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The sustainability of timber and biomass harvest in perspective of forest nutrient uptake and nutrient stocks

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ABSTRACT

The sustainability of tree harvest is questioned since harvest results in increased nutrient losses which may reduce nutrient stocks in forest soils, particularly in forests on acidified and poor soils with low base saturation. We used a new forest experiment to quantify nutrient stocks and nutrient uptake rates in mature forest stands, and to assess the forest nutrient balance in relation to different forest management scenarios: clearcutting, shelterwood and thinning; and whole-tree harvest (WTH), stem-only harvest (SOH) and wood only harvest (WOH, with on-site bark stripping). Forests were dominated by trees of *Fagus sylvatica, Pseudotsuga Menziesii* or *Pinus sylvestris*, all situated on poor, acidified soils.

We measured forest biomass and nutrient stocks based on destructive sampling of fifteen mature trees per species and by using new, calibrated allometric relationships. Aboveground stocks of N, P, S, K, Ca, Mg, Mn, Cu, Fe and Zn were calculated for foliage, branches, stem bark and stem wood. Annual forest growth and nutrient uptake were determined using tree ring measures and allometric relationships. Organic layer nutrient stocks and available nutrients in the mineral soil were determined following intensive soil sampling.

Stands of beech, Douglas fir and Scots pine differed in aboveground biomass and nutrient stocks, with highest biomass stocks in Douglas fir. However, beech stands had the highest aboveground nutrient stocks, nutrient uptake rates and nutrient losses following harvest, followed by Scots pine. Organic layer nutrient stocks generally exceeded aboveground nutrient stocks, except for the base cations and Mn. Compared to SOH, WTH increased nutrient export between 66% (Douglas fir) up to 100% (Scots pine), while WOH decreased the nutrient export between 23% (beech) up to 41% (Douglas fir).

High aboveground base cation and Mn stocks indicate potential long-term threats to forest nutrition if trees are harvested. However, in Douglas fir stands, nutrient losses through SOH may fully recover when using rotation periods of 80 years. Contrary, negative Ca balances are predicted when applying SOH in beech and Scots pine, since Ca stocks are potentially depleted within 2 final fellings. WTH poses, regardless of the species, potential threats for sustainable biomass harvest as nutrients cannot be recovered using common rotation periods. WOH conserves nutrients within the forest posing opportunities for sustainable biomass harvest. For similar temperate forest on acidified, sandy soils, we therefore recommend to limit tree harvest depending on the tree species, and to avoid WTH and consider WOH to better conserve critical nutrients required for long-term forest recovery.

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1. Introduction

Forest biomass can play a major role in the European bioeconomy in phasing-out the use of fossil-based raw materials and products (Wolfslehner, 2020; Jonsson et al., 2021). The value of forest resources leads to an increased interest in timber harvest, and the harvest of logging residues, such as crown material and trees not suited for timber production (Ericsson and Nilsson, 2006; Verkerk et al., 2019; Kumar et al., 2020). Forest harvest is therefore expected to increase over the coming decades, whereby the demand for biomass (stem wood and branches) may exceed the sustainable supply (Börjesson et al., 2017).

The sustainability of the increased harvest of forest biomass as a renewable resource is questioned since it results in increased nutrient losses which may reduce the forest nutritional status (de Oliveira Garcia et al., 2018). Nowadays, nutritional status of many forests in Europe is already deteriorating as high N deposition and CO_2 fertilization are triggering nutrient imbalance in trees (Sardans et al., 2015; Waldner et al., 2015; Du et al., 2021). These nutrient imbalances are partly induced by increased forest growth caused by CO_2 fertilization (Jonard et al., 2015; Penuelas et al., 2020), which increases biomass export and therefore nutrient export through harvest (Achat et al., 2018), and partly by the loss of base-cations due to soil acidification caused by N deposition (Bowman et al., 2008). Even though N deposition is slowly decreasing, recovery of the nutrient balance remains limited in European forests (Schmitz et al., 2019).

Biomass harvest has been argued to increase forest P limitation (Sardans et al., 2015; Du et al., 2021) and has the potential to result in negative balances of Ca, Mg and K (de Oliveira Garcia et al., 2018; de Vries et al., 2021). The effect, however, depends on the soil's capacity to counteract the negative effects of harvest and N deposition through internal nutrient supply. Effects of increased biomass harvest are therefore more pronounced on nutrient poor soils (Thiffault et al., 2011; de Vries et al., 2020). In these soils the increased biomass harvest, in combination with ongoing N deposition, may eventually limit forest growth.

Besides of soil type and fertility, harvest intensity and tree species composition also influence the effect of biomass harvest on the forest nutrient balance. Nutrient losses of timber harvest are higher in clearcutting systems compared to shelterwood systems and selection forests. Nutrient pools have been suggested to decrease over a century after a clearcutting (Richardson et al., 2017) while shelterwood systems could recover the loss of nutrients through harvest within 25 years (Carpenter et al., 2021). However, in nutrient poor systems, clearcutting decreased soil concentrations of P and Ca while other nutrients were replenished within a couple of decades (Vangansbeke et al., 2015). Selection cutting had a limited impact on the forest nutrient balance in the USA (Briggs et al., 2000), but substantial negative balances were detected following thinnings in Scots pine and Norway spruce stands in Germany (Knust et al., 2016).

The nutrient export through harvest depends on the harvested tree species. In general, harvesting of broadleaf trees results in higher nutrient exports than harvesting of coniferous species (Augusto et al., 2000; Palviainen and Finer, 2012). The effects of nutrient removal under different harvest intensities thus strongly depends on the species but also on stand age, basal area and stand productivity (Augusto et al., 2000; Soalleiro et al., 2007). The magnitude of the effect, however, is not clear. Inconsistent effects of biomass harvest are reported for both forest productivity and soil responses (Vance et al., 2018), indicating the need for species and site specific data on the effect of nutrient export through different levels of biomass harvest.

Increased harvest of forest biomass may also imply a shift from conventional stem only harvest to whole tree harvest. Whole tree harvest increases the biomass export through extraction of crown material and logging residues by up to 26 % (Mantau et al., 2010). The increase in biomass removal is dependent on the tree species with e.g. 15–20 % biomass gain for Scots pine (Mikšys et al., 2007) up to 60 % biomass gain for European beech (Andre et al., 2010). The nutrient export, however, may increase up to 5 times for P with large differences between nutrients and species (Palviainen and Finer, 2012). Because of the higher nutrient export, whole tree harvest can result in greater soil nutrient reductions compared to stem only harvest (Clarke et al., 2021) which may cause reductions of forest productivity. However, whole tree harvest did not alter forest productivity in *Pinus radiata* stands in New Zealand (Garrett et al., 2021) and further empirical evidence for lower forest productivity is lacking. Although the sustainability of whole tree harvest is debated, especially for stands on poor and acidified soils, there is not much evidence regarding the export of nutrients, the biomass gains and the remaining forest nutrient stocks allowing for forest recovery and consequences for forest productivity.

The aim of the present paper is to experimentally quantify the nutrient stocks and annual nutrient uptake of mature forest stands of three major tree species in the Netherlands: *Fagus sylvatica, Pseudotsuga Menziesii* and *Pinus sylvestris* on poor and acidified soils, and compare those stocks to the nutrient export by applying different tree harvest strategies. More specifically, we (i) investigated nutrient stocks in different crown and aboveground stem parts of trees and in the organic soil layers using an intensive field and lab campaign to measure biomass and nutrient concentrations in different tree and soil parts and newly established allometric equations for upscaling those measurements to entire forest nutrient stocks; (ii) estimated the annual nutrient uptake of a forest stand from tree ring measurements and tree nutrient concentrations; (iii) investigated the biomass and nutrient exports of different harvest intensities based on a field experiment and (iv) calculated the nutrient exports of different biomass harvest types: stem only harvest (SOH), whole tree harvest (WTH) and wood only harvest (WOH), which differs from SOH by stripping and leaving stem bark in the forest. The results on forest nutrient budgets are discussed in view of the long-term sustainability of biomass harvest.

2. Materials and methods

2.1. Experimental design

A forest experiment was established in February and March 2019 in the Netherlands. This experiment consists of monoculture stands of European beech (*Fagus sylvatica*), Douglas fir (*Pseudotsuga menziesii*) and Scots pine (*Pinus sylvestris*) in five regions (Fig. S1). In each of these fifteen stands, four 0.25 ha-subplots were installed to which the harvest intensity treatments high thinning, shelterwood, clearcutting, and unharvested control were randomly assigned. Harvest intensity was determined based on basal area reductions, whereby species-specific target basal areas per treatment were used (Table 1). All stands have a temperate maritime climate with a mean annual temperature of 10.4 °C and a mean annual rainfall of 805 mm (KNMI, 2022). The stands are located on acidic sandy soils classified as Albic or Entic Podzols or Dystric Cambisols (WRB, 2015). A general description of the study sites including stand properties, soil cover and soil classification is provided in Table 2.

