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Variations of nutrient concentrations and contents between summer and autumn within tree compartments of European beech (*Fagus sylvatica*)

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Abstract

The paradigm of sustainable forest management was initially aimed to ensure continuous wood supply but has gradually been extended for many functions and services of forest ecosystems, including the aspect of nutrient sustainability. The current tendency towards harvesting all year round and whole-tree export for energy purposes raised the question of how the input : output balance of nutrients depends on site conditions, tree species, and harvest intensity. Possible differences in nutrient export between harvesting in autumn and summer have been more or less neglected. Based on compartment-wise analyses of biomass and nutrient (Ca, K, Mg, and P) concentrations of adult European beeches (*Fagus sylvatica* [L.]), nine compartments were sampled in summer and nine in autumn. We found, for the majority of the compartments (especially in branch wood), increased levels of nutrient concentrations: 81% (Ca), 54% (K), 90% (Mg), and 96% (P) in autumn compared to summer. Upscaling our results to stand level revealed up to 10.0% and 1.6% less mineral nutrient exports of Ca and Mg, respectively, for whole-tree harvest in forest stands when carried out in summer instead of autumn. Nutrient removal was increased by 0.8% and by 13.0% for K and P, respectively, in summer. Despite lower nutrient export, many ecological, logistic, and technical reasons discourage harvesting in summer. Our findings, however, deliver an additional yet so far missing mosaic piece for a better understanding and assessment of the frame conditions for sustainable nutrient management in beech forests.

Key words: seasonal differences / calcium / potassium / magnesium / phosphorus

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1 Introduction

It has long been known that the nutrient content of beech leaves varies seasonally. As early as in 1871, *Wolff* (1871) compiled ash analyses of all important agricultural and forest plants. He documented the decrease of nutrient concentrations in autumn for the elements potassium (K), magnesium (Mg), and phosphorus (P), which is due to the translocation of nutrients from the senescing beech leaves. For calcium (Ca), however, this phenomenon was not documented, mainly due to the fact that Ca is not retranslocated *via* phloem (*Marschner*, 1995). These early findings were confirmed by the study of *Guha* and *Mitchell* (1966), who grouped the elements according to their seasonal behavior. The elements of interest in our study (Ca, K, Mg, and P) can be divided into groups. The first group shows low concentrations after budbreak, gradual increase during summer, and low (of Mg) or nearly no retranslocation (of Ca) in late autumn. The second group contains K and P, showing high concentrations after budbreak, a quick decline to almost constant values in summer, followed by a slight decrease in the time of leaf senescence.

When nutrients are retranslocated from senescent leaves, one should expect increasing nutrient contents in twigs and branches. Investigations, however, are scarce about the seasonal variation of nutrients in tree organs other than leaves. *Gäumann* (1935) did not find an increase of nutrient concentration in twigs or in the bark of branches in late autumn, although an elevated concentration of K and P in the wood of branches was found. For these two elements such an increase was also found in the bark of the stem, as well as in the younger and older wood of the stem. For Ca and Mg, his findings were inconsistent and, thus, do not support the idea that these elements are stored in wood or bark over winter. With respect to all studies mentioned, it should be stated that the nutrient content of tree compartments strongly depends on the nutrient availability at a given site (*Pretzsch* et al., 2014). The results of single studies should not be generalized. However, the knowledge of nutrient concentrations in different tree compartments is very important with respect to nutrient sustainability, which is a prerequisite for preserving the long-term stability and productivity of economically utilized forest ecosystems.

As a regenerative resource, forests can compensate for harvest-induced nutrient exports by nutrient inputs *via* weathering, deposition, and biodegradation (*Jorgensen* et al., 1975). However, highly mechanized methods, such as whole-tree harvesting, may induce nutrient exports by orders of magnitude that cannot be compensated for by forest ecosystems

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and therefore could have a negative influence on site quality and tree growth (*Kimmins*, 1977; *Hornbeck* et al., 1990; *Pretzsch* et al., 2014). *Helmisaari* et al. (2011) compared the effects of whole-tree harvesting and conventional stem harvesting on growth and tree nutrition of Scots pine and Norway spruce in boreal forests. They detected a reduced volume increment of 4% (during the first 10 years) and 8% (during the second 10 years) for pine stands and 5% and 13%, respectively, for spruce stands on the whole-tree-harvested plots. An evaluation of nutrient exports in beech forests by whole-tree harvesting, as compared to conventional stem harvesting (*Joosten* and *Schulte*, 2003), resulted in an increased rate of 18% for biomass harvesting, but an over-proportional removal of Ca (+40%), K (+24%), Mg (+23%), and P (+53%). According to *Hochbichler* et al. (1994), who evaluated biomass and nutrient contents in a 40-year-old European beech (*Fagus sylvatica* [L.]) stand, the highest nutrient contents of N, P, K, Ca, and Mg are located in the trees' leaves, barks, and twigs. In a beech forest in Southern Sweden, an evaluation of biomass primary production and nutrient distribution showed that 60% of the production is concentrated in branches of the beeches (*Nihlgård*, 1972).

This study focuses on concentrations of the macro nutrients, Ca, K, Mg, and P in different tree compartments and their seasonal changes between summer and autumn for European beech. To the authors' knowledge, studies about seasonal tree-internal variations of nutrient concentrations within European beeches do not exist so far. Thus, this work enhances knowledge about seasonal nutrient flows by comparing the differences in nutrient concentrations between summer and autumn within the above-ground tree compartments of European beech, the dominating deciduous tree species in Central Europe. This comparison of seasonal differences can be considered the main novel aspect of our study. The data used in this study were collected on an intensively monitored research plot in Southern Germany. With regard to options such as whole-tree harvesting, we also paid special attention to quantifying the biomass and seasonal nutrient removal in summer and autumn in terms of nutrient concentrations and nutrient contents.

Our work concentrates on the following two research questions: (1) Are there seasonal differences between nutrient concentrations of Ca, K, Mg, and P within different compartments of European beech trees?; (2) What do the results of question (1) mean for the practice of whole tree harvesting in European beech forests?

