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Effects of whole-tree harvesting on nutrient accumulation in the subsequent forest stand: An examination of 6 Swedish long-term experiments

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ABSTRACT

Whole-tree harvesting (WTH) is associated with increased nutrient losses compared to stem-only harvesting (SOH), potentially depleting the soil nutrient stocks and causing reduced growth and lower nutrient accumulation in biomass of the subsequent stand. This reduction in nutrient uptake, when expressed as a reduced net base cation uptake, can act as an "uptake brake", that may lead to lower biological soil acidification. We used six Swedish long-term field experiments with randomized block design on WTH vs SOH performed in final fellings or thinnings to examine the long-term effects on nutrient status. The nutrient stocks in soil and biomass were examined 25 – 37 years after final felling, and 13–20 years after thinning. Following final felling, the total aboveground biomass, as well as stocks of N, P, and base cations (BC) in biomass, were significantly larger in SOH than WTH, but no such treatment differences were revealed after thinning. The differences in growth, not element concentrations, were in general the most important factor affecting rates of element accumulation in biomass. The "total stocks" of BC (salt exchangeable fraction in the soils plus aboveground biomass) were significantly larger following SOH than WTH after both final felling and thinning. The same pattern was found for the soil C stocks while only final felling exhibited significantly larger soil N stocks in SOH compared with WTH. These results support the hypotheses that WTH in final felling results in reduced tree growth in the subsequent forest stand, leading to lower nutrient uptake and thereby lower acidification pressure of the new stand compared to SOH.

1. Introduction

The global oil embargo crisis 1973–1974, urged an interest in Sweden to save energy and secure the energy supply by replacing fossil fuels with domestic energy sources (Legnér and Leijonhufvud, 2019; Bergquist and Söderholm, 2016). Apart from the introduction of nuclear power, this caused a growing interest in replacing fossil fuels with residues from the forest industry (e.g., saw dust and bark) – but also primary biomass such as logging residues (slash; branches and tops) and other forest biomass residues available after stemwood harvest (Ericsson et al., 2004). The use of slash for energy has since then been growing and is currently on the order of 10 TW per year in Sweden (Swedish Energy Agency, 2020, 2022, 2025). This corresponds to harvesting of slash at one-third of the forest area subjected to final felling and 3 % of the thinned area, with the major part being harvested in southern Sweden (Swedish Forest Agency, 2025). The total energy supply from industrial residues, mainly derived from stem biomass, is significantly larger. In 2022 more than 100 TWh was supplied from processed solid wood biomass, and of that 55 TWh was black liquor produced in the pulp and paper industry (Swedish Energy Agency, 2025). Also in the EU, forest-based biomass has been an important supplier of renewable energy for decades (Bentsen and Felby, 2012), and corresponds to 70 % of the total bioenergy feedstock (Bioenergy Europe, 2021).

The present study is an examination of long-term Swedish experiments established in the wake of the so-called oil embargo crisis in the 1970's. During that time the main concern in forestry was the supply of

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feedstock to the traditional forest industry. Consequently, experiments were established 1974–1983 to study the impacts of harvesting nutrient-rich slash on forest growth and ecosystem nutrient stocks in the subsequent stand following final felling and in the remaining stand after thinning (Björkroth and Rosén, 1977; Egnell and Leijon, 1997). Similar field trials were also established in other Nordic countries (Helmisaari et al., 2011).

Studies of forest biomass in Sweden and Finland show that, on average, almost 70 % of N and P content of above-ground biomass is contained in branches and foliage of mature Norway spruce, and about 60 % in Scots pine. Corresponding values for K, Ca and Mg are lower and ranged 32 – 70 %. This despite the fact that the biomass of branches and foliage were on average only 33 % of aboveground biomass in Norway spruce, and 21 % in Scots pine (Authors compilation of data from Mälkönen, 1976; Björkroth and Rosén, 1977; Nihlgård, 1972; Bringmark, 1977). Whole-tree harvesting (WTH, i.e., harvest of stems and slash) will therefore result in a moderate increase in biomass harvest at a cost of a substantial increase in nutrient removals from forests compared to stem-only harvest (SOH). For this reason, most early research on WTH effects focused on soil nutrient depletion and its potential impact on future forest growth (Weetman and Webber, 1972; Kimmins, 1976; Mälkönen, 1976), and this has remained an issue also in recent research (e.g., Lim et al., 2020; Ouimet et al., 2021; Smith et al., 2022b; Klavins et al., 2023).

With a fully stocked stand, WTH in final felling of conifers means the removal of nutrient elements that quantitatively corresponds to rebuild the aboveground biomass of the subsequent stand, and in stoichiometric proportions to the nutrient demand of that stand including luxury consumption (see below). These elements play different roles for plant growth and soils. Because growth of boreal and most temperate forests on mineral soils is generally limited by nitrogen (N) (Tamm, 1991; LeBauer and Treseder, 2008; Högberg et al., 2017), growth reduction due to WTH was proposed to primarily be an effect of reduced soil N availability. Actually, few studies have demonstrated reduced soil N availability following WTH (e.g., Smolander et al., 2019). However, Nordic experiments have shown reduced tree growth following WTH, although with varying results depending on tree species and felling form (Egnell, 2017; Helmisaari et al., 2011; Egnell and Valinger, 2003; Egnell and Ulvcrona, 2015). Helmisaari et al. (2011) also found no growth reduction after WTH combined with nutrient (NPK) applied for compensation of harvest losses.

WTH may also cause lower soil C stocks. A meta-study by Achat et al. (2015b), based on a world-wide data set of 238 publications, where most sites were in temperate and boreal regions, showed that WTH generally results in lower soil carbon stocks in all soil layers. Although increased harvest losses of organic matter with WTH are inevitable, this effect is often not detected in soil C stock surveys in single field experiments. For example, Olsson et al. (1996b) observed that C and N stocks in the humus layer had decreased 15 years after final felling, but there was no significant difference between WTH and SOH at that time or at a later repeated sampling (Brandtberg and Olsson, 2012). Further, the C-to-N ratios in the soil were frequently lower in SOH than WTH treatment (Olsson et al., 1996b).

Besides WTH effects on N availability, net harvest losses of base cations (BC, i.e., Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) may be a cause of soil acidification (Van Breemen et al., 1983, Nilsson et al., 1982). In soils with low BC weathering rates, the primary mechanism for that is the potential loss of acid neutralization capacity (ANC) that comes with the loss of BC at soil particle surfaces and in soil solution resulting in lower base saturation. A lower ANC caused by this process may lower soil pH. The ultimate acidification process is driven by tree growth and the net BC accumulation in biomass throughout the forest rotation period and the corresponding exudation of protons from roots to soil to maintain charge balance. Hence, this proton production and biological soil acidification is at its maximum just before harvest when it ceases. Thereafter, the mineralization of harvest residuals initiates alkalinization processes, increasing ANC and pH. Since the BC losses are larger at WTH compared to SOH, the net acidification effects of the former are potentially larger on ANC and pH. However, regardless of harvest intensity, BC are permanently lost from the soil system.

This type of soil acidification due to WTH, that primarily depends on lack of alkalinization from decomposing residues, has been demonstrated in several Nordic field trials comparing WTH and SOH (e.g., Nykvist and Rosén, 1985; Staaf and Olsson, 1991; see also compilations in Clark et al., 2021). Further, because anion uptake in trees counteracts the acidification generated by BC uptake, subtracting anion uptake from BC is a more precise measure of the net acid load of different harvesting regimes. This is referred to as the excess, or net BC uptake (Nilsson et al., 1982; Löfgren et al., 2021). The nitrogen uptake in trees has different effect on soil acidity depending on the source of inorganic N (mineralization of organic matter or deposition), the form of N (NH_4^+, NO_3^-, or organically bound N), and whether available inorganic N is taken up by trees or lost through leaching.

The abundance of BC in forest soils is only partly reflected in plant nutrient stoichiometry (Ladanai et al., 2010). The physiological needs of Ca for tree growth are generally very low compared to the actual uptake and accumulation in trees, and is often well within the sufficiency range (Knecht and Göransson, 2004), sometimes referred to as a surplus or "luxury consumption". Uptake of Ca^{2+} is basically a passive flow with water transport. Large portions of the Ca^{2+} in trees reside in extracellular spaces as insoluble oxalate crystals or are bound to cell walls as Ca^{2+} pectate and has therefore a slow mobility in trees (Fink, 1991; Franceschi and Nakata, 2005; Dauer and Perakis, 2014). On the other hand, Ca^{2+} saturation is a major component of ANC and base saturation of soils, why variation in Ca cycling is decisive for the chemical composition and function of soils. In contrast to Ca^{2+}, plants have in general a larger need for the more mobile K^{+}, which is important as e.g., a charge counter-ion in the cell plasma, and is therefore rapidly lost when plant cells die, collapse, and decompose (e.g., Fraústo da Silva and Williams, 2001). Uptake of K^{+} in terrestrial plants is an active energy-demanding process including ion exchange with Na^{+}, that is taken up only in minute amounts and is not regarded as an essential plant nutrient (Nieves-Cordones et al., 2014). Losses of K^{+} from trees with litter shedding and foliar leaching, in combination with high demand and active uptake, is likely causing a more rapid turnover rate of K^{+} than for Ca^{2+} in trees, and this is also the case in the humus layer of forest soils (Dincher et al., 2020). The cycling characteristics of Mg^{2+} is intermediate to that of Ca^{2+} and K^{+}, with respect to mobility in both soils and plants. Mg^{2+} is pivotal for photosynthesis and concentrations in conifer needles show low variation (Ladanai et al., 2010). Accumulation of Na in trees is negligible compared to other BC ions. Marine influence with dry deposition of marine salts can be an important source of Na, indicated by higher accumulation of Na in forest biomass near the Swedish west-coast compared to boreal forests in Northern Sweden (Simonsson et al., 2015; Casetou-Gustafson et al., 2020).

