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Nutritional constraints on forest harvesting intensities in mountainous beech (*Fagus sylvatica* L.) stands on shallow calcareous soils

Ernährungsbedingte Restriktionen verschiedener Waldnutzungsintensitäten in montanen Buchenbeständen (*Fagus sylvatica* L.) auf seichtgründigen Böden auf Kalk

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Schlüsselbegriffe: Bodenfruchtbarkeit, Holzernte, Nährstoffbilanz, Ernterücklass, Kalkalpen, Waldernährung

Abstract

In the Limestone Alps, shallow soils with limited nutrient pools are common on pure limestone or dolomite, where available nutrients for vegetation growth are often restricted to the organic soil layers. Thus, loss of nutrients via forest harvest can have detrimental effects on nutritional status and productivity of the regenerating forest. To assess the risk of nutrient loss by clear cut with different harvest intensities, we compared carbon and macro nutrient stocks in the biomass and soils of twelve old mountain forest stands dominated by European beech along a fertility gradient. At

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the lower end of the fertility gradient our foliage data indicate a surplus nutrition of N, Ca and Mg, but poor nutrition of S and P and very critical values at or near the deficiency range for K. Whole tree biomass was strongly related to mineral soil stocks of exchangeable K and total P, indicating that these nutrients are key limiting factors for tree growth in this mountain forest. The percentual ratio of simulated nutrients removed via harvest to the total stock of remaining biomass on site and soil pools was consistent across the fertility gradient, except for P, because with increasing fertility a greater proportion of carbon and nutrients is stored in the above ground biomass. Mean values of K declined from 71 % (whole tree harvest during summer including foliage) to 68 % (whole tree harvest during winter excluding foliage) to 50 % (harvest of stem with bark), and to 44 % (harvest of stem without bark). Values greater than 50 % are considered critical, as nutrient supply would not be sufficient for the next forest regeneration. We conclude that, in forests on shallow soils of the Limestone Alps, harvesting must be restricted to large-sized stem wood only and foliage and branches should remain on site to support the long-term sustainability of forest regeneration.

Zusammenfassung

In den Kalkalpen sind seichtgründige Böden mit begrenzten Nährstoffvorräten auf reinem Kalkstein oder Dolomit weit verbreitet, wo die für das Pflanzenwachstum verfügbaren Nährstoffe oft auf die organischen Bodenschichten beschränkt sind. Deshalb kann Nährstoffentzug durch die Holz- und Biomassenutzung negative Auswirkungen auf die Ernährungssituation und die Produktivität des nachwachsenden Waldes haben. Um das Risiko des Nährstoffverlustes durch Kahlschlag bei unterschiedlichen Intensitäten des Biomasseentzuges zu bewerten, verglichen wir in zwölf montanen Buchenaltbeständen die Vorräte des Kohlenstoffes und der Makronährstoffe in der Biomasse mit jenen im Boden entlang eines natürlichen Fruchtbarkeitsgradienten. Am unteren Ende des Fruchtbarkeitsgradienten wiesen Blattanalysen auf eine Überversorgung mit N, Ca und Mg, eine nicht ausreichende Versorgung mit S und P und auf sehr kritische K-Werte im Mangelbereich hin. Die Tatsache, dass die oberirdische Gesamtbiomasse mit den Mineralbodenvorräten an K (austauschbar) und P (gesamt) hoch signifikant korrelierte, deutet auf die Schlüsselfunktion dieser Elemente als limitierende Wachstumsfaktoren dieser Bergwälder hin. Das prozentuale Verhältnis der durch die simulierten Ernteintensitäten entnommen Nährstoffvorräte zu den Vorräten in der auf der Schlagfläche verbleibenden Biomassekompartimente und im Boden änderte sich entlang des Fruchtbarkeitsgradienten nicht (ausgenommen P), da mit zunehmender Bodenfruchtbarkeit ein größerer Anteil an Kohlenstoff und Nährstoffen in der oberirdischen Biomasse gespeichert wird. Die Mittelwerte für K sanken von 71 % (Vollbaumnutzung im Sommer einschließlich grüne Blattmasse) über 68 % (Vollbaumnutzung im Winter ohne grüne Blattmasse) und 50 % (Stammholznutzung mit Rinde) auf 44 % (Stammholznutzung ohne Rinde). Werte über 50 % sind kritisch zu beurteilen, da die Nährstoffversorgung für die nächste Waldgenera-

tion nicht ausreichen würde. Im Sinne einer nachhaltigen Forstwirtschaft folgern wir, dass die Nutzung dieser Bergwälder auf seichtgründigen Böden der Kalkalpen auf starkes Stammholz beschränkt werden muss, und Blatt- und Astmasse am Standort zu verleiben hat.

1 Introduction

Mountain ecosystems cover about one fifth of the earth's continental area, but their ecological and economic importance extends far beyond their boundaries (Beniston *et al*. 1997). Their soil organic carbon stocks are among the highest in terrestrial biomes (Djukic *et al*. 2010; Ward *et al*. 2014). Approximately 22 % of Austria's landscape is classified as *karst* (*i.e.*, where the parent material consists of limestone and dolomite), and these areas provide drinking water for 50 % of Austria's population (Kralik 2001; Kralik 2003). For example, the city of Vienna is almost entirely dependent on karst headwaters in the north-easternmost Alps (Dirnböck and Grabherr 2000), where forests play a key role in ensuring a sustained yield of high-quality drinking water (Vacik and Lexer 2001). Furthermore, due to the typically thin soil cover of karst ecosystems (Katzensteiner 2003), forests are especially important for reducing erosion and preventing site degradation in these regions.

In the Limestone Alps, shallow soils with only small pools of exchangeable nutrients are common on pure limestone or dolomite, and nutrient cycling is often restricted to the organic soil layers (forest floor and A-horizon) and the vegetation. Consequently, nutrient loss via harvest may cause detrimental effects on the nutritional and productivity status of regenerating forests (Katzensteiner 2003). Shallow soils developed on limestone or dolomite – classified as Rendzic Leptosols and Chromic Cambsiols - cover 10 % and 9 % of Austria´s forested area, respectively (Englisch and Reiter 2009). On these sites, whole tree harvesting is considered highly problematic due to the limited supply of potassium and phosphorus, respectively (Englisch and Reiter 2009).

Many studies focus on nutrient losses via biomass exports, in particular on the differences between whole tree and stem only harvesting (*e.g.*, Freedman et al. 1986; Glatzel 1990; Kimmins 1977; Malkonen 1976; White 1974). However, limited information is available for mountain forest stands on calcareous bedrock, especially for European beech (*Fagus sylvatica*). In an extensive review by Achat *et al*. (2015), of 749 cases relating nutrient removal via biomass harvesting to soil nutrient stocks, no studies were performed in the European Alps ("nutrient stock data set"; see figure S1 in Supplementary Information). The "environmental impact data set" of that review included 168 sites, of which 92 % were located in USA (29 %), Canada (14 %) and Europe (45 %). Most European sites were provided by an experimental network in Scandinavia, with no location in the Alps.

In one of the rare case studies from the Limestone Alps in Germany, nutrient supply in soil and above ground biomass of spruce forests confirmed the relationship between site specific nutrient supply, tree nutrition and productivity (Weis and Göttlein 2016). In addition, the investigations provided clear evidence that large amounts of nutrients – about 50 % of the critical elements nitrogen (N), phosphorus (P) and potassium (K) – are stored in branches, twigs and needles. This material is frequently harvested in addition to stem wood with bark due to the rising demand for fuel wood, which can have a deteriorating effect on site quality, especially on sites with humus over bedrock, very shallow soils, or soils with high gravel content.

The mass balance approach is widely used for assessing the nutrient sustainability of forest production (*e.g.*, Sverdrup *et al*. 2006; de Vries *et al*. 2021). Taking atmospheric deposition and weathering of the bedrock as nutrient sources, and biomass uptake (harvest) and soil solution leaching as sinks, the mass balance is calculated for each nutrient. Ahrends *et al*. (2022) includes one 1,000th of the plant-available nutrient stock in the soil as an additional input (buffer) in this balance. The system is sustainable when the long-term stock of nutrients in the soil is not consumed, implying that the average value of the deficit is zero. However, such data are often not available for specific forest sites.

Hence, a simplified yet robust method for assessing the nutrient sustainability of a site prior to considering restrictions on forest biomass use is to clearly document the initial situation. Meiwes *et al*. (2008) proposed as a first guideline to compare the nutrient stocks in the biomass of a mature stand to the total stocks in the soil and stand. Severe restrictions on biomass extraction are recommended if these ratios exceed 50 % for soil exchangeable calcium (Ca), magnesium (Mg) and K, 25 % for total P and 60 % for N. If data on nutritional biomass compartments are available, this widely applied approach (see review by Achat *et al*. 2015 and references therein) can be used to evaluate the risk of nutrient extraction by forest harvest, and to what extent this risk may be minimized, if foliage, branches, and bark are left on the site.