2 Material and methods

For biomass sampling and nutrient analysis, we selected the experimental plot Freising 813 (FRE 813), which includes pure and mixed stands of Norway spruce (*Picea abies* [L.] KARST) and European beech. The beeches grow in groups that are surrounded by areas of spruces. The potential natural vegetation is a Luzulo-Fagetum (*Walentowski* et al., 2001). The experimental plot FRE 813 is comprised of six parcels (sizes ranging from 2400 m^2 to 7150 m^2) each in a differently aged stand, located in two greater forest areas called "Kranzberger Forst" (48°24′34.49′′ N, 11°38′59.53′′ E), "Grafendorfer Forst" (48°34′34.90′′ N, 11°50′41.93′′ E) close to the town of Freising (Bavaria) in the ecoregion 12 ("Tertiärhügelland") and in the growth district 12.8 ("Oberbayerisches Tertiärhügelland") at a height of approximately 500 m above sea level (*Arbeitskreis Standortskartierung in der Arbeitsgemeinschaft Forsteinrichtung*, 2003). The plot was established as an artificial time series in 1994 as a part of a long-term research program covering the most important mixed stand types. We selected three stands (age 50, 92, and 124 y) from the experimental plot Freising 813 for the study at hand. For more detailed information about the plot design, see *Häberle* et al. (2012) and *Pretzsch* et al. (1998). With an average annual precipitation of 814 mm (476 mm within the vegetation period) and an average annual temperature of 7.7°C (15.0°C within the vegetation period), this is a typical humid climate of the temperate zone (*Enders*, 1996).

The geologic parent material consists of tertiary sediments from the upper freshwater molasse with a variable coverage of loess. As a result of pedogenesis, the predominant soil types are Cambisols and Luvisols (in presence of loess) as well as stagnic or gleyic Luvisols. According to the Bavarian site classification based on *Arbeitskreis Standortskartierung* (2003), the stand with age 124 y is located on the site unit 304 (fresh silt loam), the stand with age 92 y on site unit 204 (fresh loam), and the stand with age 50 y on site unit 207 (moderately stagnic loam). Generally, the soils have a low percentage of stones and plant roots are able to penetrate them well. They show a good mineral nutrient supply and, thus, their dominating humus form is Moder. The topographic conditions of the three stands range from planar to slightly sloped with varying exposition.

2.1 Biomass and nutrient sampling

The age series Freising 813 provides trees and stands at various ages on comparable sites. The basic sampling concept included the selection of 18 differently aged beeches (young, medium-aged, old) intended for felling and subsequent sampling in August 2008 (nine beeches for summer sampling) and in November 2008 (nine beeches for autumn sampling).

In 2008, three beeches [social class by *Kraft* (1884): 1 = dominant, 2 = co-dominant, and 3 = lesser dominant] per stand were selected for summer sampling and three beeches [social class by *Kraft* (1884): 1 = dominant, 2 = co-dominant and 3 = lesser dominant] per stand for autumn sampling (*Assmann*, 1970). To guarantee the comparability of the collected material, particular attention was paid to the fact that the beeches felled in August and November were similar in size and growth patterns in the previous plot records.

Before felling the trees, their social class according to *Kraft* (1884) was recorded and each sampled beech was attributed to a biogroup together with its competitors (defined as neighbor trees touching the crown of the sampled beeches). Within these biogroups, each tree's species and its stem coordinates were determined, as well as diameter at breast height (DBH), tree height, and crown length. Crown dimension was gauged in four main geographic directions and four secondary geographic directions in-between. Table 1 shows the most important dendrometric data of the sample trees.

Before felling, six branches per tree (homogeneously distributed over the whole crown length) were selected as a representative sample in order to extrapolate the biomass of the leaves and branches with diameters $\leq$ 7 cm. To guarantee complete and intact samples, test branches were harvested by tree climbers. The knot diameter and the position of these branches within the crown were measured at the standing tree. After cutting the trees, all branch heights within the crown and their diameter at knot basis were measured, as well as the thickness of bark of the sample branches and some non-sample branches for later bark volume and biomass calculations. To determinate the total tree wood volume, stem and branch compact wood of all sampled beeches were measured section-wise in 2 m steps. Subsequently, six stem discs were cut out for later analysis of diameter over bark, bark thickness, density, and nutrients (1 × stem basis, 1 × DBH, and four discs by relative height of stem wood).

The sample branches were separated into compartments: leaves (in summer) and litter (in autumn) [see Eq. (2)], branch compact wood (Ø over bark > 7 cm) that was also measured section-wise, and branch non-compact wood (Ø $\leq$ 7 cm) that in turn was divided into the classes 1 (Ø $\leq$ 1 cm), 2 (1 cm < Ø $\leq$ 2.5 cm), and 3 (2.5 cm < Ø $\leq$ 7 cm). In the following these classes are termed branch < 1 cm (class 1), branch < 2.5 cm (class 2), and branch < 7 cm (class 3). All compartments of the six sample branches were weighed before drying. Laboratory samples of the compartments were taken for determination of specific fresh and dry weight, specific leaf area (SLA), and for later nutrient analysis. Litter was collected in catch tanks (eight catch tanks per stand, 24 in total) that were emptied four times during leaf fall in autumn 2008. The catch tanks were placed close to the beeches intended for autumn sampling. Due to the minor sample size of nine felled beeches in summer and nine felled beeches in autumn, a differentiation of nutrient concentrations by age and single tree was not taken into account.

Representative samples of all compartments (leaves as well as bark and wood from different diameter) were ground into powder and analyzed for nutrient concentration according to German forest analytical standards (*König*, 2005). Sixty-five mg of sample were digested with freshly distilled HNO_3 at 160°C in quartz vessels in a high-pressure digestion apparatus (Seiff, Germany) for 10 h. The digest was diluted to 14 mL with distilled water and analyzed for nutrient concentrations by ICP-OES (Spectro, Germany). Analytical quality was insured by repeatedly analyzing standard reference material.

2.2 Biometrical evaluation

The forest yield data were calculated using standard methods (*Pretzsch*, 2009). The volumes at forest stand level were based on the merchantable compact wood form factors by *Kennel* (1965). Testing for differences in nutrient concentrations between compartments and season-specific differences between nutrient concentrations in a given tree compartment was done by using a variance analysis with a subsequent unpaired t-test.

2.3 Biomass, nutrient, and volume calculations

2.3.1 Biomass calculations

For determination of biomass, the volumes of stem compact wood and branch compact wood, each separated into bark, sapwood, and heartwood, were calculated for all sampled beeches by assuming frustum (stems) and cylinder shapes (branches). Volumes were converted into biomass by multiplying the estimated wood density of 0.586 g cm^{-3} (calculated average density of investigated beeches in the "Kranzberger Forst") and the assumed bark density of 0.43 g cm^{-3} (*Kramer* and *Akça*, 1988), respectively. For all sampled beeches, the total biomass of stem and branch compact wood was calculated and summed up for summer and autumn.