2.2. Biomass sampling

To determine the dry biomass of the aboveground tree compartments in forests, allometric relationships were constructed to scale biomass measures from three harvested trees per stand and thus fifteen trees per species in total to the entire above-ground forest. In each stand, a dominant, intermediate and suppressed tree representing the average DBH within the canopy position class was felled in February or March 2019. Per tree, the dry biomass was determined for small branches (up to Ø 2 cm), coarse branches (2 cm > Ø < 10 cm), stem bark, stem sapwood and, in the case of Douglas fir and Scots pine, stem heartwood and needles. Total dry biomass was calculated based on within-tree crown allometric relationships (for branches and needles) and calculations of stem volume and tissue densities (for stem bark, sapwood and

Table 1
Average basal area ± s.e. ($m^2\ ha^{-1}$), realized target basal area ($m^2\ ha^{-1}$) and basal area reduction for the timber harvest intensities high-thinning and shelterwood for European beech, Douglas fir and Scots pine. Target basal area of the clearcutting was 0 for all species with a reduction of 100 %. Basal area reductions per treatment per forest stand are in table S1.

Species	Average BA	High-thinning			Shelterwood			Clearcutting
		Target BA	Reduction		Target BA	Reduction		Reduction
	$m^2\ ha^{-1}$	$m^2\ ha^{-1}$	%	$m^2\ ha^{-1}$	$m^2\ ha^{-1}$	%	$m^2\ ha^{-1}$	$m^2\ ha^{-1}$
Beech	25 ± 0.86	17	18	4.6 ± 0.28	4.5	76	19 ± 0.71	24 ± 0.96
Douglas fir	32 ± 1.6	23	20	6.4 ± 0.40	5.0	78	25 ± 1.1	32 ± 1.5
Scots pine	23 ± 1.2	18	16	3.7 ± 0.47	4.1	83	19 ± 1.0	22 ± 0.65

Table 2
Overview of stand and soil characteristics of the beech, Douglas fir and Scots pine forests of this study. The forest stand property density includes all trees with DBH > 10 cm, Dg is the root mean square DBH and H is the height based on 16 dominant trees per stand. The soil cover values are coverage percentages for the foliar litter, mosses, graminoids and ferns. Mineral soil properties include the pH_{H2O}, the soil bulk density (BD), the average Al-S saturation of cation exchange capacity (CEC) by Al per hectare and the average soil base saturation (BS) per hectare. Both Al-S and BS are based on the unbuffered CEC, with “b.d.” in the case where Ca, K, Mg and Na were below the detection limit and undetectable. Soil profiles were classified based on the field records according to the international standards (IUSS Working Group WRB 2015).

		Forest stand				Soil cover				Mineral soil (0–30 cm depth)				
Site	Species	Age (yr.)	Density ($n\ ha^{-1}$)	Dg (cm)	H (m)	Foliar litter %	Mosses %	Graminoids %	Ferns %	pH	BD $g\ cm^{-3}$	Al-S %	BS %	Soil type
1	Beech	94	260	34	22	100	0	0	0	4.3	1.0	96	2.1	Albic Podzol
2	Beech	100	140	47	26	98	2	0	0	4.3	1.0	100	b.d.	Entic/Albic podzol
3	Beech	82	220	38	25	100	0	0	0	4.2	0.98	94	1.3	Dystric Cambisol
4	Beech	98	240	34	24	97	3	0	0	4.5	1.3	83	10	Dystric Cambisol
5	Beech	46	1100	18	19	100	0	0	0	4.1	1.1	77	1.3	Dystric Cambisol
1	Douglas fir	74	120	54	41	28	72	0	0	4.2	1.3	68	3.3	Albic podzol
2	Douglas fir	59	170	50	37	37	63	0	0	4.0	1.1	75	2.0	Entic/Albic podzol
3	Douglas fir	60	140	52	37	26	69	2	0	4.2	1.2	100	3.8	Entic/Albic podzol
4	Douglas fir	66	150	51	36	93	5	0	0	4.0	1.1	74	4.0	Entic/Albic podzol
5	Douglas fir	60	240	44	28	3	2	0	95	4.2	1.2	91	7.1	Albic podzol
1	Scots pine	55	420	25	19	51	49	0	0	4.3	1.2	79	1.3	Albic podzol
2	Scots pine	48	430	24	18	54	37	9	0	4.1	0.97	88	3.2	Albic podzol
3	Scots pine	47	880	17	19	34	59	7	0	4.4	1.4	88	5.0	Dystric Cambisol
4	Scots pine	62	450	26	21	36	59	5	0	4.0	0.98	69	4.3	Albic podzol
5	Scots pine	73	470	27	16	31	24	45	0	4.2	1.1	92	5.0	Albic podzol

heartwood) (Vos et al., 2023). Nutrient samples per tree compartment were taken for the analysis of nitrogen (N) and carbon (C) contents using a CN-analyzer (LECO TruSpec CHN, USA). Concentrations of phosphorus (P), sulfur (S), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), copper (Cu), iron (Fe) and zinc (Zn) following HNO_3 extraction were analysed with ICP-AES (Thermo-Scientific iCAP 6500 DUO, USA). The selection of the sampled trees, destructive biomass sampling, calculation of the dry weight and the determination of the nutrient concentration per compartment is described in more detail in (Vos et al., 2023).

2.3. Calculation of tree biomass and nutrient stocks

To estimate above-ground biomass for all trees in each subplot, allometric relationships for the aboveground biomass were developed based on these three intensively measured trees per stand summing to 15 trees per tree species. The dry weights of small branches, coarse branches, stem bark, stem sapwood, and, in the case of Douglas fir and Scots pine, stem heartwood and needles were modelled as a function of the DBH. The following statistical model was constructed:

$$ln(DW_{TC}) = \alpha_{[l]} + \beta_{[l]} * ln(DBH) + \varepsilon_{[l]} \tag{1}$$

where DW_{TC} is the dry weight of a tree compartment (needle, small branch, coarse branch, stem bark, stem sapwood and stem heartwood). The models were nested per location (l) using random intercept and random intercept slope models. Parameters were estimated in linear form by using logarithmic transformation to increase model performance. Model performance was evaluated based on Pearson’s correlation between the log-transformed measured and fitted values, yielding average correlations of 0.95 for total stem weight and 0.89 for total tree crown weights. The constructed allometric relationships are given in Table 3.

To estimate the foliar biomass of the beech stands, published allometric models were fitted to the data. Allometric relationships were selected when based solely on European beech, using only tree DBH as a predicter and when different allometric relationships were available for the aboveground biomass, stem biomass, branch biomass and foliar biomass. Based on the review by Zianis et al. (2005), these allometric relationships were available for beech trees in the Netherlands (Bartelink, 1997), France (Le Goff and Ottorini, 2000) and Spain (Santa Regina and Tarazona, 2001). The allometric relationships of Bartelink (1997) and Le Goff and Ottorini (2000) structurally overestimated the aboveground biomass of large trees, particularly for branches. The allometric equations of Santa Regina and Tarazona (2001) provided a good fit for the aboveground biomass and stem biomass and a reasonable fit for branch biomass (R^2 in range 0.93–1.0). The allometric relationship for beech foliage of Santa Regina and Tarazona (2001) were therefore used to estimate beech foliar biomass.

The allometric relationships were used to model the biomass of the different aboveground tree compartments for each tree with a DBH > 10 cm within the 1-ha stand. To avoid bias due to back transformation of log-transformed data, we applied a correction factor to minimise mean squared error according to the method described by Shen and Zhu (2008). This correction factor resulted in the smallest bias for predicting biomass of non-sampled trees (Clifford et al., 2013). The total biomass stock per stand was the sum of the biomass of all aboveground tree compartments, while the biomass export under high-thinning, shelterwood and clearcutting was calculated as the biomass of the harvested

Table 3
Allometric relationships for the biomass of needles, branches, stem bark and stem wood for beech, Douglas fir and Scots pine. For nested models, chosen when nesting improved model AIC by Δ2 (Zuur et al., 2009), the average model is reported. Stand specific models are in table S2. Goodness of fit of the models was assessed with Pearson's correlations of the log-transformed observed values versus the log-transformed predicted values.

Treepart	Sub model	Species	Nested	Model	Pearson
Needle	None	Douglas fir	No	$\ln(NE) = -3.36 + 1.64*\ln(DBH)$	0.80
		Scots pine	Yes	$\ln(NE) = -5.44 + 2.29*\ln(DBH)$	0.98
Branches	Small branches	Beech	No	$\ln(SB) = -2.68 + 1.77*\ln(DBH)$	0.82
		Douglas fir	No	$\ln(SB) = -2.93 + 1.63*\ln(DBH)$	0.82
		Scots pine	Yes	$\ln(SB) = -5.39 + 2.47*\ln(DBH)$	0.98
	Coarse branches	Beech	No	$\ln(CB) = -3.47 + 2.40*\ln(DBH)$	0.82
		Douglas fir	No	$\ln(CB) = -5.93 + 2.65*\ln(DBH)$	0.86
		Scots pine	Yes	$\ln(CB) = -9.69 + 3.79*\ln(DBH)$	1.00
Bark	None	Beech	Yes	$\ln(BA) = -4.30 + 2.20*\ln(DBH)$	1.00
		Douglas fir	No	$\ln(BA) = -3.33 + 2.08*\ln(DBH)$	0.93
		Scots pine	No	$\ln(BA) = -3.96 + 2.03*\ln(DBH)$	0.97
Stem wood	Sapwood	Beech	Yes	$\ln(SW) = -2.09 + 2.37*\ln(DBH)$	1.00
		Douglas fir	No	$\ln(SW) = -3.36 + 2.46*\ln(DBH)$	0.93
		Scots pine	No	$\ln(SW) = -2.95 + 2.42*\ln(DBH)$	0.93
	Heartwood	Douglas fir	No	$\ln(HW) = -4.19 + 2.69*\ln(DBH)$	0.98
		Scots pine	No	$\ln(HW) = -3.94 + 2.21*\ln(DBH)$	0.86

trees per treatment:

$$B_{ts} = \sum DW_{cts} * 4 \tag{2}$$

where B is the biomass in kg ha^{-1} for treatment t and stand s, and DW is the dry weight of tree compartment c for treatment t and stand s. Because measurements were done in a 0.25 ha subplot, the total biomass was multiplied by 4 to retrieve biomass in kg ha^{-1}. Nutrient stocks were calculated per tree compartment using:

$$NS_{cs} = DW_{cs} * [Nutrient]_{cs} \tag{3}$$

where the nutrient stock (NS) is the result of the dry weight of tree compartment c within stand s times the nutrient concentration [Nutrient] of tree compartment c within stand s. The total nutrient stock per stand was the sum of the nutrient stocks per tree compartment per tree, where different tree compartments and different trees were included dependent on the treatment.