The soil acidification effect of WTH demonstrated in current field trials was ultimately caused by the nutrient accumulation in the harvested stand in combination with the reduced return of BC in slash after felling. However, the next forest rotation following WTH will place lower acid load on the soil compared to SOH, if the net BC accumulation rate in new biomass is lower. This will have a "nutrient uptake brake" effect that will tend to diminish differences in soil acidity between SOH and WTH. However, it does not compensate the acidification effect of WTH in the next forest generation. A test of the magnitude of this acidification pressure can be made from comparing the BC accumulation in new biomass following SOH and WTH.

SOH is conveniently used as a reference to WTH, in the sense that SOH has been the conventional harvesting method and WTH has been a novel practice. By shifting the perspective, SOH can be viewed as a treatment where slash is applied on a site. This perspective allows a stronger focus on dynamics of slash decomposition and the fate of nutrient released from the slash (Hyvönen et al., 2000;

Erlandsson-Lampa et al., 2019). Although the slash amount and thereby the nutrient amount is lower following thinning as compared to final felling, the thinned stand has the advantage of responding directly to any change in nutrient availability. It is therefore reasonable to expect more significant differences in nutrient uptake and thereby tree growth between WTH and SOH in thinnings than in final fellings. In the latter case, a new stand established after final felling has an initially low nutrient demand, and is also responding to other factors occurring at the clear-cut, such as interspecific competition with pioneer vegetation such as grasses and broad-leaved trees, which also can be influenced by the retention or harvest of slash (Olsson and Staaf, 1995; Brandtberg et al., 2023). Furthermore, there is a higher risk that nutrients released from slash will be lost by leaching. The potential for leaching is promoted by nitrification, which often is much stimulated at clear-cuttings (Likens et al., 1970; Kreutzweiser et al., 2008; Olsson et al., 2022).

The aim of this study was to compare the effects of WTH versus SOH on the “total” nutrient stocks i.e., soil nutrient and carbon stocks (and for BC only in the exchangeable pools), and accumulation of nutrients in aboveground biomass of the subsequent stand. For this, we used data from six Swedish long-term field experiments where WTH had been applied in either final felling or thinning, with SOH as the reference treatment. In addition, we assessed the impacts of WTH on internal element flux by measuring needle litter-fall over 11 years at one of the Norway spruce trials.

The main testable hypotheses were that (1) compared with SOH, WTH results in lower availability of plant essential nutrients in the soil, (2) reduced tree growth, and (3) reduced uptake and accumulation of nutrients in the subsequent stand. The causal relationship between these three effects as well as the acidification pressure effects of a potential “uptake break” are discussed. Further, (4) we expected that WTH in thinning will have more marked effects on tree growth and nutrient uptake than on soil, opposed to WTH in final fellings that have more marked effects on soil than tree growth and nutrient uptake. We examined this hypothesis based on the outcome of separate statistical tests for the thinning and final felling experiments.

2. Material and methods

2.1. Study sites

We used data from six experimental sites with coniferous forests in Sweden, where different harvesting intensities (SOH and WTH) of aboveground biomass had been applied. At three sites, harvesting treatments were applied in final felling (Tönnersjöheden-T103, Kosta, Lövliden) and at the other three sites they were applied in thinning (Borrestad, Granhult, Granö). The sites are located at different climate regions of Sweden representing temperate (Borrestad, Tönnersjöheden-T103), hemi-boreal (Granhult, Kosta), and boreal (Granö, Lövliden) conditions. Soil and site conditions are shown in Table 1. The experimental stands are monocultures of Norway spruce (*Picea abies* (L.) Karst.) or Scots pine (*Pinus sylvestris* L.), respectively (Table 2). Site Tönnersjöheden-T103 is denoted ‘T103’ in the following.

2.2. Experimental design

A randomized block design was applied at all sites, where SOH and WTH were randomly assigned to one plot in four blocks ($n = 4$). Each plot (25 x 25 m) was surrounded by a 5 m wide border strip. In final felling, harvesting was done with a chainsaw and at the WTH-plots all slash was manually removed. A chainsaw was used also in the thinning experiments, where the thinning form and strength was designed to equalize basal area and stem number variation within blocks following harvest (Egnell and Leijon, 1997). Logs (SOH) or tree-sections with branches (WTH) were winched out from the plots. Due to intense growth, the treatments were repeated in a second thinning in 1988 at Borrestad (Table 2). The amounts of nutrients in slash, retained in the treatment SOH after the final fellings and thinnings, are shown in Table 3 (adopted from Björkroth and Rosén, 1977; Egnell and Leijon, 1997).

2.3. Data sources

All data on element stocks in soil and biomass were previously unpublished except for the following: Soil data from T103 (2002) and Kosta (2001) was a reorganized subset originating from the same data source as that of Brandtberg and Olsson (2012). Element concentrations in tree biomass of T103 and Kosta have been used in calculations of nutrient uptake by Zetterberg et al. (2016), but nutrient concentration data were then not presented.

2.4. Biomass and nutrient content determination

Determination of biomass and nutrient content in standing biomass was made after 25–46 years in final felling experiments, when these stands were first thinned, and after 13–20 years in thinning experiments. The determination was performed in five steps. First, all trees on the plots were cross-calipered to determine diameter at breast height (DBH, 1.3 m). The mean DBH measure per tree was used for further calculations. Second, a stratified selection of trees for destructive sampling of aboveground biomass was made based on DBH data. The number of trees felled in each plot varied from 1 to 3, and always included one or two average (DBH) trees of the plot, or included in addition (T103, Kosta) a −1 or + 2 SD from the mean plot DBH (Table 4). Destructive sampling of tree biomass was performed in autumn (September – November) or in late winter or early spring (February–April).

Third, selected trees were felled with a chainsaw. Logs were cut in 3–4 parts and the physical dimensions and fresh weight were measured. The treetop was separated from the bole at stem diameter 5 cm. A 5 cm

Table 1
Characteristics of the study sites.

	T103	Kosta	Lövliden	Borrestad	Granhult	Granö
Site ID	S2443	S2442	S2444	S2449	S2448	S2447
Position	56°42’N, 13°50’E	56°52’N 15°23’E	64°16’N 19°31’E	55°52’N, 14°02’E	57°03’N, 15°13E	64°19’N, 19°02’E
Altitude	100	595	260	100	295	300
Mean temp*	7.1	6.2	2.4	7.8	6.0	2.4
Annual precip*	1146	738	624	614	738	624
Parent material	Albic podzol	Albic podzol	Albic podzol	Eutric cambisol	Albic podzol	Albic podzol
Soil	Glacial till	Glacial till	Glacial till	Glacial sediment	Glacial till	Glacial till
Soil texture**	Silt	Silt loam	Silt	Silt	Silt loam	Silt
Stoniness	Moderate	High	Moderate	None	Moderate	Moderate
Soil moisture class	Mesic	Mesic	Mesic-wet	Mesic	Mesic	Mesic
Field vegetation type	Dwarf-shrub	Dwarf-shrub	Dwarf-shrub	None	Dwarf-shrub	Dwarf-shrub

[*]) Mean annual temperature and annual precipitation are from nearest SMHI meterological station, mean values for the period 1981–2010. (Swedish Metereological and Hydrological Institute, 2021).
[**] IUSS Working Group WRB. (2015).

Table 2
Stand characteristics and experimental treatments.

	T103	Kosta	Lövliden	Borrestad	Granhult	Granö
Experiment type	Final-felling	Final-felling	Final-felling	Thinning	Thinning	Thinning
Former stand:						
Tree species	*Picea abies*	*Pinus sylvestris, Picea abies*	*Picea abies, Pinus sylvestris*	–	–	–
Age of former stand (yrs)	70	100	155–175	–	–	–
Final felling (year)	1974	1975	1976	–		–
Stem volume (m^3 ha^{-1})	325	305	290			
Site productivity (m^3 ha−1 yr^{-1})	10.1	5.9	3.8	–		–
Present stand:						
Tree species	*Picea abies*	*Pinus sylvestris*	*Picea abies*	*Picea abies*	*Picea abies*	*Pinus sylvestris*
Present stand established (year)	1975	1975	1976	1966	1955	No data
Year of treatment	1975	1975	1976	1983, 1988	1983	1982
Year of biomass sampling	2004	2000	2020	1996	2002	2002
Year of soil sampling	2002	2001	2012	1997	2002	2002
Thinning intensity % of basal area	–	–	–	25, 25	25	25
Plot size (net, ha)	0.04	0.04	0.04	0.1	0.1	0.1
Mean stem density prior to sampling (ha^{-1})				1150	1320	
Stand age at sampling (year)	28	25	45	31	48	No data

Table 3
Site index (H_{100}) and amounts of nutrients (kg ha^{-1}) in logging residues retained in treatment SOH after thinning or clear-felling. At Borrestad, WTH was made at first thinning 1984 and at a second thinning in 1988. Data for Granö and Granhult are adopted from Egnell and Leijon (1997), data from T103, Kosta and Lövliden are from Björkroth and Rosén (1977). Data for Borrestad are based on stem inventory data, Marklund's (1988) allometric function with corrections from 1984 tree sampling, and using nutrient analyses from the 1996 inventory.