The biomass of the test branches was calculated and summed up on a single-tree basis for summer and autumn and for the compartments leaf, branch < 1 cm, branch < 2.5 cm, and branch < 7 cm. The compartment branch < 7 cm was divided into bark and wood. For estimating the fresh biomass of the non-sampled branches, a linear regres-

Table 1: Dendrometric data of the felled sampled beeches at single tree level.

FRE813	50 y old stand						92 y old stand						124 y old stand					
	Summer			Autumn			Summer			Autumn			Summer			Autumn		
Kraft Class	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
DBH / cm	29.7	22.5	17.4	27.9	23.2	14.5	82.1	48.4	32.6	67.9	51.1	33.0	74.3	58.2	53.3	76.9	60.2	49.7
Height / m	21.0	21.3	20.7	21.5	19.9	20.1	36.7	35.1	33.2	34.7	33.8	30.1	40.5	39.6	39.7	37.7	37.0	33.7
Crown length / m	17.3	15.5	18.3	15.6	11.0	14.1	31.9	26.5	20.8	28.8	16.3	14.2	31.4	24.7	19.1	24.7	25.9	25.5
Crown width / m	7.3	5.7	5.6	7.1	6.4	4.1	14.4	9.9	6.1	11.6	8.8	5.8	14.4	11.3	8.7	13.0	8.2	11.7

sion model proposed by *Dieler* and *Pretzsch* (2013) was fitted compartment-wise to the sample branch data. Thereby, the compartment branch < 7 cm was divided into bark and wood:

$$\ln(BM) = a + b \times \ln(DBB) + c \times \ln(Rel.HBB) + \varepsilon, \tag{1}$$

where *BM* = branch biomass (kg), *DBB* = diameter at branch base (cm), *Rel.HBB* = relative height of branch basis to tree height, ε = i. i. d. errors, and *a, b, c* = regression parameters.

Figure 1 displays the regression lines by compartment.

Finally, the biomass of the compartments leaf, branch < 1 cm, branch < 2.5 cm, branch < 7 cm, and stem and branch compact wood was summed up for each tree.

Because it is impossible to determine single tree based litter data, litter biomass was estimated by a rule of three:

$$BM_{litter} = \frac{BM_{autum} \times BM_{leaf}}{BM_{summer}}, \tag{2}$$

where BM_{litter} = complete biomass of litter (kg), BM_{autum} = complete biomass in autumn (kg), BM_{leaf} = complete leaf biomass (kg), and BM_{summer} = complete biomass in summer (kg).

The biomass of compact wood in summer and autumn was measured completely; the branches and leaves (in summer) were estimated on the basis of sample branches [see Eq. (1)]. Complete biomass by season (biomass produced in summer and autumn) was summed up afterwards.

2.3.2 Nutrient calculations

The nutrient contents of Ca, K, Mg, and P were calculated on a single-tree basis for each compartment by multiplying the determined biomass with the average nutrient concentration of the respective compartment.

2.3.3 Calculations of solid cubic meter and nutrient contents per hectare

For the following calculations, we assumed that the different compartments' volume ratios of leaf/litter, branch < 1 cm, branch < 2.5 cm, and branch < 7 cm (in the following termed "other compartments") were the same as their biomass ratios. Subsequently, the nutrient contents of Ca, K, Mg, and P per cubic meter were calculated for each compartment on basis of seasonal average nutrient concentrations and weighted by average percentage of biomass of each compartment. Typical stand volumes were taken from the yield table for beech by *Schober* (1975): first yield class, moderate thinning (with the average heights 20.7 m, 33.9 m, and 38.0 m, and the average ages 50 y, 92 y, and 124 y) using each parcel's sample trees as input data. The volumes per hectare were multiplied by nutrient content per unit compact wood and by the arithmetical mean of biomass-weighted nutrient content for the other compartments. Leaves were included for the calculation of nutrient content per hectare for whole-tree harvesting in summer, although litter in autumn was not.

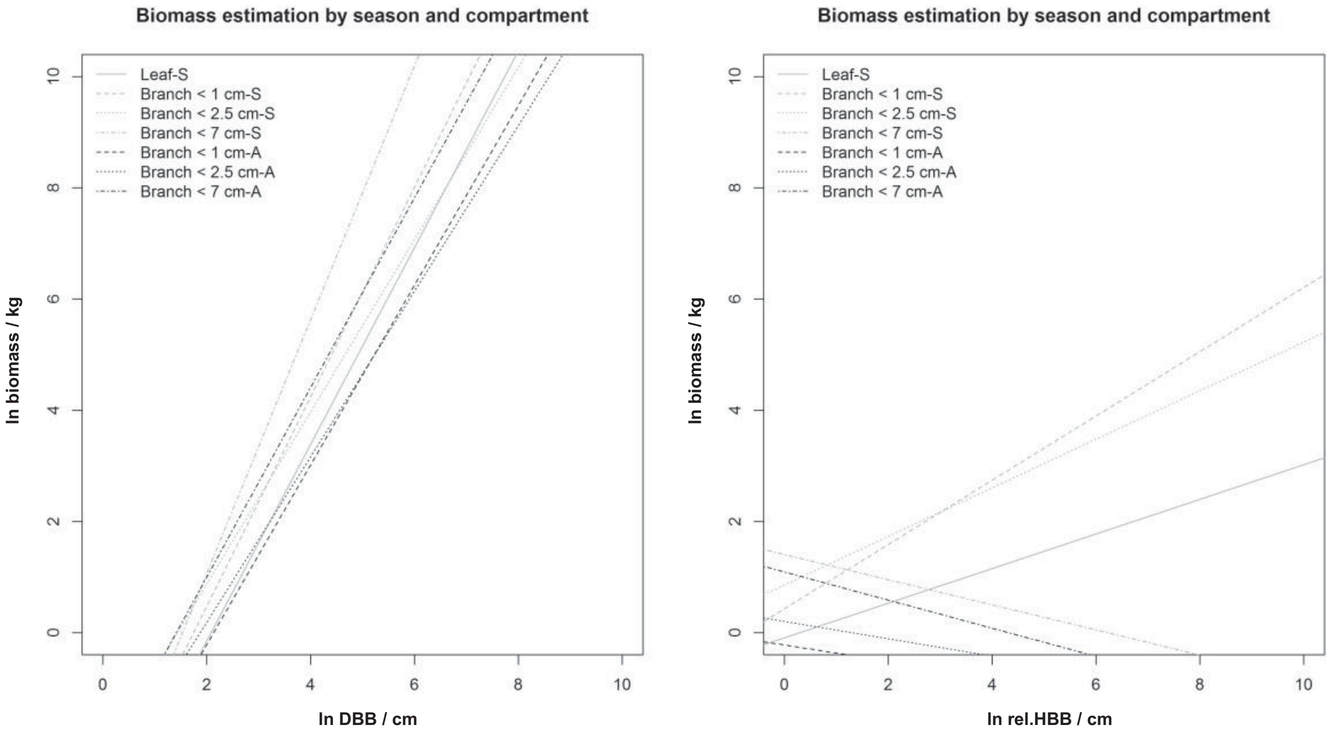

Figure 1: Regression lines of the non-test branches for biomass estimation as a function of *DBB* and *Rel.HBB* by season and compartment (*DBB*: diameter at branch base, *Rel.HBB*: relative height of branch basis to tree height, S: summer, A: autumn).