The treatments distinguished were timber harvest intensity, distinguishing high thinning (HT), shelterwood (SW) and clearcutting (CC) in which different basal areas were removed– and biomass harvest intensity consisting of whole tree harvest, stem only harvest and wood only harvest. In the "whole tree harvest" treatment all aboveground tree biomass is harvested; in the "stem only harvest" treatment, all the stem biomass is harvested (stem is defined as stem base until Ø 10 cm); and in the "wood only harvest" treatment the wood of the stem, without the stem bark, is harvested. The biomass and nutrient exports were calculated based on these timber harvest intensity treatments and biomass harvest intensities from five stands per species.

2.4. Annual nutrient uptake

Annual nutrient uptake rates were estimated for the period 2008–2018 based on diameter increment, which were linked to changes in DBH and then to changes in total aboveground biomass and nutrient stock. Stem disks from the stem base (at 30 cm height) from the 15 trees used for biomass sampling, were polished and tree-ring widths were measured to the nearest 1/100 mm on two perpendicular radii using dendrochronological measuring equipment (LINTAB, TSAP; Rinn, 2003). The COFECHA ver. 6.02P software (Grissino-Mayer, 2001) was used to assess the data quality and accuracy after cross dating. The ring width data of the last 10 years were used to calculate the average yearly diameter increase using the formula:

$$ADI = \left(\sum\left(\frac{RW_i}{d_{i-1}}\right)*100\right)/10 \tag{4}$$

where ADI is the average relative annual diameter increment (%), RW$_i$ is the ring width in year i which ranged from 2008 to 2018, d is the diameter of the stem wood of year i – 1 and 10 is the number of years included.

The annual diameter increase of Douglas fir and Scots pine was influenced by the stem diameter (table S3). Therefore, all trees per stand were assigned to annual diameter increment (%) of the sampled tree with the nearest DBH. The diameter after one year of annual growth was calculated by multiplying the *ADI* of the nearest assigned tree per forest with the DBH using:

$$DBHnew_{is} = DBH_{is} + \left(DBH_{is} * \frac{ADI_s}{100}\right) \tag{5}$$

Where the new DBH per tree i and stand s is the sum of the measured DBH per tree and forest times the ADI of the sampled tree with the nearest DBH per forest. The total biomass and nutrient stock per stand were calculated based on DBH*new* by implementing the allometric relationships for foliage, small branches, coarse branches, stem bark and stem wood (Table 3). The uptake of nutrients over 1 year is the result of the nutrient stocks based on DBH*new* minus the nutrient stocks based on DBH. This calculation assumes that the annual diameter increment is primarily due to stem wood increment by ignoring the often neglectable annual diameter increment caused by bark growth.

2.5. Soil sampling

To obtain soil nutrient stocks, the mineral soil and the organic soil layers were sampled between November 2018 and January 2019, prior to forest harvest. Five soil samples were taken in each of four subplots (one subplot per treatment), resulting in 20 (sub-)samples per stand. Sampling points were determined systematically in a cross design with the central sampling point in the geometrical centre of the subplot. For each central sampling point, the thickness of the litter layer, fragmented layer and humified layer was noted and the soil profile was described according to international standards (WRB, 2015). Samples of the organic soil layers and mineral soil were taken at each sampling point. Organic soil samples consisted of bulked samples of the ectorganic OL, OF and OH layers and were collected within a Ø 14.5 cm ring allowing to calculate the mass per unit of surface (g cm^{-2}). Bulk samples of the mineral soil were taken from the 0 to 30 cm depth directly underneath the organic soil layers sampling point using a split tube sampler (Eijkelkamp Soil & Water, Giesbeek, The Netherlands) at each sampling point. Samples were stored at 4 °C directly after the sampling before drying to a constant weight at 40 °C.

Dried samples of the organic soil layers were ground to homogenize the sample in a mill containing a 1.5 mm stainless steel screen. The weight of the organic soil sample was corrected for the admixture with mineral soil by using loss on ignition (550 °C). Samples were merged per subplot and total contents of C and N were measured using a CN-analyzer (LECO TruSpec CHN, USA). The contents of P, S, K, Ca, Mg, Mn, Cu, Fe and Zn were determined after extraction with 0.43 M HNO_3 (Groenenberg et al., 2017) on the ash of ignition (550 °C) via ICP-AES (Thermo-Scientific iCAP 6500 DUO, USA).

Mineral soil samples were sieved to 2 mm to separate gravel from the fine earth fraction. Samples were merged per subplot and direct available nutrients (P, S, K, Ca, Mg, Mn, Cu, Fe and Zn) and soil pH were measured after H_2O extraction (1:10 soil water ratio); the unbuffered cation-exchange capacity (CEC) was measured by using 0.1 M BaCl extraction. The contents of extractable nutrients and cations were determined with ICP-AES (Thermo-Scientific iCAP 6500 DUO, USA). Contents of N and P-PO_4 in the fine earth were determined with a Segmented Flow Analyzer (SFA type 4000, Skalar Analytical B.V., the Netherlands).

Soil nutrient stocks were calculated for the organic soil layers and mineral soil separately. The dry mass of the organic soil layers was corrected for the admixture with mineral soil particles before the pseudo total nutrients stocks were calculated by multiplication of the dry mass (kg ha^{-1}) and the nutrient concentration. For the mineral soil, the bulk density of the fine earth (g cm^{-3}) was multiplied with the extractable available nutrient contents and the sample depth to calculate the available nutrient stocks per hectare in the top 30-cm mineral soil.

2.6. *Statistical analysis*

Prior to statistical analysis, data on aboveground biomass and nutrient stocks, belowground nutrient stocks and nutrient uptake were scaled to a 1-ha forest using data on subplot level. To compare biomass and nutrient stocks and nutrient uptake between species, one-way ANOVA tests were performed. To test biomass increment for the different tree compartments a two-way ANOVA test was used. The analyses were performed by using linear mixed-effect models from the R package "*nlme*". Paired *t*-test was used to test the differences in the aboveground and belowground nutrient stocks by using the R package "stats". Left- or right-skewed data were log or square root transformed, respectively, to meet the normality and homogeneity assumptions. Tukey's post-hoc (HSD) test was performed following ANOVA using the R package "*emmeans*" to test for differences between species. Spatial independence of the stands within the locations was tested using random structures. The added random structure did not improve AIC (Δ 2 AIC) for any of the models.

3. Results

3.1. *Aboveground biomass and nutrient stocks and soil organic layer nutrient stocks*

The total aboveground stock of dry biomass per hectare was on average 190 ± 13 (s.e.) tons in beech, 230 ± 10 (s.e.) tons in Douglas fir and 100 ± 8.1 (s.e.) tons in Scots pine stands (Table 4). The aboveground nutrient stocks were nutrient and species dependent. The nutrient stocks decreased in the order of N > Ca > K > Mg > S > P > Mn > Zn > Fe > Cu. Beech had generally higher nutrient stocks compared to Douglas fir and Scots pine, while Douglas fir had the highest aboveground biomass (Fig. 1, Table 4). Beech had significantly higher aboveground nutrient stocks for Ca, K, Mg and Mn, with the Ca stock nearly 4 times higher compared to Douglas fir and Scots pine. Scots pine stands had in general the lowest nutrient stocks, with significantly lower stocks of N and Fe compared to both beech and Douglas fir. Stocks of S and P only differed significantly between beech and Scots pine, while species did not differ significantly in the aboveground stocks of Zn and Cu.

The total nutrient stocks in the organic soil layers (thickness 78 – 97 mm; table S5) did not significantly differ between tree species (Table 5). Largest nutrient stocks in the organic soil layers were observed for N and lowest nutrient stocks were observed for Cu (Fig. 1). The total nutrient stocks in the organic soil layers were larger than aboveground nutrient stocks, except for the base cations (Ca, K, Mg) and Mn (Fig. 1, Table S6).

Table 4

Exports of biomass (ton ha^{-1}) and nutrients (kg ha^{-1}) in a clearcutting following whole tree harvest, stem only harvest and stem wood harvest. Whole tree harvest depicts the total aboveground biomass and nutrient stocks of the forests. ANOVA F and P values are presented to compare differences in biomass and nutrient exports between species. The F value and significance of the one-way Anova based on species is displayed per biomass harvest intensity. Different letters denote significant differences among species according to Tukey's *posthoc* test with a significance level of $P < 0.05$.