Considering these knowledge gaps and the expected sensitivity of karst forest ecosystems, this study compared nutrient stocks in the biomass of mature European beech forest stands to available nutrients in shallow soils along a natural fertility gradient (change from convex to concave topography) in the Limestone Alps of Austria. The mission of this paper was to develop forest harvest management guidelines based upon potential reduction of soil nutrient stocks due to biomass export with increasing simulated management intensities. We developed our mission into the following three research questions:

1) What are the limiting macro nutrients as indicated by tree and soil nutrition?
2) Is the soil fertility gradient reflected in above ground biomass production?
3) How do different harvest intensities affect the remaining soil elemental stocks along the fertility gradient?

2 Material and Methods

2.1 Study sites

The study was conducted in the Reichraminger Hintergebirge, a mountain range located in the Northern Austrian Limestone Alps (47°49'08" N, 14°23'34" E; WGS84), near the village of Molln. The forest stands are dominated by European beech (*Fagus sylvatica* L.), with an average stand age of 146 years in 2015. The site had southern exposition, with slopes ranging from 57 % to 70 % and an elevation between 1000 to 1100 m a.s.l. Average annual precipitation and air temperature are 1645 mm and 7.8°C (Kobler *et al*., 2015). Twelve pure beech stands (approx. 30 x 30 m each) were selected in three forested blocks (West, Middle, East; four stands per block), west of existing (regenerating) clearcuts (figure 1). Stand characteristics are summarized in table 1. Stem volume increased from West (311 m^3 ha^{-1}) over Middle (499 m^3 ha^{-1}) to East (631 m^3 ha^{-1}) along a natural fertility gradient spanning roughly 700 m horizontal distance. These blocks correspond to the fertility levels classified as "low" (convex topography, shallow and stony soils) "medium", and "high" (concave topography, less shallow and loamy soils), as described by Mayer *et al*. (2021). No pre-harvesting operations had been carried out on these steep mountain slopes, as confirmed by forest management and the absence of visible stumps.

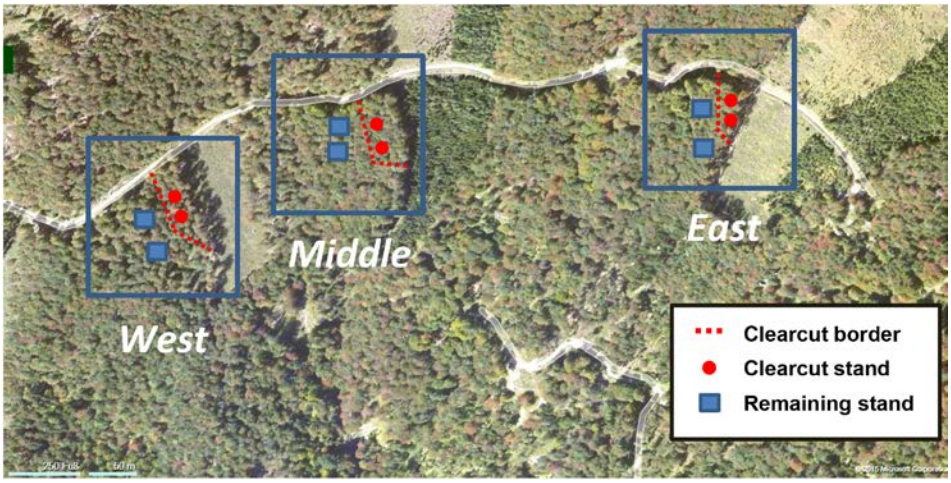


Figure 1: Map of the 12 beech forest stands assigned to the three blocks West, Middle and East along a soil fertility gradient. A forest inventory was done in 2015 before the eastern two stands of each block were cut, providing one tree with the median DBH per clearcut stand for analyzing biomass compartments. Source of the satellite image: Google Maps, 2015.

Abbildung 1: Karte der 12 Buchenwaldbestände, welche den drei Blöcken West, Mitte und Ost entlang eines Bodenfruchtbarkeitsgradienten zugeordnet wurden. Im Jahr 2015 wurde eine Waldinventur durchgeführt, bevor die zwei östlichen Bestände jedes Blockes geschlägert wurden. Der Buchenzentralbaum (medianer BHD) jedes kahlgeschlagenen Bestandes wurde für die Analyse der Biomassekompartimente herangezogen. Quelle des Satellitenbildes: Google Maps, 2015.

Soil types changed along this gradient from Rendzic Leptosol (humus type: moder; with O_i, O_e and O_a horizons above a thick mineral-organic A horizon, overlaying pure limestone and partly calcitic dolomite) to Chromic Cambisol (humus type: mull; only O_i and O_e horizons above a thin mineral-organic A horizon, gradually merging into a loamy B horizon formed by tertiary solution residues of calcareous bedrock, overlaying limestone; Kilian, 2015). The mean mineral soil depth was approximately 25 – 30 cm. The fine root fraction below 25 cm, derived from soil pits, was negligible (see Gorfer et al. 2021), indicating no arboreal nutrient uptake below that depth. The understory consisted of sparse layers of tree seedlings, grasses and herbs. Plant species such as *Carex alba*, *Helleborus niger*, and *Daphne laureola* characterize the low- and *Mercurialis perennis* and *Allium ursinum* the high fertility end of the west to east gradient.

2.2 Biomass inventory

In May 2015, diameter at breast height (DBH), tree height, and crown length were measured for all trees within a fixed-radius plot (8 or 10 m, depending on stand density) in each stand. Above ground stem wood mass per beech tree was calculated using the allometric equation by Wutzler *et al*. (2008):

$$\text{stem mass [kg]} = 0.0293 \times (\text{DBH [cm]}^2 \times \text{height [m]})^{0.974} \quad (1)$$

According to Wutzler *et al*. (2008), "stem" includes both stem wood and bark from the base to the top, excluding branches. The mean stem mass per circle, multiplied by the number of beech trees per m^2, yielded stem mass per m^2 (table 1). Stem volume (m^3 ha^{-1}) was derived from stem mass (including bark), assuming a wood density of 0.71 g cm^{-3} (Wagenführ and Wagenführ, 2022).

Mass of branches > 5 cm diameter per beech tree was calculated using the equation from Gschwantner and Schadauer (2006):

$$\text{branch mass [kg]} = e^{-9.0937+3.83316 \times \ln(\text{DBH [cm]}) + 0.56144 \times \ln(\text{crown ratio})} \times 1.38946 \quad (2)$$

The crown ratio was defined as crown length (m) divided by tree height (m). Mean branch mass per circle, multiplied by trees density, yielded branch mass (> 5 cm) per m^2 (table 1).

At the end of August 2015, the eastern part of each block (two stands per block) was clear-cut, and timber was extracted uphill by cable yarder to the forest road (see figure 1). Since only the stem with bark was harvested, most branches were kept on site. However, within each fixed-area plot, the beech tree with the median basal area was selected and felled as a whole tree – including all branches and green foliage – and extracted to the forest road for further analysis. This median basal area tree, considered the most representative for upscaling biomass data, was processed at the forest road as follows: Two cross-sectional disks including the bark were cut from the stem – one at breast height (DBH) and one at the base of the canopy. Two representative branches were cut sharp at the stem and subdivided into three diameter classes: > 5 cm, 2-5 cm, and < 2 cm. The fresh weight of each fraction per branch was measured with a hanging scale and a representative subsample of each fraction was taken to the laboratory. Finally, fresh beech leaves were collected from each branch for further analysis.

In the laboratory, all biomass samples were dried at 105°C (all values reported in this paper refer to dry weight, using conversion factors derived from fresh/dry subsamples). The bark was stripped from the stem disks, and the average bark fraction across all stands was estimated as 7.188 % of stem mass, based on all 12 stem disks (2 stands x 3 blocks x 2 disks at DBH and canopy base per median tree). For chemi-

cal analyses, representative stem wood samples were produced with a drill, while all other biomass samples were ground with a mill. Total contents (mg g^{-1}) of carbon (C) and nitrogen (N) were measured with a TruSpec CN analyzer (LECO Corp., St. Joseph, MI, USA) according to the ÖNORM L 1080. Sulfur (S), P, Ca, Mg and K were measured as total contents after microwave digestion with HNO_3 (ÖNORM L 1085) using inductively coupled plasma optical emission spectrometry (ICP-OES, Optima 8300, Perkin Elmer, Waltham, MA, USA).

For each selected beech tree in two stands per block, two samples were chemically analyzed, yielding four replicates per biomass compartment per block, except for bark, where only one pooled sample per tree (from both stem disks) was collected. Branches were not separated into wood and bark.

The mean (two branches per selected tree) dry mass ratios (branches 2-5 cm)/(branches > 5 cm) and (branches < 2 cm)/(branches > 5 cm) were calculated per tree and multiplied by the estimated mass of branches > 5 cm (g m^{-2}) to estimate the area related mass of smaller branch compartments per stand. For the remaining two stands per block, we used the mean ratios from the two adjacent cut stands in the same block.