3 Results

3.1 Nutrient concentrations

3.1.1 Characteristic leaf nutritional parameters

The leaf nutrient concentrations of the nine sampled beeches felled in the summer of 2008 were compared with the nutritional threshold values by *Göttlein* et al. (2011). Phosphorus (1.30 ± 0.02 mg kg^{-1}) and K (6.12 ± 0.13 mg kg^{-1}) were in the lower threshold, and Mg (1.45 ± 0.04 mg kg^{-1}) was in the central range of normal nutrition. Ca (6.32 ± 0.17 mg kg^{-1}), however, fell in the range of latent deficiency. Thus, based on the observed leaf nutritional parameters, the investigated beeches represent beech stands with a normal nutrient supply.

3.1.2 Comparison of nutrient concentrations by season and compartment

Table 2 gives the comparison of average nutrient concentrations of Ca, K, Mg, and P by the seasons summer and autumn and by the compartments branch < 1 cm, branch < 2.5 cm, branch < 7 cm (divided in bark and wood), and compact wood (divided in bark, sapwood, and heartwood).

The highest concentrations were found in the compartments branch < 7cm in summer and in autumn for Ca, in branches < 1 cm in summer and in autumn for K, in branches < 1 cm in autumn for Mg, and in branches < 1 cm in autumn for P. The lowest nutrient concentrations were found in compact sapwood for all four elements. The differences between the examined compartments in summer ranged from significant to highly significant for branches of < 7 cm compared to the other compartments and between bark and wood for Ca. For K, Mg, and P differences between bark and wood were only significant for compact wood. Additionally, the P concentration was significantly different for all compartments. In autumn, there were additionally significant differences in K and P between bark and wood for branches of < 7 cm. The differentiation between the compartments was also more pronounced for K and Mg.

A comparison of nutrient concentrations at the sampling dates (summer and autumn) revealed significantly greater values for all nutrients in branches of < 1 cm in autumn. Highly significant differences were observed for K within branches of < 7 cm and significant differences for Mg within compartment branches of < 2.5 cm. For branches of < 7 cm, the seasonal differences were significant, being greater in the bark for K and P in autumn, as well as greater in the wood for K and Ca in autumn. For compact wood, the concentrations of P and Mg were significantly greater in the bark in autumn as well as for Ca in sapwood.

The biggest increase in autumn was observed in the compartment of branches sized < 1cm for all examined nutrients. This was followed by the compartment of branches < 2.5 cm for Ca, branches < 7 cm for K, and branches < 2.5 cm for Mg. The subdivided compartment branches < 7 cm displayed the largest fluctuations within wood for Ca and bark for K and P. Within the segmented compartment compact wood, the seasonal fluctuations were at a lower level with an exception for P within compartment compact wood bark.

3.2 Calculations of biomass, nutrient contents and volumes

3.2.1 Biomass calculation

Table 3 displays the biomass of the felled sampled beeches. The biomass with bark showed a seasonal similarity in the compartments complete compact wood, complete branch non-compact wood, and complete biomass with marginally lower values in autumn (about –7.5%). The arithmetical means of biomass in summer and in autumn came to 21,733 kg for complete compact wood, 2,791 kg for complete branch non-compact wood and 2,4731 kg for complete biomass.

3.2.2 Percental calculations of biomass and nutrient contents

Table 4 describes the percentage distribution of biomass and nutrient contents of Ca, K, Mg, and P by seasons and by compartments stem and branch compact wood, branch non-compact wood, and leaf/litter. In comparison to its percentage of biomass, the complete compact wood showed a lower percentage of nutrient content for all analyzed nutrients in summer and autumn, especially for P. The difference (%) between stem and branch compact wood within summer and autumn was similar. The biggest variation between percentages of biomass and nutrient content was found in the stem and branch bark, especially the difference for Ca being markedly significant. Generally, P displayed the biggest differences over all compartments of compact wood equated with percentage of biomass. The distinctions between the compartments sapwood and heartwood turned out rather indifferent over all nutrients. By seasonal comparison of complete compact wood, the percentages of Ca, Mg, and P decreased and K increased in autumn. Contrary to compact wood, the percentages of all nutrient contents within complete branch non-compact wood were higher compared to percentages of biomass. The percentages of nutrient contents of Ca, K, Mg, and P within compartments of branch non-compact wood were higher in autumn than in summer, with only one exception for P with a lower percentage in branch < 7 cm. The variations between summer and autumn were relatively big for branches of < 2.5 cm and < 1 cm, while rather marginal for branch of < 7 cm. The leaf/litter displayed higher percentages of nutrient contents than biomass, with one exception for K with a lower percentage in litter. Compared to summer, the percentages of nutrient contents decreased for K, Mg, and P and increased for Ca in autumn.

3.2.3 Calculations of nutrient contents and percentage-weighted nutrient contents per solid cubic meter

Table 5 shows the nutrient contents and arithmetical mean percentages of biomass-weighted nutrient contents of Ca, K, Mg, and P per cubic meter by season and by stem and

Table 2: Comparison of average nutrient concentrations of Ca, K, Mg, and P by compartment and season (Comp.: compartments, Conc.: nutrient concentrations, cv: coefficients of variation, Diff. to summer: difference to summer, Comp. w.: compact wood). Significant differences between seasons (p A-S) and compartments (p Comp.) with $^{*}p \leq 5\%$, $^{**}p \leq 1\%$, $^{***}p \leq 0.1\%$.

