



RESEARCH PAPER

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Impacts of harvesting methods on nutrient removal in Dutch forests exposed to high-nitrogen deposition

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Abstract

Context: Forest harvest removal may cause nutrient depletion of soils, when removal of essential nutrients, including nitrogen (N), phosphorus (P), sulphur (S), calcium (Ca), potassium (K) and magnesium (Mg) exceeds their net input by deposition and wet impacts of acid atmospheric deposition on woodland after harvesting minus leaching. Nutrient removal by harvest depends on tree species and the harvesting method, i.e. whole-tree harvesting (removal of stems and branches) versus stem wood removal only.

Aim: The aim of this study was to assess the impacts of these two harvesting methods on nutrient removal in Dutch forests exposed to high-nitrogen deposition.

Methods: To assess those impacts, we measured nutrient concentrations in stem wood and branch wood of seven major tree species in the Netherlands, i.e. Japanese larch (*Larix kaempferi* Lamb.), Norway spruce (*Picea abies* L. Karst.), Douglas fir (*Pseudotsuga menziesii* Mirb.), Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), beech (*Fagus sylvatica* L.) and common oak (*Quercus robur* L.). Average nutrient concentrations in stems were based on measured concentrations in heartwood, sapwood and bark and estimated volumes and densities of these compartments. Similarly, average nutrient concentrations in branches were based on measured concentrations in coarse branches, fine branches and the bark of coarse branches and estimated volumes and densities of these compartments. Removal was assessed by using the average growth rates of these tree species on nutrient poor sandy soils in the Netherlands.

Results: Compared to other countries, N concentrations in the Netherlands were higher in stems, while phosphorus, Ca, K and Mg concentrations in both stems and branches were nearly always lower. The elevated long-term N deposition levels in the Netherlands most likely contribute to this finding, since N deposition causes soil acidification reducing the availability of Ca, K, Mg and P, that could become limiting to growth. Limits for sustainable harvest, above which outputs exceed inputs of nutrients, depend on nutrient, soil type and tree species and are mostly determined by K and P and sometimes Ca, which may already be depleted at relatively low harvest levels on poor sandy soils, in particular for broadleaved species, while depletion of Mg is not likely. Nevertheless, the average growth of forests in the Netherlands appears to be slightly higher than in most other countries in Europe.

Conclusion: Overall, we thus conclude that limited P, Ca, Mg and K availability in response to elevated N deposition is reflected in reduced contents of these nutrients in stem wood and branch wood but not in growth.

Handling Editor: Erwin Dreyer

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Key message: Nutrient concentrations in tree compartments were assessed for seven major tree species in the Netherlands. Concentrations of phosphorus, calcium, potassium and magnesium (base cations) in stems and branches are mostly lower compared to those in other countries, while nitrogen concentrations are higher. A long-term nitrogen deposition has likely contributed to these differences. The average growth has not declined, despite the low availability of phosphorus and base cations. Limiting the harvest of branch wood is suggested on nutrient poor soils to avoid depletion of phosphorus and base cations.

Keywords: Stem wood harvest, Whole-tree harvest, Wood nutrient concentrations, Nutrient balance, Nitrogen deposition, Base cation depletion

1 Introduction

In the Dutch Climate Agreement (Klimaatakkoord, 2019), reduction targets have been set at 49% reduction in CO₂ emissions in 2030 and 95% in 2050 compared to 1990. In this agreement, the ambition has been set to double the use of sustainable biomass. The Dutch nature and forestry sector thus signed an intention agreement with the Dutch Ministry of Agriculture, Nature and Food Quality, to increase the supply of biomass from forests and other land cover types, within the limits of sustainable management, implying that the soil nutrients are not depleted (LNV, 2008). Harvest of logging residues is one option to contribute to this target, being a practice that implies that stem only harvest, being the standard Dutch harvesting approach, is replaced by whole-tree harvest.

The sustainability of whole-tree harvest has, however, been questioned (De Jong, 2011), also considering that the forest in the Netherlands are mostly situated on relatively poor sandy soils. The major part of Dutch forests has been established on former heathlands and drift sands that evolved after centuries of nutrient depletion by sheep grazing and sod cutting. One of the reasons for the establishment of forest was to stop the expansion of those nutrient poor drift sands (Van der Woud, 2020). First and second generations of trees were sometimes fertilized, using phosphate and sulphate of Potash Magnesia, and sometimes a nitrogen-fixing crop (lupin) was grown for 1 or 2 years (Van den Burg et al., 1987). The effects of fertilizers on tree growth have thus been studied since the late nineteenth century to support afforestation of heathlands, and forest research even focused on growth of regenerated forests up to the second half of the twentieth century (Van de Burg, 1989). From the 1980s onwards, the effects of acid deposition on forest soils (e.g. Van Breemen et al., 1987; De Vries et al., 1995), floristic diversity (e.g. Hommel et al., 1990) and on forest vitality (e.g. Hendriks et al., 1994) have been important topics of research in The Netherlands.

Compared to stem only harvest, whole-tree harvest causes enhanced removal of essential macronutrients, including nitrogen (N) phosphorus (P), sulphur (S), calcium (Ca), potassium (K) and magnesium (Mg). This

may cause soil nutrient depletion, thus affecting the sustainability of harvesting logging residues for biomass. The need for sustainable forest nutrient management is especially relevant for the Netherlands, which is characterized by more than 40 years of elevated N deposition, mainly due to intensive livestock farming (Van Pul et al., 2018). This had led to strongly enhanced N levels in soil and foliage in combination with acidification of the poor sandy soils, which are characterized by low pH and base (Ca, Mg and K) saturation levels and low Ca, Mg and K levels in foliage (e.g. De Vries et al. 2019).

Nutrient removal by harvest depends not only on the forest management practice (whole-tree harvest versus stem only harvest) but also on the tree species, due to variation in growth and nutrient concentrations in tree compartments, i.e. stem wood, bark, thick branches, small branches and foliage (Johnson et al. 1982; Federer et al., 1989). The impact of whole-tree harvesting, including the harvest of stem wood, branch wood and foliage has been explored in the Netherlands in the early 1980s by Kofman (1983), who measured the nutrient contents in total stem wood and total crown biomass including foliage of Scots pine, Norway spruce, Japanese larch and Douglas fir. The reason was to assess the effects of whole-tree harvest in the forest, followed by delimiting at the factory, which was thought to be more efficient than stem only harvest. Since then, however, the environmental and soil conditions of Dutch forests have changed due to high nitrogen and acid deposition during several decades, thus reducing the soil base saturation (De Vries and Leeters, 2001; De Vries et al., 2017). Therefore, it is questionable that nutrient contents derived in the 1980s of the previous century, or from international literature data, are an adequate indicator for the nutrient contents in trees in the Netherlands, as concentrations are site and region specific (Augusto et al. 2000, Bauer et al. 1997). We expect that trees in the Netherlands have higher N contents and lower P, Ca, K and Mg contents in stems and branches than in other regions.

Unfortunately, we lack a quantitative overview of nutrient concentrations in the tree compartments of major tree species in the Netherlands. There are many data on

nutrient concentrations in foliage (Van den Burg, 1985), but data are extremely limited on stems and branches, which are key to assess the sustainability of harvesting methods. Furthermore, element concentrations in stems and branches are generally not based on a mass weighted mean of amounts in tree compartments. To assess a mass weighted mean, it is relevant to have insight in the proportion of heartwood, sapwood and stem bark, with varying concentrations (e.g. André et al., 2010), with both proportions and concentrations being strongly affected by stand age and diameter (Augusto et al., 2000; Miles, 2009). The mass proportions may change over time within the tree but might be site specific as well (Mencuccini and Bonosi, 2001; Jakubowski et al. 2015). Insight in current nutrient concentrations in tree wood compartments in the Netherlands is also relevant since a long-term elevated N deposition most likely have enhanced N concentrations and decreased P, S, Ca, K and Mg concentrations in those compartments.

The main aim of this study is to gain insight in the removal of nutrients (N, P, S, Ca, K and Mg) by different tree species and harvesting methods (whole-tree harvest versus stem only harvest) in an area exposed to high N deposition, by assessing current average nutrient concentrations in stem wood and branch wood in seven major tree species in the Netherlands, i.e. Japanese larch (*Larix kaempferi* Lamb.), Norway spruce (*Picea abies* L. Karst.), Douglas fir (*Pseudotsuga menziesii* Mirb.), Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), beech (*Fagus sylvatica* L.) and common oak (*Quercus robur* L.). We sampled separate woody compartments, i.e. heartwood, sapwood and stem bark, bark and wood of coarse branches, and fine branches. Based on estimated volumes and densities and thus mass proportions of these compartments, weighted average concentrations were calculated for stems and branches. Average nutrient removal was assessed by using the average growth rates of the considered tree species on nutrient poor sandy soils in the Netherlands, which is the most common soil condition (Schelhaas et al., 2014), distinguishing whole-tree harvest versus stem only harvest. Whole-tree harvest refers to harvest of stem wood with removal of logging residues only at final felling, as harvesting logging residues during thinning is not common in the Netherlands.

