Nova Acta Leopoldina NF *114*, Nr. 391, 255–265 (2013)

Tree-internal Nutrient Distribution of Beech and Spruce at the Kranzberger Forst – Implications for Efficiency of Wood Production and for Nutrient Export with Different Harvest Intensities

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With 3 Figures and 4 Tables

Abstract

Amount and tree-internal distribution of nutrients have an influence on the efficiency of production and maintenance of biomass as well as on nutrient exports by harvest. At the Kranzberger Forst, a site with optimal nutrient supply, three trees each of beech and spruce, at the age of 54 resp. 61 years, were harvested and analyzed in detail. Because of the low proportion of leafs, the green biomass of beech has a high nutrient related efficiency of wood production as well as of above ground biomass maintenance. However, for beech with its high amount of nutrients in the wood the efficiency of wood formation is rather low. Because of the smaller crown projection area for spruce most calculated space related efficiencies for this species are more favorite. Calculating the space related efficiency of biomass maintenance, however, the two species have rather similar values. Whole tree harvest of spruce leads to clearly higher nutrient exports at the site Kranzberger Forst, due to higher tree density and the higher allocation of nutrients to the crown.

Zusammenfassung

Menge und bauminterne Verteilung von Nährstoffen beeinflussen sowohl die Effizienz von Biomassebildung und -unterhalt als auch den Export von Nährstoffen bei der Biomasseernte. Im Kranzberger Forst, einem Standort mit ausgeglichenem Nährstoffangebot, wurden je 3 Fichten und 3 Buchen im Alter von 54 bzw. 61 Jahren geerntet und einer detaillierten Beprobung unterzogen. Aufgrund des geringen Gewichtsanteils an Blättern zeigen Buchen eine hohe nährstoffbezogene Effizienz der grünen Biomasse sowohl in Bezug auf die Bildung von Holz als auch in Bezug auf die Unterhaltung der gesamten oberirdischen Biomasse. Die Buche hält jedoch mengenmäßig einen sehr hohen Anteil ihrer Nährelemente im Holz und ist somit relativ ineffizient in der direkten Holzbildung. Führt man bei den Effizienzbetrachtungen einen Flächenbezug ein, so schneidet die Fichte wegen ihrer geringeren Kronenschirmfläche deutlich günstiger ab. Bei der flächenbezogenen Effizienz des Biomasseunterhalts sind sich die Baumarten jedoch sehr ähnlich. Aufgrund der bauminternen Nährstoffverteilung und der höheren Stammzahl werden bei einer Vollbaumernte im Kranzberger Forst bei Fichte deutlich mehr Nährelemente exportiert als bei Buche.

1. Introduction

Although studies of nutrient concentrations in different tree organs and in foliage are available (e.g. JACOBSEN et al. 2003, RADEMACHER 2005, WYTTENBACH et al. 1995), detailed data for the comparison of beech and spruce with respect to nutrient allocation on the same site

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are rather scarce. For a better understanding of the differences between these two species, which may also reflect different ecological strategies, a comparative study of mature beech and spruce trees growing at the Kranzberger Forst (Bavaria, Germany), a site with nearly optimal nutrient supply was carried out. Nutrient concentrations of all plant compartments in combination with the respective biomass and volume increment were used to calculate the nutrient related efficiency of wood production as well as the implications of tree internal nutrient distribution for quantification of nutrient export for different harvest intensities.

2. Material and Methods

In 2004 at the experimental site "Kranzberger Forst" (Pretzsch et al. 1998), three representative trees each of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) were chosen for total harvest and detailed nutrient analysis of above ground biomass. Tree ages were determined with 54 years for spruce and 61 years for beech. According to common practices for nutrient analysis (*BMELF* 1994) beech was harvested at the beginning of August (fully developed leaves before senescence) and spruce in November (vegetation dormancy).