Nutrients	Biomass ton ha^{-1}	N kg ha^{-1}	Ca kg ha^{-1}	K kg ha^{-1}	Mg kg ha^{-1}	S kg ha^{-1}	P kg ha^{-1}	Mn kg ha^{-1}	Zn kg ha^{-1}	Fe kg ha^{-1}	Cu kg ha^{-1}
Whole tree											
Beech	190 ± 17^{b}	520 ± 54^{b}	380 ± 76^{b}	220 ± 25^{b}	59 ± 13^{a}	27 ± 2.1^{b}	20 ± 2.1	12 ± 2.7^{a}	1.5 ± 0.27	2.3 ± 0.33^{ab}	0.35 ± 0.026
Douglas fir	240 ± 19^{b}	490 ± 50^{b}	150 ± 34^{a}	100 ± 6.2^{a}	28 ± 1.9^{a}	27 ± 2.8^{b}	20 ± 1.6	8.6 ± 2.5^{a}	5.2 ± 3.3	3.1 ± 0.53^{b}	0.53 ± 0.10
Scots pine	99 ± 7.8^{a}	290 ± 32^{a}	110 ± 11^{a}	93 ± 12^{a}	25 ± 0.93^{a}	17 ± 2.2^{a}	15 ± 2.7	4.8 ± 0.60^{a}	2.5 ± 0.84	1.6 ± 0.16^{a}	0.32 ± 0.035
F-value	27	8.7	12	11	4.6	4.9	2.6	2.6	2.4	5.0	3.8
P-value	< **0.001**	< **0.005**	< **0.001**	< **0.005**	**0.047**	**0.027**	0.11	0.11	0.15	**0.026**	0.053
Stem only											
Beech	130 ± 13^{b}	310 ± 33^{b}	240 ± 50^{b}	150 ± 20^{b}	42 ± 10^{b}	14 ± 1.2^{b}	10 ± 1.3^{b}	7.5 ± 1.6	0.88 ± 0.19	0.85 ± 0.16^{ab}	0.17 ± 0.012^{a}
Douglas fir	210 ± 17^{c}	330 ± 31^{b}	89 ± 19^{a}	63 ± 3.4^{a}	16 ± 1.1^{a}	16 ± 1.5^{b}	10 ± 0.79^{b}	5.0 ± 1.4	3.6 ± 2.3	1.5 ± 0.33^{b}	0.42 ± 0.11^{b}
Scots pine	78 ± 5.7^{a}	140 ± 16^{a}	71 ± 5.9^{a}	48 ± 4.4^{a}	16 ± 0.54^{a}	7.2 ± 0.64^{a}	5.2 ± 0.83^{a}	3.0 ± 0.31	1.4 ± 0.39	0.56 ± 0.12^{a}	0.21 ± 0.027^{a}
F-value	27	17	13	24	6.3	14	12	2.6	3.4	6.9	6.8
P-value	< **0.001**	< **0.001**	**0.001**	< **0.001**	**0.014**	< **0.001**	**0.001**	0.11	0.087	**0.010**	**0.011**
Stem wood											
Beech	130 ± 120^{b}	260 ± 28^{b}	94 ± 11^{b}	140 ± 19^{b}	38 ± 9.9^{c}	11 ± 1.1^{b}	8.1 ± 1.2^{b}	5.6 ± 1.2	0.76 ± 0.17	0.57 ± 0.17	0.14 ± 0.0096
Douglas fir	190 ± 150^{c}	250 ± 24^{b}	46 ± 5.4^{a}	35 ± 2.6^{a}	9.3 ± 0.63^{a}	8.9 ± 0.92^{b}	5.1 ± 0.53^{ab}	3.3 ± 1.1	2.0 ± 1.2	0.67 ± 0.14	0.33 ± 0.12
Scots pine	72 ± 54^{a}	110 ± 14^{a}	44 ± 3.7^{a}	38 ± 3.7^{a}	13 ± 0.52^{b}	4.8 ± 0.46^{a}	3.4 ± 0.65^{a}	2.5 ± 0.27	1.2 ± 0.32	0.38 ± 0.11	0.19 ± 0.028
F-value	27	17	14	15	12	16	9.6	2.1	1.4	1.6	2.4
P-value	< **0.001**	< **0.001**	< **0.001**	**0.002**	**0.004**	< **0.001**	**0.003**	0.16	0.29	0.25	0.14

Nutrient stocks per stand and per tree compartment are in Table S4.

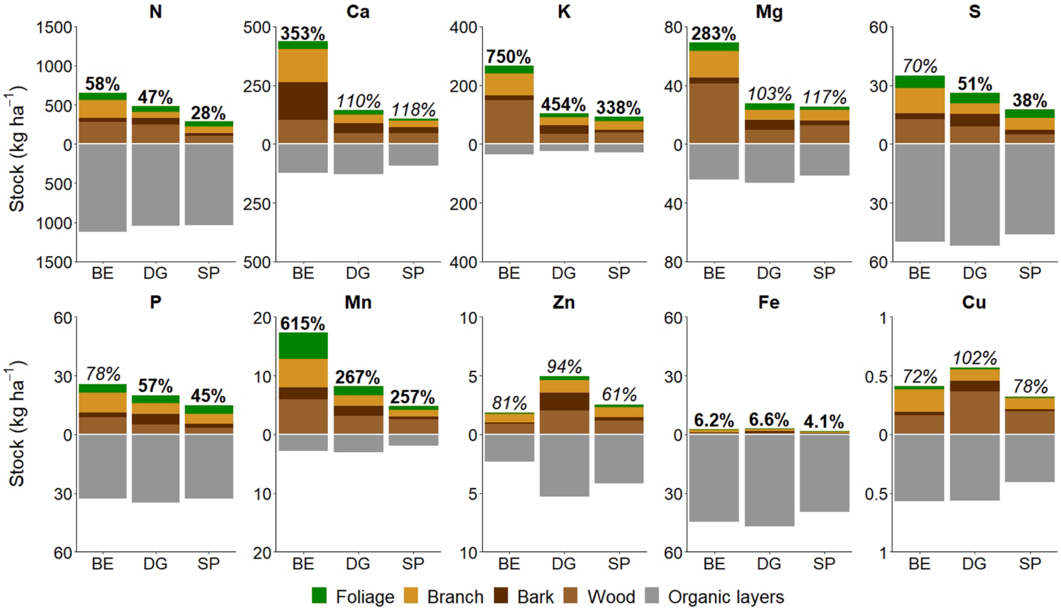

Fig. 1. Nutrient stocks (kg ha^{-1}) in the foliage, branches, stem bark, stem wood and organic layers in forest stands dominated by European beech (BE), Douglas fir (DG) and Scots pine (SP). All nutrient stock values are based on measurements, except for the foliage of European beech which were calculated based on allometric relationships and nutrient concentrations derived from literature, see method section 2.3. The percentage values present the ratios of the above-ground nutrient stocks in trees divided by the nutrient stocks in the organic layers. Bold percentages indicate statistical differences between the above ground and the organic layer nutrient stocks according to Paired *t*-test statistics (table S6).

Table 5

The means (and standard errors) of the total nutrient stocks of macro (N, Ca, K, Mg, S and P) and micro (Mn, Zn, Fe and Cu) nutrients in the organic soil layers (kg ha^{-1}) and the available stock of macro and micronutrients (kg ha^{-1}) in the upper 30 cm of the mineral soil. The F value and significance of the one-way Anova based on species per soil layer (organic layers and mineral soil) is displayed.

Species	N kg ha^{-1}	Ca kg ha^{-1}	K kg ha^{-1}	Mg kg ha^{-1}	S kg ha^{-1}	P kg ha^{-1}	Mn kg ha^{-1}	Zn kg ha^{-1}	Fe kg ha^{-1}	Cu kg ha^{-1}
Organic layers										
Beech	1100 ± 190	120 ± 15	36 ± 4.2	24 ± 2.3	50 ± 6.5	33 ± 4.0	2.8 ± 0.40	2.3 ± 0.82	45 ± 6.5	0.57 ± 0.09
Douglas fir	1000 ± 100	130 ± 8.7	23 ± 2.7	27 ± 4.3	52 ± 2.8	35 ± 2.6	3.1 ± 0.40	5.3 ± 3.7	47 ± 2.7	0.56 ± 0.05
Scots pine	1000 ± 110	92 ± 10	28 ± 2.5	22 ± 2.6	46 ± 5.5	33 ± 2.9	1.9 ± 0.28	4.2 ± 2.1	40 ± 5.9	0.41 ± 0.05
F-value	0.12	2.9	3.9	0.64	0.37	0.14	3.08	1.1	0.50	2.0
P-value	0.89	0.09	0.05	0.54	0.70	0.87	0.08	0.39	0.62	0.18
Mineral soil										
Beech	42 ± 1.8	5.2 ± 1.7	26 ± 3.7	8.0 ± 1.7	18 ± 0.78	4.3 ± 0.43	0.49 ± 0.19	0.42 ± 0.045	16 ± 1.9	0.10 ± 0.028
Douglas fir	54 ± 2.8	8.7 ± 1.8	22 ± 1.4	6.9 ± 0.69	28 ± 2.2	7.4 ± 1.3	0.71 ± 0.19	2.1 ± 0.89	21 ± 2.3	0.12 ± 0.032
Scots pine	46 ± 2.4	4.0 ± 0.50	27 ± 2.3	4.8 ± 0.86	19 ± 1.1	5.8 ± 0.72	0.15 ± 0.039	0.70 ± 0.23	15 ± 1.7	0.065 ± 0.0090
F-value	2.0	1.3	0.18	0.76	3.3	1.9	2.1	0.19	0.69	0.11
P-value	0.18	0.30	0.84	0.49	0.07	0.19	0.17	0.83	0.52	0.89

The nutrient stocks of the organic layers per stand are in Table S4, the available concentration of the mineral soil during wintertime per stand are in Table S8.