2 Material and methods

2.1 Data collection

During 2016 to 2018, samples of different wood compartments were taken to analyse nutrient concentrations. The samples were taken from seven main tree species in Dutch forests (in tables and figures, the tree species are denoted as larch, spruce, fir, pine, birch, beech and oak). Sampling locations came randomly available as sampling

took place were thinning occurred and on sites were research on nutrient leaching took place (De Vries et al., 2021). The following compartments were sampled (see Fig. 1 for a schematic presentation):

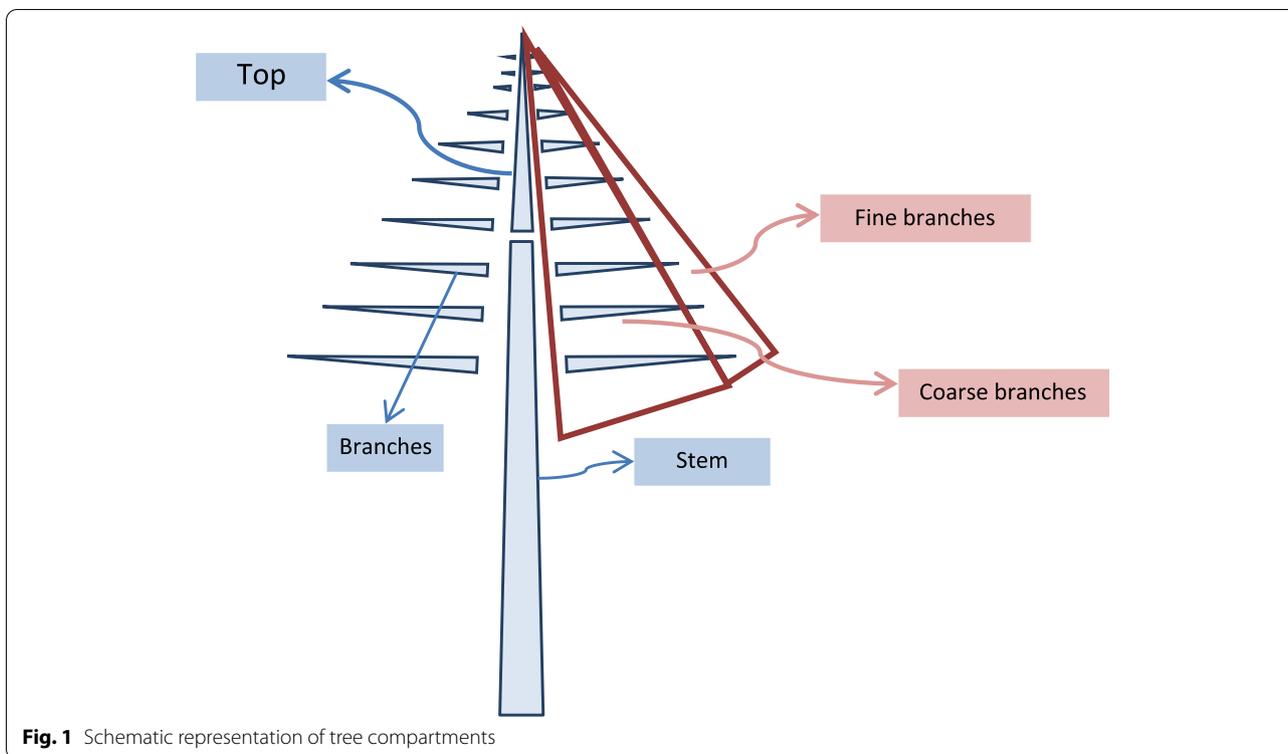
- Stems (> 10-cm diameter over (including) bark)
 - Stem wood (without bark)
 - Stem heartwood
 - Stem sapwood
 - Stem bark
- Branches
 - Coarse branches (top and branches 2–10-cm diameter over bark)
 - Coarse branch wood without bark
 - Coarse branch bark
 - Fine branches (wood and bark) (top and branches <2-cm diameter over bark)

Sapwood and heartwood were not distinguished for Norway spruce, silver birch and beech as they could not easily be distinguished in the field.

A range of diameters and bark thicknesses were measured to calculate the mass share of the compartments. Diameters were measured using a tree calliper, and bark thickness was calculated by subtracting heartwood diameter from the diameter over bark, while for thinner bark a precision calliper was used to directly measure the thickness. From these data, mean nutrient concentrations were calculated for stems and branches. Average nutrient concentrations for stems and branches were calculated from the mass proportions of the compartments over a rotation.

Samples of the wood compartments were taken during the winters of 2016/2017 and 2017/2018 in forests on dominant forest soil types in the Netherlands, i.e. a range of mineral poor (coarse) to mineral rich (loamy fine) sandy soils, based of soil types from the 1:50,000 soil map of the Netherlands. Samples were taken at 63 plots over 15 forests areas in total, with sometimes multiple tree species being sampled at one site, i.e. 18 for Japanese larch, 15 for Norway spruce, 12 for Douglas fir, 21 for Scots pine, 11 for silver birch, 7 for beech and 20 for common oak, reflecting the areal coverages of these tree species. Each sample consisted of at least three subsamples from different stem sections or branches.

Samples of stem wood, coarse branch wood and bark were taken by using a 5-mm-increment borer. For fine branch wood, 1-cm sections were taken at a



diameter of 1 cm, using regular pruning shears. Diameters of stem and branch sections over bark, under bark and heart wood were measured at harvest sites on tree and branch sections over a range of diameters over bark (mostly up to 60 cm) to calculate the mass proportions.

Samples were oven-dried and milled. The concentrations of P, S, Ca, K and Mg were analysed following a microwave digestion using nitric acid (HNO₃), hydrochloric acid (HCl) and hydrogen peroxide (H₂O₂). The addition of HNO₃ and HCl completely degraded the organic matter. The silica structure is not or only partially broken down, whereby the selected elements were dissolved. P, Ca, K and Mg were measured using ICP-OES (Inductively Coupled Plasma – Optical Emission Spectroscopy). N-concentrations were measured using C/N-analyser [LECO] after dry combustion according to the Dumas principle (Dumas, 1831). Foliage concentrations for ever green species were based on samplings carried out in the period 1990–2000 (unpublished data, Appendix Table 5). For S, no data on foliage concentrations from the Netherlands were available, so we used the middle of normal ranges from Göttlein (2015), being 1.3 mg g⁻¹ for Norway spruce and Scots pine, which we also used for Douglas fir.

2.2 Data analysis

2.2.1 Calculation of the average concentrations in stems

Calculation approach The average nutrient concentration in stems (g kg⁻¹ dry matter) was calculated as the mass weighted average concentration of (i) heartwood, sapwood and bark using formula (1) for Douglas fir, Scots pine, Japanese larch and common oak and (ii) stem wood without bark and bark using formula (2) for Norway spruce, beech and silver birch.

$$c_{stem} = \frac{V_h sw_h sf_h c_h + V_s sw_s sf_s c_h + V_b (1 - VOID) sw_b sf_b c_b}{V_h sw_h sf_h + V_s sw_s sf_s + V_b (1 - VOID) sw_b sf_b} \quad (1)$$

$$c_{stem} = \frac{V_w sw_w sf_w c_w + V_b (1 - VOID) sw_b sf_b c_b}{V_w sw_w sf_w + V_b (1 - VOID) sw_b sf_b} \quad (2)$$

where V_h , V_s , V_b and V_w are the volumes (m³ fresh wood); sw_h , sw_s , sw_b and sw_w are the densities (kg m⁻³ dry matter); sf_h , sf_s , sf_b and sf_w are the volumetric shrinkage factors (sf) from fresh to dry volume (-); and c_h , c_s , c_b and c_w are the element concentrations (g kg⁻¹ dry matter) of respectively heartwood, sapwood, bark and stem wood without bark. VOID is the fraction of air space in the bark volume. Volumetric shrinkage from fresh to dry

volume was assumed to be equal for compartments of a tree species.

Wood properties used in the calculations are given in [Appendix Table 6](#). The VOID values of Norway spruce were not available. Considering typical bark roughness, it should be less than that of common oak and higher than that of beech, and more comparable to that of ash (*F. excelsior*) and sessile oak (*Q. petraea*) for which Haygreen and Bowyer (1982) provide VOID fractions ranging from 0.13–0.23 to 0.11–0.20. Based on these data, a VOID factor of 0.15 was assumed for Norway spruce.

Volume proportions of stem compartments The volume proportions for bark, heartwood, sapwood and stem wood without bark vary with the diameter of stem segments (Miles, 2009). To determine the volume proportions of the different compartments, measurements were taken on 517 tree sections for 6 tree species (the number of sites for silver birch were too limited) ranging from 4 to 95 cm in diameter, using callipers and diameter tape. The data were used to determine linear relations between bark thickness and heartwood diameter, respectively, versus diameter of stem wood over bark, using formulas (3) for bark thickness and (4) for heartwood diameter accordingly (following Loetsch et al., 1973).

$$B_{th} = a D_{ob} + b \tag{3}$$

$$D_h = c D_{ob} + d \tag{4}$$

where B_{th} is bark thickness (cm), D_h is diameter (cm) of heartwood, and D_{ob} is diameter of stem wood over (including) bark (cm).

Bark thickness was strongly related to diameter over bark for most species, but the (linear) relationship (R^2) was weakest for Scots pine ([Appendix Table 7](#)). This is due to the species property of having an abrupt change in bark thickness at app. 30% of the tree height (Loetsch et al., 1973). Common oak had the highest correlation between bark thickness and stem diameter over bark. Heartwood diameter was also strongly related to diameter over bark ([Appendix Table 7](#)). For Scots pine, the relation was weakest as the heartwood diameter can vary strongly between trees of similar dimensions, also within an even aged stand (as observed by Jakubowski et al., 2015). Japanese larch and common oak had a notably high correlation between diameter over bark and heartwood diameter.

To calculate V_h , V_s , V_b and V_w i.e. the volumes heartwood, sapwood, bark and stem wood (under bark), respectively, for harvested wood over one rotation, yield tables

published by Jansen et al. (1996) were used. For each harvested tree over a rotation, bark, stem wood under bark, sapwood and heartwood volumes were calculated per 2-m height segment using the combination of formulas (3) and (4) with the formulas (5), (6) and (7) given below.

Bark volume per 2-m section (V_b ; in m^3) was calculated as follows:

$$V_b = 2 \frac{\pi}{4} (D_{ob}^2 - D_{ub}^2) 10^{-4} \tag{5}$$

with D_{ub} the diameter under (excluding) bark, being calculated as $D_{ob} - 2 B_{th}$ (in cm).

The volume of stem wood under bark (V_w ; in m^3) per 2-m section was calculated using formula (6):

$$V_w = 2 \frac{\pi}{4} D_{ub}^2 10^{-4} \tag{6}$$

Heartwood volume V_h was calculated according to Eq. (6), using D_h instead of D_{ub} , and the sapwood volume, V_s was calculated as V_w minus V_h .

Total volumes for bark, sapwood and heartwood were calculated by summing the sections for every tree harvested in thinnings and final felling. As there were insufficient measurements of bark thickness for BP, we used an average bark volume percentage of 12.6% of total stem volume, based on Von Dietz (1975).

Taper functions from Fonweban et al. (2011) were used to determine the stem diameter with bark (in cm) per height section over the tree height, using formula (7):

$$D_{ob} = DBH x^{(a_0 + a_1(z-1) + a_2(\exp(a_3 \cdot z)))} \tag{7}$$

with $x = (ht-h)/(ht-1.3)$, $z = h/ht$, $ht =$ tree height (in m) and $h =$ height of stem section (in m). [Appendix Table 8](#) shows the parameters a_0 , a_1 , a_2 and a_3 used per tree species. The resulting volume and mass proportions per compartment, on average over one rotation, are given in [Appendix Table 9](#).