Site	Site index[a]	N	P	K	Ca	Mg
Thinning experiments						
Borrestad 1984	36	185.1	36.3	58.8	168.9	16.0
Borrestad 1988		167.4	32.5	52.8	152.6	14.5
Borrestad sum		352.4	68.8	111.5	321.5	30.5
Granhult 1983	30	84.7	9.65	28.6	n.d.	n.d.
Granö 1982	25	45.85	4.85	17.75	n.d.	n.d.
Final felling experiments						
T103 1975	30	271.6	22.6	65.0	128.1	27.9
Kosta 1975	24	233.2	22.9	101.9	120.2	22.2
Lövliden 1976	20	160.6	18.84	81.6	229.2	19.4

a) Height (m) of dominant trees at age 100 years according to Hägglund and Lundmark (1977). Data from Egnell and Leijon (1997).

thick disc was taken from the lower end of each bole segment and placed in a sealed plastic bag for further analyses. The fresh weight of the branch biomass, and the treetop, were determined according to the sectioning of the boles. Subsamples of live and dead branches were taken and placed in sealed plastic bags for further analyses. At the laboratory, subsamples of stems and branches were weighed and further separated in stem wood, stembark, needles, living branches, and dead branches. The needles were allowed to fall off from the twigs by drying at room temperature. Dead branches also included dead twigs attached to living branches. Determination of sample dry weight (dw) was made after drying at 70°C to constant weight. Determination of dry weight of each tree part used total and sample fresh weight measured in the field, and fresh and dry weight measured in the laboratory. Dry weight of the needles and branches were determined based on the dry-to fresh weight ratios of sampled branches, and the sample-to-total branch fresh weight.

Fourth, determination of tree biomass at the plot level was made by applying generic allometric equations by Marklund (1988) to all trees in a plot and, based on sample tree data, corrected for systematic local deviations of biomass partitioning in relation to the generic equations (Table 4). The corrections were calculated from linear regressions of observed and predicted biomass, where the term (*a*) in the regression

Table 4
Selection of sample trees, Marklund (1988) biomass functions used for different tree fractions, and corrections factors estimated from sample trees.

	T103	Kosta	Lövliden	Borrestad	Granhult	Granö
Total number of trees sampled	30	36	12	24	24	24
Number of mean DBH trees	12	12	12	24	24	24
Number of DBH +/- 1 SD trees	18	24	0	0	0	0
Functions						
Stem	G−1	–	–	–	–	–
Stemwood	–	T−5	G−5	G−4	G−4	T−5
Stembark	–	T−9	G−8	G−7	G−7	T−9
Needles	G−15	T−17	G−16	G−15	G−15	T−17
Branch + needles	G−11	T−13	G−12	G−11	G−11	T−13
Dead branches	G−19	T−21	G−20	G−19	G−19	T−21
Correction factors						
Stem	1.24	–	–	–	–	–
Stemwood	–	1.00	1.067	1.211	1.154	1.065
Stembark	–	1.38	1.38	0.809	1.26	1.208
Needles	0.796	1.06	0.852	0.756	0.536	0.655
Branch + needles	0.505	1.56	0.531	0.597	0.463	0.615
Dead branches	4.28	4.68	2.644	3.136	1.255	2.722

was set to 0. Biomass functions based on DBH data only was used for all sites, except for Lövliden where tree height (H) was used in addition to DBH (Table 4). Height (H, m) data for all trees at Lövliden was calculated with Eq. (1), based on DBH (D, cm) and H data from a subsample of trees (n = 138) at the site:

$$H = 1.3 + \left(\frac{D}{(1.2869 + D \times 0.36)}\right)^3 \tag{1}$$

The total biomasses in different fractions of all trees in a plot were summed up into kg dry weight ha^{-1}.

Fifth, nutrient stocks in aboveground biomass were calculated from biomass in different fractions (kg ha^{-1}) and nutrient concentrations data in that fraction (mg g^{-1} dw). Nutrient concentration in different biomass fractions, including needle litter-fall collected in site T103, was determined by first milling dried biomass samples prior to chemical analyses. Grinding was performed in several steps using different mills to obtain the size fraction required for the analyses, and representative subsamples were taken in each step. Determination of nitrogen (N) content in biomass was made with dry combustion methods. Fine milled samples were analysed using a Carlo-Erba NA 1500 instrument, except for Lövliden samples which were analysed with a LECO instrument and using IR detection for S and TCD detection for N. Analyses of the other elements were made after an acid wet digestion procedure in two steps (HNO_3, $HClO_4$). Samples were analyzed for P, K, Ca, Mg, and Na by ICP-atomic emission spectrophotometer (Jobin Yvon JY-70 Plus). In these chemical analyses, reference materials were used for quality assurance checks. Other elements than N from Lövliden were analysed with ICP-SFMS according to SS EN ISO 17294–2: 2016 and EPA-method 200.8: 1994, following oxidation in HNO_3/ H_2O_2.

2.5. Soil element stock determinations

2.5.1. Soil sampling, and chemical analyses

Soil samples have been taken repeatedly in the final felling experiments by approximately decadal intervals (e.g., Brandtberg and Olsson, 2012). Here, we used soil data that made the best match in time with a corresponding biomass sampling, i.e., 2002 (soil) and 2004 (biomass) for T103, 2001 (soil) and (2000) biomass for Kosta, and 2012 (soil) and 2020 (biomass) for Lövliden (Table 2). See 2.3 for details on data sources. In two of the thinning experiments (Granhult, Borrestad), soil analyses were made at the time of the first thinning, i.e., at the start of the experiment, as well as at the second (Granhult), and third (Borrestad) thinning. The first soil sampling, denoted 't1', was carried out shortly after thinning in June through October. The second soil sampling, denoted 't2', was made after 13 (Borrestad) –19 years (Granö, Granhult), in the same season as for the first sampling.

The procedures for sampling, soil preparation and chemical analysis in the experiments were largely identical, as described below. In each experimental plot, samples were taken from the litter (L), humus layer (FH), and the mineral soil (0 – 20 cm divided into four 5 cm segments), on 25 spots in the plots, to make one composite sample for each plot and soil layer. The sampling positions were allocated in a grid where the starting position was chosen randomly. A sampling spot that was located on a boulder or stump was not replaced by a new spot. A corer (Ø 107 mm) was used for sampling the organic layers, and a steel corer (Ø 27 mm) was used for sampling the mineral soil. Litter and humus samples were sieved through a 5 mm mesh net, and the mineral soil was passed through a 2 mm mesh net. Fresh homogenized samples were dried at 85° C overnight for dry matter determinations.

Soil extracts for determination of exchangeable cations were prepared by adding 5 g of fresh material from the humus layer, and 20 g from the mineral soil in 250-ml polyethylene bottles and adding 100 ml of 1 M NH_4Cl. Extractions were made for 2 h. Chemical analysis of Na, K, Ca, and Mg in the filtered (Munktell OOK, Grycksbo, Sweden) extracts was performed with ICP atomic Emission Spectrometer (Jobin-Yvon JY-70 plus). Determinations of K in soil extracts from the first sampling occasion was made using an AAS. Determinations of total organic C and N was made by dry combustion methods, where Carbo-Erba elementar analyser model NA 1500 was used except for Lövliden (2012) where a LECO instrument was used.

2.5.2. Bulk density determinations

In the thinning experiments, bulk density (BD) of the mineral soil of the 0–10 cm and 10–20 cm horizons were determined from excavation of 0.5×0.5 m soil pits. The pits were located at the plot borders, and one pit per plot and site was excavated. The fresh weight of the soil (< 8 mm) was determined in the field, and samples were taken to the laboratory for further analyses of texture and dry weight of the < 2 mm soil fraction. A site mean value of the dry weight of mineral soil (<2 mm) per horizon was used for further calculation of element stocks in the mineral soil. In the final felling experiments, site mean BD data was also calculated from soil pit excavations and with the data adopted from Björkroth and Rosén (1977). BD values are shown in Supplement Table S1.