Autumnal litterfall was collected five times from 25th of Aug. to 26th of Nov. 2015 using two to three litter traps per remaining stand (52 cm diameter), dried (105°C), and weighed. Total litterfall per trap was summed and converted to g m^{-2} $year^{-1}$ for each stand. For the two cut stands per block, we used the mean annual litterfall flux of the two adjacent remaining stands within the same block. The dry mass of fresh foliage in 2015 was estimated by multiplying the annual litterfall flux by a factor of 1.43, assuming that leaf dry mass in litter decreases on average to 70 % of its original value (Ostman and Weaver 1982).

Finally, carbon and nutrient stocks for above ground beech biomass compartments (foliage; branches with bark < 2 cm, 2-5 cm and > 5 cm diameter; bark of the stem and stem wood) were calculated by multiplying analysed element contents with the corresponding area related dry masses per m^2.

Table 1: Characteristics of 12 mountain beech stands (elevation between 1000 and 1100 m; age of ca. 146 years) along a fertility gradient from low (block West) over medium (block Middle) to high (block East) according to a 2015 survey. Values per block are means of 4 stands.

Tabelle 1: Merkmale von 12 Bergbuchenbeständen (Höhenlage zwischen 1000 und 1100 m; Alter ca. 146 Jahre) entlang eines Fruchtbarkeitsgradienten von niedrig (Block West) über mittel (Block Mitte) bis hoch (Block Ost) gemäß einer Erhebung im Jahr 2015. Die Werte pro Block sind Mittelwerte von 4 Beständen.

Parameter	West		Middle		East		total mean	sd	min	max
Number per ha	202	*a*	701	*b*	659	*b*	521	286	141	1044
Diameter at breast height (cm)	43	*b*	30	*a*	34	*a*	36	6	28	47
Tree height (m)	27	*b*	22	*a*	24	*a*	24	2	21	28
Basal area (m^2 ha^{-1})	29	*a*	53	*ab*	63	*b*	48	19	25	71
Stem volume (m^3 ha^{-1})	311	*a*	499	*ab*	631	*b*	481	175	275	728
Foliage (g m^{-2})	293	*a*	340	*ab*	401	*b*	345	56	277	441
Branches < 2 cm diameter (g m^{-2})	934	*a*	1757	*b*	1940	*b*	1544	537	810	2554
Branches 2-5 cm diameter (g m^{-2})	1581	*a*	3409	*b*	3364	*b*	2785	908	1459	3783
Branches > 5 cm diameter (g m^{-2})	4161	*a*	4135	*a*	5415	*a*	4570	1496	1765	7013
Bark of the stem (g m^{-2})	1590	*a*	2549	*ab*	3223	*b*	2454	891	1403	3715
Stem wood (g m^{-2})	20526	*a*	32910	*ab*	41613	*b*	31683	9223	18121	47964
Whole tree (g m^{-2})	29084	*a*	45099	*ab*	55955	*b*	43380	9223	25032	62818
Aspect (from N to S)	161		156		208					
Slope (%)	57		70		59					
N coordinate (WGS84)	47°49'07"		47°49'08"		47°49'08"					
E coordinates	14°23'11"		14°23'19"		14°23'38"					

A one-way ANOVA (factor block) was performed for each parameter and results of Scheffé multiple range tests are given (different letters indicate significant differences, $p < 0.05$; *a* represents the lowest mean; $N = 4$ stands x 3 blocks = 12)

2.3 Soil inventory

In June 2015, forest floor and mineral soil samples were collected at four subplots per beech stand. Litter (O_i and O_e) and humus horizons (O_a, if present) were sampled by hand within a 19-cm-diameter ring and carefully separated from the underlying mineral soil, which was then sampled with a small shovel at depth of 0-5 and 5-10 cm depth. The mineral soil from 10-25 cm was sampled using a soil auger (2 cm diameter, half-open steel pipe). Samples were pooled per stand and horizon. Area related total dry masses (105°C) of forest floor samples was determined by weighing, with roots removed. Forest floor samples were chemically analyzed as described for the biomass samples above, and corresponding element stocks calculated by multiplying dry mass of forest floor with element content.

Mineral soil samples were sieved (2 mm), and stones and roots were removed. Mineral soil chemical parameters were determined by routine procedures following Blum *et al*. (1989) for the standardization of Austrian soil surveys. Soil acidity was measured as pH using a glass Ag/AgCl combination electrode with KCl reference electrode: 10 g fresh soil was mixed with 25 ml of both 0.01 M $CaCl_2$ and deionized H_2O, stirred, and pH was measured the next morning, 30 min after re-stirring (ÖNORM L 1083). Total C and N contents were measured on a 300 mg oven-dried (105°C) subsample, as for biomass samples. Organic C was calculated as total C minus C_{CaCO3} (Scheibler method: reaction of carbonates with HCl and volumetric determination of released CO_2, according to ÖNORM L 1084). In this paper, C always refers to organic C. Total S and P contents were measured for 700 mg subsamples using aqua regia digestion (ÖNORM 1085) and ICP-OES analysis (Optima 8300, Perkin Elmer, Waltham, MA, USA). Calcium, Mg, K, sodium (Na), manganese (Mn), iron (Fe) and aluminum (Al) were measured as exchangeable cations (0.1 M $BaCl_2$ extraction, ÖNORM L 1086) in the mineral soil by ICP-OES.

In June 2015, one soil pit per block was excavated down to the bedrock (Gorfer et al. 2021). Stone content was visually estimated with a grid frame, and bulk density was calculated from pooled undisturbed soil samples using steel cylinders (diameter: 5.6 cm; height 4.2 cm; 3 to 5 replications per soil horizon per pit). Stone fraction decreased from West (0.188, 0.413, 0.810) to Middle (0.088, 0.213, 0.548) to East (0.010, 0.050, 0.170) for the 0-5, 5-10, and 10-25 cm soil depth, respectively ($cm^2\ cm^{-2}$). Bulk density (fine soil < 2 mm) increased along the same gradient: West (0.269, 0.355, 0.482) to Middle (0.520, 0.523, 0.538) to East (0.695, 0.734, 0.877; all data in $g\ cm^{-3}$), with increasing fertility level from "low" to "medium" to "high". Fine soil masses ($g\ m^{-2}$) were calculated as bulk density × (1 - stone fraction) × horizon depth (cm) × 10,000. Elemental stocks in the mineral soil were then calculated as the product of dry (105 °C) fine soil masses (area and soil depth related) and corresponding element contents.

2.4 Data evaluation and statistics

A one-way ANOVA (grouping factor: block; *N* = 3 blocks) was performed for selected stand and biomass parameters, and for each element in soil and biomass compartments. Scheffé's multiple range test was used to test differences along the fertility gradient. Bivariate linear correlations (Pearson) were performed between dry masses of biomass compartments and nutrient contents or pools. All statistical analyses were performed with IBM SPSS Statistics 29 (IBM Corporation, Armonk, NY, US).

3 Results

3.1 Above ground biomass along the fertility gradient

All biomass compartments, expressed in g m^{-2} (table 1), increased significantly along the fertility gradient from low (block West) to high (block East), except for branches > 5 cm diameter, which did not differ between blocks. Medium fertility (block Middle) revealed intermediate biomass values for foliage, bark of the stem, stem wood, and whole tree, but did not differ significantly from either low or high fertility stands. Soil fertility increased the whole tree biomass primarily via higher stand density (number of trees per ha), since the individual trees had lower diameters at breast height. Among the 12 beech stands, the smallest relative range was observed for fresh foliage (277 to 441 g m^{-2}), while the largest range was found in branches > 5 cm (1765 to 7013 g m^{-2}). The whole tree biomass within the 12 stands ranged from 250 to 628 t ha^{-1}.

3.2 Soil nutrition along the fertility gradient

Mean mineral soil properties per gram dry soil are given in table 2. Organic C contents and C/N ratios decreased with increasing soil fertility. Total contents of S and P (mg g^{-1}) were strongly linked to soil organic matter and thus also decreased along the fertility gradient. The low-fertility West block was characterized by very high C_{org} contents in the mineral organic A horizon, ranging from 213 mg g^{-1} (0-5 cm) to 137 mg g^{-1} (10-25 cm, directly above limestone bedrock). According to the Austrian soil classification key (Kilian 2015), organic C contents above 200 mg g^{-1} are considered hol-organic forest floor (O horizon), with an exception for Rendzic Lepthosols, where the threshold is set at 250 mg g^{-1} due to stable mineral-humus complexes formed by macrofauna activity. As a result of the high exchange capacity of organic compounds, the effective cation exchange capacity (CEC_{eff}) was roughly twice as high at low fertility (block West: 730-806 μmol_c g^{-1}) as at high fertility (block East: 341-395 μmol_c g^{-1}). Calcium and Mg together accounted for 96.6 to 97.6 % of CEC_{eff}. Exchangeable contents of K were very low (0.33 to 1.57 % of CEC_{eff}) and were mainly associated with soil texture rather than organic matter, increasing with higher loam content along the fertility gradient from low (Rendzic Lepthosol) to high (Chromic Cambisol).