For the three harvested trees of beech, three main branches each were chosen and representatively sampled for leaves in different distances from the top, as well as twigs and branches of different diameter classes. For branch samples > 1 cm diameter wood and bark were analyzed separately. For the three harvested trees of spruce, one representative branch each of the whorls 1, 4, 7, 10, 15 and 20 was chosen for analysis. For each branch representative samples from needles of each age class as well as twigs from each age class were taken. Samples from branches were grouped by diameter classes and analyzed separately for bark and wood. For beech and spruce stem discs were cut in different stem heights and separately analyzed for bark and wood. For more details with respect to the sampling scheme see Göttlein et al. (2013).

All samples were dried, ground to powder and analyzed for nutrient elements by acid digestion with HNO_3 and subsequent ICP-OES spectroscopy (for metals, P and S) as well as by combustion in an elemental analyzer (for N). For detailed description of the analytical methods used see *Gutachterausschuss Forstliche Analytik* (2005). Biomasses of the trees were calculated using the detailed measurements during harvest and the model Silva (Pretzsch et al. 2002). All data were specified resp. calculated on a dry weight basis. Growth increment of woody biomass of the selected trees was derived as an annual average from a five years period before harvest (1999–2004). The data given for the area of one hectare were calculated on the basis of all measured 482 beech trees respectively 553 spruce trees and subsequent extrapolation.

The soil at Kranzberger Forst is characterized as a luvisol derived from loess, layered above tertiary sediments and showing a tendency to stagnant moisture in the deeper mineral soil (according to the German soil classification: "im Unterboden schwach haftnässe-pseudovergleyte Parabraunerde aus Löß über tertiären Molassesedimenten"). The combination of low pH in the topsoil and high base saturation in the deeper soil enables an optimal nutrition for beech and spruce for macro and micro nutrients (Göttlein et al. 2013).

Although statistics with only three random samples per group are very critical, mean values of beech and spruce were compared using t-Test, supposing that there is an approximately normal distribution of the collectives and that their variances are homogeneous.

3. Results and Discussion

3.1 Tree Internal Nutrient Distribution of Beech and Spruce

For beech and spruce at Kranzberger Forst about three quarter of the biomass is allocated to trunk wood, in Figure 1 divided into the fractions stem and crown. The rest of the biomass is distributed between branches, twigs, bark and foliage, with differences emerging between species. Beech has a high proportion of branch biomass, with a considerable amount allocated to branches greater 7 cm in diameter which is the smallest diameter for merchantable wood. In contrast, spruce shows a higher amount of biomass allocated to needles and bark. Although the proportion of bole wood is similar for beech and spruce there are large differences in the proportion of nutrients stored in this compartment. Beech allocates much more nutrients into the wood than spruce, with highest differences found for K and Mg. With respect to branches (< 7 cm) and twigs the very high proportion of Ca allocated to these compartments by beech is striking. In contrast spruce allocates a much higher proportion of K, Mg and Ca into the bark. Due to its evergreen character spruce holds more biomass in its green parts and also incorporates there a higher proportion of nutrients (Tab. 1). It is well known since long time (Wolff 1880, Fiedler et al. 1973) that usually nutrient concentrations in plant tissues of beech are higher than in spruce. However, studies on nutrient partitioning within mature trees of beech and spruce are scarce especially with the focus to compare the two species on the same forest site. Weis and Göttlein (2002) compared nutrient storage in beech and spruce at the experimental site "Höglwald", however, in the period of vegetation dormancy so that the green biomass of beech was not included in their study. For beech a study on nutrient partitioning was done in Brandenburg/Germany (Krauss and Heinsdorf 2008), resulting in a very similar biomass distribution as compared to the Kranzberger Forst. However, for the partitioning of nutrients there were marked differences with beech at Kranzberger Forst incorporating a lower proportion of P and K to stem wood, whereas the proportion of Ca in this compartment was considerably higher. These differences are on the one hand due to different site conditions, on the other hand genetic differences (provenance) may be of importance. Because it is long known, that nutrient contents in plant tissues vary dependent on soil chemical properties (Becker-Dillingen 1939) the detailed results obtained at Kranzberger Forst may only be extrapolated to comparable site conditions, cautioning generalization for beech or spruce. However, the obvious and general differences between the two species with respect to biomass and nutrient allocation can lead to universally valid conclusions about aspects of efficiency of wood production and nutrient exports by harvesting as described in the following chapters.