The organic soil stock of Ca, K, Mg and Mn were smaller than the aboveground stocks, but differences were only large and significant for K and Mn, and for Ca and Mg in beech (Fig. 1). The highest biomass nutrient stock to soil nutrient stock was observed for K, with an aboveground nutrient stock between 338 % and 750 % of the stock present in the organic soil layers (Fig. 1). In contrast, high stocks in the organic soil layers as compared to the aboveground tree stock were observed for Fe, where 4 to 6 % of the organic soil layers stock was present in the aboveground tree biomass. The organic layer nutrient stocks of major nutrients N, P and S were similar to (in case of beech) or larger than the aboveground nutrient stocks.

3.2. *Annual nutrient uptake and nutrient availability*

The estimated annual aboveground biomass increment was 4700 ± 430 kg ha^{-1} yr^{-1} in beech stands, 7800 ± 910 kg ha^{-1} yr^{-1} in Douglas fir stands and 3900 ± 430 kg ha^{-1} yr^{-1} in Scots pine stands. The biomass increment is significantly higher in Douglas fir compared to both beech and Scots pine and is driven by a higher biomass increment of the stem wood and bark (Table S7). Annual nutrient uptake was largest for N and lowest for Cu (Fig. 2). Base cation uptake differed between species, beech had 2.4 times higher uptake rates than Douglas fir and Scots pine stands for Ca, and 1.5 and 1.9 times higher for K and Mg respectively (Fig. 2, Table S8). There was no significant difference in Mn uptake between the species, although beech tended to have a higher uptake than Douglas fir and Scots pine.

The concentrations of available nutrients in the mineral soil did not differ between species and decreased in the order of N > S > K > Fe > Mg > Ca > P > Zn > Mn > Cu. The base saturation was on average 3.6 % while the average CEC-Al equaled 85 %. The annual nutrient uptake was generally lower than the available nutrients in the mineral soil which was measured during wintertime (Table 5). Only the annual uptake of Ca in beech and Mn in Scots pine exceeded the available nutrients in the mineral soil (Fig. 2, Table 5). The nutrient stock of the organic soil layers was over 50 times higher than the annual nutrient uptake for N, P and S, and<10 times bigger than the annual nutrient uptake of K and Mn (in case of beech).

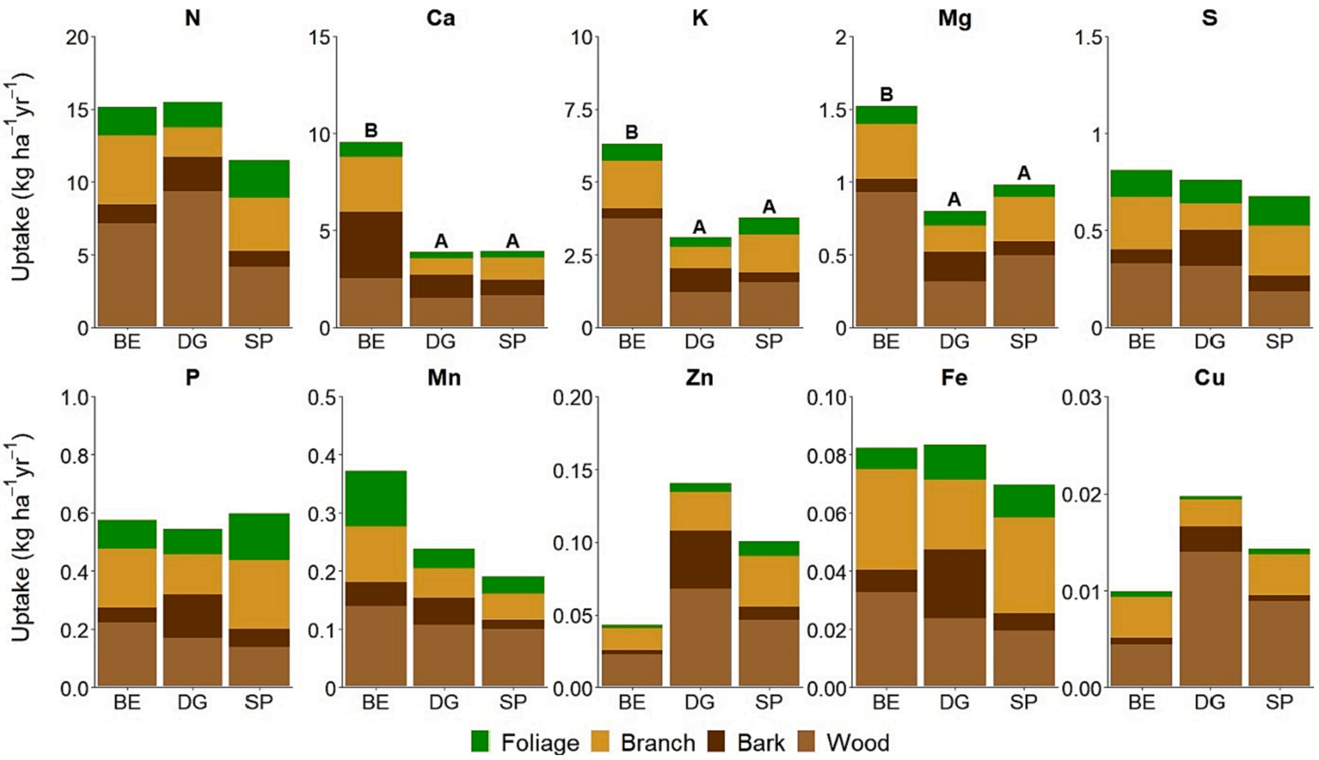

Fig. 2. Estimated mean annual nutrient uptake rates in the foliage, branches, stem bark and stem wood for forest stands dominated by European beech (BE), Douglas fir (DG) and Scots pine (SP) over the period 2008–2018 (kg ha^{-1} yr^{-1}). Different capital letters indicate significant differences (ANOVA, $p < 0.05$) among species. Absence of capital letters indicate no significant differences between species.

3.3. Impact of timber harvest intensity on biomass and nutrient export

The reduction to the target basal area for the treatments yielded an average basal area export between 3.7 to 6.4 m^2 for high thinning, 19 to 25 m^2 for shelterwood and 22 to 34 m^2 for clearcutting (Table 2). Basal area reductions were comparable between beech and Scots pine but higher for Douglas fir corresponding to much higher absolute biomass exports in Douglas fir compared to beech and Scots pine (Fig. 3, Table 4). Biomass reductions for the different timber- and biomass harvest intensities ranged from 12 % (SOH) to 21 % (WTH) in high thinning, 55 % (SOH) to 86 % (WTH) in shelterwood and 67 % (SOH) to 100 % (WTH) in a clearcutting (Table S9).

Nutrient export was highest for N and lowest for Cu for all timber harvest intensities, proportional to nutrient stocks (Table 4). Differences in biomass and nutrient export were substantial between high thinning and shelterwood and high thinning and clearcutting, while shelterwood and clearcutting resulted only in a slight difference in biomass and nutrient export (Fig. 3).

Nutrient export differed between species. In a conventional stem only harvest clearcutting of beech, significantly higher stocks of Ca and K and, although not significant, higher stocks of Mg were exported. In a Scots pine stem only clearcutting, significant lower stocks of N, P and S were exported (Fig. 3). Differences in biomass and nutrient exports were more pronounced when comparing whole tree harvest but less when comparing stem wood harvest (Fig. S2, Table 4).

3.4. Impact of biomass harvest intensity on biomass and nutrient export

The biomass and nutrient export were compared between stem only harvest and whole tree harvest, and between stem only harvest and wood only harvest. Compared to stem only harvest, whole tree harvest increased the biomass export on average by 35 % (52 tons ha^{-1}) for beech, 12 % (26 tons ha^{-1}) for Douglas fir and 27 % (21 tons ha^{-1}) for Scots pine following clearcutting harvest. The average increase of nutrient export was highest in Scots pine (100 %), intermediate in beech (87 %) and lowest in Douglas fir (66 %). Highest increase of nutrient export was observed for Fe where whole tree harvest increased export up to 220 % (Fig. 4). Large increase in export was also observed for P, whole tree harvest resulted in an increased P export of 92 % in Douglas fir, 96 % in beech and 180 % in Scots pine. The average increase of the base cations (Ca, K, Mg) and Mn export resulting from whole tree harvest was 55 % in beech, 66 % in Scots pine and 68 % in Douglas fir.

Compared to stem only harvest, wood only harvest (excluding the bark) in a clearcutting decreased the biomass export by 5.9 % in beech (7 tons ha^{-1}), 9.8 % in Douglas fir (21 tons ha^{-1}) and 7.5 % in Scots pine (6 tons ha^{-1}) (Fig. 4). Yet, the decrease of nutrient losses was much higher: wood only harvest resulted in an average decrease in nutrient export of 23 % in beech, 25 % in Scots pine and 41 % in Douglas fir compared to stem only harvest. The highest decrease of nutrient export was observed for Ca in beech (58 %) and P and Fe in Douglas fir (resp. 51 % and 56 %). The export of base cations Ca, K, Mg and Mn following wood only harvest decreased by 23 % in Scots pine, 26 % in beech and 43 % in Douglas fir.

