in Scots pine, Norway spruce and birch stands as a function of stem volume (m^3 ha^{-1}). *Solid lines* are predictions of Eq. 1 for stems and *dashed lines* are predictions of Eq. 1 for above-ground biomass (Table 7). The correction terms (Eq. 2, Table 7) were included into the equations when calculating predicted values. Note the different scales of the figures. The figure at lower right shows differences between tree species in the predicted stem (*lower line*) and above-ground biomass (*upper line*)

smallest in pine stands, but the difference between spruce and birch is small.

Discussion

We succeeded in formulating regression equations with high degrees of determination for N, P, K, and Ca content in stem wood or total above-ground biomass and stem volume as the independent variable for pine, spruce, and birch stands. We used these equations for showing the differences in harvesting intensities, tree species, and stand developmental stages on nutrients removals from forest stands. The nutrient removals will be compared with the other nutrient fluxes and soil nutrient pools to enable the evaluation of their importance on the maintaining nutrient balance in Fennoscandian boreal forest stands.

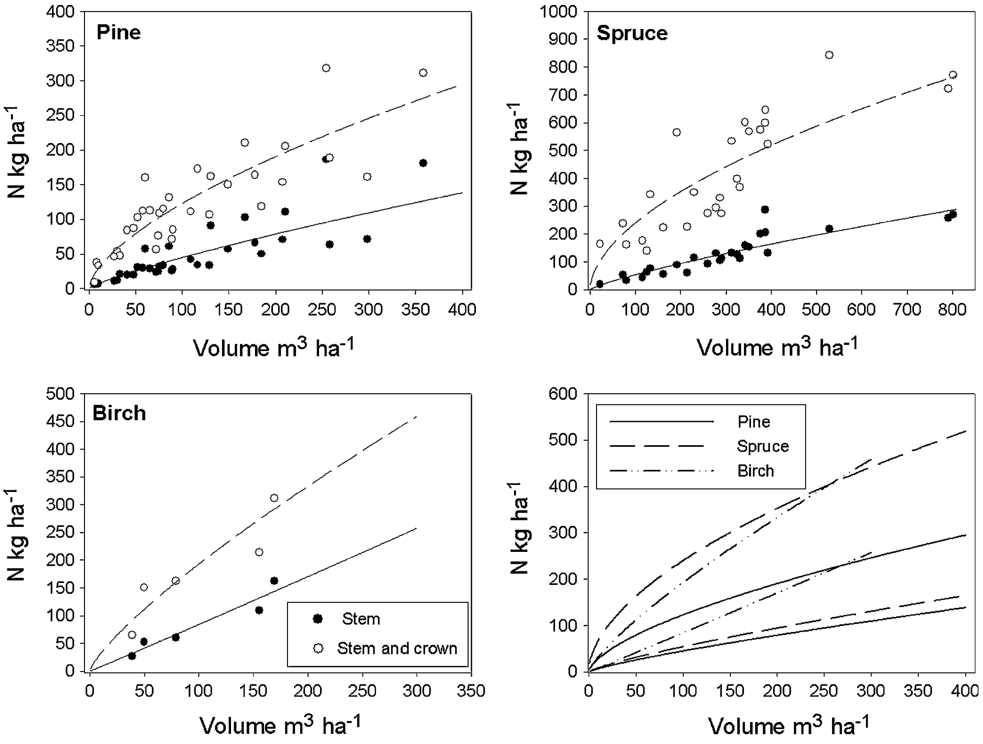

Fig. 2 The amount of nitrogen (kg ha^{-1}) in Scots pine, Norway spruce and birch stems (stem wood and stem bark) and above-ground biomass (stem and crown) as a function of stem volume (m^3 ha^{-1}). *Solid lines* are predictions of Eq. 1 for stems and *dashed lines* are predictions of Eq. 1 for above-ground biomass (Table 7). The correction terms (Eq. 2, Table 7) were included into the equations when calculating predicted values. Note the different scales of the figures. The figure at lower right shows differences between tree species in the predicted amount of nitrogen in stems (*lower line*) and above-ground biomass (*upper line*)