Tab. 1 Percentage of biomass and nutrients allocated to the green biomass of beech and spruce; lower values are printed in italics; significant differences between species are indicated by * for $p < 0.05$

	Biomass	N	P	K	Ca	Mg
Spruce needles	5.1*	22.0*	27.4*	20.8*	13.3*	14.7*
Beech leaves	*1.0*	*9.4*	*11.5*	*6.1*	*3.4*	*5.7*

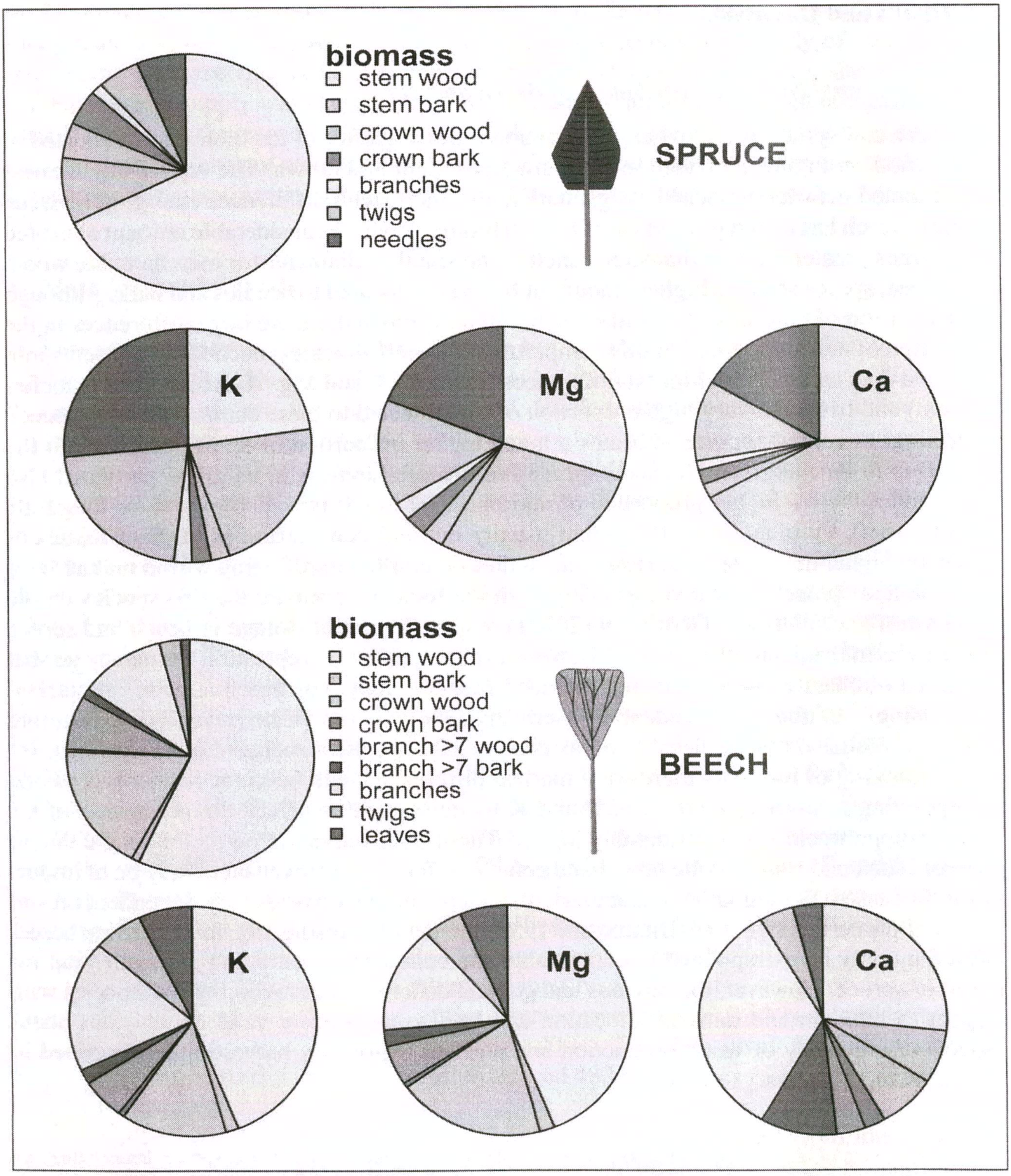

Fig. 1 Allocation of biomass and nutrients to different compartments of spruce and beech