Table 2: Mean mineral soil properties in 0-5, 5-10 and 10-25 cm soil depth of the 12 beech forest stands along a fertility gradient from block West over block Middle to block East (4 stands per block). Total contents of C_{org}, N, S and P in mg g^{-1}, pH (in H_2O and $CaCl_2$), effective cation exchange capacity (CEC_{eff}) in µmolc g^{-1}, contents of exchangeable ions in % of the exchange complex and base saturation in %. Stone fraction (cm^2 cm^{-2}) and bulk density (g cm^{-3}) were estimated from pooled samples of one soil pit per block.

Tabelle 2: Durchschnittliche mineralische Bodeneigenschaften in 0-5, 5-10 und 10-25 cm Bodentiefe der 12 Buchenwaldbestände entlang eines Fruchtbarkeitsgradienten von Block West über Block Mitte bis Block Ost (4 Bestände pro Block). Gesamtgehalt an C_{org}, N, S und P in mg g^{-1}, pH-Wert (in H_2O und $CaCl_2$), effektive Kationenaustauschkapazität (CEC_{eff}) in µmol_c g^{-1}, Gehalt an austauschbaren Ionen in % des Austauschkomplexes und Basensättigung in %. Der Grobbodenanteil (cm^2 cm^{-2}) und die Lagerungsdichte (g cm^{-3}) wurden anhand von gepoolten Proben aus einer Profilgrube pro Block geschätzt.

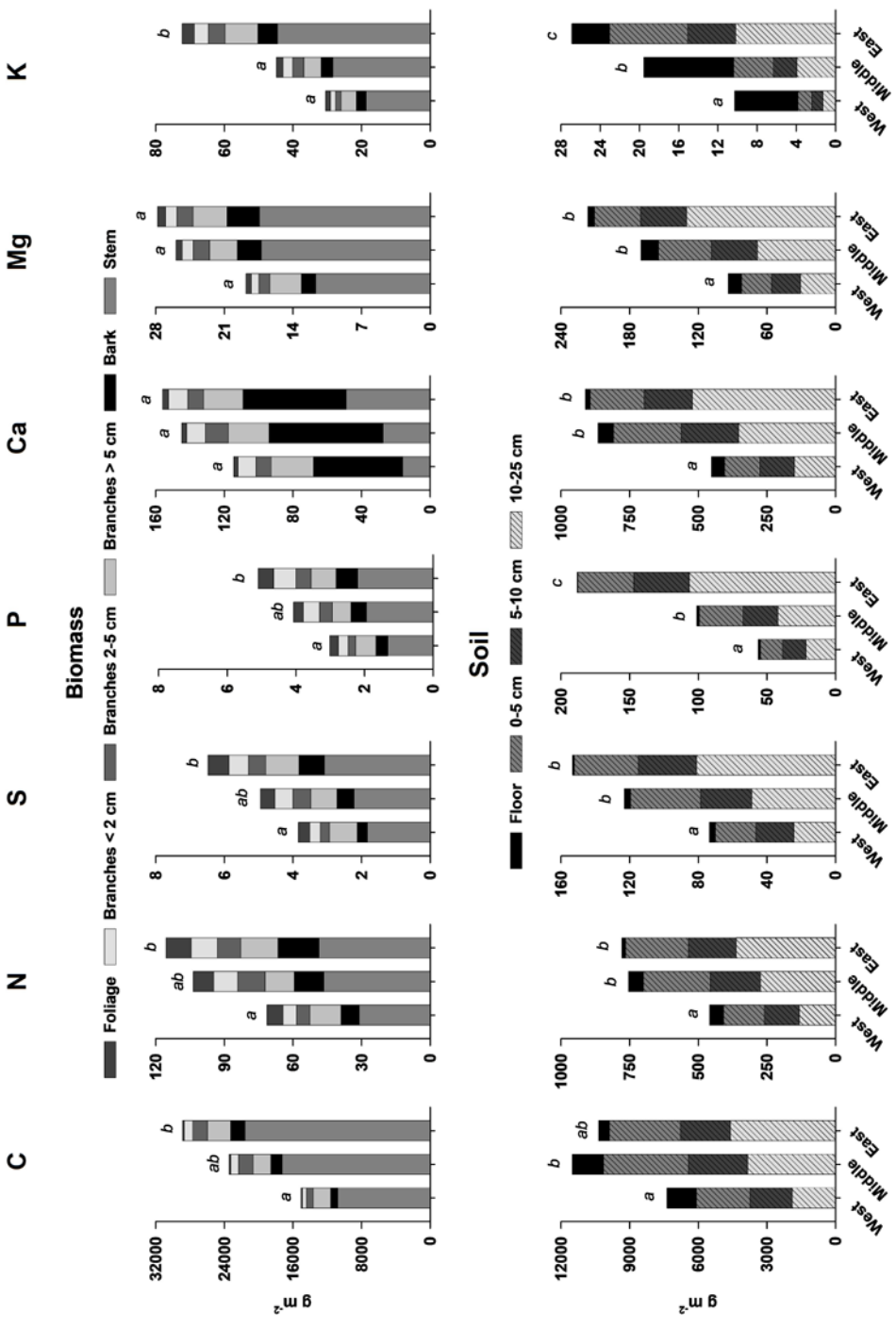
Parameter	0-5 cm			5-10 cm			10-25 cm		
	West	Middle	East	West	Middle	East	West	Middle	East
Stone fraction (cm^2 cm^{-2})	0.19	0.09	0.01	0.41	0.21	0.05	0.81	0.55	0.17
Bulk density (g cm^{-3})	0.27	0.52	0.69	0.36	0.52	0.73	0.48	0.54	0.88
C (mg g^{-1})	213.72 *b*	156.86 *ab*	90.42 *a*	177.89 *c*	126.01 *b*	62.60 *a*	137.16 *c*	105.11 *b*	42.05 *a*
N (mg g^{-1})	13.55 *b*	10.27 *ab*	6.63 *a*	12.21 *c*	8.88 *b*	5.00 *a*	9.62 *c*	7.48 *b*	3.31 *a*
C/N	15.63 *a*	15.22 *a*	13.66 *a*	14.51 *b*	14.17 *b*	12.48 *a*	14.24 *b*	14.04 *b*	12.63 *a*
S (mg g^{-1})	2.15 *b*	1.72 *ab*	1.09 *a*	2.13 *b*	1.45 *b*	0.97 *a*	1.77 *c*	1.34 *b*	0.74 *a*
P (mg g^{-1})	1.47 *a*	1.34 *a*	1.18 *a*	1.64 *b*	1.24 *b*	1.16 *a*	1.56 *b*	1.15 *a*	0.97 *a*
pH (H_2O)	7.43 *a*	7.25 *a*	7.00 *a*	7.58 *a*	7.53 *a*	7.03 *a*	7.85 *a*	7.65 *a*	7.68 *a*
pH ($CaCl_2$)	6.78 *a*	6.60 *a*	6.30 *a*	6.95 *a*	6.86 *a*	6.38 *a*	7.13 *b*	7.03 *ab*	6.93 *a*
CEC_{eff} µmol_c g^{-1}	793.64 *b*	691.12 *b*	395.10 *a*	806.40 *b*	671.55 *b*	353.29 *a*	730.48 *b*	641.76 *b*	341.43 *a*
Ca (% of CEC)	74.36 *a*	75.24 *a*	72.54 *a*	74.22 *ab*	75.13 *b*	71.00 *a*	74.32 *b*	75.35 *b*	69.69 *a*
Mg (% of CEC)	24.73 *a*	23.30 *a*	24.06 *a*	25.07 *a*	23.92 *a*	26.63 *a*	25.00 *ab*	23.89 *a*	28.84 *b*
K (% of CEC)	0.42 *a*	0.63 *a*	1.57 *b*	0.35 *a*	0.44 *a*	1.06 *b*	0.33 *a*	0.43 *a*	0.71 *b*
Na (% of CEC)	0.16 *a*	0.25 *a*	0.30 *a*	0.12 *a*	0.21 *ab*	0.25 *b*	0.20 *a*	0.16 *a*	0.34 *b*
Al (% of CEC)	0.03 *a*	0.04 *a*	0.07 *a*	0.05 *a*	0.05 *a*	0.07 *a*	0.06 *a*	0.06 *a*	0.20 *b*
Fe (% of CEC)	0.01 *a*	0.01 *a*	0.01 *a*	0.01 *a*	0.01 *a*	0.02 *a*	0.02 *a*	0.02 *a*	0.06 *b*
Mn (% of CEC)	0.29 *a*	0.53 *a*	1.43 *a*	0.18 *a*	0.23 *a*	0.97 *a*	0.07 *a*	0.11 *a*	0.17 *b*
H (% of CEC)	0.00 *a*	0.00 *a*	0.01 *a*	0.00 *a*	0.00 *a*	0.01 *a*	0.00 *a*	0.00 *a*	0.00 *b*
Base saturation (%)	99.67 *a*	99.43 *a*	98.48 *a*	99.77 *a*	99.70 *a*	98.93 *a*	99.85 *b*	99.82 *b*	99.57 *a*

A one-way ANOVA (factor block) was performed for each parameter per soil depth and results of Scheffé multiple range tests are given (different letters indicate significant differences, $p < 0.05$; *a* represents the lowest mean; $N = 4$ stands x 3 blocks = 12)

With increasing soil fertility, bulk density increased as organic C contents and stone fractions decreased, resulting in higher fine earth masses (< 2 mm; chemically analyzed fraction): 35 kg m^{-2} (West), 81 kg m^{-2} (Middle), and 178 kg m^{-2} (all values for 0-25 cm soil depth). Consequently, nutrient soil stocks per unit area (g nutrient m^{-2}) showed a different pattern than nutrient soil contents (mg nutrient per g soil). As shown in figure 2, soil stocks (forest floor plus mineral soil) of all macro nutrients increased from low to high fertility. Nutrient stocks in the forest floor accounted for less than 13 % of total soil stocks (down to 25 cm) for N, S, P, Ca and Mg. However, for K, a very large proportion was stored in the forest floor (West: 63 %; Middle: 47 %; East: 14 %), indicating that weathering release from calcareous bedrock is very small.