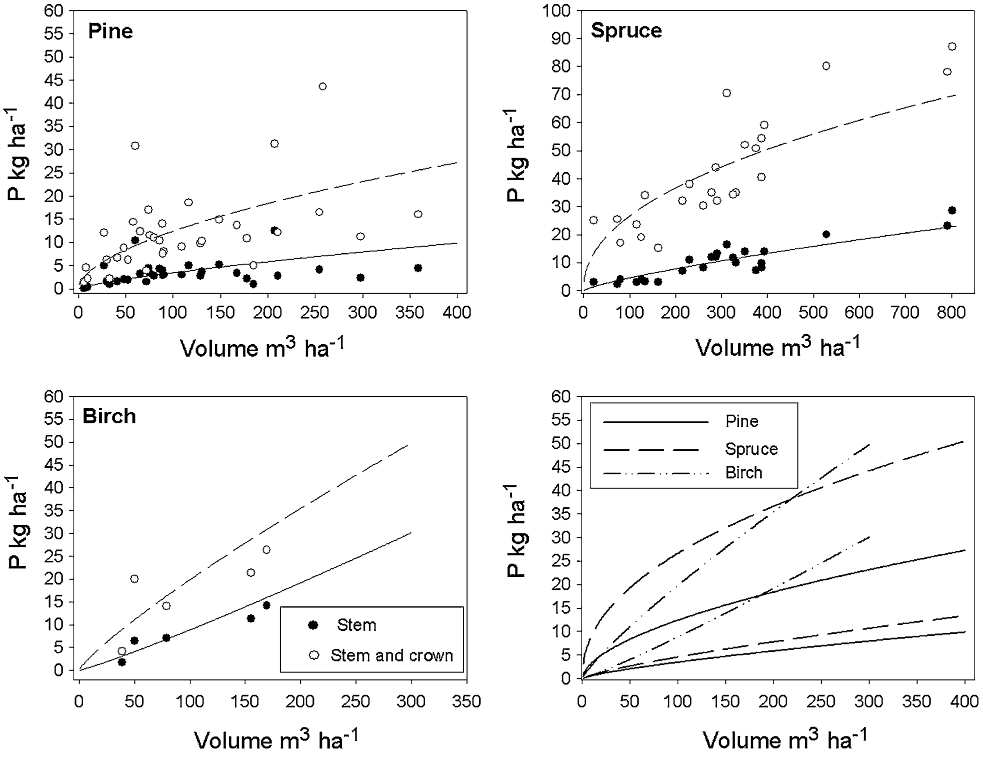

Fig. 3 The amount of phosphorus (kg ha^{-1}) in Scots pine, Norway spruce and birch stems (stem wood and stem bark) and above-ground biomass (stem and crown) as a function of stem volume (m^3 ha^{-1}). *Solid lines* are predictions of Eq. 1 for stems and *dashed lines* are predictions of Eq. 1 for above-ground biomass (Table 7). The correction terms (Eq. 2, Table 7) were included into the equations when calculating predicted values. Note the different scales of the figures. The figure at lower right shows differences between tree species in the predicted amount of phosphorus in stems (*lower line*) and above-ground biomass (*upper line*)

The formulated nutrient equations were based on data representing relatively well the variation in stand age, fertility, and geographical location in pure Scots pine and Norway spruce stands in boreal region of Fennoscandia, whereas the equations for birch were based on a very limited number of stands. The equations may not be applicable for mixed stands, e.g., because the nutrient concentrations of different tree fractions may differ between pure and mixed stands (Thelin et al. 2002). The validity of the equations depends not only on the number of stands but also on the