2.2.2 Calculation of the average concentrations in branches

The average element concentrations of coarse branches were calculated from the element concentrations in coarse branch wood without bark and coarse branch bark according to the following:

$$c_{bc_i} = \frac{V p_{bw_i} sw_{bw_i} sf_{bw} c_{bw_i} + V p_{bb_i} sw_{bb_i} sf_{bb} c_{bb_i}}{V p_{bw_i} sw_{bw_i} sf_{bw} + V p_{bb_i} sw_{bb_i} sf_{bb}} \tag{8}$$

with $V_{p_{bw}}$ en $V_{p_{bb}}$ being the volume proportions (%), sw_{bw} en sw_{bb} the densities (kg m^{-3} dry matter) and c_{bw} and c_{bb} the element concentrations (g kg^{-1} dry matter) of coarse branch wood under bark and coarse branch bark, respectively. The densities were assumed to be equal to those of stem wood and stem bark, respectively (Appendix Table 6). The volumetric shrinkage from fresh to dry volume was assumed to be equal for compartments within a species.

The average nutrient concentrations in (total) branches were calculated as the weighted average concentrations of coarse and fine branches, according to the following:

$$c_{br} = mp_{bc} c_{bc} + mp_{bf} c_{bf} \quad (9)$$

where mp_{bc} and mp_{bf} are the mass proportions (%) and c_{bc} en c_{bf} are the nutrient concentrations (g kg^{-1} dry matter) of the coarse and fine branches.

2.2.3 Volume proportions of branch compartments

The volume proportions of wood and bark for branches strongly depends on diameter (Loetsch et al., 1973; Haygreen and Bowyer, 1982). Proportions in coarse branches were based on 142 measurements of branch diameter over and under bark. Average volumes proportions were calculated from weighted average cross-section areas under bark and over bark per tree species. No correction for bark VOID was made since branch bark was fairly smooth and thickness was measures without VOID.

Bark proportions of coarse branch wood differs strongly between tree species, with Scots pine having the smallest proportion of bark due to the fairly thin bark, even for larger branch diameters (Appendix Table 10). Common oak has the largest proportion of bark in branch wood. The bark proportions of branch wood are indicative, as they are strongly dependent on branch and tree size (Morhart et al. 2016) and detailed data are not available.

The mass proportions for coarse and fine branches are based on André et al. (2010), de Boer (2020), Genet et al. (2011), Christophe et al. (2017), Husmann et al. (2018), Svoboda et al. (2006) and Grote (2002), who published biomass quantities per diameter class for branch wood of several relevant tree species. Their data show that biomass proportion is related to stand age. For this study, proportions at mature age are relevant, since branch wood is only harvested at final fellings in the Netherlands. The studies mentioned above apply different limits between fine and coarse branches. The proportions at a limit of 2 cm, used in this study, can thus not be derived directly. Based on the data of André et al. (2010), a linear relation between the cumulative biomass at different diameter limits was assumed

(Appendix Fig. 3). In Appendix Table 11, the extrapolated proportions of branch wood < 2 cm for each study are given. Based on these data, the mass proportion of fine branch wood for broadleaved species was set to 25% and for coniferous species at 40%.

2.2.4 Calculation of nutrient removal through timber harvesting

The annual removal of nutrients through harvest was based on the average growth rate of the seven tree species on sandy soils over one rotation period, using yield tables for the Netherlands (Jansen et al., 1996). Growth classes were selected that corresponded with the median growth according to the national forest inventory (Schelhaas et al., 2014) (Appendix Fig. 4).

The nutrient concentrations were assumed to be constant over the rotation period since average harvest levels over a whole rotation were calculated. The mass of the branches and needles at final felling were based on GrowUp (Bonten et al., 2016, De Vries et al., 2021), a tree growth model that calculates the uptake, retention and removal of nutrients per tree species per year based on the amount of biomass and the nutrient contents in stems, branches, roots, leaves and needles. GrowUp uses data from Vilén et al. (2005), as used in EFISCEN (Schelhaas et al., 2007), on the ratio of branches to stem wood and the mass of needles (Scots pine, Douglas fir, Norway spruce) at final felling. Other biomass components (especially roots) were assumed to remain in the forest and are thus not included in the calculations.

Limits for sustainable harvest, above which outputs exceed inputs of nutrients, were calculated using wood nutrient contents and net availability of nutrients. The net availability of nutrients was calculated using data from de Vries et al. (2021) on the average inputs of nutrients by weathering and deposition minus outputs by leaching. The net nutrient availability (in $\text{kg ha}^{-1} \text{ year}^{-1}$), thus calculated for moderately poor sandy soils was 4.46 for Ca, 2.09 for K, 3.03 for Mg and 0.20 for P 0.20^1 , being is 9 to 64% higher than in poor sandy soils (Ca is 4.11, K is 1.90, Mg is 1.85 and P is 0.16 $\text{kg ha}^{-1} \text{ year}^{-1}$).

3 Results

3.1 Nutrient concentrations in wood compartments

Overall, the nutrient concentrations were highest in branch bark and fine branches (Table 1). Branch bark had the highest concentrations of N for most species, though concentrations in fine branches and stem bark were relatively high as well, compared to stem and

Table 1 Average concentrations (g kg^{-1}) and standard errors (SE) of major nutrients in tree compartments of seven tree species with numbers of samples analysed for P, S, Ca, K and Mg (n_a) and N (n_b). Note that for spruce, birch and beech there is no distinction in sapwood and heartwood, and results are directly given as stem wood

	N g kg⁻¹	SE	P g kg⁻¹	SE	S g kg⁻¹	SE	Ca g kg⁻¹	SE	K g kg⁻¹	SE	Mg g kg⁻¹	SE	n_a / n_b
Stembark													
Larch	4.63	0.32	0.260	0.03	0.343	0.02	1.962	0.16	1.51	0.13	0.409	0.03	18/17
Spruce	5.58	0.13	0.395	0.03	0.389	0.02	9.311	0.96	2.28	0.17	0.835	0.06	15/15
Fir	3.60	0.35	0.171	0.02	0.263	0.02	1.617	0.20	0.950	0.17	0.253	0.04	12/11
Pine	4.55	0.51	0.109	0.01	0.260	0.02	2.560	0.38	0.595	0.08	0.155	0.02	21/14
Birch	5.61	0.50	0.183	0.02	0.325	0.04	2.925	0.29	0.700	0.09	0.375	0.03	11/11
Beech	8.43	0.34	0.387	0.03	0.429	0.02	13.41	2.53	2.00	0.21	0.547	0.08	7/7
Oak	7.47	0.65	0.216	0.01	0.546	0.02	11.19	1.06	1.46	0.09	0.771	0.05	20/17
Stem sapwood													
Larch	1.44	0.12	0.0650	0.01	0.0811	0.01	0.344	0.03	0.378	0.04	0.0961	0.01	18/17
Fir	1.29	0.10	0.0583	0.005	0.0700	0.004	0.335	0.03	0.558	0.13	0.0958	0.01	12/12
Pine	1.41	0.18	0.0738	0.02	0.0905	0.01	0.616	0.12	0.490	0.03	0.162	0.03	21/17
Oak	2.85	0.33	0.134	0.01	0.160	0.01	0.489	0.04	1.27	0.07	0.152	0.01	20/19
Stem heartwood													
Larch	1.21	0.08	0.0161	0.005	0.0500	0.005	0.189	0.02	0.200	0.05	0.0478	1.21	18/18
Fir	1.35	0.11	0.0108	0.001	0.0517	0.004	0.226	0.08	0.225	0.2	0.0425	1.35	12/12
Pine	1.25	0.13	0.0124	0.002	0.0633	0.004	0.787	0.04	0.267	0.01	0.168	1.25	21/18
Oak	1.94	0.09	0.0215	0.004	0.113	0.003	0.302	0.02	0.395	0.03	0.0310	1.94	20/20
Stem wood													
Spruce	1.29	0.07	0.0313	0.004	0.0547	0.001	0.744	0.04	0.453	0.03	0.140	1.29	15/15
Birch	1.78	0.12	0.0818	0.01	0.0809	0.004	0.555	0.04	0.591	0.04	0.241	1.78	11/11
Beech	1.98	0.15	0.0871	0.01	0.123	0.01	0.747	0.06	0.929	0.09	0.250	1.98	7/7
Branch bark													
Larch	6.84	0.38	0.545	0.03	0.524	0.04	3.88	0.19	2.96	0.15	0.885	0.06	18/18
Spruce	8.25	0.37	0.608	0.04	0.576	0.03	11.87	1.17	2.41	0.13	1.06	0.06	15/15
Fir	6.11	0.53	0.463	0.05	0.472	0.05	4.88	0.39	2.38	0.26	0.845	0.06	12/12
Pine	6.87	0.64	0.508	0.05	0.505	0.05	6.42	0.83	2.56	0.26	0.889	0.10	17/17
Birch	7.16	0.31	0.396	0.03	0.44	0.03	5.07	0.48	1.89	0.14	0.683	0.03	11/11
Beech	7.62	0.35	0.384	0.04	0.419	0.02	8.94	2.57	1.69	0.18	0.507	0.03	7/7
Oak	9.69	0.37	0.431	0.03	0.742	0.03	8.20	1.20	2.45	0.18	1.15	0.10	20/20
Coarse branch wood													
Larch	1.74	0.19	0.0756	0.02	0.100	0.01	0.944	0.16	0.544	0.07	0.233	0.02	18/17
Spruce	1.72	0.14	0.0807	0.01	0.0900	0.01	1.29	0.21	0.553	0.05	0.235	0.02	15/15
Fir	1.58	0.10	0.0492	0.01	0.0875	0.005	0.705	0.06	0.358	0.06	0.193	0.02	12/12
Pine	1.77	0.19	0.0629	0.01	0.105	0.01	1.08	0.13	0.571	0.08	0.280	0.03	17/17
Birch	2.86	0.30	0.159	0.03	0.135	0.01	1.01	0.14	0.764	0.05	0.345	0.04	11/10
Beech	2.58	0.25	0.167	0.04	0.133	0.01	0.846	0.08	1.04	0.10	0.306	0.03	7/7
Oak	3.55	0.37	0.188	0.03	0.231	0.02	0.875	0.11	1.35	0.11	0.296	0.03	20/20
Fine branches													
Larch	6.10	0.37	0.477	0.02	0.422	0.03	2.63	0.13	2.10	0.11	0.616	0.03	18/18
Spruce	6.48	0.35	0.499	0.05	0.476	0.03	3.34	0.23	2.09	0.22	0.703	0.05	15/15
Fir	4.34	0.26	0.346	0.03	0.325	0.02	3.26	0.28	1.88	0.16	0.536	0.04	12/12
Pine	5.35	0.50	0.341	0.03	0.405	0.04	1.97	0.19	1.93	0.19	0.500	0.05	17/17
Birch	7.59	0.24	0.513	0.05	0.460	0.02	2.79	0.26	1.65	0.10	0.650	0.03	11/11
Beech	5.78	0.40	0.459	0.07	0.344	0.01	2.29	0.24	1.50	0.21	0.399	0.03	7/7
Oak	7.72	0.30	0.427	0.03	0.529	0.02	2.84	0.31	1.90	0.12	0.670	0.03	20/20

branch wood. For silver birch, N concentrations were highest in fine branches and Norway spruce had the highest concentrations in stem bark. Heartwood generally had the lowest N concentrations, but the differences with sapwood concentrations was not so large compared to other nutrients. Concentrations of P were particularly high in branch bark and fine branches. Heartwood clearly had the lowest concentrations of P, and the difference between heartwood and sapwood concentrations were largest of all measured nutrients. Concentrations patterns of S were mostly similar P concentration patterns, although heartwood concentrations were not as low and differences between heartwood and sapwood were not so large.