Figure 2: Carbon and nutrient stocks of the soil (horizons: forest floor; 0-5 cm, 5-10 cm and 10-25 cm mineral soil) and the above ground beech biomass (compartments: foliage; branches < 2 cm, 2-5 cm and > 5 cm diameter; bark of the stem and stem wood) in g m^{-2} along a fertility gradient from block West over block Middle to block East (four stands per block). All stocks are based upon total element contents, except mineral soil stocks of base cations represent exchangeable stocks. A one-way ANOVA (factor block) was performed for each parameter and results of Scheffé multiple range tests are given (different letters indicate significant differences, p < 0.05; a represents the lowest mean; N = 4 stands x 3 blocks = 12).

Abbildung 2: Kohlenstoff- und Nährstoffvorräte des Bodens (Horizonte: Auflage; 0-5 cm, 5-10 cm und 10-25 cm Mineralboden) und der oberirdischen Buchenbiomasse (Kompartimente: Blattmasse; Äste < 2 cm, 2-5 cm und > 5 cm Durchmesser; Rinde des Stammes und Stammholz) in g m^{-2} entlang eines Fruchtbarkeitsgradienten von Block West über Block Mitte nach Block Ost (vier Bestände pro Block). Alle Vorräte basieren auf den Gesamtelementgehalten, außer bei der Berechnung der Mineralbodenvorräte der basischen Kationen wurden austauschbare Gehalte verwendet. Für jeden Parameter wurde eine einseitige ANOVA (Faktor Block) durchgeführt und die Ergebnisse eines multiplen Mittelwertvergleiches nach Scheffé angegeben (unterschiedliche Buchstaben zeigen signifikante Unterschiede an, $p < 0,05$; *a* steht für den niedrigsten Mittelwert; *N* = 4 Bestände x 3 Blöcke = 12).


C
N
S
P
Ca
Mg
K
Biomass
Foliage
Branches < 2 cm
Branches 2-5 cm
Branches > 5 cm
Bark
Stem
Soil
Floor
0-5 cm
5-10 cm
10-25 cm
g m-2
West
Middle
East

3.3 Tree nutrition along the fertility gradient

The fertility gradient was reflected in increasing contents (mg g^{-1} dry biomass) of K, S and P in fresh foliage from West to East (table 3). No differences were observed for foliar N, Ca and Mg. Potassium was significantly higher in the branches of all diameter classes towards more fertile blocks, matching increasing exchangeable K stocks in the soil. In contrast, calcium and Mg contents in thin branches (< 2 cm and 2-5 cm) were higher on Rendzic Lepthosols than on Chromic Cambisols. Bark Ca contents increased significantly towards the low-fertility end, which was characterized by fewer but trees with higher diameters (table 1). No significant differences were observed for other elements or biomass compartments (table 3).

Element stocks (g m^{-2}) within the biomass are plotted in figure 2, divided into the five studied biomass compartments. Differences between fertility blocks are indicated by different letters for the whole tree biomass (sum of all five biomass compartments). For all macro nutrients, there was a clear trend of increasing stocks parallel to the corresponding soil nutrient stocks from low to high fertility.

To point out that element contents (mg g^{-1}) and element stocks (g m^{-2}) can show different patterns due to very different masses of biomass compartments, means of all 12 beech stands are shown in figure 3. Distributing nutrient contents (mg g^{-1}) in percent among above ground biomass compartments is somewhat unusual but underlines general textbook knowledge that the highest nutrient contents are typically found in fresh foliage. This was the case for all macro nutrients, except Ca, which was most concentrated in the bark of the stem bark. However, the distribution of nutrient stocks (figure 3) showed that 57 to 74 % of the whole tree's macro nutrient stocks were sequestered in bark plus stem wood. For Ca, 43 % of the whole above tree biomass stock was stored in bark alone. For Mg and K, 64 % and 62 %, respectively, were found in stem wood without bark, highlighting that harvest of stem wood may severely impact nutrient budgets for these nutrients in old mountain beech forests.

Table 3: Mean nutrient contents of biomass compartments in mg g^{-1} (dry mass) along a fertility gradient from block West over block Middle to block East. Two samples were taken from cut beech trees with the median DBH of two study stands per block, yielding four replicates per block (except for bark only one sample per tree was collected).

Tabelle 3: Durchschnittlicher Nährstoffgehalt der Biomassekompartimente in mg g^{-1} (Trockengewicht) entlang eines Fruchtbarkeitsgradienten von Block West über Block Mitte nach Block Ost. Zwei Proben wurden vom gefällten Buchenzentralstamm von zwei Untersuchungsbeständen pro Block entnommen (somit vier Wiederholungen pro Block mit Ausnahme der Rinde, von welcher nur eine Probe pro Baum entnommen wurde).

Biomass compartment	West		Middle		East		West		Middle		East		West		Middle		East	
	---------- N ----------						---------- S ----------						---------- P ----------					
Foliage	24.09	*a*	26.26	*a*	27.61	*a*	1.11	*a*	1.23	*a*	1.52	*b*	0.85	*a*	0.86	*a*	1.12	*b*
Branches < 2 cm	6.36	*a*	6.02	*a*	5.92	*a*	0.33	*a*	0.30	*a*	0.29	*a*	0.32	*a*	0.27	*a*	0.34	*a*
Branches 2-5 cm	3.76	*a*	3.53	*a*	3.05	*a*	0.17	*a*	0.15	*a*	0.15	*a*	0.13	*a*	0.11	*a*	0.13	*a*
Branches > 5 cm	3.22	*a*	3.07	*a*	3.01	*a*	0.19	*a*	0.18	*a*	0.18	*a*	0.14	*a*	0.13	*a*	0.13	*a*
Bark of the stem	4.98	*a*	5.03	*a*	5.61	*a*	0.19	*a*	0.20	*a*	0.23	*a*	0.22	*a*	0.18	*a*	0.20	*a*
Stem wood	1.50	*a*	1.42	*a*	1.16	*a*	0.09	*a*	0.07	*a*	0.07	*a*	0.06	*a*	0.06	*a*	0.05	*a*
	---------- Ca ----------						---------- Mg ----------						---------- K ----------					
Foliage	8.38	*a*	8.73	*a*	8.74	*a*	1.88	*a*	1.85	*a*	1.96	*a*	4.73	*a*	5.45	*a*	8.88	*b*
Branches < 2 cm	11.24	*b*	6.16	*a*	5.82	*a*	0.83	*b*	0.65	*a*	0.62	*a*	1.62	*a*	1.61	*a*	2.12	*b*
Branches 2-5 cm	5.61	*b*	3.99	*ab*	2.74	*a*	0.70	*b*	0.48	*a*	0.48	*a*	1.00	*ab*	0.96	*a*	1.45	*b*
Branches > 5 cm	5.88	*a*	5.68	*a*	4.27	*a*	0.78	*a*	0.67	*a*	0.64	*a*	1.06	*a*	1.24	*a*	1.75	*b*
Bark of the stem	32.72	*c*	26.25	*b*	18.69	*a*	0.92	*a*	0.97	*a*	1.03	*a*	1.84	*a*	1.34	*a*	1.81	*a*
Stem wood	0.78	*a*	0.83	*a*	1.17	*a*	0.56	*a*	0.53	*a*	0.42	*a*	0.89	*a*	0.86	*a*	1.06	*a*

A one-way ANOVA (factor block) was performed for each nutrient per biomass compartment and results of Scheffé multiple range tests are given (different letters indicate significant differences, $p < 0.05$; *a* represents the lowest mean; $N = 4$ replicates x 3 blocks = 12; except for bark: $N = 2$ replicates x 3 blocks = 6)