		Sampling summer			Sampling autumn			Comparison A-S	
Element	Comp.	Conc. (mg kg $^{-1}$)	cv (%)	p Comp.	Conc. (mg kg $^{-1}$)	cv (%)	p Comp.	Diff. to summer (%)	p A-S
Ca	Branch 1	3.21	24		5.80	54		81	*
Ca	Branch 2.5	2.73	21	*	3.87	62	*	42	
Ca	Branch 7	1.31	13	*** ***	2.10	30	***	60	**
Ca	Compact wood	1.27	11	*** ***	1.47	21	*** **	15	
Ca	Branch 7 bark	12.15	26		14.98	47	***	23	
Ca	Branch 7 wood	0.81	8		1.29	21		58	***
Ca	Comp. w. bark	15.13	23		16.91	32		12	
Ca	Comp. w. sap	0.68	10	***	0.81	19	***	18	*
Ca	Comp. w. heart	0.94	18	***	0.94	15	***	0	
K	Branch 1	1.83	19		2.81	12		54	***
K	Branch 2.5	1.57	16		1.87	21	***	19	
K	Branch 7	1.49	21	*	1.87	16	***	25	*
K	Compact wood	1.27	19	*** *	1.27	10	*** *** ***	0	
K	Branch 7 bark	1.54	22		3.10	12	***	101	***
K	Branch 7 wood	1.49	22		1.81	18		22	*
K	Comp. w. bark	3.04	26		2.74	18		-10	
K	Comp. w. sap	0.99	18	***	1.03	15	***	3	
K	Comp. w. heart	1.42	24	***	1.40	15	*** *	-2	
Mg	Branch 1	0.45	26		0.86	18		90	***
Mg	Branch 2.5	0.41	35		0.62	25	**	50	*
Mg	Branch 7	0.49	31		0.65	44	*	34	
Mg	Compact wood	0.32	18	* ***	0.31	31	*** *** ***	-1	
Mg	Branch 7 bark	0.53	18		0.65	37		25	
Mg	Branch 7 wood	0.49	33		0.67	46		37	
Mg	Comp. w. bark	0.59	17		0.79	31		35	*
Mg	Comp. w. sap	0.20	26	***	0.24	25	***	18	
Mg	Comp. w. heart	0.41	27	*** ***	0.35	46	***	-15	
P	Branch 1	0.76	33		1.48	11		96	***
P	Branch 2.5	0.53	34	**	0.66	24	***	24	
P	Branch 7	0.31	48	*** *	0.31	68	*** ***	0	
P	Compact wood	0.15	41	*** ***	0.13	37	*** *** *	-15	
P	Branch 7 bark	0.33	16		0.53	7	**	58	***
P	Branch 7 wood	0.31	50		0.28	81		-9	
P	Comp. w. bark	0.38	17		0.53	6		37	***
P	Comp. w. sap	0.14	39	***	0.12	43	***	-15	
P	Comp. w. heart	0.14	51	***	0.11	50	***	-26	

Table 3: Summed-up biomass of the felled sampled beeches by season and compartment (BM: biomass, Diff. S-A: difference between summer and autumn, Ø S-A: arithmetic mean values of summer and autumn, c.w.: compact wood, b.n.c.w.: branch non compact wood). The percental differences between summer and autumn by compartment are given in brackets.

Compartment	BM with bark / kg		BM without bark / kg		BM bark / kg		BM heartwood / kg		BM sapwood / kg	
Season	**Summer**	**Autumn**	**Summer**	**Autumn**	**Summer**	**Autumn**	**Summer**	**Autumn**	**Summer**	**Autumn**
Compact wood stem	16544	16459	16084	15910	460	549	8394	8266	7690	7644
Compact wood branch	6017	4446	5752	4223	265	223	2866	2021	2885	2202
Sa. compact wood	**22561**	**20905**	**21836**	**20133**	**725**	**772**	**11260**	**10287**	**10576**	**9846**
Diff. S-A c.w.	**1656 (–7.3%)**		**1703 (–7.8%)**		**–47 (+6.5%)**		**973 (–8.6%)**		**730 (–6.9%)**	
Ø S-A c.w.	**21733**		**20985**		**749**		**10774**		**10211**	
Branch < 1 cm	327	363								
Branch < 2.5 cm	476	514								
Branch < 7 cm	2097	1805	2004	1697	92	107				
Sa. b.n.c.w.	**2900**	**2682**								
Diff. S-A b.n.c.w.	**218 (–7.5%)**									
Ø S-A b.n.c.w.	**2791**									
Leaf	215									
Litter		199								
Sa. complete	**25676**	**23786**								
Diff. S-A complete	**1890 (–7.4%)**									
Ø S-A complete	**24731**									

branch compact wood, branch non-compact wood, and leaf/litter. The nutrient contents of Ca, K, Mg, and P per cubic meter reflected the distribution and the relation of nutrient concentrations between compartments and seasons. The highest nutrient contents of Ca, K, Mg, and P were located in the leaves and litter, while compact wood displayed the lowest values for Ca, K, Mg, and P in summer and autumn. An autumnal ascent of nutrient contents per cubic meter became obvious within compact wood and litter for Ca and within branch non compact wood for all investigated nutrients.

3.2.4 Exemplary calculation of nutrient contents per hectare by season and compartment

Figure 2 displays nutrient contents per hectare of Ca, K, Mg, and P for three differently aged exemplary beech forests by season and by compartments of compact wood and complete tree including compact wood, branch non-compact wood, and leaves (in summer). The corresponding percentage differences are given in Table 6.

The differences (%) of nutrient contents per hectare of Ca, K, Mg, and P between the three differently aged beech stand types were similar for seasons and compartments. The percentage differences of nutrient contents between complete tree and compact wood amounted to 18.7% for Ca, 17.0% for K, 19.1% for Mg, and 30.1% for P in summer, and 20.0% for Ca, 16.8% for K, 21.8% for Mg, and 33.4% for P in autumn. The seasonal comparison showed higher nutrient contents per hectare in autumn for Ca within the complete tree (+10.0%) and compact wood (+8.5%) and for Mg within the complete tree (+1.6%). A decrease in autumn was observed for K within the complete tree (–0.8%) and compact wood (–0.5%), for Mg within compact wood (–1.8%), and for P within the complete tree (–13.0%) and compact wood (–18.7%).

4 Discussion

4.1 Research questions

Although several studies have dealt with biomass and nutrient distributions in compartments of tree species in general (*Helmisaari* et al., 2002; *Jacobsen* et al., 2003) and European beech in particular (*Rademacher* et al., 2009; *Göttlein* et al., 2013), information about seasonal differences of nutrient concentrations in above-ground compartments of European beech are limited. Thus, a comparison of our findings to other investigations proves difficult. This is due to missing comparisons of seasonal variations and significant species-specific differences in biomass percentages and nutrient allocations

Table 4: Percentage distribution of biomass and nutrient contents of Ca, K, Mg, and P by season and compartment (S: summer, A: autumn, A/S: quotient of autumn and summer rounded to one decimal). The percentage values are based on natural biomass and nutrient data.