2.5.3. Element stock caclulations

The amounts of elements in the humus layer were determined using the mass of humus per unit sampling area at each sampling occasion whereas the stocks of elements in each mineral soil layer and experimental plot were calculated using the BD for the different soil layers. Sum of exchangeable base cations (BC_{ex}) was calculated as the equivalent sum of Na^+, K^+, Ca^{2+} and Mg^{2+}.

2.6. Litter-fall study of T103

Litterfall was measured continuously over 11 years (1991–2001) at site T103. At each plot, 10 litterfall traps were distributed in a grid pattern. The cylindrical pipe-formed traps were constructed from thin stainless steel (50 cm Ø, 40 cm height), with a stretched mesh net (1 mm) fixed horizontally above 30 cm from the ground. The rationale of the design was to collect needles falling from the lower branches, which at the start of the sampling period were at about height 1 m. The total sampling area per plot was 1,96 m^2. During the first year, litter was sampled at monthly intervals, and thereafter 2–3 times per year depending on snow conditions. It was discovered that a fraction of the needle litterfall could escape through the mesh net. This fraction was measured, and to correct for a systemic underestimation a factor of 1.2649 was used in all calculations of dry mass and nutrient fluxes in needle litterfall. Litter samples were separated in needles and other litter, and dry weight was determined after drying at 70°C. Chemical analyses of milled needle litter were made using the same methods as for the biomass samples from T103.

2.7. Statistical analyses

Statistical tests of the effect of treatment, site, block, and interaction site × treatment on dependent variables were made using an ANOVA (Standard Least Squares module in JMP Pro 26.0.0. software) model based on the randomized block design of each site. Response variables were biomass and element stocks in biomass, in soil, and in total expressed as Kg ha^{-1} or $Kmol_c$ ha^{-1} (extractable BC), and element concentrations in biomass. Statistical tests on element stocks in biomass were made separately for the two types of experiments, given the fundamental differences between final felling and thinning stands. However, soil element stocks were additionally tested for data of all sites due to their potential effects on soil nutrient stocks and tree growth, respectively. Treatment effects on the total C sequestration (biomass +soils) will be handled in a separate article. No transformation of data was considered necessary, based on visual inspection of residuals.

3. Results

3.1. Biomass effects

Total aboveground biomass, and stocks of N, P, BC in biomass were significantly larger in SOH than WTH following final felling, whereas no treatment differences were revealed in thinning experiments for these variables (Table 5, Figs. 1, 2). The treatment effect on biomass BC was due to increased amounts of Ca and Mg in biomass, not of K or Na. Interactions between site and treatment were not significant (Table 5). The Borrestad site was exceptional with respect to biomass and element stocks in biomass, with about two times larger biomass, N and BC stocks, and three times larger P stocks compared to the other sites (Figs. 1, 2).

Treatment effects on element stocks in biomass could be due to an influence on growth, element concentrations in biomass, or both. Concentrations of N, P, and BC elements in stem wood, stem bark, needles, and living branches were tested for treatment effects. With three exceptions, there were no significant differences between treatments (Supplement Table S2): Ca concentrations in stem wood were lower in WTH than in SOH stands in final felling experiments, and Ca concentrations in living branches in thinning experiments were lower in WTH

Table 5
Effect of harvesting logging residues (WTH) at final felling or thinnings on dry mass and element stocks in aboveground tree biomass in the subsequent stand. Stem-only harvesting (SOH) is reference to WTH effects. Mean values across 3 sites (n = 12) and *P*-values from statistical analyses; LSD = Least Significant Difference. n.s. = not significant, i.e., $P > 0.05$. Treatment S, SOH=stem-only harvest; W, WTH=whole-tree harvest.

Variable	Experiment	SOH	WTH	Treatment LSD	*P*-value	Treatm. x Site LSD	*P*-value
Biomass (Tonnes ha^{-1})	Final felling	108	88.1	**S>W**	**< 0.001**	n.s.	0.676
	Thinning	179	174	n.s.	0.103	n.s.	0.977
N (Kg ha^{-1})	Final felling	320	277	**S>W**	**0.027**	n.s.	0.689
	Thinning	375	358	n.s.	0.117	n.s.	0.845
P (Kg ha^{-1})	Final felling	37.4	30.5	**S>W**	**0.007**	n.s.	0.746
	Thinning	66.5	67.0	n.s.	0.699	n.s.	0.069
BC (Kmol$_c$ ha^{-1})	Final felling	20.7	15.9	**S>W**	**0.004**	n.s.	0.830
	Thinning	27.3	26.9	n.s.	0.603	n.s.	0.365
Ca (Kg ha^{-1})	Final felling	271	197	**S>W**	**0.003**	n.s.	0.355
	Thinning	380	373	n.s.	0.581	n.s.	0.636
Mg (Kg ha^{-1})	Final felling	39.7	33.8	**S>W**	**0.032**	n.s.	0.363
	Thinning	46.4	46.1	n.s.	0.857	n.s.	0.142
K (Kg ha^{-1})	Final felling	144	124	n.s.	0.124	n.s.	0.269
	Thinning	167	166	n.s.	0.942	n.s.	0.394
Na (Kg ha^{-1})	Final felling	3.09	2.23	n.s.	0.284	n.s.	0.633
	Thinning	3.72	3.26	n.s.	0.161	n.s.	0.933

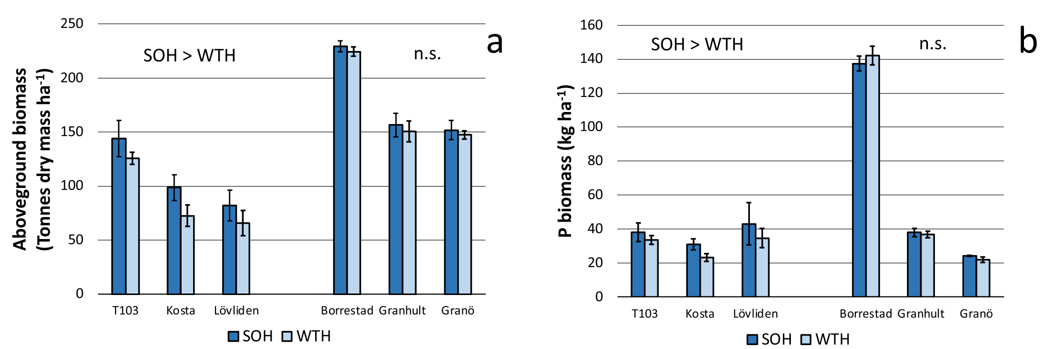

Fig. 1. Effects of WTH compared with SOH on aboveground biomass (a), and P in biomass (b). Bars are grouped in final felling experiments (3 to the left) and thinning experiments (3 to the right). Treatment means with standard deviation shown in error bars. Significant differences between treatments within each group are indicated ($p < 0.05$); n.s. = not significant. Statistical results are given in detail in Table 5.

than in SOH. N concentrations in live branches of final felling sites were higher in WTH than SOH treatments. Element-to-N ratios in the total needle biomass indicated ratios for Ca and Mg to be well over physiological needs for growth at all sites, but with relatively low supply of K and P at T103 (Supplement Table S3).

3.2. Soil effects

There was no statistically significant difference in soil C stocks when the SOH and WTH treatments were evaluated for separate experimental types, although it was close to significant in the final felling experiments ($p = 0.058$) (Table 6, Fig. 3). The soil N stocks showed a similar pattern, with statistically significant larger soil N stocks in SOH than WTH after final felling, but not after thinning. Interactions between site and treatment were not significant. Additional statistical tests were made that included data from both experiment types, which showed significantly larger soil C and N stocks in SOH than WTH. The C-to-N ratios of the humus layer ranged from low values at temperate southern sites to higher valuer at the boreal sites (Fig. 3). There was no treatment effect on the C-to-N ratio for separate experimental types, or for both types combined.

In contrast to the effects on biomass, the soil stocks of exchangeable BC were significantly higher in SOH than WTH in the thinning experiments, whereas the final felling experiments showed no significant difference between treatments (Table 6, Fig. 2). However, a similar BC_{ex} trend as after thinning also appeared after final felling with a *p*-value close to statistical significance ($p = 0.053$). Test of the two experimental types combined revealed significantly higher BC_{ex} stocks in SOH than WTH.

Among the BC elements, Ca and K responded differently to treatments (Fig. 2). Exchangeable Ca stocks were larger in SOH than WTH in both final felling and thinning experiments, and when these experimental types were combined. Despite large variations in mean exchangeable Ca stocks across sites (97–476 kg ha^{-1} after thinning, 75–216 kg ha^{-1} after final felling), there was no significant interaction between site and treatment. The exchangeable soil stock of K was significantly larger in SOH than in WTH in thinning experiments and when the two experimental types were combined, but no difference was detected in final felling experiments. Despite a narrow range of soil mean exchangeable K stocks across sites (48–67 kg ha^{-1}), the site × treatment interaction was significant after thinning, indicating a larger difference between treatments at sites with larger exchangeable K soil stocks.

Soil BC_{ex} and N stocks varied differently with sites. For example, site T103 had apart from Granö the lowest BC_{ex} stocks, but the highest N stocks. The soil BC_{ex} stocks at Borrestad was about twice as large as at Kosta, Lövliden and Granö (Fig. 2).