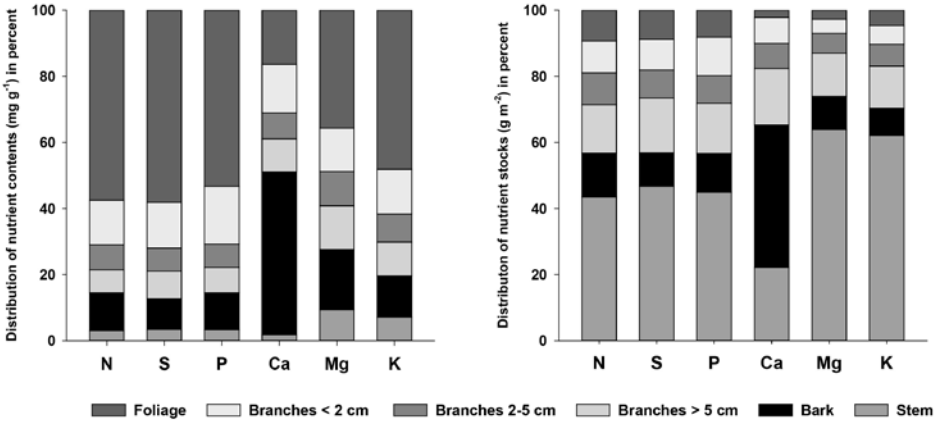


Figure 3: Mean (N = 12 beech forest stands) distribution of nutrient contents (mg g^{-1}) in percent (e.g., foliage N in % = 100 × foliage N in mg g^{-1} / (foliage N in mg g^{-1} + all three diameter branches N in mg g^{-1} + bark N in mg g^{-1} + stem N in mg g^{-1})) and distribution of nutrient stocks (g m^{-2}) in percent among above ground biomass compartments (foliage; branches < 2 cm, 2-5 cm and > 5 cm diameter; bark of the stem and stem wood).

Abbildung 3: Mittlere (*N* = 12 Buchenwaldbestände) Verteilung der Nährstoffgehalte (mg g^{-1}) in Prozent (z. B., Blatt N in % = 100 × Blatt N in mg g^{-1} / (Blatt N in mg g^{-1} + Ast N aller drei Durchmesser in mg g^{-1} + Rinde N in mg g^{-1} + Stamm N in mg g-1)) sowie Verteilung der Nährstoffvorräte (g m^{-2}) in Prozent auf die oberirdischen Biomassekompartimente (Blatt; Äste < 2 cm, 2–5 cm und > 5 cm Durchmesser; Rinde des Stammes und Stammholz).

3.4 Chemical foliar condition along the fertility gradient

The classification system for macro nutrient contents, according to Stefan *et al.* (1997), is given in the legend of figure 4. The authors summarized the results of a survey of the chemical content of needles and leaves carried out on a systematic grid (16x16 km; level I) within 16 European countries. Due to high weathering rates of calcareous and dolomitic bedrock, calcium and Mg contents in foliage were within the high surplus range (figure 4). All blocks showed foliar N contents at the lower end of the surplus range. In contrast, foliar contents of S, P and K were in the deficiency range for the block West (Rendzic Leptosol) and Middle, but in the lower (S, P) or higher (K) optimum range at the most fertile block East (Chromic Cambisol).

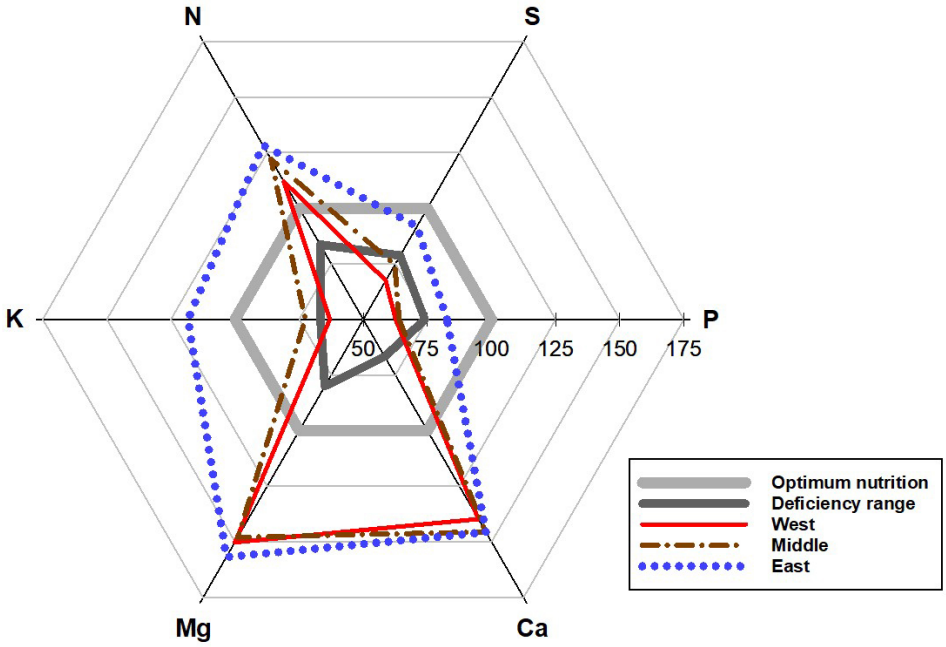


Figure 4: Mean (N = 4 stands per block) macro nutrient contents of fresh beech foliage expressed as percentage of optimum nutrition (mean value of class range 2 according to Stefan et al. (1997): N: 21.50; S: 1.65; P: 1.35; Ca: 6.00; Mg: 1.25; K: 7.50; data in mg g^{-1}) along a fertility gradient from block West over block Middle to block East in 2015. Deficiency range: upper value of class 1: N: 18.0; S: 1.3; P: 1.0; Ca: 4.0; Mg: 1.0; K: 5.0; data in mg g^{-1}.

Abbildung 4: Durchschnittlicher (*N* = 4 Bestände pro Block) Makronährstoffgehalt von frischen Buchenblättern, ausgedrückt in Prozent der optimalen Versorgung (Durchschnittswert der Klassenstufe 2 nach Stefan *et al.* (1997): N: 21,50; S: 1,65; P: 1,35; Ca: 6,00; Mg: 1,25; K: 7,50; Werte in mg g^{-1}) entlang eines Fruchtbarkeitsgradienten von Block West über Block Mitte nach Block Ost im Jahr 2015. Mangelhafte Versorgung: oberer Wert der Klasse 1: N: 18,0; S: 1,3; P: 1,0; Ca: 4,0; Mg: 1,0; K: 5,0; Werte in mg g^{-1}.

3.5 Correlation between biomass- and soil parameters

The highest positive Pearson correlation coefficients (table 4) were recorded between nutrient foliage contents (mg nutrient g^{-1}) and mineral soil stocks (g nutrient m^{-2}; 0-25 cm soil depth) for K (0.93), P (0.93) and S (0.78), which were in the deficiency range for the blocks West and Middle according to foliar nutrition guidelines (figure 4). Since there was a positive relation between foliage nutrition (mg nutrient g^{-1}) and foliage biomass (g DM m^{-2}) for all nutrients (R: 0.73 to 0.79), except for Ca and Mg, foliage biomass was related to mineral soil stocks for most nutrients as well. Because

only 39 % (R = 0.63; table 4) of the relation between the whole above tree biomass and foliage biomass can be explained by the regression model, the whole tree biomass was finally related only to mineral soil stocks of exchangeable K (R = 0.68) and total P (R = 0.70).

Nutrient stocks within the forest floor were generally negatively related with above ground biomass parameters (*i.e.*, nutrient foliage content and – stocks, foliage – and whole tree biomass; level of significance are given in table 4), since the formation of thick organic layers is commonly associated with reduced tree growth (Kazda and Pichler 1998). Slow decomposition of litter, buildup of forest floor and consequently sequestration of nutrients in the forest floor slows down nutrient cycling, hampering forest productivity (Berger *et al.* 2002; Berger and Berger 2012).

Table 4: Coefficients of correlation (Pearson) between dry masses (DM) of biomass compartments and nutrient contents or pools (N = 12 beech forest stands; level of significance is indicated by different shading).

Tabelle 4: Korrelationskoeffizienten (Pearson) zwischen Trockenmassen (DM) der Biomassekompartimente und Nährstoffgehalten oder -vorräte (N = 12 Buchenwaldbestände; das Signifikanzniveau wird durch unterschiedliche Schattierungen angezeigt).