3.2 Nutrient Related Efficiency Parameters of Wood Production

In Table 2 the nutrient related efficiency of wood production of single trees is calculated on three different principles. With respect to the amount of nutrients allocated to the green biomass for all elements beech is much more effective in wood production than spruce. This is valid for calculations based on volume (cm^3 wood per g nutrient) as well as on weight (g wood per g nutrient). This differentiation is important because of the large difference in wood density of the two species. Especially for P the efficiency of beech is very high, leading to significant differences, although there are only three trees per species with considerable tree to tree variation. With respect to the efficiency of carbon incorporation (g wood per g nutrient) also N and K reach the range of significance. The clear advantage of beech against spruce for this calculation base is not surprising, because of the comparatively low amount of nutrients allocated to the green biomass (Tab. 1).

Tab. 2 Single tree efficiency of wood production of beech and spruce in relation to nutrients allocated to the green biomass, to the total aboveground biomass and to wood biomass; lower values are printed in italics; significant differences between species are printed in bold and indicated by ^{x} for $p < 0.10$ and * for $p < 0.05$

		Nutrient related efficiency of wood production basis: green biomass		Nutrient related efficiency of wood production basis: above ground biomass		Nutrient related efficiency of wood production basis: wood biomass	
		cm^3 wood per g nutrient	g wood per g nutrient	cm^3 wood per g nutrient	g wood per g nutrient	cm^3 wood per g nutrient	g wood per g nutrient
Spruce	N	*63*	*32*	14	*7*	**1165***	*590*
	P	*820*	*415*	226	*115*	45 269	22 906
	K	*205*	*104*	**42**^{x}	21	**4842***	**2450***
	Ca	*170*	*86*	23	*11*	**2646***	*1339*
	Mg	*1025*	*518*	150	76	**14 263***	**7217***
Beech	N	133	**92**^{x}	*13*	9	*924*	638
	P	**2577**^{x}	**1778**^{x}	302	208	*29 181*	*20 135*
	K	470	**324**^{x}	*28*	*19*	*1623*	*1120*
	Ca	630	435	*21*	14	*2054*	1417
	Mg	1741	1201	*104*	*71*	*5026*	*3468*

Regarding the efficiency of wood production in relation to the nutrients incorporated to the whole above ground biomass for N, Ca and Mg the differences between the two species are almost vanishing. For P there is still an advantage of beech, however, far away from getting significant. For K, however, only on a volume basis the efficiency of spruce is significantly higher. Although there are no big differences on the basis of individual trees as calculated in Table 2 there are still marked differences between beech and spruce on the basis of stand area. At our site there are 550 spruce trees per ha, as compared to 296 beech trees on the same area. This means, that for hypothetical pure stands of beech or spruce on an area basis spruce is more effective in wood production than beech (see also Tab. 3).

Regarding the efficiency of wood production based on the amount of nutrients invested to the wood biomass the results are completely changing, with spruce being much more effective on a volume basis than beech, significant for all elements except of P. On the weight basis, this clear advantage of spruce, however, disappears for the elements N, P and Ca. For K and Mg spruce still is about twice as effective as beech on the weight basis.