3.3. Effects on total stocks – the sum of soil and biomass

Total stocks of BC, here defined as the sum of soil BC_{ex} and aboveground biomass BC, were significantly larger following SOH than WTH in both final felling and thinning experiments (Table 7). Total stocks of N were significantly larger in SOH than WTH stocks after final felling, but

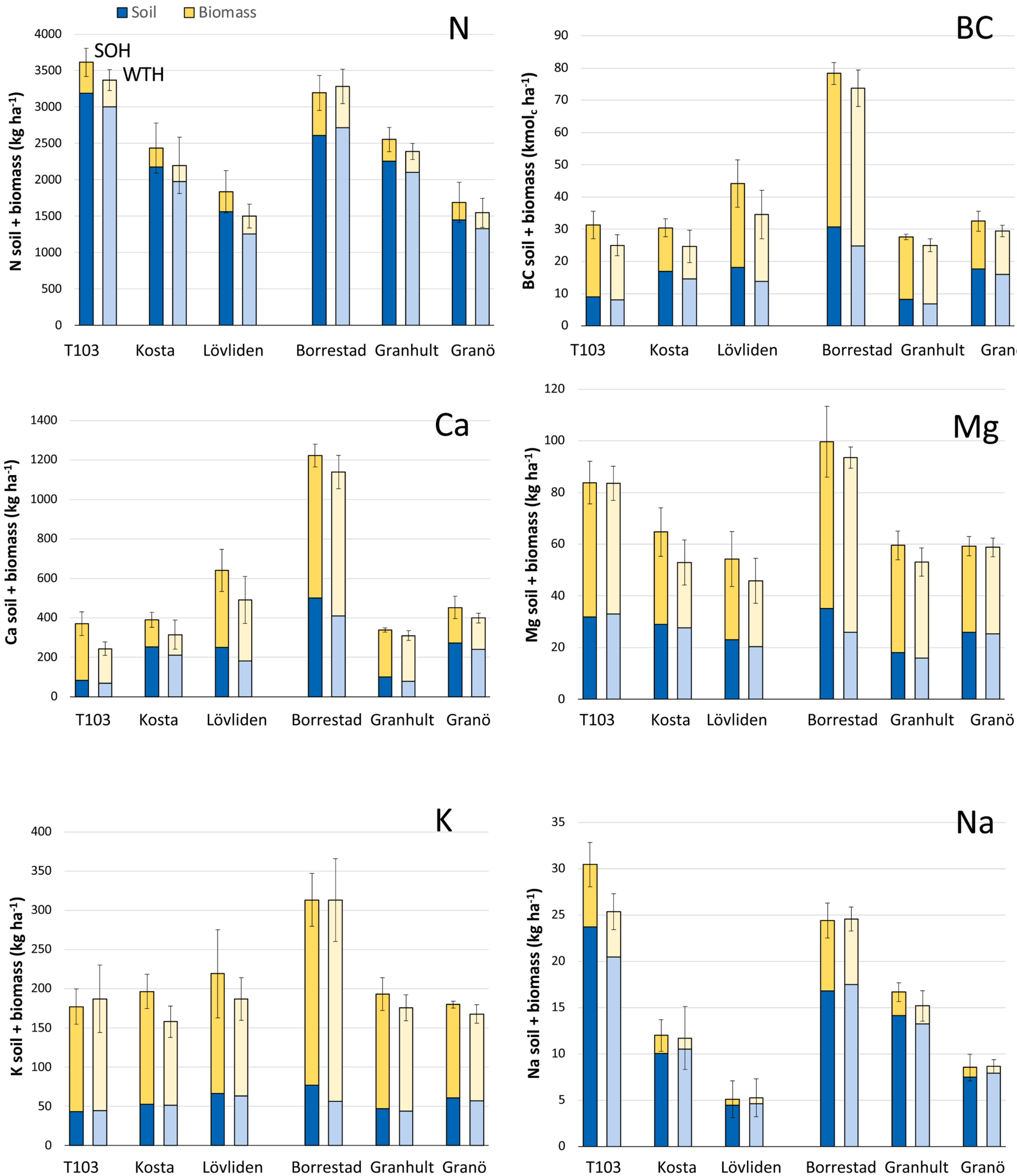

Fig. 2. Effects of WTH (light blue and yellow bars) compared with SOH (dark blue and yellow bars) on element stocks in soil (blue) and aboveground tree biomass (yellow). Soil N stocks are total stocks, whereas soil stocks in BC, Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+} are exchangeable stocks. Bars are grouped in sites of final felling experiments (3 to the left) and thinning experiments (3 to the right). Bars show treatment means, error bars show standard deviation of the sums of stocks in soil and aboveground biomass. Statistical results are given in detail in Tables 5 and 6.

not after thinning. Interactions between site and treatment were not significant.

3.4. *Temporal changes in soil stocks in thinning experiments*

Soil data from the time of initiation of the thinning experiments allowed for estimates of temporal soil changes (Fig. 4). There was no significant temporal change in soil N and C stocks (O horizon and

Table 6
Effect of harvesting logging residues (WTH) at clear-felling or thinning on element stocks in soil in the subsequent stand. Stem-only harvesting (SOH) is reference to WTH effect. Mean values across 3 sites (n = 12) and *P*-values from statistical analyses; LSD = Least Significant Difference. n.s. = not significant, i.e., $P > 0.05$. Treatment S=stem-only harvest; W=whole-tree harvest.

Variable	Experiment	SOH	WTH	Treatment LSD	*P*-value	Treatm. x Site LSD	*P*-value
C (Tonnes ha^{-1})	Final felling	67.5	61.3	n.s.	0.058	n.s.	0.565
	Thinning	46.8	44.6	n.s.	0.279	n.s.	0.544
	All	57.1	52.9	**S>W**	**0.024**	n.s.	0.585
N (Tonnes ha^{-1})	Final felling	2.31	2.08	**S>W**	**0.036**	n.s.	0.862
	Thinning	2.10	2.05	n.s.	0.535	n.s.	0.415
	All	2.21	2.06	**S>W**	**0.036**	n.s.	0.587
C/N	Final felling	30.5	31.1	n.s.	0.105	n.s.	0.064
	Thinning	23.3	23.0	n.s.	0.522	n.s.	0.394
	All	26.9	27.1	n.s.	0.421	n.s.	0.052
BC_{ex} ($Kmol_c$ ha^{-1})	Final felling	14.0	11.7	n.s.	0.053	n.s.	0.573
	Thinning	18.7	16.1	**S>W**	**0.014**	n.s.	0.202
	All	16.7	14.1	**S>W**	0.007	n.s.	0.478
Ca_{ex} (Kg ha^{-1})	Final felling	196	154	**S>W**	**0.031**	n.s.	0.516
	Thinning	294	246	**S>W**	**0.023**	n.s.	0.304
	All	244	198	**S>W**	**0.004**	n.s.	0.654
K_{ex} (Kg ha^{-1})	Final felling	54.1	53.0	n.s.	0.711	n.s.	0.784
	Thinning	62.4	53.4	**S>W**	**0.001**	*	**0.009**
	All	57.9	52.8	**S>W**	**0.017**	n.s.	0.053

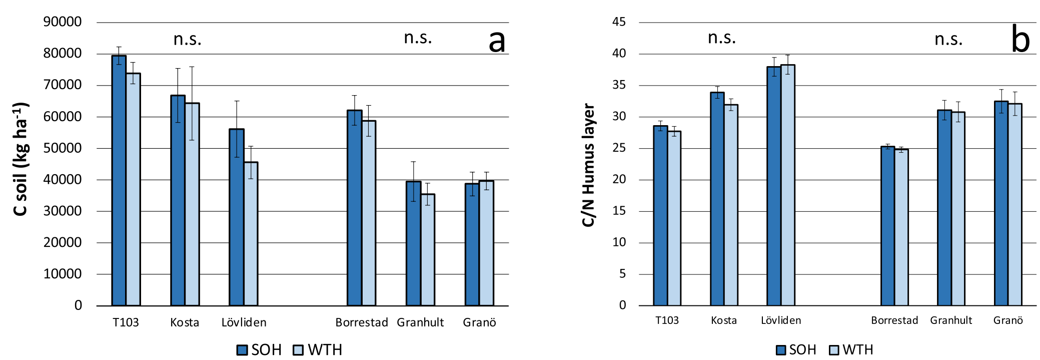

Fig. 3. Effects of WTH compared with SOH on total soil C stocks (a), and C-to-N ratios in the humus layer (b). Bars are grouped in sites of final felling experiments (3 to the left) and thinning experiments (3 to the right). Treatment means with standard deviation shown in error bars. Significant differences between treatments within each group are indicated ($p < 0.05$); n.s. = not significant. Statistical results are given in detail in Table 6.

Table 7
Effect of harvesting logging residues (WTH) at clear-felling or thinning on total N, BC, Ca and K stocks in soil and aboveground biomass in the subsequent stand, and on tree-to-soil ratio of Ca and K. Stem-only harvesting (SOH) is reference to WTH effect. Mean values across 3 sites (n = 12) and *P*-values from statistical analyses; LSD = Least Significant Difference. n.s. = not significant, i.e., $P > 0.05$. Treatment S=stem-only harvest; W=whole-tree harvest.