	Biomass / %			**Ca / %**			**K / %**			**Mg / %**			**P / %**		
Compartment	S	A	A/S	S	A	A/S	S	A	A/S	S	A	A/S	S	A	A/S
Stem bark	1.79	2.31	1.3	17.73	23.62	1.3	3.68	5.04	1.4	3.24	5.41	1.7	4.04	7.32	1.8
Stem sapwood	29.95	32.13	1.1	15.87	14.90	0.9	20.95	24.46	1.2	18.66	22.05	1.2	22.12	23.49	1.1
Stem heartwood	32.69	34.75	1.1	24.04	20.43	0.8	36.01	35.91	1.0	36.90	33.62	0.9	24.75	21.60	0.9
Sa. stem compact wood	**64.43**	**69.19**	**1.1**	**57.64**	**58.95**	**1.0**	**60.64**	**65.41**	**1.1**	**58.80**	**61.08**	**1.0**	**50.91**	**52.41**	**1.0**
Branch bark	1.03	0.94	0.9	9.48	8.59	0.9	2.20	2.02	0.9	1.86	2.34	1.3	2.41	2.88	1.2
Branch sapwood	11.24	9.26	0.8	6.26	4.03	0.6	8.06	7.03	0.9	7.73	6.57	0.8	8.74	5.81	0.7
Branch heartwood	11.16	8.49	0.8	8.23	4.54	0.6	11.58	8.61	0.7	12.32	7.15	0.6	7.06	3.77	0.5
Sa. branch compact wood	**23.43**	**18.69**	**0.8**	**23.97**	**17.16**	**0.7**	**21.84**	**17.66**	**0.8**	**21.91**	**16.06**	**0.7**	**18.21**	**12.46**	**0.7**
Sa. complete compact wood	**87.86**	**87.88**	**1.0**	**81.61**	**76.11**	**0.9**	**82.48**	**83.07**	**1.0**	**80.71**	**77.14**	**1.0**	**69.12**	**64.87**	**0.9**
Branch < 7 cm	8.17	7.59	0.9	8.05	8.91	1.1	10.02	10.12	1.0	12.06	13.14	1.1	13.26	11.42	0.9
Branch < 2.5 cm	1.85	2.16	1.2	3.73	4.45	1.2	2.04	2.85	1.4	2.08	3.57	1.7	5.40	7.93	1.5
Branch < 1 cm	1.28	1.53	1.2	3.02	4.69	1.6	1.75	3.12	1.8	1.69	3.53	2.1	5.87	13.04	2.2
Sa. branch non compact wood	**11.30**	**11.28**	**1.0**	**14.80**	**18.05**	**1.2**	**13.81**	**16.09**	**1.2**	**15.83**	**20.24**	**1.3**	**24.53**	**32.39**	**1.3**
Leaf/litter	0.84	0.84	1.0	3.59	5.84	1.6	3.71	0.84	0.2	3.46	2.62	0.8	6.35	2.74	0.4

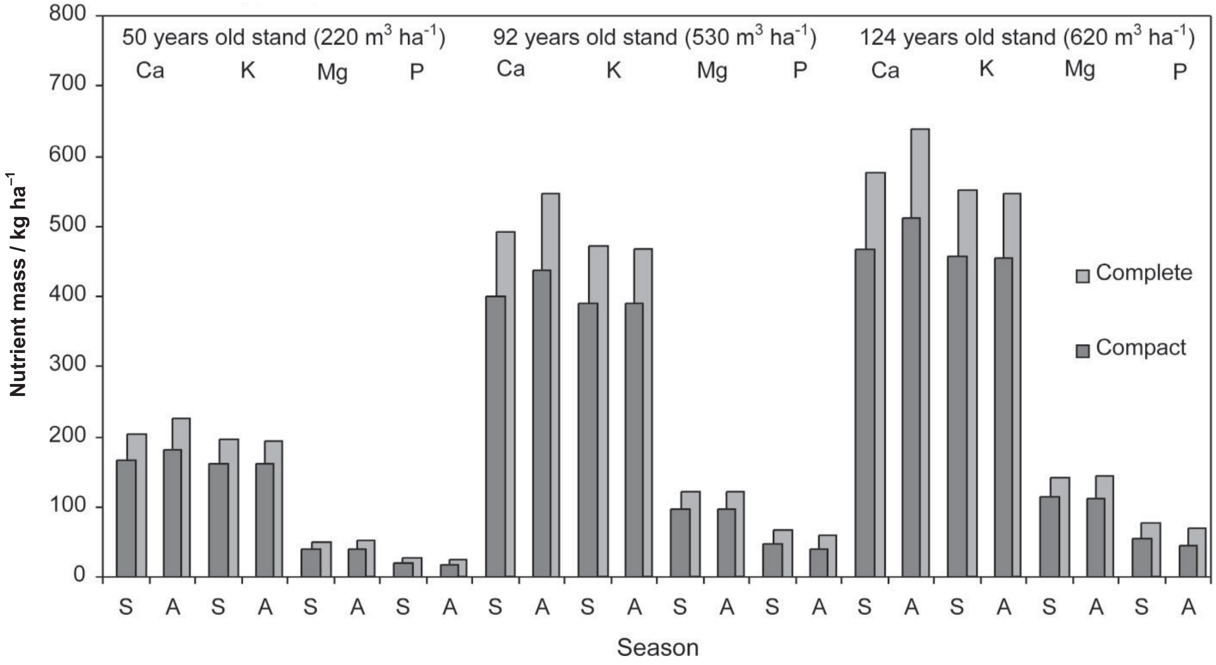

Figure 2: Calculation of nutrient contents per hectare of Ca, K, Mg, and P for three differently aged typical beech forests by season and compartment. The volume values conform to data of the yield table by *Schober* (1975): European beech, I. Class, moderate thinning (S: summer, A: autumn, Compact: compact wood, Complete: complete trees).

among tree components, documented by several authors (*Nihlgård*, 1972; *Kimmins*, 1977; *Perala* and *Alban*, 1982).

(1) Our results partly show significant differences of nutrient concentrations of Ca, K, Mg, and P between the seasons. The largest variations can always be found in branches of

Table 5: Nutrient contents and percentage of biomass-weighted nutrient contents of Ca, K, Mg, and P per cubic meter by season (S: Summer, A: Autumn) and compartment (c.w.: compact wood, b.n.c.w: branch non compact wood). The percental average mean values of biomass by compartment in summer and autumn are shown in column Ø-% Comp. and the differences between summer and autumn are located in rows Diff. S-A. The weighted nutrient contents per cubic meter are displayed in rows compartment weighted. Bark is included for all compartments of compact wood and branch non compact wood.