Dependant parameter	Independant parameter	N	S	P	Ca	Mg	K	DM
Corresponding nutrient foliage content (mg nutrient g^{-1})	Forest floor (g nutrient m^{-2})	-0.57	-0.77	-0.83	-0.15	-0.45	-0.67	
	Mineral soil (g nutrient m^{-2})	0.70	0.78	0.93	0.57	0.53	0.93	
Foliage biomass (g DM m^{-2})	Foliage (mg nutrient g^{-1})	0.73	0.79	0.73	0.19	0.36	0.76	
Corresponding nutrient foliage stock (g nutrient m^{-2})	Forest floor (g nutrient m^{-2})	-0.68	-0.77	-0.81	-0.62	-0.56	-0.63	
	Mineral soil (g nutrient m^{-2})	0.59	0.74	0.91	0.61	0.71	0.90	
Foliage biomass (g DM m^{-2})	Forest floor (g nutrient m^{-2})	-0.65	-0.67	-0.66	-0.66	-0.51	-0.34	
	Mineral soil (g nutrient m^{-2})	0.53	0.66	0.77	0.56	0.65	0.71	
Whole tree biomass (g DM m^{-2})	Foliage biomass (g DM m^{-2})							0.63
Whole tree biomass (g DM m^{-2})	Forest floor (g nutrient m^{-2})	-0.39	-0.42	-0.50	-0.43	-0.58	-0.50	
	Mineral soil (g nutrient m^{-2})	0.55	0.57	0.70	0.55	0.51	0.68	

	> 0.05		< 0.01
	< 0.05		< 0.001

4 Discussion

4.1 Foliar chemistry as indicator of nutrient deficiency

Foliar nutrient ratios (deduced from table 3) were in the harmonious range for N/Ca, N/Mg and Ca/Mg according to Stefan *et al*. (1997). However, ratios of N/P (24.7-30.4; 25.0), N/S (18.2-21.6; 19.2) and N/K (3.1-5.1; 5.0; last number is the highest optimal value) were all within a critical high range, indicating nutritional imbalances. Obviously, high total N stocks in the organic horizons are quickly mineralized and become plant available at low soil C/N ratios and high soil pHs (table 2) but simultaneous uptake of P, S and K is hindered. Foliar ratios of K/Ca (0.6-1.0; 0.6) and K/Mg (2.5-4.5; 3.3; last number is the lowest optimal value) were within a critical low range, indicating potential K limitations (compare figure 4).

4.2 Relations between above ground biomass parameters and soil nutrition

Correlation coefficients between biomass - and soil parameters (table 4) indicate that K and P availability are key limiting factors for tree growth in these mountain forests, which is consistent with the general limited supply of these nutrients on calcareous bedrock. The slope of the regression line, relating above ground biomass (g dry mass m^{-2}) to mineral soil nutrient stocks (g m^{-2}), was steeper for exchangeable K (1147) than for total P (169), suggesting that even small increases in soil K can have a high positive effect on tree growth. In line with Liebig's law of the minimum (Liebig 1840), stating that growth is dictated not by total resources available, but by the scarcest resource (limiting factor), potassium seems to play a key role for the fertility of these mountainous beech forests on calcareous bedrock.

Reduced plant uptake of P due to immobilization in form of Ca phosphates (De Schrijver *et al*. 2012; Kruse *et al*. 2015) is put forward to explain the observed foliar deficiency of P at the less fertile blocks West and Middle (figure 4). There is a general trend that soil pH values (both in H_2O and $CaCl_2$; for all 3 soil horizons) were lower at block East (table 2), increasing mobility of P, resulting in significantly higher P foliage contents (table 3).

4.3 Impact of harvest intensity on remaining elemental soil stocks

One main goal of this study was to develop forest harvest management guidelines for these mountain beech forest stands. Hence, simulated removed organic carbon and nutrients via clear cut with different harvest intensities of the above ground biomass compartments were expressed in percent of organic carbon and nutrient stocks

(biomass plus forest floor and mineral soil down to 25 cm) in table 5. Values greater than 50 % for quickly exchangeable base cations, and higher than 25 % and 60 % for slower released total P and N, respectively (Meiwes *et al.* 2008), are critical, since nutrient supply would not be sufficient for the next forest regeneration without external net inputs.

Among the six macro nutrients, these limit values (assuming the same value for total S than for total P) were exceeded only for exchangeable K. Mean simulated values declined from 71 % (whole tree harvest during summer; including foliage), over 68 % (whole tree harvest during winter; excluding foliage), over 50 % (harvest of stem with bark) to 44 % (harvest of stem without bark). It is striking these ratios did not change along the soil fertility. This means, that with increasing fertility relatively more K is stored in the higher above ground biomass without changing the ratio of removed to remaining K. According to our simple model whole tree harvesting will inevitably reduce site sustainability and forest productivity with respect to K. Accounting for inputs (atmospheric deposition and weathering) and outputs (leaching via soil solution) does little to alter the predicted K limitation at these sites for several reasons: (i) most K bulk deposition fluxes in remote forests is attributable to internal cycling (*i.e.*, plant-derived material) rather than true external inputs to the ecosystem (Likens *et al*., 1994); (ii) weathering rates are low, since pure limestone ($CaCO_3$) and pure dolomite ($CaMg[CO_3]_2$) do not release K; and (iii) leaching losses in undisturbed forest ecosystems are very small (Likens *et al.* 1994; Ahrends *et al*. 2022). The fact that K harvest losses are particularly high for beech is in accordance with de Vries *et al*. (2021) who compared nutrient balances of beech, oak, spruce, Douglas fir, larch and pine in the Netherlands. Negative K balances were calculated for beech and oak, even for stem only harvest (not separated into stem wood and bark). Stem only harvest extractions of K were highest for beech.

Although organic carbon is not considered a macro nutrient,- since it is abundantly supplied by photosynthesis of atmospheric CO_2 - it is striking that forest harvesting removed substantial proportions of total ecosystem C stocks: 69 % for whole tree harvest during summer including foliage, 68 % for whole tree harvest during winter excluding foliage, 54 % for harvest of stem with bark, and 50 % for harvest of stem without bark. The fact that above ground C stocks exceed soil C stocks is unique for these mountain forests on shallow soils, since C stocks in above- and below ground biomass typically represent 6.2 to 31.3 % of the total ecosystem C pools in boreal and temperate IPCC climate regions (Scharlemann *et al.* 2014). The mechanisms of soil C storage and how they are impacted by harvest residue removal still need to be better understood (Mayer *et al.* 2020). Johnson and Curtis (2001) reported in a meta-analysis that whole tree harvesting decreased soil C stocks by about 6 %, whereas stem with bark harvesting increased soil carbon by around 18 %. However, this positive effect seemed restricted to coniferous species. Another meta-analysis by Achat et al. (2015) indicated that removing harvesting residues caused significant losses of soil C in both the forest floor (10-45 %, depending on harvest intensity) and even deep

Table 5: Simulated removed (a) and remaining (b) organic carbon and nutrients depending on harvest intensity in g m^{-2} and removed nutrients in percent of total stocks (a + b) for the overall mean (12 beech forest stands, including the range) as well as for the individual blocks (4 stands per block; increasing fertility from West over Middle to East). All stocks are based upon total element contents, except for calculating soil stocks (forest floor and mineral soil down to 25 cm) exchangeable base cations within the mineral soil were used.

Tabelle 5: Simulierte entnommene (a) und verbleibende (b) Vorräte von organischem Kohlenstoff und Nährstoffen in Abhängigkeit von der Ernteintensität in g m^{-2}, sowie entnommene Nährstoffe in Prozent der Gesamtvorräte (a + b) für den Mittelwert aller 12 Buchenwaldbestände (einschließlich der Schwankungsbreite) als auch für die einzelnen Blöcke (4 Bestände pro Block; zunehmende Bodenfruchtbarkeit von West über Mitte nach Ost). Die Vorräte basieren auf Gesamtelementgehalten, außer bei der Berechnung der Bodenvorräte (Auflage und Mineralboden bis zu einer Tiefe von 25 cm) wurden für die basischen Kationen des Mineralbodens austauschbare Gehalte verwendet.

Harvest intensity	**C**	**N**	**S**	**P**		**Ca**	**Mg**	**K**
Harvest of whole tree during summer								
a) Whole tree (g m^{-2})	22464.4	96.9	5.1	4.1		138.5	24.2	49.2
b) Soil (g m^{-2})	9742.8	663.9	116.6	115.2		743.1	160.3	18.9
Removed nutrients (% of total stocks)	68.8	13.0	4.4	3.9		16.6	14.0	71.4
range	56-79	9-17	3-6	2-6		9-24	8-21	58-80
West	67.2	13.5	5.0	5.1	*b*	20.4	16.7	73.6
Middle	65.6	12.3	4.0	4.0	*ab*	14.6	13.7	68.1
East	73.6	13.2	4.2	2.7	*ab*	14.9	11.7	72.6
Harvest of whole tree during winter								
a) Whole tree - foliage (g m^{-2})	22284.1	87.9	4.6	3.7		135.5	23.5	46.9
b) Soil + foliage (g m^{-2})	9923.0	672.9	117.1	115.5		746.1	160.9	21.2
Removed nutrients (% of total stocks)	68.2	11.8	4.0	3.6		16.3	13.6	68.0
range	55-78	8-16	2-6	2-6		9-23	8-20	53-78
West	66.5	12.2	4.6	4.7	*b*	19.9	16.2	69.9
Middle	65.1	11.2	3.7	3.7	*ab*	14.3	13.3	65.1
East	73.1	11.9	3.8	2.4	*ab*	14.6	11.4	69.0
Harvest of stem with bark								
a) Whole tree - foliage - branches (g m^{-2})	17809.9	55.0	2.9	2.3		90.4	17.9	34.6
b) Soil + foliage + branches (g m^{-2})	14397.3	705.8	118.8	116.9		791.2	166.6	33.6
Removed nutrients (% of total stocks)	54.2	7.4	2.5	2.2		10.7	10.3	49.8
range	41-64	4-11	1-4	1-4		6-14	6-15	37-62
West	51.7	7.4	2.8	2.8		12.1	11.6	51.2
Middle	51.7	7.1	2.2	2.3		9.5	10.4	47.7
East	59.3	7.6	2.5	1.5		10.4	8.7	50.3
Harvest of stem without bark								
a) Whole tree - foliage - branches - bark (g m^{-2})	16556.0	42.1	2.4	1.8		30.8	15.4	30.5
b) Soil + foliage + branches + bark (g m^{-2})	15651.1	718.7	119.3	117.4		850.8	169.0	37.6
Removed nutrients (% of total stocks)	50.4	5.7	2.1	1.8		3.4	8.9	43.6
range	39-60	3-8	1-3	1-3		2-6	5-14	29-56
West	48.2	5.9	2.4	2.2		2.9	10.3	43.8
Middle	48.1	5.5	1.8	1.9		2.8	9.1	42.6
East	55.0	5.6	2.0	1.2		4.7	7.4	44.4