Variable	Experiment	SOH	WTH	Treatment LSD	*P*-value	Tream. x Site LSD	*P*-value
N (Tonnes ha^{-1})	Final felling	2.63	2.36	**S>W**	**0.022**	n.s.	0.914
	Thinning	2.48	2.41	n.s.	0.441	n.s.	0.969
BC ($Kmol_c$ ha^{-1})	Final felling	35.3	28.1	**S>W**	**0.004**	n.s.	0.742
	Thinning	46.0	43.0	**S>W**	**0.007**	n.s.	0.717
Ca ($Kmol_c$ ha^{-1})	Final felling	23.3	17.5	**S>W**	**0.002**	n.s.	0.641
	Thinning	33.5	30.7	**S>W**	**0.008**	n.s	0.504
Mg ($Kmol_c$ ha^{-1})	Final felling	5.56	5.00	n.s.	0.062	n.s.	0.384
	Thinning	5.99	5,64	n.s.	0.103	n.s.	0.546
K ($Kmol_c$ ha^{-1})	Final felling	5.05	4.54	n.s.	0.151	n.s.	0.304
	Thinning	5.85	5.60	n.s.	0.417	n.s.	0.831
Na ($Kmol_c$ ha^{-1})	Final felling	0.555	0.517	n.s.	0.213	n.s.	0.075
	Thinning	0.558	0.560	n.s.	0.922	n.s.	0.400
Ca tree/soil	Final felling	1.89	1.61	n.s.	0.115	n.s.	0.104
	Thinning	1.49	1.75	n.s.	0.127	n.s.	0.508
K tree/soil	Final felling	2.71	2.42	n.s.	0.202	n.s.	0.391
	Thinning	2.67	3.14	**W>S**	**0.015**		**0.001**

mineral soil 0–20 cm), except for decreased C stocks and lowered C/N-ratio at Granö. In contrast, BC_{ex} stocks had decreased at all sites, and BC_{ex} stocks were also generally lower following WTH than SOH at Borrestad

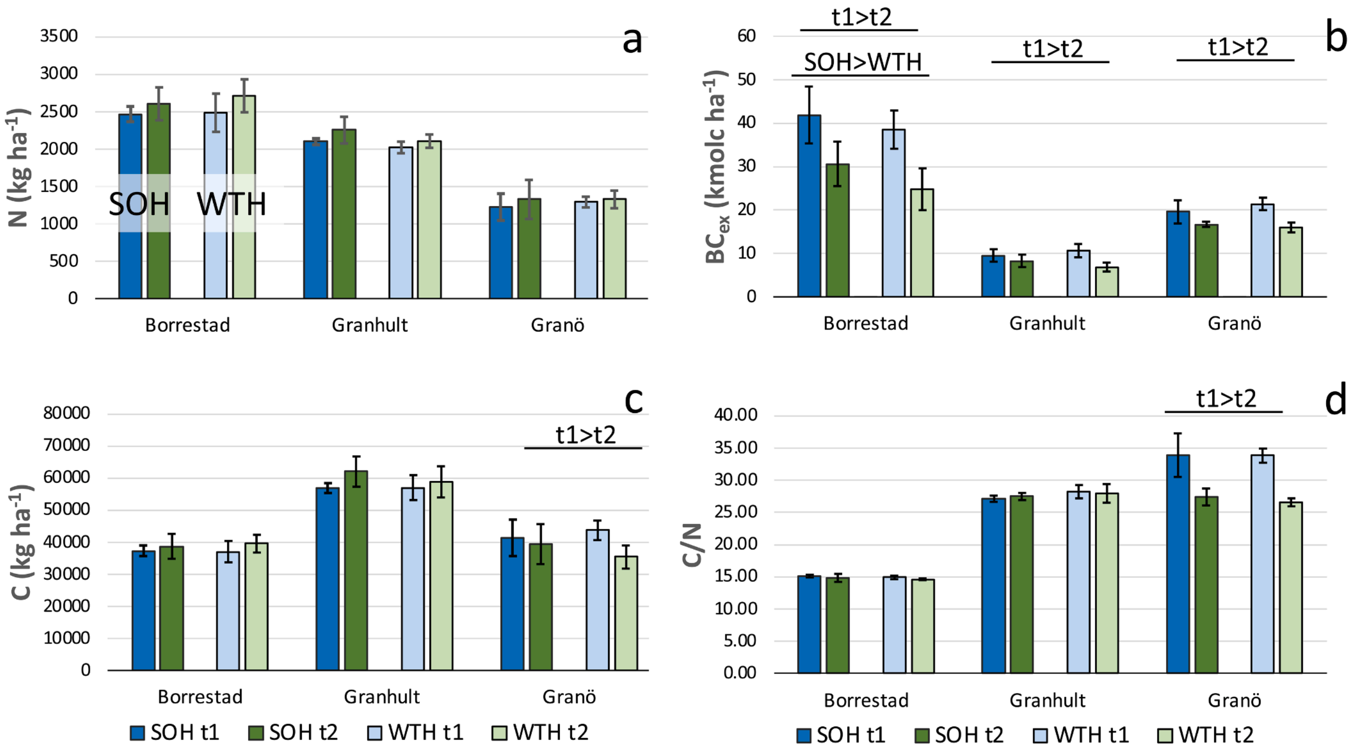

Fig. 4. Soil stocks of total N, C, and exchangeable BC in soils of thinning experiments following the first thinning and slash treatment (t1), compared with soil stocks following a second or third (Borrestad) thinning (t2). Temporal changes “t1” and “t2” are shown pair-wise with darker and lighter bars, respectively. C/N ratios are ratios from C and N stocks in the humus and 0–20 cm layers. Treatment means with standard deviation shown in error bars. Significant temporal changes (differences between t1 and t2) across treatments, and significant differences between treatments across time are indicated ($p < 0.05$).

3.5. Litter-fall study

The annual needle litter-fall at site T103 (1991–2001) contained significantly larger (45 %) flux of Ca in treatment SOH than WTH (Fig. 5). There was no significant difference between treatments regarding dry mass of needle litter-fall, or content of N, P, and K in needle litter. Measurements of the live needle biomass in 2004 at this site revealed no significant treatment effect. Arithmetic mean values of Ca concentrations and stocks in living needle biomass at site T103 in 2004 indicated higher values in SOH than WTH, but the differences were not statistically significant (Table 8).

Table 8
Live needle biomass, Ca concentration, and Ca stock in needle biomass at site T103 in 2004. Mean values with standard deviation in parenthesis.

	Biomass	Ca conc.	Ca stock
	Tonnes ha^{-1}	mg g^{-1}	Kg ha^{-1}
SOH	16.1 (1.75)	3.61 (1.33)	57.4 (20.1)
WTH	17.9 (0.73)	2.21 (0.42)	39.5 (7.9)
P	0.181	0.130	0.228

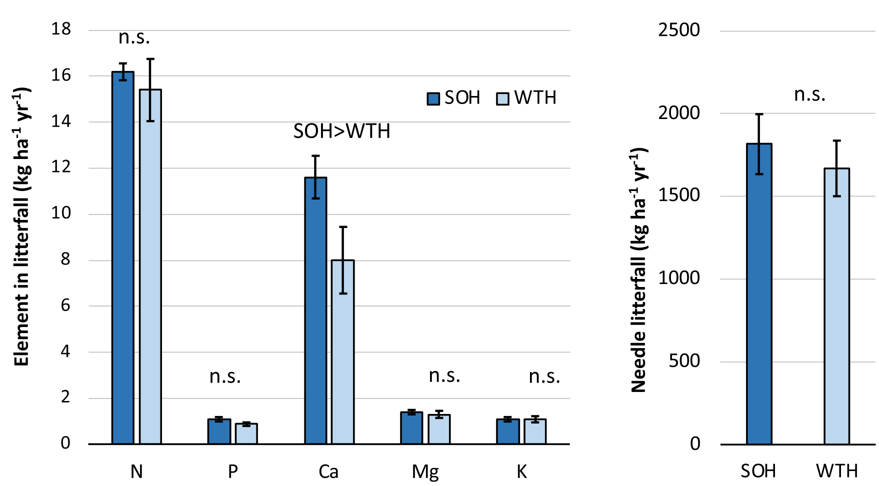

Fig. 5. Effects on WTH compared with SOH on needle litter-fall including its nutrient content at the Norway spruce site Tönnersjöheden-T103. Bars show mean values and standard deviation of annual litter-fall fluxes of dry matter and nutrient elements. Litter-fall was measured over a 11-year period, 16–27 years after final felling. Statistically significant differences between treatments are indicated ($p < 0.05$).

4. Discussion

4.1. Overview

The results of our examination of six long-term field experiments showed that out of 31 tests half of them revealed lower soil nutrient stocks (H1), lower biomass (H2), and lower nutrient stocks in biomass (H3) following WTH compared to SOH, and no test showed the opposite result (Tables 5, 6, 7). No significant interactions between site and treatment exclude site-specific effects (Table 3). The main result agrees well with other studies as they concern effects on soil and forest growth, but there is a scarcity of experimental data comparing SOH and WTH with respect to nutrient content and accumulation in biomass (H3).