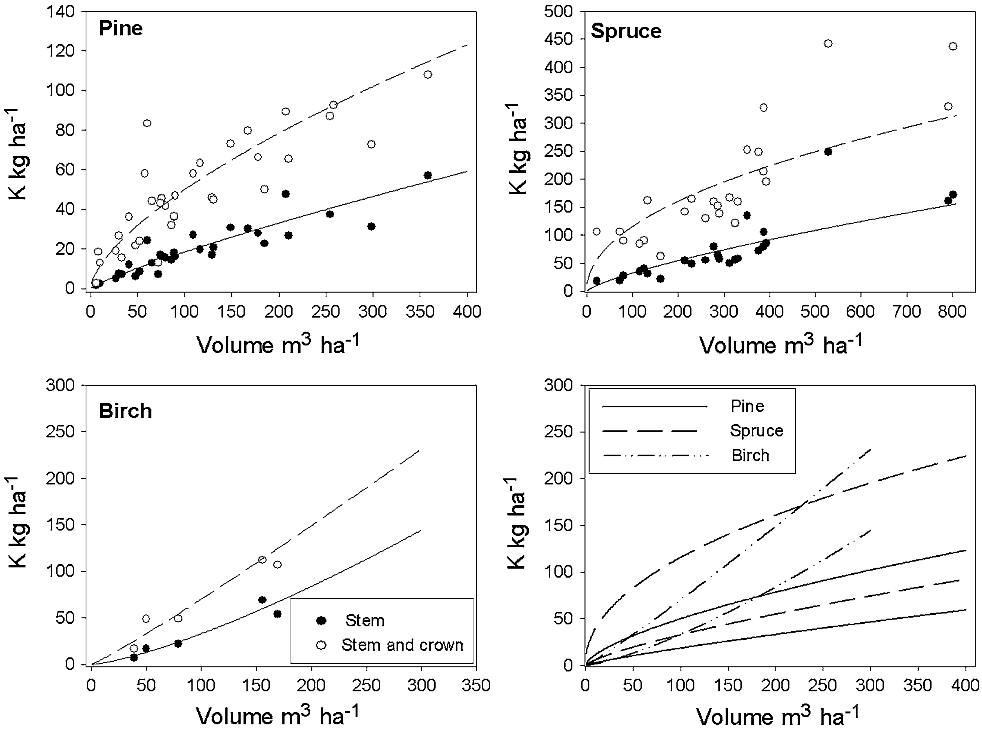

Fig. 4 The amount of potassium (kg ha^{-1}) in Scots pine, Norway spruce and birch stems (stem wood and stem bark) and above-ground biomass (stem and crown) as a function of stem volume (m^3 ha^{-1}). *Solid lines* are predictions of Eq. 1 for stems and *dashed lines* are predictions of Eq. 1 for above-ground biomass (Table 7). The correction terms (Eq. 2, Table 7) were included into the equations when calculating predicted values. Note the different scales of the figures. The figure at lower right shows differences between tree species in the predicted amount of potassium in stems (*lower line*) and above-ground biomass (*upper line*)

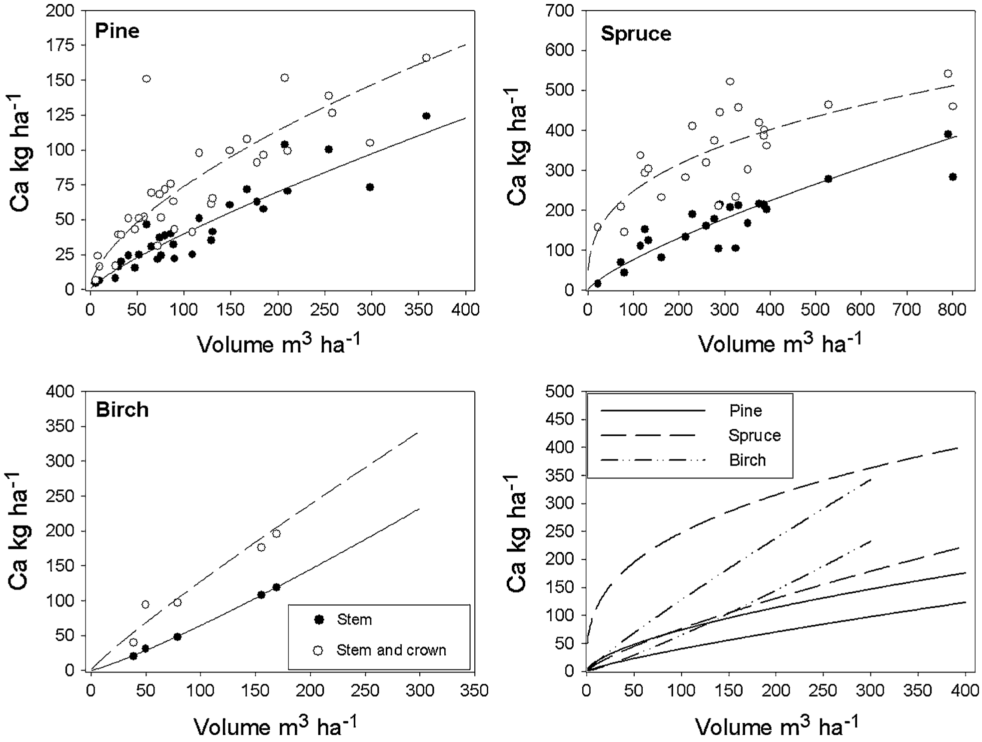

Fig. 5 The amount of calcium (kg ha^{-1}) in Scots pine, Norway spruce and birch stems (stem wood and stem bark) and above-ground biomass (stem and crown) as a function of stem volume (m^3 ha^{-1}). *Solid lines* are predictions of Eq. 1 for stems and *dashed lines* are predictions of Eq. 1 for above-ground biomass (Table 7). The correction terms (Eq. 2, Table 7) were included into the equations when calculating predicted values. Note the different scales of the figures. The figure at lower right shows differences between tree species in the predicted amount of calcium in stems (*lower line*) and above-ground biomass (*upper line*)

level of precision of individual studies in determining stand nutrient content. It has been pointed out that the sample tree material has to be large enough in order to determine stand nutrient content precisely (Comerford and Leaf 1982a, b).