The concentrations of Ca were highest in stem bark of common oak, beech and Norway spruce. The differences in Ca concentrations in stem bark between tree species were large, with beech having eight times higher concentrations compared to Douglas fir. Ca concentrations were high in branch bark as well, for Norway spruce in particular. Stem wood, sapwood, heartwood, and to a lesser extent branch wood had low Ca concentrations compared to bark and fine branches.

Concentrations of K were highest in branch bark and fine branches, but also in stem bark of Japanese larch, Norway spruce, beech and common oak. Sapwood concentrations of K in common oak were higher compared to sapwood of other species. Branch bark had the highest Mg concentrations, followed by stem bark of Norway

spruce and common oak. Concentrations of Mg in heartwood of Japanese larch, Douglas fir and common oak were notably low (Table 1).

Overall, results did not show significant higher nutrient concentrations on the moderate poor soils ($n = 59$) compared to the poor soils ($n = 41$). In most cases, both soil categories showed comparable patterns in nutrient levels. In some instances, concentrations were higher on average on the poorer soils, for example P and Ca concentrations of in stem bark of beech or N concentrations in branch bark of Japanese larch, Norway spruce, beech and common oak, but the opposite was true for P and K in Douglas fir branch bark. Overall, in 113 (58%) out of 195 combinations of tree compartment and species, the average concentrations on the poor soils were higher than on moderate poor soils. Using a two-tailed t test, we found a significant difference for 15 combinations, with 13 of these with higher concentrations on poor soils compared to moderate poor soils. Notable were the higher concentrations in sapwood of Japanese larch on the poorer sandy soils for both P, S, Ca, K and Mg.

The mass weighted mean nutrient concentrations for harvested stem wood (including bark) over one rotation shows that N and P concentrations in stems of broad-leaved species were on average higher than in stems of coniferous trees (Table 2). However, Ca concentrations were relatively high in stems of Norway spruce, caused by relatively high concentrations of Ca in stem bark. K

Table 2 Average concentrations (g kg^{-1}) of major nutrients in stems, both including bark, according to Jacobsen et al. (2003) and this paper and the relative difference (%) between both datasets (% difference = (this paper / Jacobsen et al. - 1) \times 100%)

Species	Nutrient concentrations (g kg^{-1})					
	N	P	S	Ca	K	Mg
Jacobsen et al. (2003)						
Larch	1.21	0.32	n.a.	0.74	0.73	0.26
Spruce	1.22	0.15	n.a.	1.41	0.77	0.18
Fir	1.01	0.13	n.a.	0.75	0.87	0.12
Pine	1.09	0.11	n.a.	1.08	0.65	0.24
Birch	1.70	0.17	n.a.	1.20	0.75	0.20
Beech	1.54	0.14	n.a.	1.80	1.04	0.26
Oak	2.10	0.12	n.a.	2.47	1.05	0.18
This paper and difference this paper vs. Jacobsen et al. (2003)						
Larch	1.60(+32%)	0.0565 (-82%)	0.0875	0.403 (-46%)	0.383 (-47%)	0.0980 (-62%)
Spruce	1.68 (+38%)	0.0646 (-57%)	0.0852	1.528 (+8%)	0.620 (-19%)	0.204 (+13%)
Fir	1.54 (+52%)	0.0548 (-58%)	0.0834	0.428 (-43%)	0.494 (-43%)	0.0949 (-21%)
Pine	1.60 (+47%)	0.0689 (-37%)	0.0987	0.768 (-29%)	0.471 (-28%)	0.162 (-32%)
Birch	2.12 (+25%)	0.0908 (-47%)	0.103	0.765 (-36%)	0.601 (-20%)	0.253 (+26%)
Beech	2.31 (+50%)	0.102 (-27%)	0.138	1.392 (-23%)	0.983 (-5%)	0.265 (+2%)
Oak	2.99 (+42%)	0.0889 (-26%)	0.186	1.763 (-29%)	0.865 (-18%)	0.171 (-5%)

and S concentrations were higher for common oak and beech compared to the other species, whereas Mg-concentrations were highest for Norway spruce and silver birch. The concentrations of N were up to approximately 50% higher compared to the average concentrations of multiple sources published by Jacobsen et al. (2003), with an average difference over the seven tree species of +40%. The concentrations of other nutrients were clearly lower, especially for P (−26 to −82%), but also for Ca (+8 to −46%) and K (−5 to −47%), but the differences were not so large for Mg (+26 to −62%) (Table 2).

The nutrient concentrations in branches were in most cases 2 to 4 times higher than in stems (Table 3). P concentrations were particularly higher for branches compared to stems. The differences between concentrations in branches compared to stems of Japanese larch and to a lesser extend Douglas fir were the largest. For Scots pine, the levels in branches were approximately twice as high as in stems. The differences in nutrient concentrations in stems and branches of beech on the other hand, were relatively small, varying from +23% for K up to +151% for P in branches as compared to stems. Although common oak had the highest concentrations of N, S, K and Mg in branches, the differences in nutrient concentrations in branches between broadleaved and coniferous species are less apparent as for stems. The concentrations of nutrients in branches were lower compared to the average concentrations published by Jacobsen et al. (2003) in all but two cases (Table 3).

3.2 Nutrient removal

Calculated nutrient removals differed strongly between species and harvest regimes (Table 4). Removals for broadleaved species were relatively high for all nutrients, while growth and harvest levels were lower compared to the coniferous species. Nitrogen removals for stem only harvest for common oak were over twice as high as for Scots pine. Removals of P were small compared to N, Ca and K and are particularly small for Japanese larch and Scots pine. Removal of Ca through stem harvest was high for common oak, beech and Norway spruce, compared to the other species. This was largely due to higher than average concentrations in bark for common oak and Norway spruce and in stem wood for Norway spruce and beech. Removals of K were notably high for beech, which was due to relatively high levels in stem wood. Removals of Mg were relatively small for Japanese larch, with Mg removals for beech, Norway spruce and silver birch being approximately three times as high.

Branch wood harvest at final fellings leads to a significantly higher removal of nutrients compared to stem only harvest. For some combinations of nutrients and coniferous tree species, the removal almost doubled. For example, in Norway spruce and Douglas fir, the removal of P through whole-tree harvest increased by 96% and 81%, respectively, compared to stem only harvest, while removal of S increased by 66% and 65% and removal of K increased 44% and 54%. This relatively strong additional removal is largely due to the removal of nutrients

Table 3 Average concentrations (g kg^{-1}) of major nutrients in branches, both including bark, according to Jacobsen et al. (2003) and this paper and the relative difference (%) between both datasets (% difference = (this paper / Jacobsen et al. − 1) × 100%)

Species	Nutrient concentrations (g kg^{-1})					
	N	P	S	Ca	K	Mg
Jacobsen et al. (2003)						
Larch	6.19	0.71	n.a.	2.49	2.71	0.66
Spruce	5.24	0.65	n.a.	3.33	2.39	0.53
Fir	2.98	0.43	n.a.	4.22	1.65	0.41
Pine	3.61	0.34	n.a.	2.07	1.67	0.73
Birch	5.40	0.62	n.a.	4.60	2.00	0.50
Beech	4.27	0.48	n.a.	4.02	1.50	0.36
Oak	6.19	0.43	n.a.	4.41	2.00	0.44
This paper and difference this paper vs. Jacobsen et al. (2003)						
Larch	3.79 (-39%)	0.265 (-63%)	0.254	1.796 (-28%)	1.31 (-52%)	0.425 (-36%)
Spruce	4.08 (-22%)	0.285 (-56%)	0.278	2.852 (-14%)	1.30 (-46%)	0.480 (-10%)
Fir	2.30 (+1%)	0.196 (-54%)	0.209	2.015 (-52%)	1.11 (-33%)	0.375 (-9%)
Pine	3.36 (-7%)	0.188 (-45%)	0.238	1.599 (-23%)	1.18 (-30%)	0.387 (-47%)
Birch	4.39 (-19%)	0.267 (-57%)	0.244	1.781 (-61%)	1.07 (-47%)	0.448 (-10%)
Beech	3.78 (-11%)	0.257 (-46%)	0.209	1.856 (-54%)	1.21 (-19%)	0.345 (-4%)
Oak	5.29 (-15%)	0.275 (-36%)	0.363	2.204 (-50%)	1.61 (-19%)	0.487 (+11%)

Table 4 Nutrient removal (kg ha⁻¹ yr⁻¹) for stem only harvest and whole tree harvest at final felling, for given yield classes (max. average increment, m³ ha⁻¹ yr⁻¹), average stem harvest over the rotation (m³ ha⁻¹ yr⁻¹), rotation length (yr) and biomass expansion factors at final felling (BEF) for branch wood (-). The table also gives foliage removal at final felling of Scots pine, Douglas fir and Norway spruce when applying whole tree harvest (10³ kg dm ha⁻¹)

Spec.	Yield class	Stem harvest	Rotation length	BEF branch wood	Foliage removal	Nutrient removal for stem only harvest						Nutrient removal for whole tree harvest					
						(kg ha ⁻¹ yr ⁻¹)						(kg ha ⁻¹ yr ⁻¹)					
	m ³ ha ⁻¹ yr ⁻¹		yr	(-)	10 ³ kg dm ha ⁻¹	N	P	S	Ca	K	Mg	N	P	S	Ca	K	Mg
Larch	10	7.8	80	0.20		5.2	0.18	0.29	1.3	1.2	0.32	6.4	0.27	0.37	1.9	1.7	0.46
Spruce	12	12	80	0.16	9.2	6.8	0.26	0.35	6.2	2.5	0.83	10	0.51	0.58	7.4	3.6	1.1
Fir	16	12	100	0.17	12.9	7.4	0.27	0.40	2.1	2.4	0.46	11.3	0.49	0.66	3.4	3.7	0.79
Pine	8	6.7	100	0.18	3.7	4.6	0.20	0.28	2.2	1.3	0.46	6.1	0.29	0.39	2.7	1.9	0.58
Birch	6	5.7	90	0.15		6.3	0.27	0.30	2.3	1.8	0.75	7.3	0.33	0.36	2.7	2.0	0.86
Beech	6	6.0	100	0.16		7.9	0.35	0.48	4.8	3.4	0.91	8.9	0.42	0.53	5.2	3.7	1.0
Oak	6	5.9	100	0.16		9.5	0.28	0.59	5.6	2.7	0.54	11	0.34	0.67	6.1	3.1	0.65
Av.						6.8	0.3	0.4	3.5	2.2	0.6	8.7	0.4	0.5	4.2	2.8	0.8

in foliage. The additional removal of nutrients in broad-leaved species is much less (approximately 10–20%), since no foliage is removed.