4. Discussion

4.1. The potential of forest regrowth from a soil nutrient stock perspective

The potential of forest regrowth after tree harvest depends largely on soil nutrient stocks. The nutrient stocks in organic soil layers are particularly important for long-term site nutrition for forest on low fertility sites, such as acidic soils (Prietzel and Stetter, 2010; Garrett et al., 2021). Many forest soils are sensitive to acidification resulting from long lasting acid deposition. The sampled forest soils were strongly acidic with a low base saturation (Table 2), which represent the conditions of many other European forests on acidified soils (Riek et al., 2012; Binkley and Högberg, 2016).

We found that the nutrient stocks of the organic soil layers were

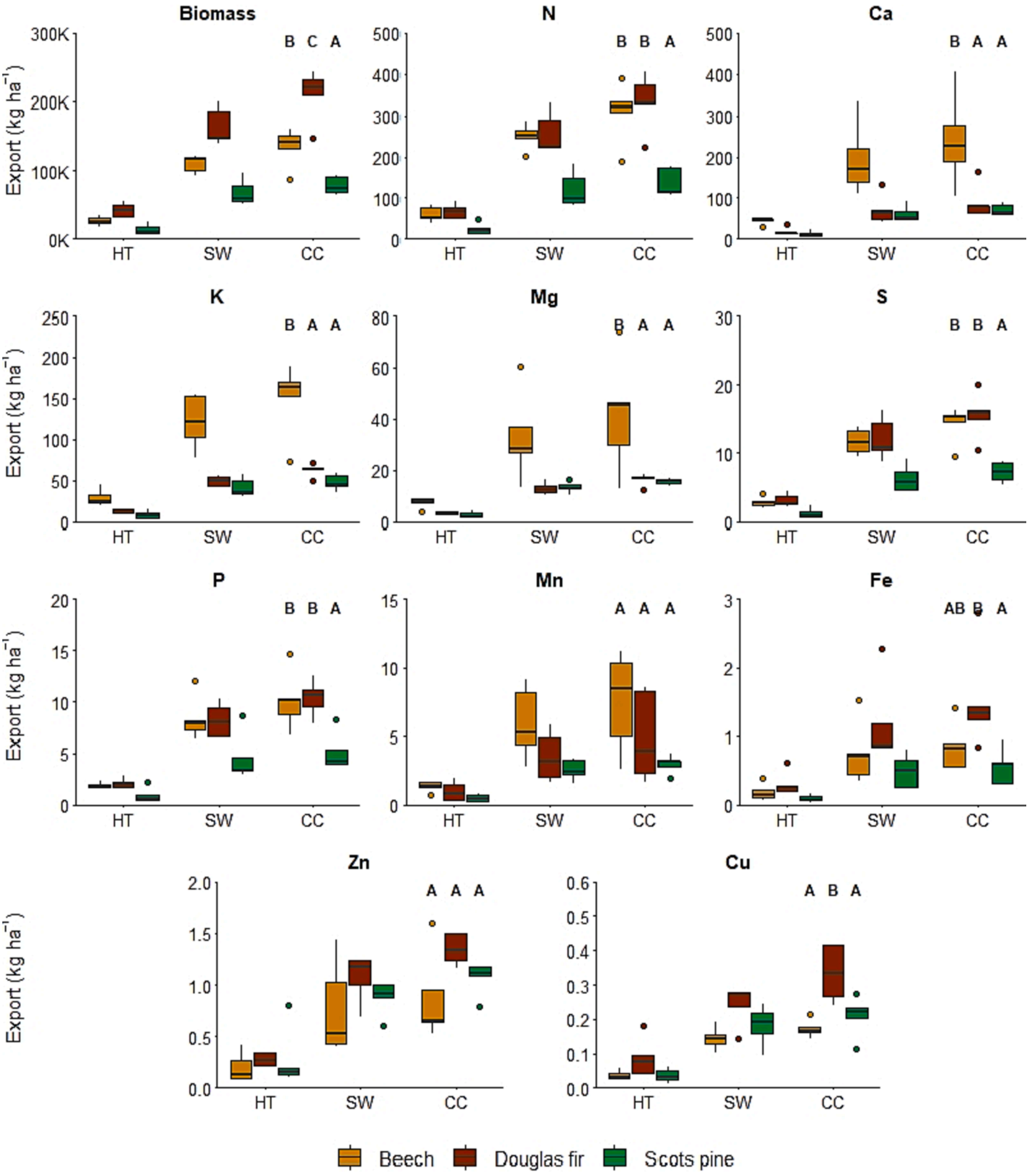

Fig. 3. Export of biomass, macronutrients (N, P, K, S, Ca and Mg) and micronutrients (Mn, Cu, Fe, Zn) under the different timber harvest intensities: high-thinning (HT), shelterwood (SW) and clearcutting (CC). The biomass harvest intensity considered here is stem only harvest, the biomass harvest intensities whole tree harvest and stem wood harvested are in Figure S2. Coloured dots are outliers. Different capital letters indicate significant differences (ANOVA, $p < 0.05$) among species for the clearcutting treatment. Same magnitude, but with less pronounced differences is expected for the high-thinning and shelterwood treatments.

higher than in (aboveground) trees for most nutrients, except for Ca, K, Mg (base cations) and Mn, regardless of the tree species (Fig. 1). Aboveground stocks, however, differed between tree species with higher base cation stocks in beech. Overall, comparing annual nutrient uptake in aboveground woody tree biomass (i.e. immobilization) and the nutrient stocks of the organic layers, we observed that the current organic layer nutrient stock could support up to 20 years of annual K and Mn uptake and up to 50 years of Ca and Mg uptake. This indicates that, with too limited external nutrient supplies, the base cation stocks of organic soil layers may be insufficient for long-term site nutrition. High nutrient uptake demands by roots caused by high turnover rates (Brunner et al., 2013), which is not taken into account in this study,

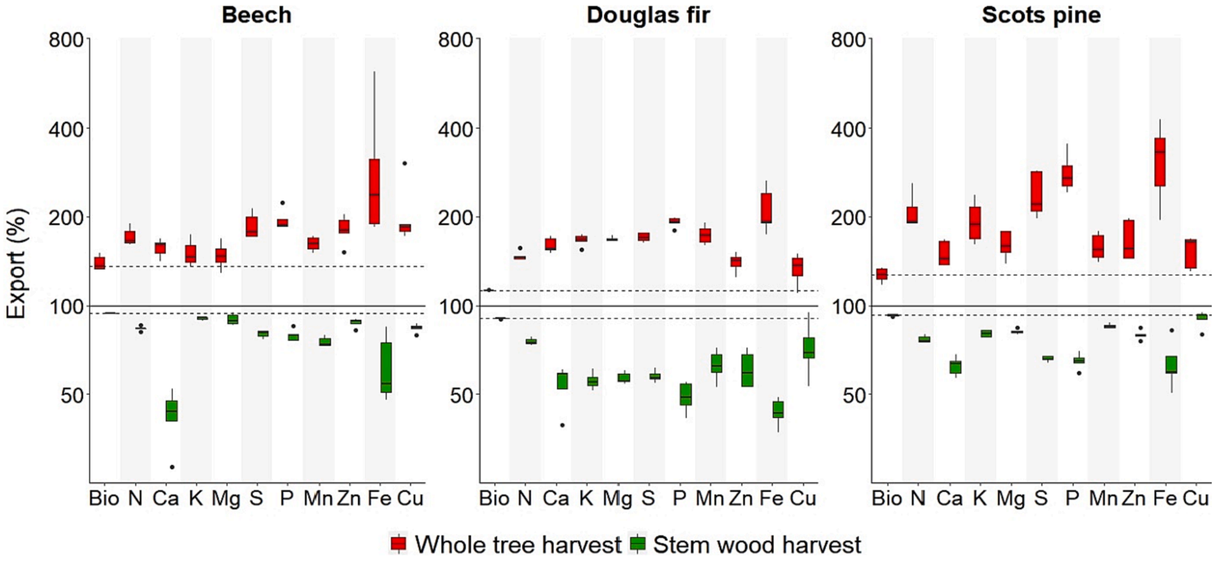

Fig. 4. Effects of whole tree harvest (WTH) and wood only harvest (WOH, with bark removed and left in forest) on biomass and nutrient export relative to stem only harvest (SOH, wood and bark). The total export per nutrient in SOH is set to 100% and is denoted with a solid line. The red bars indicate the increased losses due to WTH, and the green bars the reduction in losses following WOH. The dashed lines refer to the average biomass lost in WTH and WOH relative to SOH. Note that biomass loss (Bio) is also indicated by the first bar in each plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

could further limit the period of growth supported by the organic layers. As the organic soil layers are the major source of base cations (Kuehne et al., 2008), base cation nutrition is a potential limiting factor for long-term forest growth when harvests are continued. Organic soil layers provide sufficient stocks of other nutrients to supply long-term forest growth. The current organic soil layers stocks potentially supply the current annual uptake in woody tree biomass of N, P and S for forest growth for > 80 years, which is a common rotation period.

The dependency on the organic soil layers as a nutrient source, however, differs per species. For example, the superficial fine root distribution of Scots pine suggests a high dependency on the organic soil layers for nutrient uptake (Vanninen and Mäkelä, 1999; Helmisaari et al., 2007), while Douglas fir roots also appear in the top of the mineral soil (Nnyamah and Black, 1977; Olsthoorn, 1991). Deep soil uptake has been demonstrated for beech which reduces the dependency on the organic soil layers as a nutrient buffer (Berger et al., 2006; Turpault et al., 2019). Comparison of the nutrient stocks of the organic layers solely may therefore underestimate the potential of the soil nutrient stock to support forest growth.