Even though the degree of the determination was high in most nutrient equations, the error terms were relatively high. Several factors, like site fertility (Kellomäki and Väisänen 1986; Vanninen et al. 1996; Kärkkäinen 2005), geographical location (Kärkkäinen 2005), stand density (Kellomäki and Väisänen 1986; Nilsson and Gemmel 1993; Mäkelä and Vanninen 1998; Ilomäki et al. 2003), and stand age (Albrektson 1980; Hakkila 1989; Helmisaari

Table 7 The estimates, standard errors and p-values of parameters and the adjusted R^2 values, standard error of the estimates (SEE), the correction factors (k, see Eq. 2) and the number of observations (n) of equations ($Y = aX^b \rightarrow \ln(Y) = \ln(a) + b \ln(X) + k$ for the biomass and nutrient content (kg ha^{-1}) of stem and total above-ground biomass as a function of the volume of tree stand (m^3 ha^{-1}) in Scots pine, Norway spruce and birch forests

Dependent variable	Tree species	Parameter ln(a)			Parameter b			Model				
		Value	SE	*p*	Value	SE	*p*	R^2	SEE	*k*	*p*	*n*
Stem biomass	Pine	6.120	0.113	<0.001	0.981	0.025	<0.001	0.983	0.124	0.008	<0.001	28
	Spruce	6.206	0.151	<0.001	0.968	0.027	<0.001	0.984	0.099	0.005	<0.001	22
	Birch	6.343	0.376	<0.001	0.992	0.084	0.001	0.979	0.111	0.006	0.001	5
Above-ground biomass	Pine	7.096	0.146	<0.001	0.831	0.033	<0.001	0.957	0.182	0.017	<0.001	31
	Spruce	7.747	0.117	<0.001	0.750	0.021	<0.001	0.985	0.077	0.003	<0.001	22
	Birch	6.871	0.414	<0.001	0.917	0.093	0.002	0.970	0.122	0.007	0.002	5
N in stems	Pine	0.004	0.305	0.989	0.812	0.067	<0.001	0.824	0.347	0.060	<0.001	33
	Spruce	0.274	0.346	0.436	0.801	0.063	<0.001	0.872	0.241	0.029	<0.001	26
	Birch	−0.280	0.744	0.732	1.018	0.167	0.009	0.925	0.219	0.024	0.009	5
N in above-ground biomass	Pine	1.856	0.250	<0.001	0.631	0.056	<0.001	0.799	0.316	0.050	<0.001	34
	Spruce	2.864	0.457	<0.001	0.557	0.083	<0.001	0.654	0.319	0.051	<0.001	26
	Birch	1.590	1.002	0.211	0.788	0.225	0.039	0.804	0.296	0.044	0.039	5
P in stems	Pine	−2.387	0.505	<0.001	0.754	0.112	<0.001	0.609	0.562	0.158	<0.001	31
	Spruce	−2.112	0.538	0.001	0.773	0.097	<0.001	0.741	0.374	0.070	<0.001	24
	Birch	−3.051	1.531	0.140	1.114	0.343	0.048	0.779	0.452	0.102	0.048	5
P in above-ground biomass	Pine	−0.202	0.379	0.599	0.566	0.085	<0.001	0.582	0.479	0.115	<0.001	34
	Spruce	1.109	0.458	0.024	0.461	0.083	<0.001	0.585	0.318	0.051	<0.001	24
	Birch	−1.034	1.929	0.629	0.838	0.432	0.148	0.557	0.569	0.162	0.148	5
K in stems	Pine	−0.996	0.246	<0.001	0.841	0.055	<0.001	0.891	0.273	0.037	<0.001	31
	Spruce	−0.015	0.481	0.975	0.748	0.087	<0.001	0.771	0.334	0.056	<0.001	24
	Birch	−2.704	0.871	0.053	1.340	0.195	0.006	0.940	0.257	0.033	0.006	5
K in above-ground biomass	Pine	0.839	0.313	0.012	0.650	0.070	<0.001	0.729	0.396	0.078	<0.001	34
	Spruce	2.487	0.503	<0.001	0.478	0.091	<0.001	0.556	0.349	0.061	<0.001	24
	Birch	−0.811	1.128	0.524	1.087	0.253	0.023	0.860	0.333	0.055	0.023	5
Ca in stems	Pine	−0.090	0.243	0.713	0.812	0.054	<0.001	0.887	0.270	0.036	<0.001	31
	Spruce	0.726	0.400	0.083	0.775	0.072	<0.001	0.839	0.278	0.039	<0.001	24
	Birch	−1.210	0.196	0.009	1.167	0.044	<0.001	0.996	0.058	0.002	<0.001	5
Ca in above-ground biomass	Pine	1.370	0.271	<0.001	0.624	0.061	<0.001	0.768	0.343	0.059	<0.001	34
	Spruce	3.877	0.337	<0.001	0.349	0.061	<0.001	0.597	0.234	0.027	<0.001	24
	Birch	0.669	0.893	0.508	0.900	0.200	0.020	0.871	0.263	0.035	0.020	5