A growing amount of data from studies of forest harvesting effects, and comparisons of different harvest intensities have been compiled and reviewed in several meta-studies, most of them with focus on soil C and N stocks (Johnson and Curtis, 2001; Nave et al., 2010; Achat et al., 2015b; Clark et al., 2015; Hume et al., 2018, Wan et al., 2018; James et al., 2021). Fewer meta-studies have compiled results including other soil properties (Thiffault et al., 2011; Achat et al., 2015a; Clark et al., 2021), and there is to our best knowledge only two compilations of growth effects based on data from the Nordic countries (Egnell, 2017; Helmisaari et al., 2011). Results of the present study, for example depleted soil nutrient stocks and reductions in forest production following WTH, agree with results from some of these meta-studies. Previously published data from the sites of the present study have been used in several of these compilations (e.g., Olsson et al., 1996a; Olsson et al., 1996b; Egnell and Leijon, 1997; Egnell and Leijon, 1999; Egnell, 2011, Egnell and Valinger, 2003). Thus, data redundancy to some extent explains the agreement between the findings of the present study and some of these meta-studies.

4.2. Causal relationship between soil nutrient stocks and forest growth

The logging residues left on site in the SOH treatment contained substantial amounts of all nutrient elements required for growth (Table 3), and the generally higher soil stocks of N and BC_{ex} in the SOH treatment was therefore an expected effect (Table 6). Was this load of nutrients causing higher growth in the SOH treatment, and what nutrient element was most likely to be limiting and thus controlling the growth effect? Experiments in the Nordic countries with WTH/SOH treatments in thinnings have shown that growth reduction due to WTH can be compensated for with NPK fertilization (Helmisaari et al., 2011). However, their experimental design revealed only an effect of a broad nutrient compensation, not specifically a N effect. It is not possible to directly determine the limiting nutrient element in the sites of the present study, but comparisons with other studies on comparable soil conditions can give a strong indication on nutrient limitation. For example, Tamm (1991) used a factorial experiment with Norway spruce in boreal Sweden and showed strong N limitation, where additions of P, K and Mg only increased growth further when combined with very high doses of N. Later studies have concluded that growth of boreal and most temperate forests on mineral soils are in general limited by nitrogen supply (LeBauer and Treseder, 2008; Högberg et al., 2017). N limitation is restricted to forests where the root system has contact with mineral soil. The situation is very different in peat soils. Fertilization with P and K, or wood-ash containing P and K but no N, can significantly increase forest growth on peat soils (Huotari et al., 2015), whereas application of N-free wood-ash has in general no effect on forest growth on mineral soil (Jacobson et al., 2014).

Nutrient ratios in needles can indicate nutrient status and limitation (Linder, 1995). A previous study of foliar nutrient status in the final felling experiments showed that logging residues treatment (SOH) enhanced nutrient uptake, but with different dynamics for different elements (Olsson et al., 2000). Foliar N concentrations were higher in SOH than WTH treatment when the new stands were 8 years old. There was no difference in N concentrations between treatments at stand age 16–18 years, but Ca, Mg, and Mn, were higher in SOH treatments. At stand age 22 years, only the effect on Ca concentrations remained. Foliar K concentrations showed a different response and was lower in SOH treatment than in WTH (Olsson et al., 2000). In the present study, element-to-N ratios in the total needle biomasses of the sites are presented in Supplement Table 3, with target values for optimum nutrition according to Linder (1995). These ratios indicated that growth was in general limited by N supply at all sites, but low values for K/N and P/N at T103 suggested that K and P could also be critically low. Ca/N ratios were well above target for optimum, why Ca limited growth was not likely. However, decline in soil BC stocks due to acid deposition and harvesting has been associated with Ca deficiency and growth decline of sugar maple in northeastern USA (eg., Schaberg et al., 2006). To our best knowledge, similar decline in tree vigor linked to Ca deficiency has not been reported in the Nordic countries.

If N mineralization from decomposing logging residues is the cause to higher tree growth in SOH treatment, nutrient release and growth response should be linked in time.

A detailed study of growth responses at the boreal site Lövliden showed that the growth stimulation effect of slash had diminished after ca. 20 years (Egnell, 2011), suggesting that N mineralization from slash had then largely ceased. This dynamic in time is also in line with temporal changes in treatment effects on foliar N (Olsson et al., 2000). Model simulations of N mineralization from logging residues indicated that N net mineralization from slash can occur over a similar period (Hyvönen et al., 2000). However, predicted N net mineralization from residues showed a marked peak about 5 years after final felling at the site T103 in southern Sweden, whereas N started to be released after an initial lag-period of 5 years at a boreal nutrient poor pine site. The N release continued at a low rate for several decades (Hyvönen et al., 2000).

The reasoning above allows us to compare the N-fertilization effect of slash with inorganic N fertilizers. Hyvönen et al. (2008) examined the long-term effects of repeated N fertilization on C sequestration in tree biomass and soil, i.e., the N-efficiency of fertilization, C sequestered per N applied (Kg C/ Kg N), by compiling data from Nordic fertilization trials. A similar N-efficiency relationship can be applied for the N load in slash left in the SOH treatment. Hence, we adopted values of N-efficiency from Hyvönen et al. (2008) from stands in the same or similar region as of the present study and from the same tree species. Observed values of N inputs were calculated from N content in harvesting residues left in SOH treatment (Table 3), whereas C sequestration was calculated from treatment differences in C contents in soil (Table 6), and biomass (Table 5), assuming a 50 % C content of biomass. The comparison showed that slash had comparable N-use efficiency for C sequestration in biomass as inorganic N fertilizers (Table 9). However, the N-use efficiency of residues to soil C sequestration was markedly higher than for corresponding N-fertilization. This difference was likely attributed to that undecomposed slash in SOH treatment could have contributed to

Table 9
The N-use efficiency of logging residues on C sequestration (Tonnes (C) kg (N) ha^{-1}).

Compartment	Site	Tree species	Predicted from N-efficiency[a]	Observed This study
Biomass	T103	Picea abies	11–14	9
	Kosta	Pinus sylvestris	6–8	13
	Lövliden	Picea abies	6–9	8
Soil	T103	Picea abies	3	6
	Kosta	Pinus sylvestris	1	3
	Lövliden	Picea abies	1–2	11

a) Adopted from Hyvönen et al. (2008)

higher observed differences in soil C.

4.3. Hypothesis 3: larger nutrient accumulation in the new stand following SOH

Our results give experimental evidence that WTH cause a reduced accumulation of BC in the biomass of the subsequent stand after final felling (but not after thinning), and thus a lower growth induced acid load pressure compared to SOH. The results showed that reduced BC uptake was mostly due to reduced growth since the BC concentrations in biomass were little affected.

The findings demonstrate a negative feed-back, that depends on both acid-base state of the soil and the nutrient demand of trees. Zetterberg at el. (2016), Erlandsson-Lampa et al. (2019), and McGivney et al. (2019) have used different ecosystem model approaches to estimate nutrient uptake in the next rotation, resulting in different ways of expressing a "nutrient uptake brake", and the former two studies used data from the three final felling experiments of the present study.

Zetterberg et al. (2016) used the MAGIC model to focus on changes in exchangeable Ca^{2+} soil stocks. MAGIC simulations described a long-term depletion of exchangeable Ca^{2+} stocks from the time the former stands were established until logging in 1975 (time is indicated by former stand age in Table 1). Final felling caused a short-term increase in Ca^{2+}, which was higher in SOH than WTH, and thereafter followed a continued depletion of Ca^{2+}. The simulations partly agreed with measured data, but exaggerated soil Ca^{2+} depletions at stand age 15–35 years and did not reproduce the diminishing differences between WTH and SOH measured by Brandtberg and Olsson (2012). Zetterberg et al. (2016) suggested that these discrepancies could have been caused by uncertainties in model parameters, underestimated soil Ca^{2+} pools, and biological feed-backs such as reduced growth or lowered "luxury consumption"; the latter explanation is supported by the present study.

Erlandsson-Lampa et al. (2019) used the ForSAFE model to describe the BC dynamics, with focus on how BC released from decomposing slash was distributed to soil, tree uptake and leaching losses. At stand age $\approx$ 30 years, about 50–70 % of BC left in the slash of the SOH treatment remained in the soil and biomass, and in the order of 30 % was contained in soil organic matter (non-exchangeable). These proportions are reasonably similar with the relationship between BC left in slash and BC stock difference (SOH-WTH) of the present study (Fig. 2). Thus, both Zetterberg et al. (2016) and Erlandsson-Lampa et al. (2019) show that about 1/3 of the BC content of the slash in SOH have been lost, probably through leaching. A difference between the studies is that Erlandsson-Lampa et al. (2019) estimated non-exchangeable BC contained in soil organic matter, and stressed the importance of this pool for long-term BC balance.