When calculating the efficiencies listed in Table 2 in relation to the crown projection area, space related efficiencies of wood production can be derived (Tab. 3). With respect to

Tab. 3 Space related efficiency of wood production of beech and spruce with relation to nutrients allocated to the green biomass, to the whole aboveground biomass and to wood biomass; space is defined as the crown projection area; lower values are printed in italics; significant differences between species are printed in bold and indicated by ^{x} for $p < 0.10$ and * for $p < 0.05$

		Nutrient related efficiency of wood production basis: green biomass		Nutrient related efficiency of wood production basis: above ground biomass		Nutrient related efficiency of wood production basis: wood biomass	
		cm³ wood per g nutrient	g wood per g nutrient	cm³ wood per g nutrient	g wood per g nutrient	cm³ wood per g nutrient	g wood per g nutrient
Spruce	N	5	3	**1.2***	**0.6**^{x}	**99***	**50***
	P	71	*36*	19.9	10.1	4082	2066
	K	18	9	**3.7***	**1.9***	**402***	**203***
	Ca	*15*	*7*	**1.9***	**1.0***	**224***	**113***
	Mg	89	45	**12.8***	**6.5***	**1171***	**593***
Beech	N	*3*	*2*	*0.3*	*0.2*	*23*	*16*
	P	*67*	46	*7.8*	*5.4*	*735*	*507*
	K	*12*	*8*	*0.7*	*0.5*	*41*	*28*
	Ca	17	11	*0.5*	*0.4*	*52*	*36*
	Mg	*45*	*31*	*2.7*	*1.9*	*129*	*89*

nutrients in the green biomass the efficiencies of beech and spruce were rather similar with no significant differences. However, area related efficiencies of spruce on the basis of nutrients in the total above ground biomass and on the basis of nutrients in wood were much higher, being significant for all elements, except of P.

Leaving the anthropocentric view of wood production, in Table 4 efficiencies of biomass maintenance (total aboveground biomass) by the green biomass were calculated. On the individual tree level, this efficiency is significantly higher for all elements for beech. However, because the crown area of beech (average 39.9 m²) is more than three times higher than that of spruce (average 12.2 m²), on an area basis this advantage of beech is vanishing and no significant differences were detected.

Beech is the naturally dominating tree species in Central Europe with a high physiological tolerance and competitiveness (Ellenberg 1996). The high efficiency of its green biomass to support biomass and growth is important for the competitiveness of beech trees. Because with relation to crown area this advantage is not given, the key of success of beech is its capability of space occupation (Pretzsch and Schütze 2005). Beech is very shade tolerant as seedling and also produces very dark stands as adult tree (Lyr et al. 1996). Furthermore, its plasticity of crown formation is high, and thus the potential of space sequestration and filling gaps in the forest canopy (Roloff 2001). Once the canopy space has been occupied the maintenance costs for the tree are relatively low. This advantage of beech is given in the range of its ecological optimum. At the edges of this range the high potential for space sequestration and space occupation is getting lower, and thus the advantage of low maintenance costs cannot be established.

The benefit or disadvantage of the relatively high proportion of nutrients incorporated in beech wood (stem and branches) remains unclear. Compared to other important central Eu-

Tab. 4 Efficiency of biomass maintenance (g total biomass per g nutrient in green biomass) of beech and spruce; lower values are printed in italics; significant differences between species are printed in bold and indicated by ˣ for $p < 0.10$ and * for $p < 0.05$

		g total biomass per g nutrient	g total biomass per g nutrient and m² crown
Spruce	N	*1453*	124
	P	*18878*	*1623*
	K	*4717*	403
	Ca	*3922*	*334*
	Mg	*23551*	2032
Beech	N	**4379***	*111*
	P	**83823***	2130
	K	**15363***	*390*
	Ca	**19844***	510
	Mg	**55755***	*1417*

ropean tree species (spruce, oak, pine, fir, maple) nutrient concentrations in wood are rather high (Jacobsen et al. 2003), which is the reason why in former times especially beech wood was burned for producing potash (Stinglwagner et al. 2005). The investment for acquiring relatively high nutrient contents in woody compartments, however, could also be a competitive strategy to withhold nutrients from potential competitors, to keep nutrients in the habitat and to slowly reallocate them for the next beech generation during decomposition. Such a strategy of beech may be of advantage in natural forests, even on nutrient poor sites. In managed forests, however, high nutrient contents in woody parts lead to higher nutrient export by wood harvest. Thus, forest management has to consider such differences in nutrient contents between beech and spruce in order to warrant nutrient sustainability for future tree generations, as shown in the following paragraph.