The top of the mineral soil (down to 30 cm depth) however, hardly provides an additional nutrient stock for base cations as base saturation levels are generally below 4 % (Table 2). The overall influence of the deep mineral soil (>30 cm depth) as a nutrient source in beech remains ambiguous. Generally, the biochemical cycling is inferior to nutrient uptake from biological nutrient cycling (Berger et al., 2006; van der Heijden et al., 2015). The uptake from organic soil layers and the biological cycling of nutrients account for a large part of the base cation uptake in beech (45–60 %) (Göransson et al., 2006; van der Heijden et al., 2015; Turpault et al., 2019). This is reflected by the low organic layer stock of Ca, K and Mg stock of beech, which equaled the organic layer stocks in Douglas fir and Scots pine despite the higher aboveground nutrient stocks of beech. Therefore, despite of the deep soil uptake of beech, beech stands, as well as Douglas fir and Scots pine stands, depend on external nutrient supply of base cations for forest regrowth after harvest on the long term.

Finally, remarkable high stocks of N, S and Fe were present in the organic soil layers, with the Fe stock up to 500 times the annual Fe uptake. These high stocks are clear indicators of the ongoing effects of S and N deposition. Reduction of the N deposition is expected to result in only a marginal response of forest stands (Schmitz et al., 2019), while accumulation of S in the organic soil layers is linked to a 50 % reduction of the soil Ca and Mg pool (Prietzel et al., 2004). The organic soil layers therefore hold legacies with negative impacts on (base cation) nutrition for the coming decades.

4.2. Growth and nutrient uptake

Species differ in both growth rate and nutrient uptake rates. Douglas fir grew faster in aboveground biomass than beech and Scots pine (Table S7) but was similar in nutrient uptake compared to Scots pine (Fig. 2). This higher nutrient use efficiency, resulting from the lower nutrient concentration of Douglas fir (Vos et al., 2023), may contribute to the competitive superiority of Douglas fir over beech and Scots pine on low fertile sites.

Uptake of the macronutrients N, P and S did not differ between species. The annual uptake of base cations in aboveground tree biomass (including foliage), however, was up to 3 times higher in beech stands compared to Douglas fir and Scots pine stands (Fig. 2). This high base cation uptake was not reflected in high annual biomass growth, which implies a low base cation use efficiency in beech. This low efficiency may lead to more rapid depletion of soil exchangeable base cation stocks and nutrient imbalances, which result in growth reductions on nutrient poor sites (Balcar et al., 2011; Calvaruso et al., 2017; Cremer and Prietzel, 2017; Court et al., 2018). Such growth reductions may already occur as the studied beech stands were of medium to poor yield contrary to Douglas fir and Scots pine stands, that were of excellent and good yield, respectively, according to traditional yield tables for such sites (Jansen et al., 2018). Also the within tree nutrient imbalances are likely to occur in beech stands as we found 24 % lower annual aboveground uptake rates for K, 30 % lower for Mg and around 50 % lower for P and Ca compared to a forest stand with similar biomass production (5.1 tons ha^{-1} yr^{-1}) in France (Calvaruso et al., 2017). From this, we hypothesize that the growth of beech might be impaired by low mineral supply of base cations. Such impaired growth may limit further use of beech for timber and biomass production, also because nutrient imbalances have been previously related to increased sensitivity to drought and forest dieback (Bal et al., 2015; González de Andrés et al., 2021). From this we speculate that the sustainability of beech stands on soils with low reservoirs of base cations (K, Ca, Mg) and Mn may be at risk with respect to the mineral supply.

Surprisingly, despite lower concentrations of base cations and P in aboveground tree biomass (Vos et al., 2023), the direct available nutrient stock in wintertime (Table 5) was overall higher than the annual nutrient uptake (Fig. 2) indicating no direct nutrient limitation for base cations, Mn and P in the short term. Caution for interpretation is however required since we did not take annual nutrient uptake rates in roots into account, therefore potentially underestimating the actual annual nutrient uptake rate by trees. Nevertheless, available P in wintertime was 10 times greater than the annual P uptake although this available P was far below the optimum for tree growth (Van den Burg and Schaap, 1995). On an European level, P limitation is increasing as indicated by foliar concentrations (Du et al., 2021). Nonetheless, the relatively high available P concentrations in the mineral soil relative to tree uptake indicated no P limitation. Foliar concentrations did however indicate P limitation but not base cation limitation (Vos et al., 2023). We do not know how these ambiguous responses emerge from underlying mechanisms, which may include decreased mycorrhizal uptake efficiency (Braun et al., 2010), the preferential uptake of N over other elements (Vanguelova and Pitman, 2019) or a mismatch in decomposition and uptake. Based on the soil organic stock and the availability of nutrients in the mineral soil, we argue that P limitation is not caused by a small total soil P stock contrary to base cations which are at risk of soil stock limitation.

4.3. *Base cation balance for forest growth*

The long-term recovery after harvest not only depends on the nutrient stocks in the soil, but also on the fluxes driving the dynamics of these stocks. The fluxes include losses by tree uptake and leaching from the soils on the one hand and the gain via deposition and weathering on the other hand. To quantify the nutrient balances of base cations for our forest stands, we compared the estimated nutrient uptake rates in aboveground woody biomass (including bark) with the estimated total deposition based on wet-only deposition (RIVM, 2015) and leaching and weathering data of comparable forest stands (de Vries et al., 2021). We focused on nutrient uptake of the woody biomass and bark and not the foliage, because the stem accumulates nutrients whereas the foliage recycles nutrients to soil within few years. This assumption is reasonable for mature forest of this study, which are supposed to have relatively constant annual needle production and low natural tree mortality rates (Turner and Long, 1975; Flower-Ellis, 1985; Albrektson, 1988). The leaching and weathering fluxes, however, add considerable uncertainty to the balance as site specific leaching and weathering fluxes are needed for balance calculations (Pare and Thiffault, 2016) and conclusions on balances remain therefore uncertain too. Nevertheless, the thus calculated nutrient balances were predominantly negative for K, Ca and Mg, indicating an annual reduction of the soil nutrient stock up to 4.2 kg ha^{-1} yr^{-1} for K, 1.1 kg ha^{-1} yr^{-1} for Mg and 8.6 kg ha^{-1} yr^{-1} for Ca (Table 6). The most negative balances were present for beech, which had the highest uptake rates, while balances for Douglas fir were least negative.

Negative annual balances for base cations in beech, together with P limitation (Sverdrup et al., 2006; Schmidt et al., 2015) and negative balances of Ca in Douglas fir (Sverdrup et al., 2006) have been observed throughout Europe. Deficiencies, resulting from long-term negative balances, were observed for Mg and K in needles of Douglas fir in Czech Republic (Šrámek et al., 2019), indicating that negative balances of base cations in both beech and Douglas fir are widespread. Even on a global scale, K fertilization was found to increase tree growth in 69 % of the forest ecosystems (Tripler et al., 2006), indicating that base cation nutrition is potentially limiting forest growth on continental to global scale. Base cation nutrition is currently still deteriorating due to high N deposition. The uptake of K is negatively affected by N uptake in beech stands (Vanguelova and Pitman, 2019) and even though N deposition is decreasing, recovery of the nutrient imbalance remains limited in European forests (Schmitz et al., 2019). Although, the loss of base cations can be (partly) mitigated by deep soil uptake in beech, no such mechanisms can possibly compensate for nutrient losses in Douglas fir and Scots pine (Nnyamah and Black, 1977; Olsthoorn, 1991; Vanninen and Mäkelä, 1999; Helmisaari et al., 2007). Overall, despite high uncertainty in the nutrient balance, there are multiple indicators suggesting possible growth limitation due to negative balances of K, Ca and Mg. These negative balances may result in long-term growth reductions and can be a risk for timber and biomass production as well as forest health.

Table 6
Annual nutrient uptake in stem wood, bark and branches (kg ha^{-1} yr^{-1}) and the nutrient inputs via weathering (kg ha^{-1} yr^{-1}) and leaching (kg ha^{-1} yr^{-1}). Weathering and leaching rates are based on published data of forest nutrient budgets in the Netherlands (de Vries et al., 2021), deposition is based on bulk deposition data (RIVM, Table S10) multiplied by the correction factor to calculate total deposition within a forest stand (Table S11). The balance is the sum of weathering and deposition minus uptake and leaching. The net external nutrient input is the sum of nutrients coming in by soil weathering and atmospheric deposition minus leaching, and thus excludes the nutrient uptake by trees.

Flux		K	Mg	Ca
Uptake[1] (-)	Beech	5.7 ± 0.53	1.4 ± 0.16	8.8 ± 1.2
	Douglas fir	2.8 ± 0.27	0.70 ± 0.094	3.5 ± 0.63
	Scots pine	3.2 ± 0.47	0.89 ± 0.091	3.6 ± 0.48
Leaching (-)	Beech	2.3	2.9	5.8
	Douglas fir	1.3	1.6	3.2
	Scots pine	1.9	2.4	4.8
Weathering (+)		2.0	1.8	3.0
Deposition (+)	Beech	1.1	1.2	2.0
	Douglas fir	1.0	1.4	2.3
	Scots pine	1.0	1.2	1.5
Balance	Beech	**−4.9**	**−1.3**	**−9.6**
	Douglas fir	**−1.1**	0.90	**−1.4**
	Scots pine	**−2.1**	**−0.29**	**−3.9**
External nutrient input	Beech	0.8	0.1	**−0.8**
	Douglas fir	1.7	1.6	2.1
	Scots pine	1.1	0.6	**−0.3**

[1] uptake in wooden parts (stem wood, stem bark and branches).