Limits for sustainable harvest are reached at very different harvest levels, depending on nutrient, soil type and tree species. On poor sandy soils, even at relatively low harvest levels (< 5 m³ha⁻¹year⁻¹) depletion may occur for K and P, in particular for broadleaved species, but

also on moderate sandy soils (Fig. 2). Limits for Ca may be reached at low harvest levels for common oak and beech as well. For coniferous species, limits for K are reached only at higher harvest levels (>8 m³ha⁻¹year⁻¹), but at lower levels for P for Scots pine and Japanese larch. Ca depletion may occur for spruce at harvest levels >8 m³ha⁻¹year⁻¹. Depletion of Mg is not likely for all tree species since the limit is far above the likely growth rates.

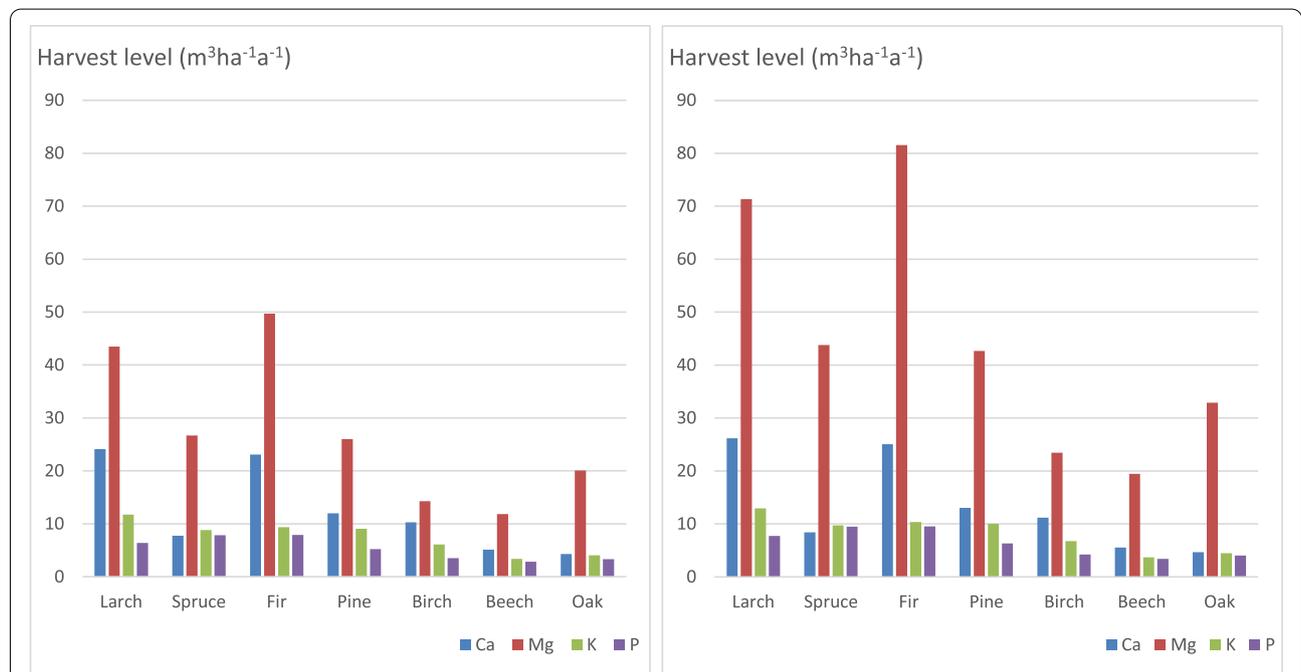


Fig. 2 Limits for sustainable harvest for the seven tree species, avoiding nutrient depletion depending on the element considered, for poor sandy soils (left) and moderate poor sandy soils (right) in the central sandy soil region in the Netherlands

4 Discussion

4.1 Impacts of sampling and site factors on measuring nutrient concentrations

The sampling method in this study may have had some effect on these results as samples were taken in stands in the second half of their rotation. For base cations, it is known that concentrations of some species may decrease with increasing stem diameter as cation binding capacity can be negatively related to distance from pitch (Momoshima and Bondietti, 1990). Sampling only in the later stages of a rotation may therefore have had a negative effect on the concentrations of base cations measures in stem wood. However, loggings in the yield tables and in practise for the largest extend take place in the late thinnings and final felling, so sampling was in accordance with this.

Another aspect of the method in this study that has an effect on the results is the fact that most of the harvesting in the yield tables take place in the late thinnings and final felling. This has an effect on the average proportions of tree compartments used to calculate the nutrient concentrations in stems. In particular the proportions of heartwood—with relatively low-nutrient concentrations—increase with increasing tree size, as observed in this study and by Ojansuu and Maltamo (1995), thus having an negative impact on the average nutrient concentrations of stems. Both aspects may to some extent explain the lower concentrations of base cations and P in this study compared to the data of Jacobsen et al. (2003), which also include younger stands, but it does not provide an explanation for the differences of N.

The mass weighted mean concentrations in branches in our study are affected by the fractions fine branches, branch bark and branch wood we used. The fractions are based on the idea that branches are harvested only at final felling, having a relatively large maximum diameter, thus having a large proportion of (coarse) branch wood and a relatively small proportion of branch bark and fine branches compared to branches harvested in thinnings of the first half of the rotation. For beech and common oak, the proportions of branch bark mass compare well to the proportions that can be derived from the data by André et al. (2010): 9–15% for common oak and 7–10% for beech for larger trees. Haygreen and Bowyer (1982) however mention 21% bark in branches > 2.5-cm diameter for white pine and red maple. Data from Duviigneaud and Denaeyer-De Smet (1970) show the relation between branch diameter and bark mass proportion for common oak, which ranged from 13% (15–25-cm diameter) to 32% (1–7 cm). The average was 27% bark, clearly higher than in this study. Increasing the proportions of branch bark (+50%) and fine branches (+25%) in this study would lead to more similar levels of N compared to

data in Jacobsen et al. (2003), while the differences for P, Ca, K and Mg get smaller, although they are still notable (Appendix Table 12). For branches—maybe more than for stems—the mix of compartments has a large effect and so has the sampling of branch wood. When comparing concentrations in branches, it is not always clear what parts of branches have been taken as a sample. It may be a whole branch of which the size is not known or it may be some part of a branch. In some cases, foliage is included in branch biomass and concentrations (Erikson and Rosen, 1994).

We suggest additional measurements of the proportions of different compartments of branches and stems and for branch and foliage biomass expansion factors as well to improve the calculations. This type of information is not widely available, but is highly relevant for nutrient budget calculation.

The nutrient concentrations in wood cannot be explained by differences in soil properties at the investigated sites. As we showed, there is no clear difference in concentrations between poor or moderately poor sandy soils. However, soils of all sampled sites all had low base saturations, mostly < 10%. In that aspect, they can all be categorised as poor on base cations, although at the moderate poor sites input from weathering will be larger. Bijlsma et al. (2020) found in Dutch forests clearly higher base cation levels in common oak stems on (rich) clay soils, compared to sandy soils.

4.2 Nutrient concentrations and the impacts of atmospheric deposition

4.2.1 Comparison of nutrient concentrations with literature data

Compared to the concentrations from Japanese larch, Norway spruce, Douglas fir and Scots pine in eight stands in the Netherlands by Kofman (1983), N concentration in this study is indeed mostly higher and they tend to be lower for P, Ca, K and Mg, even though tree samples by Kofman (1983) were relatively young: mostly < 50 years and *DBH* < 20 cm. Similarly, the comparison with data published by Jacobsen et al. (2003), based on measurements between 1958 and 2002, except for the N concentration in branch wood (Tables 3). In stems, the N concentrations in our study appear 25–52% higher. Concentrations of P, Ca and K are 5–82% lower, except for Ca in Norway spruce (Table 2), with differences being larger for conifers than for broadleaves. For Mg, however, concentrations are lower in four tree species and higher in three tree species (Table 2). Comparison with international data from De Vries et al. (1990) shows similar results. Comparison of stem bark nutrient concentrations with Jacobsen et al. (2003) shows smaller differences in N concentrations and mostly lower concentrations of P,

Ca, K and Mg in this study (Appendix Table 13) as well. For stem wood (under bark), N concentrations are clearly higher, while P, Ca, K and Mg are lower in this study (Appendix Table 14). The differences in N concentrations are even larger than in total stems. Remarkable are the higher concentrations in stem wood for P in Scots pine and Mg in Norway spruce and Douglas fir in this study (Appendix Table 14). In branches, the concentrations of P, Ca and K and to a lesser extent of Mg are also lower than those reported in Jacobsen et al. (2003), but surprisingly N concentrations are mostly up to 39% lower too (except for Douglas fir, Table 3).

For sapwood and heartwood, Jacobsen et al. (2003) does not provide data, and individual references are not abundant. Comparing with averaged data provided by Duvigneaud and Denaeyer-De Smet (1968), Duvigneaud and Denaeyer-De Smet (1970) (South of Belgium) and Mussche et al. (1998) (West of Belgium) and Lévy et al. (1996) (North of France) however show the same pattern of higher average N concentrations and lower average concentrations of P, Ca, K and Mg in this study, compared to references (Appendix Table 15). Some of the references have lower P or base cation concentrations compared with this paper, and some have almost as high N concentrations. Nutrient concentration data in these references originating from Belgium, however, may have also been affected by high N deposition, in particular the data by Mussche et al. (1998) in the West of Belgium. Sampling years may also be a factor affecting the differences.