1995; Vanninen et al. 1996; Lehtonen et al. 2004; Kantola and Mäkelä 2006) affect the allocation of biomass between stems and crowns in Fennoscandian boreal forests. In addition, the nutrient concentrations of tree stands are affected by geographical location (Ericsson et al. 1993; Oleksyn et al. 2003), stand age (Augusto et al. 2000), and to small extent also site fertility (Reinikainen et al. 1998; Augusto et al. 2000). These factors are among the ones, which could possibly improve the nutrient equations, if they are included in the equations. The inclusion of these factors as independent variables is problematic since many of the variables are confounded with each other, and the more there are independent variables the more data are needed for deriving the equations. In all cases, more data are needed to improve and to independently validate the equations.

We found that WTH increases nutrient removals 2- to 4-fold compared with SOH in pine, spruce, and birch stands (Fig. 6) and was attributed to the fact that the proportion of crown out of the total above-ground nutrient amount decreases with increasing stand volume. This finding is comparable to the estimates based on the previous experimental (Mälkönen 1972; Kubin 1977; Mälkönen and Saarsalmi 1982) and modeling (Raulund-Rasmussen et al. 2008) studies in single tree species stands, which indicate WTH to remove from 2 to 7 times more nutrients

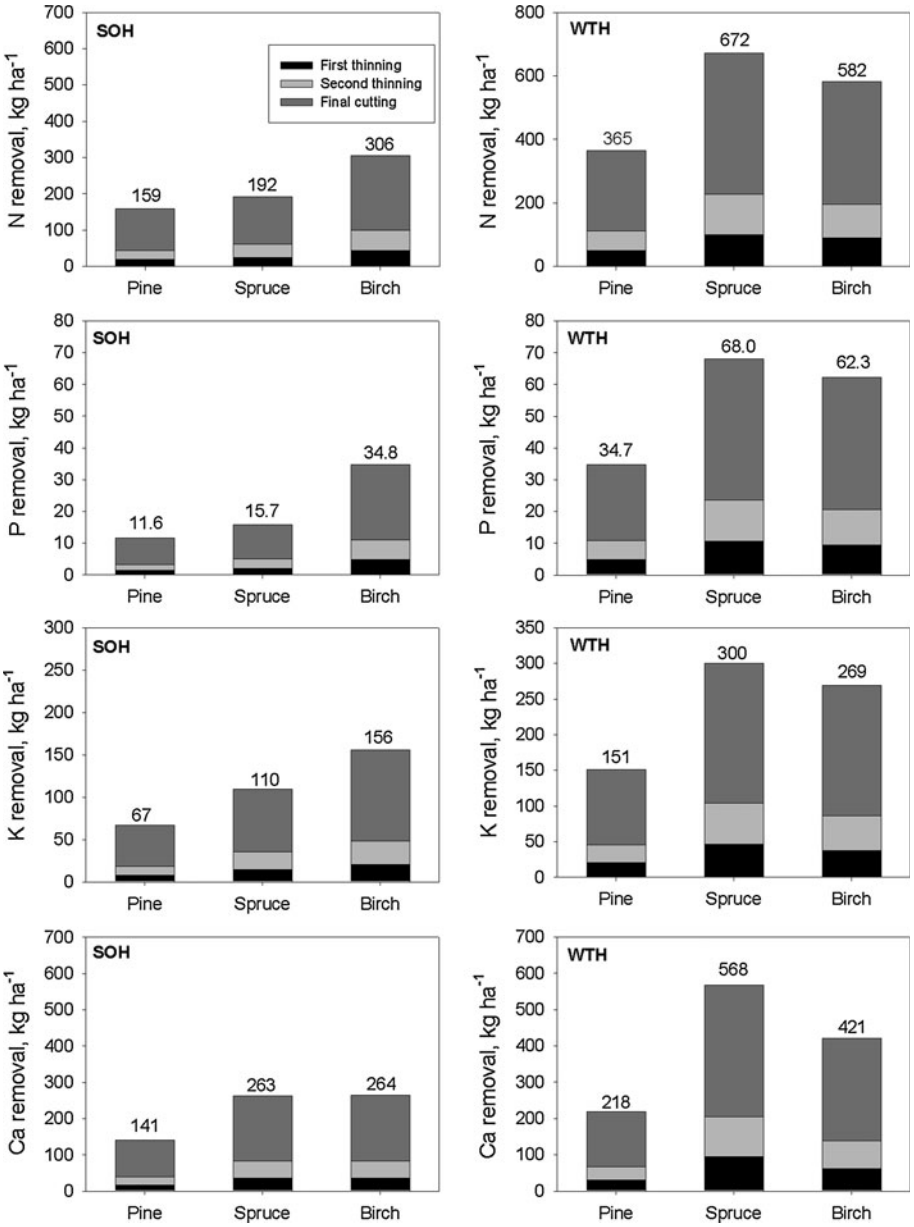

Fig. 6 Nitrogen, phosphorus, potassium and calcium removals caused by thinnings and final cutting in pine, spruce and birch stands during the rotation period in stem-only harvesting (SOH) and whole-tree harvesting (WTH) in Central Finland on medium fertile Myrtillus type sites

than SOH in Scots pine, Norway spruce, and birch stands. So far, little attention has been paid on how the developmental stage of the stand affects nutrient removals. We found that the nutrient removals are the same in thinnings and final cuttings in SOH but considerably larger in thinnings than final cuttings in WTH, especially in pine and spruce stands when the same volume of stem is harvested.

It has also been shown earlier that the nutrient removals in SOH are higher in birch stands compared with pine or spruce stands (Finér 1989; Hakkila 1989). This is probably due to that stem biomass is higher in birch stands compared with pine and spruce stands with similar stem volume (Fig. 1). The results on the effects of nutrient removals could be somewhat biased for birch, since the data originated from younger stands with smaller trees than those for pine and spruce. Tree nutrient concentrations decrease with the size and age of the trees (Augusto et al. 2000, 2008). In WTH, nutrient removals were found to be smallest in pine stands, which is probably because the nutrient concentrations were lowest in pine stems and crowns (Table 5). Considerably smaller nutrient removals in pine than in spruce WTH can be also explained by the fact that the biomass of crown is two times smaller in pine than in similar size spruce trees (Repola 2009).

The intensification of the utilization of forest biomass has increased the concern about its impact on the nutritional status of forests. In this study, nutrient removals by harvesting were assumed to be equal to the accumulated nutrient amounts. In reality, the nutrient removals are somewhat smaller because, in practice, part of the logging