3.3 Implications of Tree Internal Nutrient Distribution on Nutrient Export by Harvesting

For biomass, as well as for all nutrients the proportion allocated to wood is higher for beech than for spruce (Fig. 2), especially for P, K and Mg for which the allocation to wood is more than doubled compared to spruce. Adding the proportions of wood and bark, which corresponds to the conventional harvesting, the difference between beech and spruce for biomass is vanishing. It should be noted that for this approach all woody biomass compartments of beech larger than 7 cm in diameter were included, with respect to fact that considerable fractions of thick branches being especially important for pulpwood or fire wood. Furthermore, beech leaves were not included in the calculations of nutrient export because beech in general is harvested in the winter half year. However, for all nutrients, except for Ca, the relative proportion of nutrients stored in wood and bark for beech is still higher, even though spruce incorporates a high amount of nutrients to the bark. Comparing beech and spruce at Kranzberger Forst nutrient export by harvest may be more efficiently reduced in spruce stands by leaving bark and crown material in the stand. For beech the potential for a reduction of nutrient export by optimized harvesting strategies is much lower.

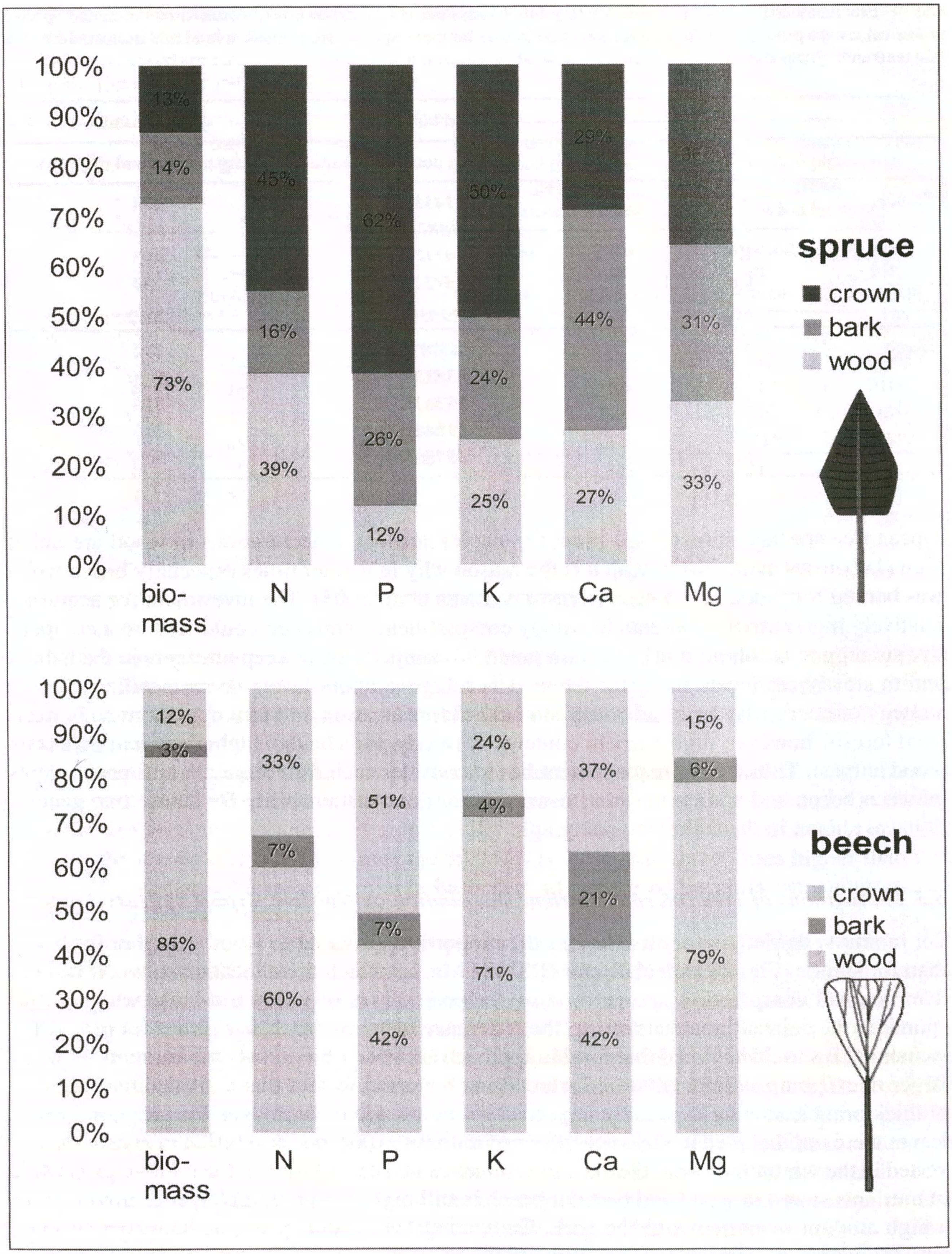

Fig. 2 Implication of different harvest intensities on biomass and nutrient removal; average value per tree; for beech the leaves were not included because beech is normally harvested in winter time.