Among the BC elements, Ca appears to be quantitatively most important and most affected by WTH. This was shown in the litter-fall study at site T103 (Figure 6), where Ca was the most responsive element to WTH. Further, soils with high base (Ca^{2+}) saturation are more likely to supply trees with Ca^{2+} and Mg^{2+} than acid soils with low BS, and high BS soils will show greater absolute depletion in BS from the nutrient demand of a growing stand. This was indicated by the marked temporal decline in BC stocks for 13 years at Borrestad (-27 % SOH, −36 % WTH; Fig. 4) and following repeated thinning. Of all study sites, the largest Ca stocks (soil + biomass) was observed in Borrestad and Lövliden. In the latter, the high Ca-to-N ratio in one-year-old needles in 1998 was in the order of 100 % which is several times higher than the level for physiological needs, and three times higher than at Kosta and T103 (Olsson et al., 2000). This surplus uptake of Ca in trees is often regarded as a "luxury consumption", but as shown by Dauer and Perakis (2014) it should be viewed as a significant part of the ecosystem Ca cycle that maintains base saturation via litter input.

4.4. Hypothesis 4: WTH in thinnings and final fellings cause different effects on tree growth and nutrient uptake

Treatment responses were clearly different between the type of harvesting, since the effects on biomass or nutrient stocks in biomass were only statistically significant in the final-felling experiments, whereas significant effects on soil stocks were mostly found in the thinning experiments. It was only in the tests of total BC and Ca stocks (sum of biomass and soil content) that significant treatment effects were revealed for both types of experiments. This outcome was not in agreement with our fourth hypothesis. However, the present study provides no perfect comparison of WTH effects between thinning and final felling because they cover different periods of time elapsed following treatments, with final felling experiments showing more long-term effects. There is also a risk that long-term effects on growth mirrors a difference obtained earlier but is maintained because a larger growing stock will have a higher production, although the growth stimulation effects of nutrients from residues have largely ceased (Egnell, 2011). Assessments of temporal changes in WTH effects need to be considered carefully. For example, Zetterberg et al. (2013) observed diminishing differences between WTH and SOH in soil water chemistry at the three final felling experiments. Their study covered two periods (2003–2005, 2008–2010), at stand ages ranging from 28 to 35 years. On average, Ca^{2+} concentration in soil water (50 cm soil depth) was 40 % lower in WTH than SOH treatments during the first sampling period. In the later period, treatment differences in ANC and Ca^{2+} concentrations diminished at all sites, but was still significant at Lövliden owing to its well-buffered soil. If differences between WTH and SOH in exchangeable soil BC stocks and soil solution have gradually diminished from stand age 15–35 years, there is a risk that the results of this study underestimate WTH effects on soil in final felling compared to the thinning experiments simply because differences in time of soil sampling. We used soil data sampled 25 or 37 (Lövliden) years following final felling, whereas soil data from thinning experiments were sampled 13 (Borrestad) to 19–20 years after thinning. Thus, for this reason WTH/SOH differences in element soil stocks would be more likely detected in thinning than in final felling experiments.

Another reason to be cautious on differences between the two harvest type experiments is that the study included a small number of study sites (3 +3). Studies comprising larger number of experimental sites provide more confident conclusions. Helmisaari et al. (2011) analyzed 22 experiments with WTH thinning in the Nordic countries and observed significantly lower volume increment in Norway spruce over two consecutive 10-year periods, and significantly lower growth in Scots pine over the second 10-year period. Further, there was no growth reduction after WTH combined with nutrient (N) compensations. Egnell (2017) surveyed WTH studies from the Nordic countries, partly including the same sites as Helmisaari et al., (2011), and of the present study. Data from final felling experiments indicated a moderate decrease in Norway spruce growth after WTH, but no effect on the Scots pine growth.

4.5. Representativity of this study

Taken as a whole, our study was not symmetric in design with respect to equal representation of different tree species, soil type or climate, thus inference on these factors should be cautious. In a wider perspective this study comprised a rather narrow range of soil types, with Borrestad as an exception (Table 1), and included only two tree species. The climatic range was probably more marked. In sites such as Granö and Lövliden in the boreal zone, N limited growth is often pronounced. Sites in the temperate zones in south Sweden (T103, Borrestad), are characterized by higher site productivity and historically high N and acid deposition (Pihl Karlsson et al., 2024). However, the fact that there were no significant interactions between sites and treatment (Tables 5, 6, 7) underscores that WTH effects show little variation along site productivity climatic ranges. This probably reflects the fact that nutrient losses from slash harvest is roughly proportional to site productivity. However, Egnell (2017) suggest that low productivity sites with Norway Spruce may be more sensitive to WTH in final fellings. This could be the case when WTH is made in old-growth forests at low productivity sites such as Lövliden (155–175 years).

The importance of diversity of site conditions to examine WTH effects was demonstrated by Ouimet et al. (2021) who revisited 196 sites subjected to either WTH or SOH 30 years earlier in Quebec, Canada. They found lower soil nutrient stocks and forest productivity following WTH. Their study sites were divided in four soil provinces, where the two provinces characterized by coarse-textured podzolic soils on granitic or gneissic bedrock were the most sensitive to WTH, soil types that also dominate in Swedish forests.

Comparisons of long-term WTH/SOH experiments in the Nordic countries with North American experiments may be hampered by differences in experimental conditions originating from common forest management practices. In the present study, the target tree species had been planted, and competing self-established tree species were removed, as is a common practice in Nordic forest management, but was also needed to achieve best experimental conditions to detect differences in forest growth. In contrast, a long-term (35 years) experiment comparing WTH and SOH in Maine, USA, were managed to "represent the 'intensive' end of the forest management spectrum in northeastern North America" (Smith et al., 2022a). They found no significant effects neither on the aboveground biomass production and nutrient uptake of the dominant tree species (*Abies balsamea, Picea rubens*) (Smith et al., 2022b), nor on the soil C and nutrient stocks (Smith et al., 2022a). In contrast to the present study, all trees were naturally regenerated trees. However, some of the applied management practices could potentially have diminished WTH effects such as aerially applied herbicides to release conifer growth and fertilizer applications. Thus, comparisons of long-term experiments on WTH/SOH at global or regional scales need to consider that experiments are designed in the context of the local management practices.

Another aspect of representativity is the difference between experimental conditions and design versus how harvest of slash is performed in practical forestry. The effects of WTH shown in this study were based on experimental designs aimed at studying the impact of a full utilization of slash. In current forestry practices in Sweden, this potential is hardly met. The Swedish Forest Agency recommends that at most 70 % of the slash should be harvested (Swedish Forest Agency, 2019), and there are often practical limitations to what can be recovered as shown by Nilsson et al. (2018). Furthermore, slash on SOH plots was evenly distributed, whereas slash in practical forestry is unevenly distributed.

4.6. Conclusions

We used data on element stocks in soil and biomass from six Swedish long-term field experiments where WTH had been applied in either final felling or thinning, with SOH as the reference treatment. The results supported the hypothesis that WTH in final fellings results in reduced tree growth in the subsequent forest stand, but did not show growth reduction following WTH in thinnings. A reduction in nutrient availability, particularly of N, was assumed the likely cause to growth reduction although this was not directly demonstrated. Reduced growth following WTH in final fellings also resulted in reduced accumulation of N, P, Ca, Mg (and BC, but not K and Na) in biomass. Reduced element accumulation in biomass was mostly an effect of reduced growth, and only occasionally due to reduced element concentrations in biomass. According to the concept of ANC (Van Breemen et al., 1983; Nilsson et al., 1982), this finding implies that the acid load due to forest growth was lower following WTH than SOH in the consecutive stands after final felling. Further, this study also shows that among the BC elements, Ca was quantitatively the most important element behind SOH–WTH differences. The reduced cycling of Ca following WTH is a concern for maintaining the acid-base status of soils, and soil biota, but is of no immediate concern for tree growth because Ca concentrations at all sites were well above physiological needs.

In contrast to the final felling experiments, we found no effect on tree growth nor on nutrient accumulation in biomass in thinning experiments, but significantly lower stocks of exchangeable Ca^{2+}, K^{+}, and BC in the soil. A possible explanation is that a shorter time elapsed between treatment and sampling in thinning experiments than in final felling experiments, which caused a biased comparison. Previous studies in final felling experiments have shown that soil effects of WTH gradually decrease over the course of several decades. The time dimension in assessments of SOH–WTH differences is therefore of vital importance. In practical forestry, treatment effects demonstrated by the experiments of this study will be of the same kind, but will likely be less pronounced since the recovery rate of slash normally is lower. The long-term perspective needed to examine effects of WTH in experiments, demonstrated in this study, also means that there is plenty of time for compensatory management, such as N fertilization or wood-ash application.

CRediT authorship contribution statement

Stefan Löfgren: Writing – review & editing, Funding acquisition, Conceptualization. **Therese Sahlén Zetterberg:** Writing – review & editing, Data curation, Conceptualization. **Bengt Axel Olsson:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jon Petter Gustafsson:** Writing – review & editing, Funding acquisition, Conceptualization. **Gustaf Egnell:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123240.

Data availability

Data will be made available on request.

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