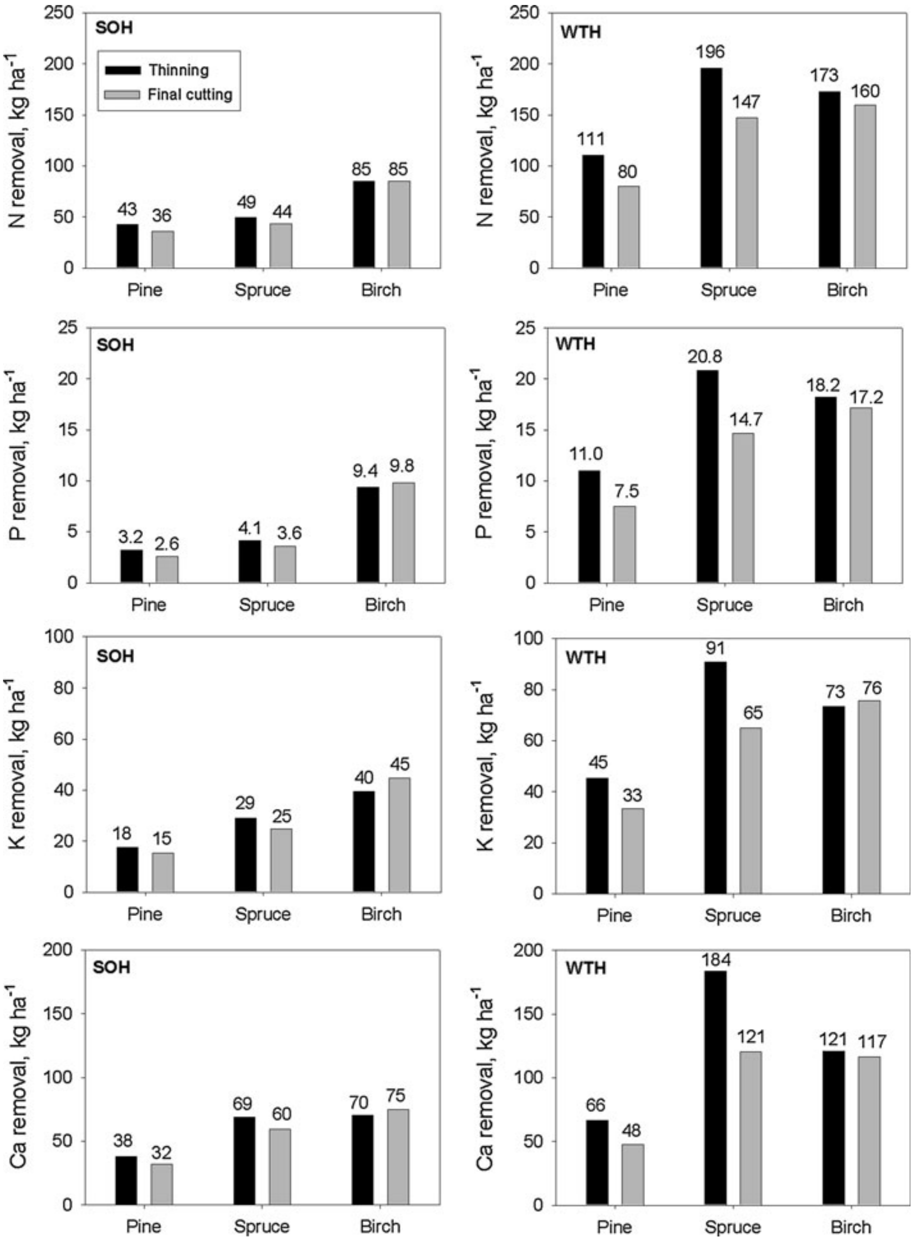

Fig. 7 Nitrogen, phosphorus, potassium and calcium removals in pine, spruce and birch stands in stem-only harvesting (SOH) and whole-tree harvesting (WTH) in first thinning and final cutting when 100 m^3 of wood is harvested

residues will remain on the site in WTH (Hakkila 2002). It should also be noted that nutrient removals are smaller in birch stands if WTH is done during the leafless period. About 20–30% of the above-ground tree nutrients are in the leaves in birch stands (Tamm 1969; Mälkönen 1977). A part of the nutrients contained in the leaves are, however, translocated to storage tissues during leaf senescence. In addition to harvesting, nutrients are lost from the forest ecosystem through leaching which is increased after final cutting (Table 8). Nutrients removed in harvesting operations can be compensated by inputs from atmospheric deposition and in mineral soils also by weathering. Nutrient deposition is highest in southern Fennoscandia and decreases toward the north (e.g., Ruoho-Airola et al. 2003; Akselsson et al. 2010). In a typical tree stand in southern Finland (Table 4), the removals of N caused by SOH (Fig. 6) are smaller in pine, spruce, and birch stands than the inputs by N deposition during the rotation (Table 8). Deposition and weathering together can compensate P and K losses caused by SOH during the rotation in pine and spruce stands but in birch stands, more P (35 kg P ha^{-1}) and K (156 kg K ha^{-1}) are removed in SOH than are received through weathering and deposition (17 kg P ha^{-1} and 102 kg K ha^{-1} at maximum). If we take into account the leaching of P and K, the balance can come negative also in pine and spruces stands. Deposition and weathering were sufficient to compensate for the Ca losses caused by SOH during the rotation in all studied tree species. On