A one-way ANOVA (factor block) was performed for each nutrient and results of Scheffé multiple range tests are given only if differences were significant, i.e., for P (different letters indicate significant differences, $p < 0.05$; *a* represents the lowest mean; $N = 4$ stands x 3 blocks = 12)

soil layers (10 %). Following Jandl *et al*. (2007), we conclude that forest management activities have high potential to influence soil C stocks. Maintaining or enhancing soil C stocks offers multiple benefits beyond C sequestration, including improved soil and site productivity (see figure 2), increased water-holding capacity, and enhanced below ground biodiversity (Mayer *et al*. 2020). Additionally, because organic soil compounds dominate the exchange complex of the studied soils, a decline in soil C content will directly reduce CEC_{eff} and consequently the availability of nutrients such as K (see table 2).

Exchangeable Ca and Mg were sufficiently supplied by weathering of limestone ($CaCO_3$) and partly calcitic dolomite ($CaMg[CO_3]_2$), occupying most of the (organic) soil exchanger (> 96 % of CEC_{eff} ; see table 2). Consequently, forest harvesting does not pose any restrictions regarding Ca and Mg availability. Even with whole tree harvest during summer, which represents the scenario with the greatest nutrient removal (including foliage), only 17 % of total Ca and 14 % of total Mg stocks were extracted – clearly below the critical threshold of 50 %.

Estimated harvesting-related removals of total N and total S were also moderate, reaching less than 17 % for N and 6 % for S (maximum range, table 5) even at the highest intensity (whole tree harvest during summer). However, total nutrient contents do not necessarily reflect their availability for plant uptake. Foliage N contents were in the surplus range (as discussed above; figure 4). One source is assumed quick mineralization of organic soil N due to small C/N soil ratios (Berger and Berger 2012; compare table 2) and preferential plant uptake in form of ammonium which is less subject to leaching via seepage than nitrate at the nearby (4 km distance, same altitude) comparable long-term monitoring LTER- Europe site "Zöbelboden" (Vuorenmaa *et al*. 2018). At Zöbelboden mean (1993-2015) catchment output fluxes of nitrate (46) are even slightly higher than bulk deposition in the open (44), while output fluxes of ammonium (0.15) are negligible in comparison to bulk deposition (70; data in meq m^{-2} yr^{-1}; Vuorenmaa *et al*. 2018). At the mixed beech study site at Zöbelboden mean (1997 to 2012) uptake of inorganic N via the canopy is estimated 0.81 (NH_4-N: 0.69; NO_3-N: 0.12), yielding together with throughfall (N_{tot} 1.37) and stemflow (N_{tot} 0.29) a total N deposition of 2.47 (all data in g m^{-2} yr^{-1}; Dirnböck *et al.* 2023). Thus, total N deposition at the Zöbelboden site exceeded recommended critical loads for European forests (1.6 g m^{-2} yr^{-1}), despite its remote location away from local emission sources (Dirnböck *et al*. 2023).

Plants take up S primarily in form of inorganic sulfate (Buchner *et al*. 2004). However, only a minor fraction of soil S is available in this form, since the majority is contained in organic material (Hanousek *et al*., 2017). At Zöbelboden, mean (1993-2015) catchment output fluxes of sulfate (22 meq m^{-2} yr^{-1}) were low in comparison to bulk deposition in the open (35 meq m^{-2} yr^{-1}; Vuorenmaa *et al.*, 2018). Currently, in many regions mass balance estimates of S are negative, since previously stored, historic S is released via mineralization of the organic soil S pool or desorption from the soil

exchanger (Likens *et al.* 2002; Berger *et al.* 2009a, b; Berger and Muras 2016; Berger *et al.* 2016; Dolschak and Berger 2020). Positive input-output S balances as recorded for the site Zöbelboden, which is comparable to our study sites, are rare (*e.g.*, in the study by Vuoernmaa *et al.* 2018, only 3 LTER sites out of 19 showed a positive balance). This means, that solute flux profiles through the soil indicate a sink for sulfate-S, *e.g.*, caused by low sulfate release rates via microbial mineralization of organic S. This would explain the fact that S nutrition is below the optimum (block East) or even within the deficiency range (blocks West and Middle; figure 4) though total soil S contents are high in comparison to biomass S contents. Emissions of SO_2 declined continuously since the 1990s, which is reflected in an annual decline of bulk deposition of -0.08 meq m^{-2} yr^{-1} for this period (Vuorenmaa *et al.* 2018), resulting in a SO_2-S bulk deposition around 0.4 g m^{-2} yr^{-1} at Zöbelboden in 2015, when part of the study sites were cut. This sharp decline in S deposition has reduced sulfate in the soil solution and led to lower S uptake from the soil. Furthermore, direct foliar uptake of S has diminished (Jonard *et al.* 2015).

Estimated P removal through forest harvesting was low - less than 6 % (maximum range, table 5) of total ecosystem P stocks even under the most nutrient extractive harvesting method (whole tree harvest during summer), similar to the findings for S. This indicates that, in terms of total stock, phosphorus resources are not limiting and are unlikely to be affected by forest harvesting operations. As discussed above, total P content does not necessarily reflect the size of plant-available pools. Foliage P contents indicated clear deficiencies in the lower and medium fertility blocks (West, Middle), and only low optimum supply in the high fertility block (East), based on the thresholds proposed by Stefan *et al.* (2007; see figure 4). Mean foliar N/P ratios (West: 28.5; Middle: 30.4; East: 24.7; deduced from table 3) were very high in comparison to published upper normal ranges of, *e.g.*, 25 (Stefan *et al.* 2007) or 18.9 (Mellert and Göttlein 2012). These alarming high foliar N/P ratios indicate severe nutritional imbalance. Long-term increases of N/P ratios in beech foliage are reported in other studies as well (Berger *et al.* 2016; Jonard *et al.* 2015). Our data do not give an explanation for the observed deterioration of P nutrition, but plausible mechanisms are: (i) high soil pH may reduce plant P uptake by promoting P immobilization as calcium phosphates (see above); (ii) as suggested by Jonard *et al.* (2015), increasing tree productivity – driven by high N deposition and rising atmospheric CO_2 – could raise P demand to levels not met by the available P pool, resulting in increased foliar N/P ratios (as observed both here and across Europe; *e.g.*, Duquesnay *et al*. 2000; Flückiger and Braun 1998; Jonard *et al.* 2012, 2015); iii) large decreases in beech foliar P content may be partly explained by a reduction in mycorrhizal abundance due to high atmospheric N deposition (Duquesnay *et al.* 2000), since mycorrhizae play a major role for P uptake in beech trees.

5 Conclusions

A straightforward method for assessing the nutrient site sustainability before considering restrictions in the use of forest biomass is a clear documentation of the initial situation. We compared macro nutrient stocks within the biomass of ca. 146-year-old beech forest stands (without any pre-harvest losses) to available nutrients in shallow soils along a natural fertility gradient from "low" over "medium" to "high" (four stands per fertility class) in the Northern Limestone Alps.

Whole tree biomass was positively correlated with mineral soil stocks of exchangeable K and total P, highlighting these nutrients as limiting factors for tree growth on calcareous bedrock (question 1, see Introduction).

All above ground beech biomass compartments (foliage; branches < 2 cm, 2-5 cm, and > 5 cm diameter; bark of the stem and stem wood) increased along the fertility gradient, confirming the close relationship between site-specific nutrient availability, tree nutrition, and productivity (question 2).

Removed organic carbon and macro nutrients via different harvest intensities of the above ground biomass compartments were expressed in percent of organic carbon and nutrient stocks (remaining biomass on site plus forest floor and mineral soil down to 25 cm). Soil fertility gradient did not affect these ratios (except for P). This means, that with increasing fertility relatively more carbon and nutrients are stored in the above ground biomass without changing the ratio of removed to remaining element. Potassium supply is the main limiting factor (question 3). In contrast to spruce stands, much higher K stocks are sequestered in bark plus stem wood of beech (74 % of the whole above ground tree´s stock).

We conclude that forest harvesting on these sites must be restricted to thick stem wood only, leaving foliage and branches on site. Furthermore, debarking harvested stems directly at the site will markedly improve calculated nutrient balances.

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