When comparing with data provided by Wright and Will (1957) and Häsänen and Huttunen (1989) for sapwood and heartwood of Scots pine, we see on average higher N concentrations and lower concentrations of P, Ca and Mg in this study and for K only in sapwood. Penninck et al. (2001) noted similar differences when comparing oak heartwood nutrient concentrations from acidic soils from the Netherlands and the central Belgium with richer soils in France.

Part of the differences for stem wood may be related to differences in factors such as stand age, since the sources in Jacobsen et al. (2003) provide data on a mixture of younger to older stands. Nutrient concentrations tend to decrease as stands grow older (Jacobsen et al., 2003; Augusto et al., 2000; Augusto et al. 2008), what can partly be related to the mix of compartments evolving with age. However, this aspect does not explain the large differences with reported literature values and the most plausible explanation is the impact of elevated atmospheric deposition of nitrogen, reflected in higher N contents and lower P, Ca, Mg and K contents in view of ongoing soil acidification. The impact on P availability is in line with Prietzel et al. (2020) who found a generally low P

status of Scots pine needles in Germany. Lower nutrient concentrations of P, Ca, Mg and K may be influenced by increased growth due to increased N availability, causing a dilution in P, Ca, Mg and K contents, combined with ongoing soil acidification. Despite the low availability of P, Ca, Mg and K, the average increment of forests in the Netherlands appear to slightly higher (in order of magnitude 15%) compared to that of most other countries in Europe (Forest Europe, 2015). Apparently, the limited availability is not reflected in growth but in dilution of nutrient contents in stem wood and heartwood.

4.2.2 Atmospheric deposition most likely affects nutrient concentrations

A long-term monitoring at fixed locations is needed in order to assess unequivocally the impact of elevated N and acid deposition on nutrient concentrations in forest compartments. The ICP level II forest sites is such a monitoring network, but unfortunately, this only includes the assessment of nutrient contents in foliage and not in stems and branches. This monitoring network indicates clear changes in N, P and base cations in foliage response to deposition changes (e.g. Schmitz et al., 2019; Du et al., 2021). Circumstantial evidence for those changes may however be obtained from a comparison with nutrient concentrations in stems and branches of Dutch forests measured in the past (Kofman, 1983) and in other countries (Jacobsen et al., 2003), both experiencing lower N and acid input levels.

Our hypothesis that current nutrient concentrations would differ from those found in the past in the Netherlands and in other countries, experiencing lower N deposition levels, was clearly confirmed in this study. The results are in line with literature, showing that multiple decades with high N deposition, leading to N enrichment of the soil, may cause higher N contents in woody tissues (Balster et al., 2009; Saurera et al. 2004) and to soil acidification causing lower P, Ca, K and Mg depletion of the soil (De Vries et al. 2019), which may lead to lower contents in woody tissues (Bondietti et al., 1989). The results underline the importance of using region-specific and up-to-date nutrient concentrations. Using data from literature or from past measurements may lead to over or underestimation of sustainable harvest levels at least for The Netherlands. It may have resulted in mostly unneeded restrictions of wood harvest as the concentrations of Ca, K, Mg and P tend to be higher in literature compared to the data in this study.

4.3 Implications of changes in carbon to nitrogen stoichiometry on forest carbon sequestration

The carbon to nitrogen ratio in woody compartments is an important indicator that is used in so-called

stoichiometric scaling approaches in models that assess global scale impacts of N deposition on forest carbon sequestration. Considering that carbon presents 50% of the wood biomass, the C/N ratio can be derived from the measured N concentrations. The stoichiometric scaling approach is based on the assumption that C to N ratios in forest biomass and soils are constant. The C–N response ratio, defined as the additional mass unit of sequestered C per additional mass unit of N deposition, is calculated by multiplying: (i) the fraction of external N inputs that is retained in the forest ecosystem with (ii) the fraction of retained N allocated to different forest compartments (woody biomass, non-woody biomass, and soil), and (iii) the C to N ratio of each compartment (De Vries et al., 2014; Du and de Vries, 2018). A fixed C to N ratio is sometimes not assumed, in the so-called flexible stoichiometric approaches, since N deposition is known to affect foliar N concentrations and thus the C/N ratios in foliage. However, in those approaches, the effect on woody C/N ratios is generally not included, also since information on impacts is lacking.

This study however shows that N concentrations in stems were app. 25–50% higher than those published in literature overviews. Considering that the average N contents in broadleaves varied from 2.1 to 3.0 g kg⁻¹, this implies C/N ratios ranging from 170 to 240, while is normally near 1.5 to 2.1 g kg⁻¹, being C/N ratios ranging from 240 to 330. Similarly, the average N contents in coniferous trees are all near 1.6 g kg⁻¹ (C/N ratios near 300), while is normally ranging from 1.0 to 1.2 g kg⁻¹, implying C/N ratios ranging from 400 to 500). So a tree can apparently adjust its C/N content in wood in regions with prolonged high N input due to luxury consumption. The Netherlands encountered more than 40 years of elevated N deposition, on average near 40–50 kg N ha⁻¹ year⁻¹ around 1980 to near 25 kg N ha⁻¹ year⁻¹ at present, dominated by ammonia deposition (Van Pul et al., 2018). This effect in regions with prolonged high N input is in line with other approaches such as the assessment of growth responses to experimental N addition and field N gradient studies, showing that there is a flattening of the growth response to a plateau near 15–30 kg N ha⁻¹ year⁻¹ and a reversal above that level (De Vries et al., 2014). This effect is mainly due to soil acidification, implying reduced P, Ca, K and Mg availability, which is also reflected in the P, Ca, K and Mg concentrations in this study, which were app. 5–80% lower than those published in literature overviews (Jacobsen et al., 2003).

This effect should preferably be included in global scale carbon sequestration models even though it is likely only relevant in small parts of the world, since about 90% of

the global forests receive an N deposition below 15 kg N ha⁻¹ year⁻¹ (Schwede et al., 2018), likely implying a constant C/N ratio for most forest. This is in line with a comparison of model predicted and measured site-averaged ($n = 22$) ecosystem carbon (C) changes resulting from nitrogen (N) fertilization, showing the best comparisons when using a flexible C/N ration in leaves and roots, linked to NPP, but a constant ratio for the woody parts, linked to NEP (Meyerholt and Zaehle, 2015).

4.4 Nutrient removal and the impacts of management measures

In this study, we presented the nutrient removal for the considered tree species, i.e. Scots pine, Douglas fir, Norway spruce, Japanese larch, common oak, beech and silver birch, considering both whole-tree harvesting and stem wood removal only, by using the average growth rates of these tree species on relatively nutrient poor sandy soils in the Netherland. N removals through harvest of 5–11 kg N ha⁻¹ year⁻¹ are relatively small compared to N deposition, which is typically over 1700 mol or 24 kg ha⁻¹ year⁻¹ (Hoogerbrugge et al. 2019). For S, deposition has decreased from 80 kg ha⁻¹ year⁻¹ in the 1980s to app. 15 kg ha⁻¹ year⁻¹ currently, which is still clearly larger compared to potential removals of 0.3–0.7 kg ha⁻¹ year⁻¹ through harvest. Removals of P range from 0.18 to 0.35 kg ha⁻¹ year⁻¹ for stem harvest up to 0.51 kg ha⁻¹ year⁻¹ when including harvest of branches at median growth levels. This exceeds the P inputs of app. 0.25 kg ha⁻¹ year⁻¹ (De Vries et al., 2021). For the base cations, at median growth levels, removals are lower than the inputs of weathering and deposition. Removals of K (being 1.2–3.7 kg ha⁻¹ year⁻¹) in most cases are lower but in some cases (namely whole-tree harvest of Douglas fir, Norway spruce and beech) approach the inputs of weathering and deposition of app. 4 kg ha⁻¹ year⁻¹ (De Vries et al., 2021). The removals of Ca (1.3–7.4 kg ha⁻¹ year⁻¹) are lower than inputs (9 kg ha⁻¹ year⁻¹, De Vries et al., 2021) and removals of Mg (0.32–1.07 kg ha⁻¹ year⁻¹) are strongly lower than inputs (6 kg ha⁻¹ year⁻¹, De Vries et al., 2021). However, taking into account leaching, outputs of K and Ca may exceed inputs, in particular of common oak, Beech and Norway spruce.

We found that the harvest of logging residues at final felling increased nutrient removals with 20% (Ca for Scots pine) to 128% (P for Norway spruce) for coniferous species. This is in the low range of the findings of Raulund-Rasmussen et al. (2008), who noted that the nutrient removal may vary considerably depending on growth model, biomass equations and nutrient concentrations in different tree compartments. For broad-leaved species, the additional removals were only 10%

(Ca for common oak) to 25% (P for silver birch) higher, due to relative high-nutrient contents in stems, and no removal by foliage. Besides, less than half of the stem volume (42%) for broadleaved species beech and common oak is harvested at final felling with branches, meaning that a large part of branch biomass over one rotation remains in the stand at thinnings. For the coniferous species on the other hand, app. 50–55% of the stem wood volume is harvested at final fellings. For common oak and beech, the applied biomass expansion factors for branch wood (0.16) are lower than data by Baritz and Strich (2000), who give a biomass expansion factors for branch wood of broadleaved species of 0.24. Duvigneaud and Denaeyer-De Smet (1970) and André et al. (2010) give biomass expansion factors up to 0.30 for branches < 7 cm. We thus may have used too low biomass expansion factors for these species, and the effect of whole-tree harvest compared to stem only harvest may be larger. The biomass expansion factor for coniferous species given by Baritz and Strich (2000), however, is 0.14, which is lower compared to those used in this study (0.16–0.20).

Removals averaged over one rotation are in line with removals given by Raulund-Rasmussen et al. (2008) for Norway Spruce and Scots pine and with Palviainen and Finér (2012) for Norway spruce, Scots pine and silver birch. Nitrogen removals through stem only harvest reported by Raulund-Rasmussen et al. (2008) e.g. are up to 10 kg ha⁻¹year⁻¹, similar to our results. But they are based on different average biomass removals. When correcting for total biomass removal for Norway spruce to match Raulund-Rasmussen et al. (2008), we see mostly higher N removals and lower Ca, Mg—even more notable—P removals in this study as compared to Raulund-Rasmussen et al. (2008) (excluding the data for the Rääkkylä site which are very low for all nutrients). Removals of K, based on the data in this study, were higher for Scots pine and lower for Norway spruce. Correcting for total biomass removal rates is however not straight forward as differences in rotation length affect tree compartment proportions (André et al. 2010) and thus average stem nutrient concentrations and average branch biomass removals.