Table 8 Nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) deposition (Helmisaari 1995; Ruoho-Airola et al. 2003; Piirainen et al. 2004), weathering rates (Starr et al. 1998; Fisher and Binkley 2000), background leaching from forested areas (Finér et al. 2004; 2010), the total increase in leaching caused by final cutting (Finér et al. 2005; 2010) and the total and plant-available N, P, K and Ca pools in the soil in mineral soil (Mälkönen 1974; Helmisaari 1995; Tamminen 1998; Palviainen 2005) and peatland sites (Starr and Westman 1978; Kaunisto and Paavilainen 1988; Laiho 1997; Westman and Laiho 2003)

	N (kg ha^{-1})	P (kg ha^{-1})	K (kg ha^{-1})	Ca (kg ha^{-1})
Annual deposition	2–6	0.04–0.25	0.3–0.6	0.3–2.1
During whole rotation (64–69 years)	128–414	2.6–17.3	19.2–41.4	19.2–144.9
Annual weathering rate		0.02	1.0	3.0
During whole rotation (64–69 years)		1.28–1.38	64–69	192–207
Annual background leaching	0.29–2.3	0.017–0.15	0.50–2.5	1.95–14.8
During whole rotation (64–69 years)	19–159	1.1–10.1	32–169	125–1,021
Total increase in leaching after final cutting				
Mineral soil sites	5.03	0.251	5.91–22.95[a]	
Peatland sites	25.87	0.638		
Total pools in the rooting zone				
Mineral soil sites	920–2,650	665–1,550	381–605	852–1,440
Peatland sites	3,000–7,000	90–380	30–300	500–2,100
Plant-available pools in the rooting zone				
Mineral soil sites	6–18	12–32	32–111	75–730
Peatland sites	30–110	3–20	25–75	100–1,200