	Ø -%	**Ca**		**K**		**Mg**		**P**	
	Comp.	**/ kg fm^{-1}**		**/ kg m^{-1}**		**/ kg fm^{-1}**		**/ kg fm^{-1}**	
Compartment	S-A	Summer	Autumn	Summer	Autumn	Summer	Autumn	Summer	Au-tumn
Stem compact wood		0.725	0.791	0.736	0.733	0.185	0.181	0.087	0.073
Diff. S-A stem c.w.		0.066		–0.003		–0.004		–0.014	
Stem c.w. weighted	75.9	0.550	0.600	0.559	0.556	0.140	0.137	0.066	0.055
Diff. S-A stem c.w. weighted		0.050		–0.002		–0.003		–0.011	
Branch compact wood		0.849	0.933	0.742	0.737	0.184	0.183	0.089	0.076
Diff. S-A branch c.w.		0.084		–0.005		–0.001		–0.013	
Branch c.w. weighted	24.1	0.205	0.225	0.179	0.178	0.044	0.044	0.021	0.018
Diff. S-A branch c.w. weighted		0.020		–0.001		0.000		–0.003	
Sa. compact wood weighted	100.0	0.755	0.825	0.737	0.734	0.185	0.181	0.087	0.074
Diff. S-A c.w. weighted		0.070		–0.003		–0.003		–0.014	
Branch < 7 cm		0.811	1.163	0.868	1.092	0.283	0.387	0.181	0.171
Diff. S-A branch < 7 cm		0.352		0.224		0.104		–0.01	
Branch < 7 cm weighted	9.0	0.073	0.105	0.078	0.098	0.025	0.035	0.016	0.015
Diff. S-A branch < 7 cm weighted		0.032		0.020		0.009		–0.001	
Branch < 2.5 cm		1.517	2.174	0.871	1.066	0.23	0.344	0.297	0.373
Diff. S-A branch < 2.5 cm		0.657		0.195		0.114		0.076	
Branch < 2.5 cm weighted	2.3	0.035	0.050	0.020	0.025	0.005	0.008	0.007	0.009
Diff. S-A branch < 2.5 cm weighted		0.015		0.004		0.003		0.002	
Branch < 1 cm		1.757	3.244	1.001	1.574	0.249	0.483	0.414	0.814
Diff. S–A branch < 1 cm		1.487		0.573		0.234		0.4	
Branch < 1 cm weighted	1.6	0.028	0.052	0.016	0.025	0.004	0.008	0.007	0.013
Diff. S–A branch < 1 cm weighted		0.024		0.009		0.004		0.006	
Sa. branch non compact wood weighted	112.9	0.136	0.207	0.114	0.148	0.035	0.050	0.030	0.037
Diff. S–A b.n.c.w.		0.071		0.034		0.016		0.007	
Leaf/Litter		3.788	6.662	3.719	0.786	0.875	0.699	0.785	0.323
Diff. leaf/litter		2.874		–2.923		–0.176		–0.462	
Leaf/Litter weighted	1.0	0.038	0.067	0.037	0.008	0.009	0.007	0.008	0.003
Diff. leaf/litter weighted		0.029		–0.029		–0.002		–0.005	
Sa. complete (= weighted)	113.9	0.929	1.098	0.889	0.890	0.228	0.239	0.125	0.114
Diff. S/A complete (= weighted)		0.170		0.001		0.011		–0.011	
Sa. complete without litter			1.032		0.882		0.232		0.111

Table 6: Calculation of nutrient masses per hectare of Ca, K, Mg and P for three differently aged typical beech forests by season and compartment. The volume values conform to data of the yield table by *Schober* (1975): European beech, I. Class, moderate thinning. The differences between complete nutrient mass and nutrient mass of compact wood by seasons summer and autumn are displayed in rows Diff. C./C.. The seasonal disparity of complete nutrient mass and nutrient mass of compact wood in summer and autumn are illustrated in columns Diff. A-S. The percental differences of nutrients between summer and autumn and between whole tree and compact wood are enclosed in brackets.

Age / y	50			92			124		
Height / m	20.7			33.9			38.0		
Yield / m^3 ha^{-1}	220			530			620		
	Summer	**Autumn**	**Diff. A-S**	**Summer**	**Autumn**	**Diff. A-S**	**Summer**	**Autumn**	**Diff. A-S**
Ca-Complete / kg ha^{-1}	204.33	227.00	22.67 (10.0%)	492.24	546.85	51.61 (10.0%)	575.83	639.71	63.89 (10.0%)
Ca-Compact / kg ha^{-1}	166.07	181.55	15.47 (8.5%)	400.09	437.37	37.28 (8.5%)	468.03	511.64	43.61 (8.5%)
Diff. C./C. Ca / kg ha^{-1}	38.25 (18.7%)	45.45 (20.0%)		92.15 (18.7%)	109.49 (20.0%)		107.80 (18.7%)	128.08 (20.0%)	
K-Complete / kg ha^{-1}	195.54	194.03	–1.51 (–0.8%)	471.07	467.43	–3.64 (–0.8%)	551.06	546.81	–4.25 (–0.8%)
K-Compact / kg ha^{-1}	162.24	161.47	–0.77 (–0.5%)	390.85	389.00	–1.85 (–0.5%)	457.22	455.06	–2.16 (–0.5%)
Diff. C./C. K / kg ha^{-1}	33.30 (17.0%)	32.56 (16.8%)		80.22 (17.0%)	78.43 (16.8%)		93.84 (17.0%)	91.75 (16.8%)	
Mg-Complete / kg ha^{-1}	50.22	51.03	0.81 (1.6%)	120.97	122.93	1.96 (1.6%)	141.52	143.81	2.29 (1.6%)
Mg-Compact / kg ha^{-1}	40.65	39.93	–0.72 (–1.8%)	97.92	96.19	–1.74 (–1.8%)	114.55	112.52	–2.03 (–1.8%)
Diff. C./C.Mg / kg ha^{-1}	9.57 (19.1%)	11.10 (21.8%)		23.05 (19.1%)	26.75 (21.8%)		26.97 (19.1%)	31.29 (21.8%)	
P-Complete / kg ha^{-1}	27.52	24.36	–3.16 (–13.0%)	66.29	58.68	–7.61 (–13.0%)	77.55	68.64	–8.90 (–13.0%)
P-Compact / kg ha^{-1}	19.25	16.22	–3.03 (–18.7%)	46.37	39.07	–7.29 (–18.7%)	54.24	45.71	–8.53 (–18.7%)
Diff. C./C. P / kg ha^{-1}	8.27 (30.1%)	8.14 (33.4%)		19.93 (30.1%)	19.61 (33.4%)		23.31 (30.1%)	22.94 (33.4%)	