4.4. *Effect of timber harvest intensity*

Nowadays, current forest management tends to shift towards less intense harvest intensities in which a continuous cover is maintained. These less intense forest management practices are favoured because of the greater resistance of forest to biotic and abiotic damages (Knoke, 2009). The biomass export in a stem only harvest high thinning, a low intensity forest management, leads to limited biomass (13–43 tons ha^{-1}) and nutrient exports (0.12–220 kg, Fig. 3). However, effects of low intensity forest management will be comparable to nutrient exports in high intensity forest management as the frequency of the low forest management is higher, diminishing possible advantages for forest nutrient balances.

Regardless of harvest intensity, we expected the species in our study to have large export differences since they differ in biomass growth, biomass distribution and nutrient concentrations. Our results confirm earlier work on Douglas fir, showing higher biomass yield than beech and Scots pine on well-drained nutrient poor sites (Fig. 3) (Bastien, 2019; Thomas et al., 2022). Despite this higher yield, nutrient export in all harvest intensities was generally lower compared to the other two species. Due to the low nutrient export, there is no direct threat of negative nutrient balances for Douglas fir timber harvest. For example, loss of base cations can be recovered within 9 years after a stem only high thinning up to 42 years after a stem only clearcutting (Table 4, Table 6). Contrary, negative nutrient balances were reported previously for Douglas fir stands (Ranger et al., 2002; de Vries et al., 2021), with more negative balances during stand development due to higher nutrient uptake and leaching (Ranger et al., 2002). The nutrient dynamics during stand development were not considered in this study. In the nutrient export balance, the annual uptake of nutrients in foliage was not considered, although this short-term uptake flux is known to result in negative balances (Table 6). It is therefore possible that nutrient budgets become temporarily negative during stand development following harvest which may decrease tree growth.

Timber harvest in beech and Scots pine is likely to impede forest nutrition within two final felling's using common rotation periods. These final felling's could be either two clearcutting harvest intensities or a series of thinning's, both resulting in the harvest of all stems. Timber harvest, regardless of harvest intensity, in both beech and Scots pine resulted in negative balances of base cations with no natural refill of exported Ca due to the negative external supply (Table 6). To fully replace the loss of the other base cations in beech, rotation periods of 70 years should be used for a stem only high thinning up to a rotation period of 420 years for a stem only clearcutting. These rotation periods can be calculated by dividing the nutrient export (Fig. 3) by the external nutrient supply (Table 6). For Scots pine, the Mg and K stock will be recovered within 30 years following clearcutting harvest up to 60 years following stem only clearcutting harvest. Although deep layer uptake could provide another nutrient influx for beech, this influx may have only a limited effect on tree nutrition (Berger et al., 2006; van der Heijden et al., 2015). Negative nutrient budgets for base cations due to harvest were reported previously (Růžek et al., 2019; de Vries et al., 2021), together with possible P limitation (de Vries et al., 2021). We did not find risks of declining P stocks as P stocks of all species following stem only harvest in a clearcutting can recover within 50 years considering leaching, weathering (de Vries et al., 2021) and deposition (RIVM, 2015). Negative balances of Ca and P have been found previously (Vangansbeke et al., 2015; de Vries et al., 2021) as well as negative balances of K and Mg which were linked to elevated S deposition (Schaaf et al., 1995) and risks for negative K balances were mentioned for Scandinavia (Palviainen and Finer, 2012). Finally, we predict that harvest in beech stands leads to negative nutrient balances, regardless of harvest intensity. We also have indications that the nutrient balances following stem only harvest in Scots pine seem solely hampered by negative Ca inputs. The annual decreasing soil nutrients stocks, resulting from negative external nutrient input, imply that additional measures are necessary to counteract the loss of base cations if trees will be harvested in these forests in the long term.

4.5. Effect of biomass harvest type

The biomass harvest type, i.e., harvest of crown materials in case of whole tree harvest (WTH) or stripping the bark in case of wood only harvest (WOH), strongly influenced the nutrient export by harvest but had relatively small effects on biomass exports. The highest biomass gain (beech: 140 %, taking stem only harvest as the 100 %-reference) after WTH was accompanied by nutrient losses up to 310 %. The biomass gain following whole tree harvest for Scots pine (130 %) is in line with earlier reports for Scots pine (Palviainen and Finer, 2012; Węgiel et al., 2018) but the export in beech in this study was higher which could be caused by wider crowns (Göttlein et al., 2012; Ulbricht et al., 2016). Whole tree harvest caused considerable increase in base cation (150–190 %) and P (190–280 %) export. These increased losses of scarse nutrients will cause more negative nutrient balances or unrealistic long rotation periods for both beech and Scots pine. Whole tree harvest in Douglas fir seems more sustainable, since base cation losses due to whole tree harvest are replenished by external nutrient input within 70 years. However, because of low stocks of especially K and Mn in the organic soil layers, there seems hardly any nutrient buffer in the system to recover from disturbances. Such disturbances impact soil nutrient stocks as, for example, leaching temporarily increases after harvest (Katzensteiner, 2003; Rothe and Mellert, 2004; Gundersen et al., 2006; Piirainen et al., 2007). Therefore, although nutrient stocks can be replenished by external nutrient supply assuming stable conditions, the poor soil nutrient buffers for base cations, Mn and P makes whole tree harvest potentially unsustainable and a risk for nutrition and forest growth (Thiffault et al., 2011) within a single rotation period for such forests on poor and acidified soils.

Wood only harvest, thus removing stem without stem bark, resulted in a 6–10 % lower biomass export (again compared to stem only harvest as the 100 %-reference) but saves up to 50 % of the base cation and P export. Highest reductions in nutrient exports were shown for Douglas fir while reductions were lowest for beech (Fig. 4). Wood only harvest will lower the base cation export with 10 % to 60 % and the P export by 30 to 50 % compared to stem only harvest. High stocks of base cations in the bark are observed across multiple species, including an up to 50 % decrease of base cation export following wood only harvest (Andre et al., 2010; Achat et al., 2015). Although this study confirms that leaving the bark in the forest is a sustainable management practice (Pyttel et al., 2015; Manolis et al., 2019), the effects differ per nutrient and per species. Wood only harvest will allow rotation periods of 50 years following a clearcutting in Douglas fir but cannot counteract the negative external nutrient input in beech and Scots pine, indicating that harvest in beech and Scots pine will still lead to negative Ca balances. However, wood only harvest can prevent depletion of soil K and Ca stocks in both beech and Douglas fir which has previously been observed for coppice oak systems (Pyttel et al., 2015). Furthermore, wood only harvest will keep the main stock of micronutrients in the forest (Manolis et al., 2019). We strongly advocate to shift conventional stem only harvest to wood only harvest. In-situ debarking has been done for Spruce where 91 % of the bark was left in the forest in the final felling (Mergl et al., 2021). High debarking efficiencies using harvesters were reported in multiple studies, concluding that in-situ debarking is a potential addition to existing harvesting methods (Heppelmann et al., 2019; Holzleitner and Kanzian, 2022). Debarking of trees may therefore not lead to technical impossibilities but will considerably improve nutrient balances for forests on low-fertile soils.

4.6. Conclusions

Many forests occur on acidified, poor and well-drained forest soils, i.e., soils with low base saturation that are at risk of base cation and Mn limitation. For 15 Dutch forest stands on such soils, we measured nutrient stocks for macro- and micronutrients and calculated potential limitations in nutrient supply for forest recovery. The aboveground base cation and Mn stocks are generally larger than the soil stocks, posing an immediate threat to forest nutrition if the trees are harvested. Even without harvest, negative external nutrient inputs like the negative input of Ca in both beech and Scots pine forests poses threats to forest growth and vitality. This negative external Ca balance limits also timber harvest in both beech and Scots pine as exported nutrients cannot be recovered, resulting in a depletion of the Ca nutrient stock within 2 final fellings. Contrary, timber harvest in Douglas fir stands will not result in negative base cation balances using rotation periods of 80 years as base cation losses by harvest are fully replaced by external input. However, temporary negative nutrient balances resulting in lower growth might occur as aboveground K and Mn stocks are larger than the soil stocks. We show that on such nutrient poor forest soils, whole tree harvest should be avoided as harvesting crown materials results in negative nutrient balances, with particularly base cation nutrient removal exceeding the base cation nutrient stocks. Whole tree harvest also resulted in extraordinary high export losses of P, which may limit future forest growth. Instead, wood only harvest, where the bark is stripped in the field, may pose opportunities for sustainable biomass harvest as it can conserve up to 50 % of the nutrients in the system compered to regular timber harvest. We therefore recommend that use of such forests on acidified, poor soils will be limited to low intensity harvesting, and recommend debarking trees to conserve large quantities of nutrients within the forest system upon harvest.

Author contributions

Marleen A.E. Vos, W. de Vries, J. den Ouden and Frank J. Sterck conceived the ideas, methodology was designed by Marleen A.E. Vos and J. den Ouden. The soil sampling was conducted by M. Valtera and Marleen. A.E. Vos. Statistical analysis was performed by Marleen A.E. Vos. Marleen A.E. Vos led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120791.

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