Forest managers have several options to mitigate the effects of nutrient removal through harvest. Addition of nutrients (fertilisation) is an obvious way to mitigate the effects of nutrient removals through wood harvest. Fertilisation was common practice in the late nineteenth and first half of the twentieth century, but nowadays, it is hardly practised anywhere in Dutch forests. The use

of slow release base cation fertilisers (rock powder) is now evaluated, to avoid any unwanted effects on pH, accelerated mineralisation of organic matter and loss through leaching (De Vries et al., 2019). The costs for this type of nutrient additions are relatively high and is only advised at sensitive sites with vitality issues.

Leaving branches in the forest for 6 months before removal will retain part of the nutrients in the forest. This may be effective for K, which may leach for 40–80% from needles and 30–40% from branches (Palviainen et al., 2004). However, P, Ca and Mg hardly leach from needles or branches in that time span (Palviainen et al., 2004; Staaf and Berg, 1982), but depending on species, 24–42% (Lehtikangas, 1991) of the needles may fall off in 4 months. From the perspective of logistic and forest road maintenance, this option is not preferred. Limiting the harvest of branch wood is still suggested as the favourable way to avoid depletion of P and base cations on nutrient poor sites.

5 Conclusions

Nutrient concentrations in tree wood of forests in the Netherlands are different from those in other countries. Concentrations of P, Ca and K are 5–82% lower, except for Ca in pine, with differences being larger for conifers than for broadleaves, while N concentrations in stems are app. 25–52% higher. This demonstrates the importance of using region-specific nutrient concentrations for wood in the Netherlands, where decades of high nitrogen and acidic deposition in the Netherlands may not only have affected nutrient concentrations in foliage but also in stems and branches. The estimated median removal of P in stems and branches exceeded the estimated input by deposition and weathering. In contrast, the median removals of base cations did not exceed these estimated inputs, but in case of K approached them. When considering higher than median harvest levels and leaching losses, the depletion of K and Ca may occur and should be taken into account when whole-tree harvest is considered.

Considering that the average growth of forests in the Netherlands is comparable, or even slightly higher, than in most other countries in Europe, limited P, Ca, K and Mg availability is not reflected in growth but in reduced contents of these nutrients in stem wood and heartwood. Apparently, trees can adapt to nutrient poor circumstances by changes in the stoichiometry of nutrients in woody compartments.

Appendix

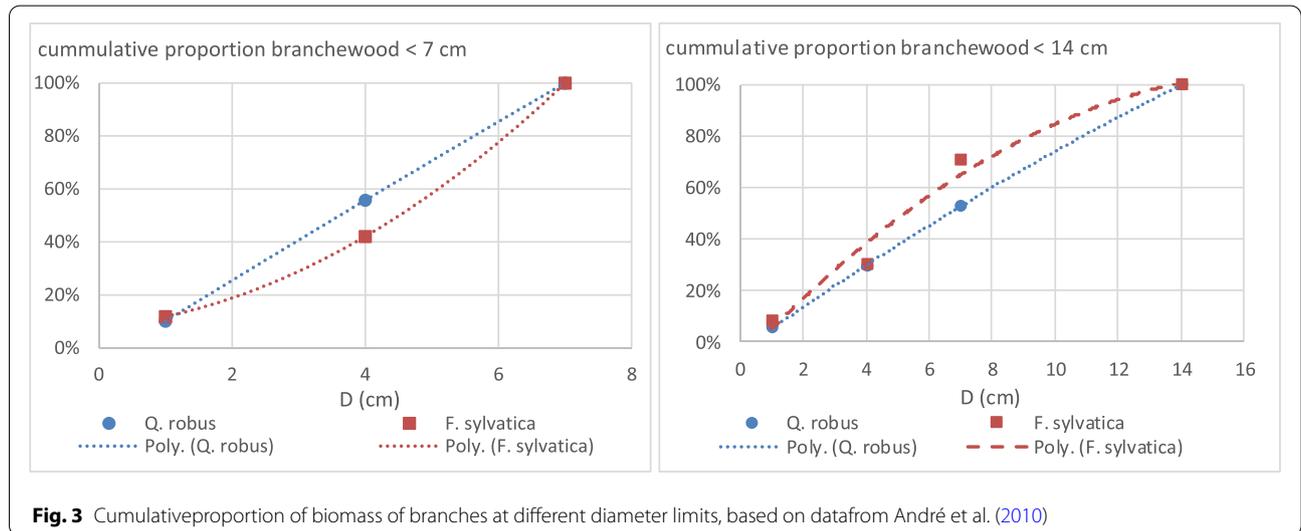


Fig. 3 Cumulative proportion of biomass of branches at different diameter limits, based on data from André et al. (2010)

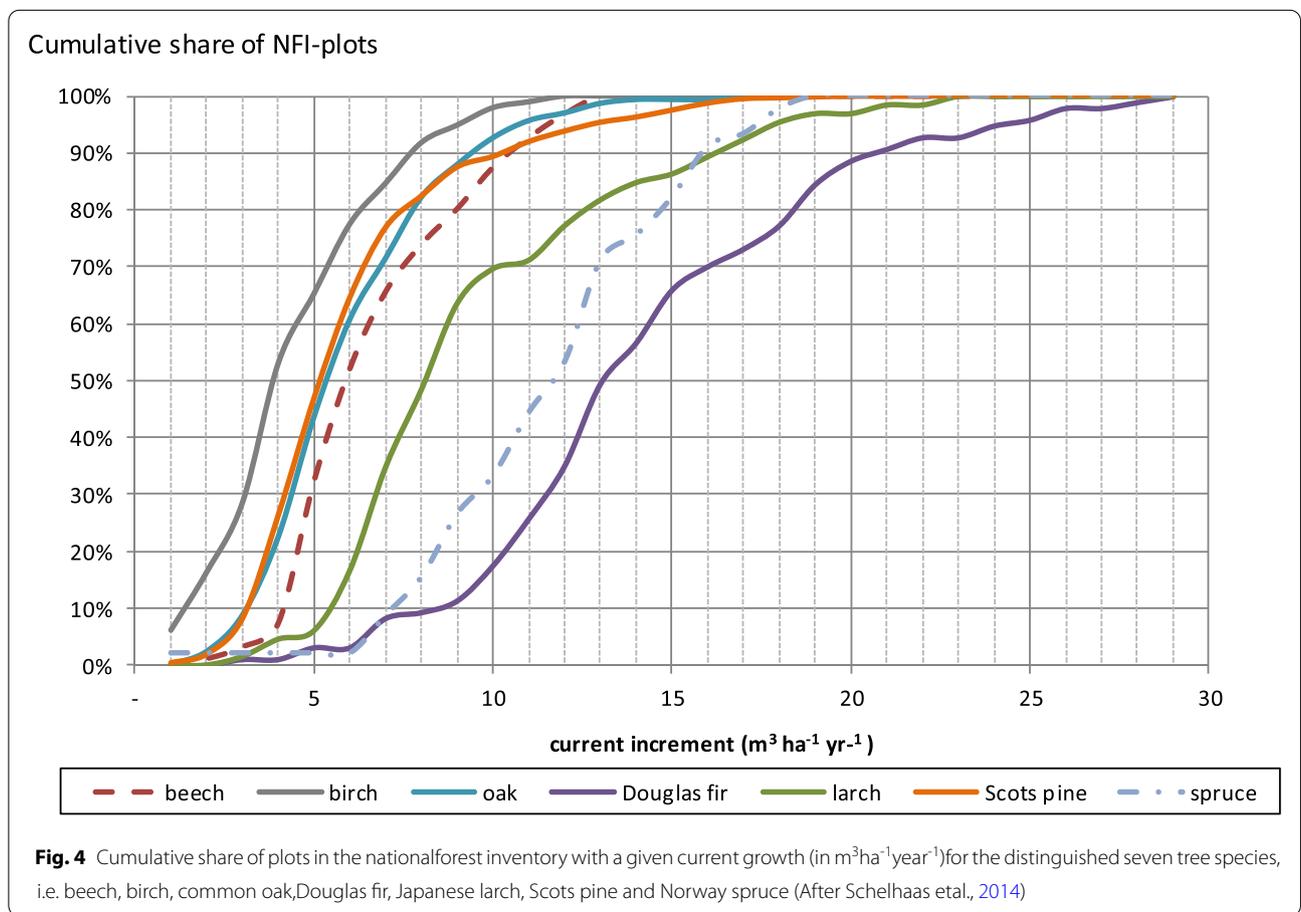


Fig. 4 Cumulative share of plots in the national forest inventory with a given current growth (in $m^3 ha^{-1} yr^{-1}$) for the distinguished seven tree species, i.e. beech, birch, common oak, Douglas fir, Japanese larch, Scots pine and Norway spruce (After Schelhaas et al., 2014)

Table 5 Nutrient concentrations in foliage (mean and standard error, SE) for ever green species

Tree species	n	N		P		Ca		K		Mg	
		g kg ⁻¹	SE								
Spruce	366	18.65	0.28	1.40	0.02	3.36	0.11	5.85	0.10	0.91	0.02
Pine	1706	19.70	0.14	1.35	0.01	2.17	0.02	6.30	0.04	0.74	0.01
Fir	755	20.45	0.23	1.10	0.01	3.53	0.07	6.41	0.08	1.35	0.02

Table 6 Properties of wood based on wood-database.com, Miles et al. (2009) and Dietz (1975). For Norway spruce, the VOID value was based on European ash (*Fraxinus excelsior* L.) and sessile oak (*Q. petraea* matt)

Tree species	Density(kg dry matter/m ³ dry volume)		VOID (%)
	sapwood and heartwood	Bark	
Larch	538	342	27%
Spruce	405	391	15%
Fir	510	375	27%
Pine	550	352	27%
Birch	640	562	23%
Beech	710	625	5%
Oak	675	480	25%

Table 7 Regression coefficients in the correlation of bark thickness (B_{th}) and of diameter of heartwood (D_h) with diameter of stem wood including bark (D_{ob}), according to Eqs. (3) and (4). Note that heartwood is not distinguished for Norway spruce and beech. For silver birch, insufficient measurements of bark thickness were available

Tree species	Bark thickness (-)				Heartwood diameter (-)			
	a	b	R ²	n	c	d	R ²	n
Larch	0.045	0.010	0.75	60	0.86	-2.82	R ² = 0.99	39
Spruce	0.024	-0.085	0.77	67				
Fir	0.049	-0.093	0.81	111	0.69	-3.02	R ² = 0.89	132
Pine	0.046	-0.15	0.53	156	0.46	-1.76	R ² = 0.57	140
Beech	0.011	0.14	0.77	62				
Oak	0.055	0.060	0.87	64	0.81	-2.95	R ² = 0.99	35