< 1 cm, followed by branch sizes of < 2.5 cm, and with an exception for K in branches of < 7 cm, while the lowest fluctuations can always be found in compact wood. Mostly the nutrient concentrations are higher in autumn with the exception of K in compact wood. Ca and Mg follow the pattern of seasonal variations in the stem (a strong increase of nutrient concentrations in early spring, a lower level in summer, and again an increase in autumn and winter) and conform to results of *Glavac* et al. (1990); but by contrast, a maximum of K in autumn was not observed. *Gäumann* (1935) analyzed the nutrient balance of European beeches on the basis of raw ash in the course of a year by comparing stem, branches and twigs. Although the absolute values cannot be compared to our findings due to different analytical methods, the seasonal relationship of nutrient distributions are similar to our results and follow the same patterns for all investigated compartments throughout the year (Table 2).

(2) A seasonal comparison between removed nutrient contents reveals a higher export in autumn for Ca in whole tree (10.0%) and compact wood (8.5%), and marginal differences in nutrient exports for K (–0.8% whole tree, –0.5% compact wood) and for Mg (1.6% whole tree, –1.8% compact wood). In contrast, lower removals in autumn can be observed for P (–13.0% whole tree, –18.7% compact wood). A seasonal comparison between nutrient removals by whole-tree harvesting and conventional harvesting results in higher losses of Ca in summer (18.7%) and autumn (20.0%), K (17.0% summer, 16.8% autumn), Mg (19.1% summer, 21.8% autumn), and in particular P (30.1% summer, 33.4% autumn) for whole-tree harvesting (Fig. 2, Table 6). Thus, compared to the proportion of biomass, the percentage of exported nutrient amounts by whole-tree harvesting is over-proportional for all of the investigated nutrients, especially for P. With an exception for Mg in summer as well as in autumn, our findings (especially for Ca and P) differ from results by *Joosten* and *Schulte* (2003), who estimated a higher biomass by 18% but an over-proportional

export of Ca (40%), K (24%), Mg (23%), and P (53%) through whole-tree harvesting. Besides the negative effect on nutrient balance, the cumulative damages to the remaining stands by skidding whole trees also should be taken into account. Compared to stem-only harvesting, at least two-thirds of the wounds in the remaining stands are caused by skidding whole trees (*Kelly*, 1983). In summary, whole-tree harvesting can deplete stands more easily, which would lead to degeneration associated with a decrease in volume increment (*Helmisaari* et al., 2011). Applications of artificial and cost-intensive fertilizers would be necessary in order to compensate for nutrient loss. By contrast, bark, branches and twigs could also be considered as a natural fertilizer, resisting exploitation, and worth leaving in forest stands. Though a trend in accumulation of nutrients in autumn leads to higher nutrient exports, the disadvantages of timber harvesting predominate in summer. Timber harvesting should take place within the vegetation-free period to avoid larger damages to trees and soils by skidding trees and a higher risk of calamities caused by insects. Other ecological aspects (*e.g.*, breeding season and rearing offspring) also discourage timber harvesting within the vegetation period.

4.2 Physiological relevance

On the basis of our calculated data, approximately 88% of the biomass are located in compact wood and approximately 11% in branch non-compact wood (for whole tree = 100%) (Tables 3 and 4). Nutrient concentrations per compartment decrease in the order of leaf > twigs > branches > compact wood and nutrient concentrations per sub-compartment decline in the order of bark > wood. The level of nutrient content is in the order of Ca > K > Mg > P. The patterns of distribution comply with allocations of biomass and nutrients in aspen stands reported by *Wang* et al. (1995). Our results show that the investigated nutrients are mainly concentrated in compact wood bark (Ca, K, Mg, P), branch < 7 cm bark (Ca), and in the branches of < 1 cm (K, P). Compared to wood, bark presents higher nutrient concentrations (*Hochbichler* et al., 1994) but a minor percentage of biomass. As a consequence, branch non-compact wood is over-proportionate in its percentage of biomass; it is higher in nutrient concentration due to its larger proportion of nutrient-rich bark, but the majority of nutrient amounts is accumulated in compact wood (*Jacobsen* et al., 2003; *Göttlein* et al., 2013). Similar to bark, the effect of leaf on nutrient amount can, in spite of high compartmental nutrient concentration, be regarded as marginal due to the smallest proportion of biomass (approx. 1%). Comparing leaf and litter reveale declining nutrient contents in autumn by factor (A/S) 0.2, 0.8, and 0.4 for K, Mg, and P, respectively. In contrast, the amount of Ca in litter is enhanced by factor 1.6 (Table 4). As an immobile nutrient, Ca is accumulated in litter, while P and K, as mobile and soluble nutrients, are translocated easily to the tree before leaf fall. The seasonal shifts of nutrients and the translocation patterns between leaf and litter agree well with findings by *Bockheim* et al. (1991) and *Helmisaari* (1992).

4.3 Critique and generalizability

As a consequence of data acquisition and experimental design, both collectives of sampled beeches in summer and in autumn differ in biomass and nutrient concentrations and cannot be simply compared without biomass correction. This was achieved by averaging summer and autumn biomass. For volume calculations of the leaf/litter, the percentages of biomass were transferred to percentages of volume, although the density differs from the density of wood. Thus, the volumes of leaf/litter only describe artificial values, otherwise an integration of the leaves in the volume calculations would not have been possible. Due to the time-consuming and cost-intensive data acquisition and nutrient analyses, repetitions over multiple years could not be conducted; however, it can be assumed that seasonal variations of nutrient concentrations can be influenced by antecedent conditions of moisture and temperature. Such factors can affect nutrient uptake, storage, and loss, but they cannot be quantified. Our findings cannot be simply transferred to other locations with varying climatic and geological conditions. The examined sampled beeches only represent beech forests with a normal nutrient supply, and trees will react differently on various sites dependant on the availability of nutrients (*Rademacher* et al., 2009). According to *Von Fircks* et al. (2001), the concentrations of Ca, K, Mg, and P in all tree compartments are positively correlated to the rate of nutrient supply. In conclusion, trees of locations with a higher nutrient supply can absorb nutrients more efficiently than those of locations with low nutrient supply, but even marginal nutrient exports from stands with substandard nutrient supply will cause an over-exploitation (*Joosten* and *Schulte*, 2003).

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