The effect of final cutting on nutrient leaching can be seen for 10 years after treatment. The data represents nutrient pools and fluxes in Finland

[a] Estimate for the first 6 years after final cutting

stands where the Ca leaching is high, the balance can be negative. If all biomass is removed, the nutrient inputs cannot compensate the nutrients removed from the forest. Even if WTH is done only at final felling, the removals of N are greater than N deposition in spruce and birch stands, and the removals of P exceed the inputs through deposition and weathering in all tree species. Deposition and weathering are also insufficient to compensate for the losses of K in spruce and birch stands and the losses of Ca in spruce stands. These nutrient input–output comparisons suggest that in most cases, nutrient balance is negative if WTH is practised, and especially in birch stands, the balances of P and K can be negative even in SOH. These results are consistent with nutrient balance studies, which have demonstrated that there is a depletion of N and base cations in many parts of Fennoscandia in the long-term if WTH is practised (Sverdrup and Rosen 1998; Joki-Heiskala et al. 2003; Akselsson et al. 2007). The N balance has been found to be positive in WTH only in southern Sweden where N deposition is high (Akselsson et al. 2007). Some uncertainties are always involved in these nutrient balance calculations because nutrient fluxes vary temporally and spatially and it is technically difficult to determine some of them (Raulund-Rasmussen et al. 2008). The estimates of weathering rates are probably most uncertain because there are only a very few studies on boreal forest soils, and the estimates have varied greatly depending on the method of investigation (Jacks 1990; Starr et al. 1998). Nitrogen may also be lost though denitrification and gained through N-fixation (Rosén and Lindberg 1980; DeLuca et al. 2002; Maljanen et al. 2006). These fluxes are, however, small compared with the nutrient removals caused by harvesting (Rosén and Lindberg 1980; DeLuca et al. 2002; Maljanen et al. 2006).

The capacity of forest soil to sustain the tree production in the long term can also be assessed by comparing nutrient removals associated with harvesting to total and plant-available nutrient pools in the soil. In cases where the pools are small compared the removals, the risk for unbalanced tree nutrition is high and there is a need for compensating fertilization. The amounts of N removed with harvested biomass during the rotation were relatively large compared with the total soil N pools in mineral soil sites, and the removed P and K amounts were relatively large compared with the total soil P and K pools in peatland sites particularly in WTH (Fig. 6, Table 8). The removals of Ca with harvested biomass were relatively large in both mineral soil and peatlands. Other studies have also suggested that wood production and especially WTH may be a threat for the sufficiency of K in peatlands because the K pools in trees are of a similar order of magnitude as total K pools in the surface peat (Holmén 1964; Kaunisto and Paavilainen 1988; Finér 1989; Laiho 1997). Only a small part of soil nutrients are in a form available for trees (Table 8). The amounts of nutrients removed during the rotation are considerable compared with the plant-available nutrient pools in the rooting zone. Although nutrient budget calculations can be imprecise, comparisons with the size of soil nutrient pools confirm that WTH causes considerable nutrient losses in north European boreal forests, and if forests are not fertilized, the soil nutrient pools might be depleted and the growth of trees reduced as has already been shown in a few studies (Olsson et al. 1996a, b; Jacobson et al. 2000; Egnell and Valinger 2003; Saarsalmi et al. 2010). Tree stands are probably the most sensitive to nutrient removals caused by WTH at the thinning stage (Jacobson et al. 2000) when the nutrient demand is greatest (Mälkönen 1974).

Conclusions

We conclude that we could formulate regression equations where stand volume is used as an independent variable and provide an easy tool to get estimates of the nutrient content of stems and above-ground biomass in boreal Scots pine, Norway spruce, and birch stands. More data would be needed to increase the validity of the equations. Tree species, harvesting method, and the stage of stand development have a pronounced influence on nutrient removals. Nutrient removals per harvested stem m^3 are smallest in pine stands both in SOH and WTH. Nutrient removals by WTH can be reduced by harvesting energy wood from mature forests instead of young thinning forests because the nutrient-rich crown accounts for a relatively higher proportion of biomass in young forests. If WTH is done at final cutting, nutrient export by harvesting is in many cases greater than the nutrient inputs through deposition and weathering during the rotation. In forests stands where nutrient leaching is high, the balances of P, K, and Ca can be negative even in SOH. In mineral soil sites, N removals, and in peatland sites, P and K removals by WTH during the rotation are relatively large compared with the respective soil nutrient pools.

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