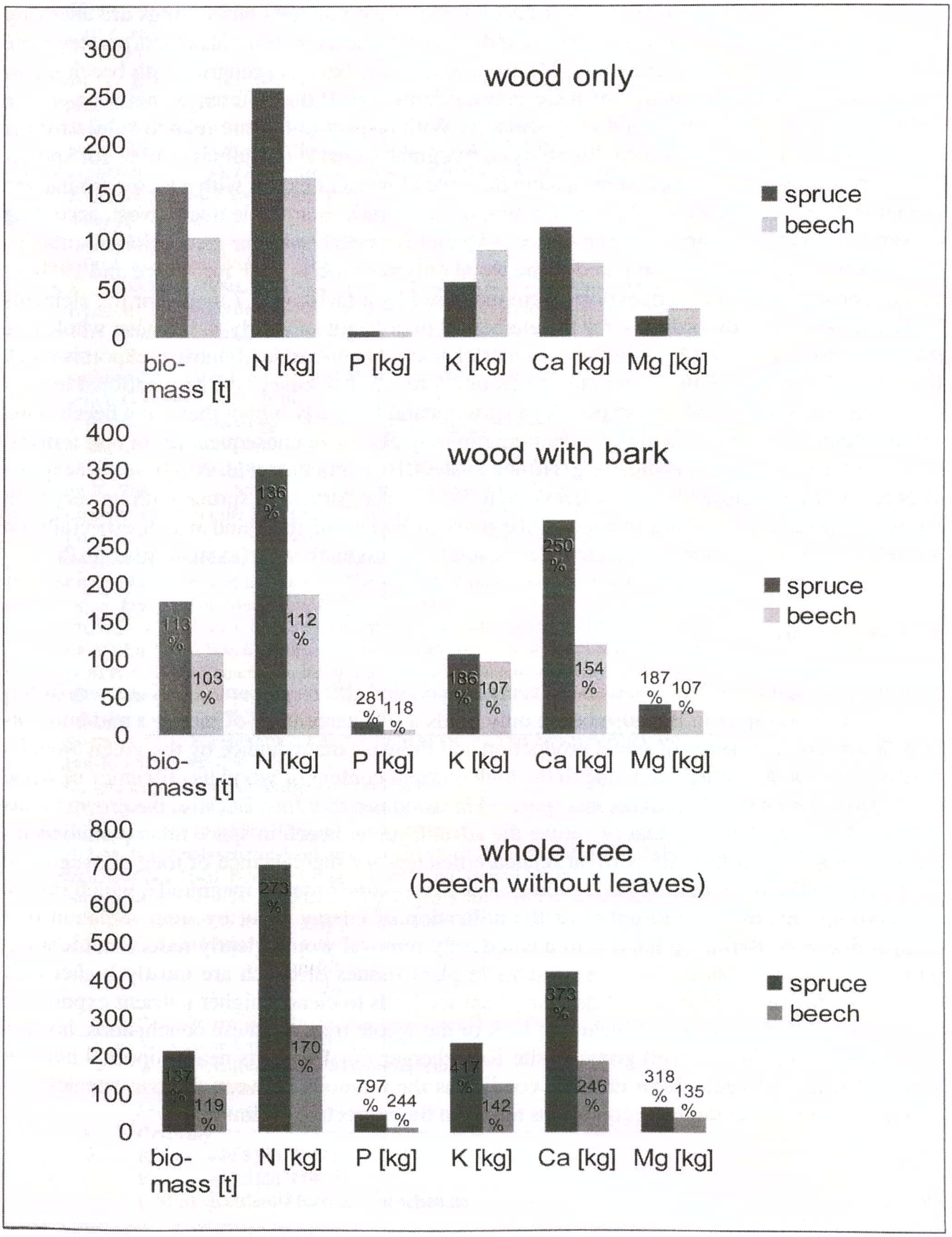

Fig. 3 Biomass and nutrient removal with different harvest scenarios for the existing stand, on a per hectare basis; per cent values refer to the wood only scenario.

Because there are more spruce trees per hectare, looking on an area basis things are changing (Fig. 3). Spruce produces more biomass, and thus with some exceptions also incorporates more nutrients. These exceptions are K and Mg for a wood-only harvest scenario, with beech incorporating clearly higher amounts of these two nutrients. For P the differences between spruce and beech are small for the wood-only scenario. With respect to hectare related values for the conventional harvest (wood including bark) a marginal increase of biomass (13 % for spruce, 3 % for beech) leads to a disproportionately increase of nutrient export with a factor around and greater than two for the elements P, K, Ca and Mg for spruce. For whole tree harvest, according to common practices calculated for spruce with and for beech without green biomass, the increase of biomass removal compared to the wood only scenario is 37 % for spruce and 19 % for beech. For spruce the nutrient exports were increased by a factor of 2.7 to 4.2 for the elements N, K, Ca, Mg and extraordinary for the element P by a factor of nearly 8. Because whole tree harvest of beech does not include the nutrient rich leaves the increase of nutrient export is much lower than for spruce with factors ranging from 1.4 to 2.5. Looking at the conventional harvest (wood including bark) nutrient export for a spruce stand is clearly higher than for a beech stand for the elements P and Ca which on the long run may also have consequences for soil fertility. At present, nitrogen input is high (e.g. Huber et al. 2010, Mellert et al. 2004), so that exports of N are of minor relevance for the ecosystem. Whole tree harvest of spruce with its very high nutrient exports has a strong impact on the nutrient budget of the stand which especially on nutrient poor sites my rapidly lead to a decrease of site productivity (Helmisaari et al. 2011).

4. Conclusions

Tree-internal nutrient distribution and thus nutrient related efficiency parameters are very different for beech and spruce. Because beech only holds a low percentage of biomass and nutrients in its leaves, its efficiency of wood production and biomass maintenance by the green biomass is very high. On the other hand, due to the high nutrient content of wood its efficiency of wood production in relation to nutrients incorporated in wood is rather low. Because the crown radius of a beech was higher than that of spruce the advantages of beech in space related efficiencies are vanishing. Regarding the nutrient related efficiency for maintenance of total aboveground biomass per m² crown area the two species range in the same order of magnitude, which shows, that both species are able to optimize the utilization of energy input by solar radiation in a comparable way. Reducing harvest to a wood-only removal would clearly reduce nutrient exports for spruce. Although nutrient contents in plant tissues of beech are mostly higher than for spruce, the higher biomass production of spruce leads to clearly higher nutrient exports for spruce, when harvesting wood including bark or the whole tree. All these conclusions, however, are only valid for the well growing site Kranzberger Forst with its nearly optimal nutrient supply. Under different site or climatic conditions the relations between the two species will change, the more, the farer the conditions are from the respective optimum.

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