Table 8 Parameters for the taper function according to Eq. (7) (Fonweban et al., 2011)

Tree species	Parameters			
	a0	a1	a2	a3
Pine, oak, beech	0.8120	0.6257	2.5258	-5.5031
Fir, spruce, larch	0.7906	0.2954	3.5997	-11.7161

Table 9 Volume (including bark VOID) and mass proportions (%) per compartment for sapwood, heartwood and bark for seven tree species. Note that sapwood and heartwood are not distinguished for Norway spruce, birch and beech

Tree species	Volume proportion (%)			Mass proportion (%)		
	Sapwood	Heartwood	Bark	Sapwood	Heartwood	Bark
Larch	36	47	17	40	51	9
Spruce			11			9
Fir	55	28	17	59	31	10
Pine	76	11	14	81	12	7
Birch			13			9
Beech			6			5
Oak	35	46	19	38	49	13

Table 10 Volume and mass proportions (%) of bark in coarse branch wood of seven tree species

Tree species	Bark volume	Bark mass
Larch	15%	8%
Spruce	11%	9%
Fir	15%	9%
Pine	8%	4%
Birch	10%	7%
Beech	12%	10%
Oak	19%	13%

Table 11 Mass proportions for fine branch wood of total branch wood per tree species using the diameter limit for fine branches given in the source, and estimated proportion using a 2-cm limit. Twig refers to leave carrying parts of branches

Source	Tree species	Diameter limit fine branches (cm) in source	proportion fine branches of total branches (%) according to source	Estimated proportion (%) of fine branches at 2 cm diameter limit based on source
André et al. (2010)	<i>Q. robur</i>	< 1	5–10	14–26
André et al. (2010)	<i>F. sylvatica</i>	< 1	8–12	17–29
Boer (2020)	<i>P. sylvestris</i>	< 2	43	43
Boer (2020)	<i>P. menziesii</i>	< 2	34	34
Genet et al. (2011)	<i>F. sylvatica</i>	< 4	22–44	11–22
Christophe et al. (2017)	<i>F. sylvatica (young)</i>	< 4	49–68	25–34
Husmann et al. (2018)	<i>Q. robur and Q. petraea</i>	< 1	20	40
Husmann et al. (2018)	<i>F. sylvatica</i>	< 1	15	30
Grote (2002)	<i>F. sylvatica (rel. young stand)</i>	“twig”	35	> 35
Grote (2002)	<i>P. abies</i>	“twig”	26	> 26
Svoboda et al. (2006)	<i>P. abies</i>	< 0.5	14–21	> 40

Table 12 Average nutrient concentrations (g kg^{-1}) in branches, assuming larger proportions of fine branch wood ($\times 1.25$) and bark in coarse branch wood ($\times 1.5$), according to this paper and Jacobsen et al. (2003) and relative difference (%) between both datasets (% difference = (this paper/Jacobsen et al. - 1) $\times 100\%$)

Tree species	Nutrient concentrations (g kg^{-1})				
	N	P	Ca	K	Mg
Jacobsen et al. (2003)					
Larch	6.19	0.71	n.a.	2.49	2.71
Spruce	5.24	0.65	n.a.	3.33	2.39
Fir	2.98	0.43	n.a.	4.22	1.65
Pine	3.61	0.34	n.a.	2.07	1.67
Birch	5.40	0.62	n.a.	4.60	2.00
Beech	4.27	0.48	n.a.	4.02	1.50
Oak	6.19	0.43	n.a.	4.41	2.00
This paper and difference this paper vs. Jacobsen et al. (2003)					
Larch	4.32 (-30%)	0.313 (-56%)	2.02 (-19%)	1.51 (-44%)	0.475 (-28%)
Spruce	4.67 (-11%)	0.336 (-48%)	3.24 (-3%)	1.48 (-38%)	0.541 (+2%)
Fir	3.36 (+13%)	0.234 (-46%)	2.35 (-44%)	1.30 (-21%)	0.422 (+3%)
Pine	3.76 (+4%)	0.220 (-35%)	1.73 (-16%)	1.33 (-20%)	0.415 (-43%)
Birch	4.82 (-11%)	0.296 (-52%)	2.02 (-56%)	1.16 (-42%)	0.478 (-4%)
Beech	4.14 (-3%)	0.282 (-41%)	2.20 (-45%)	1.26 (-16%)	0.357 (-1%)
Oak	5.83 (-6%)	0.301 (-30%)	2.66 (-40%)	1.67 (-15%)	0.549 (+25%)

Table 13 Average nutrient concentrations in stem bark (g kg^{-1}) according to Jacobsen et al. (2003), and relative difference (%) with dataset in this paper (see Table 1 for data; difference (%) = this paper/Jacobsen et al. - 1) $\times 100\%$). Silver birch is not given in Jacobsen et al., 2003

Tree species	Nutrient concentrations (g kg^{-1})				
	N	P	Ca	K	Mg
Jacobsen et al. (2003)					
Larch	4.32	0.45	2.50	1.36	0.68
Spruce	5.17	0.65	8.17	2.83	0.77
Fir	3.58	0.66	2.94	3.83	0.46
Pine	3.85	0.46	5.03	2.08	0.61
Beech	7.35	0.50	20.52	2.34	0.59
Oak	5.16	0.30	21.49	2.00	0.65
Difference this paper vs. Jacobsen et al. (2003)					
Larch	7%	-42%	-22%	11%	-40%
Spruce	8%	-39%	14%	-19%	8%
Fir	1%	-74%	-45%	-75%	-45%
Pine	18%	-76%	-49%	-71%	-75%
Beech	15%	-23%	-35%	-15%	-7%
Oak	45%	-28%	-48%	-25%	19%

Table 14 Average nutrient concentrations in stem wood (without bark, g kg⁻¹) according to Jacobsen et al. (2003) and this paper and relative difference (%) between both datasets (difference (%) = this paper/Jacobsen et al. - 1) x 100%). Silver birch is not given in Jacobsen et al. (2003). Japanese larch, Douglas firs, Scots pine and common oak are calculated from mass proportions of sapwood and heartwood

Species	Nutrient concentrations (g kg ⁻¹)					
	N	P	S	Ca	K	Mg
Jacobsen et al. (2003)						
Larch	0,61	0,11	n.a.	0,50	0,39	0,21
Spruce	0,83	0,06	n.a.	0,70	0,46	0,11
Fir	0,60	0,06	n.a.	0,36	0,43	0,06
Pine	0,76	0,05	n.a.	0,62	0,42	0,18
Beech	1,21	0,10	n.a.	0,95	0,93	0,25
Oak	1,56	0,08	n.a.	0,46	0,95	0,09
This paper and difference this paper vs. Jacobsen et al. (2003)						
Larch	1.31 (+115%)	0.0375 (-66%)	n.a.	0.257 (-49%)	0.278 (-29%)	0.069 (-67%)
Spruce	1.29 (+56%)	0.0313 (-48%)	n.a.	0.744 (+6%)	0.453 (-1%)	0.140 (+27%)
Fir	1.31 (+118%)	0.0421 (-30%)	n.a.	0.298 (-17%)	0.444 (+3%)	0.0776 (+29%)
Pine	1.39 (+83%)	0.0659 (+32%)	n.a.	0.638 (+3%)	0.462 (+10%)	0.163 (-10%)
Beech	1.98 (+64%)	0.0871 (-13%)	n.a.	0.747 (-21%)	0.929 (0%)	0.250 (0%)
Oak	2.33 (+50%)	0.0703 (-12%)	n.a.	0.383 (-17%)	0.772 (-19%)	0.0835 (-7%)

Table 15 Average nutrient concentrations in sapwood and heartwood (g kg⁻¹) for common oak according to references and relative difference (%) with this paper (difference (%) = this paper/average references - 1) x 100%

Sapwood					Heartwood					Reference
N	P	Ca	K	Mg	N	P	Ca	K	Mg	
Nutrient concentrations (g kg ⁻¹)										
2.50	0.20	0.60	2.20	0.30	1.20	0.02	0.40	0.60	0.03	Duvigneaud and Denaeyer-De Smet, 1968
2.15	0.16	1.25	1.75	0.60	1.45	0.03	0.95	0.90	0.17	Duvigneaud and Denaeyer-De Smet, 1970
1.80	0.33	0.53	1.75	0.19	1.10	0.05	0.40	0.65	0.04	Lévy G., Bréchet, and Becker, 1996
2.15	0.12	0.48	1.20	0.19	1.20	0.15	0.24	0.30	0.08	Mussche et al. 1998
2.09	0.21	0.72	1.69	0.37	1.25	0.06	0.49	0.59	0.04	Average, references
2.9	0.13	0.49	1.27	0.15	1.9	0.022	0.30	0.40	0.031	Average, this paper
36%	-36%	-32%	-25%	-59%	55%	-64%	-38%	-33%	-22%	Difference, %;

Acknowledgements

We thank Borgman Forestry Consultants for the sampling and providing locations for sampling in the winter of 2016–2017, and Staatsbosbeheer, the Dutch State Forest Service (SFS), for providing sampling locations for the winter of 2017–2018. We greatly appreciate the SFS, VBNE, Het Loo Royal Estate, Borgman Forestry Consultants, Bosgroepen (Dutch Forestry Groups), Central Government Real Estate Agency, Landschappen NL, Estate Twickel, Natuurmonumenten and Forestry Contractor Association (AVIH) for their comments and suggestion on the approach of this research.

Code availability

Not applicable.

Authors' contributions

Conceptualization: Anjo de Jong, Wim de Vries, and Hans Kros. Methodology: Anjo de Jong, Wim de Vries, and Hans Kros. Formal analysis and investigation: Anjo de Jong. Writing—original draft preparation: Anjo de Jong and Wim de Vries. Writing—review and editing: Wim de Vries, Hans Kros, and Joop Spijker. Funding acquisition: Joop Spijker. Supervision:

Joop Spijker and Wim de Vries. The authors read and approved the final manuscript.

Funding

This study was funded by the Dutch Ministry of Agriculture, Nature and Food Quality through the Wageningen University Knowledge Base program: Biodiversity in a Nature Inclusive Society (KB-36-003-019) and the Dutch Forest and Nature reserve owners' association (VBNE).

Availability of data and materials

The datasets generated during and/or analysed during the current study are available in the repository <https://doi.org/10.4121/19705156>.

Declarations

Ethics approval and consent to participate

The authors declare integrity of the research and compliance to the rules of good scientific practice.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no competing interests. The funders had no role in the design of the study; in the collection, analyses or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Received: 5 January 2022 Accepted: 10 June 2022

Published online: 22 July 2022

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