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**Original article**

# Macronutrients in tree stems and foliage: a comparative study of six temperate forest species planted at the same sites

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**Abstract –** Common European tree species (oak, ash, beech, birch, lime and spruce) planted in adjacent stands on six sites were compared in terms of macronutrient concentrations in foliar and stem wood (including bark) biomass. The nutrient concentrations in both biomass compartments were much more dependent on species than on site although soil conditions differed between the sites. Differences between species regarding stem wood nutrient concentrations only partly corresponded to the differences in species foliage. The concentrations in spruce were considerably lower than in deciduous species, except P in foliage, and Ca in both stem wood and foliar biomass. Differences were also observed between the deciduous species both regarding foliar and stem wood nutrient concentrations. The differences should be considered when modelling nutrient circulation in forest stands and when evaluating the long-term sustainability of forest management.

**nutrient / hardwood / Norway spruce / stemwood / foliage**

**Résumé – Éléments minéraux dans le tronc et le feuillage : une étude comparative de six essences tempérées plantées sur les mêmes sites.** Les essences européennes communes (chêne, frêne, hêtre, bouleau, tilleul et épicéa commun) plantées dans des parcelles adjacentes sur six sites ont été comparées en termes de concentrations en macro-éléments minéraux dans la biomasse foliaire et dans le tronc (écorce y compris). Ces concentrations dépendaient plus de l'espèce que du site, bien que les conditions de sol étaient différentes entre les sites. Les différences entre les espèces observées dans le bois de tige ne correspondaient que partiellement à celles observées dans le feuillage. L'épicéa commun était plus pauvre en éléments minéraux que les feuillus excepté concernant le P dans le feuillage, et le Ca dans le tronc ainsi que dans la biomasse foliaire. Des différences de concentrations minérales ont également été observées entre les espèces de feuillus dans le bois ainsi que dans le feuillage. Ces différences devraient être considérées pour la modélisation de la circulation des éléments minéraux dans les peuplements forestiers et dans l'évaluation des aménagements forestiers dans le cadre d'une gestion durable.

**nutriment / feuillu / épicéa commun / bois de tige / feuillage**

## 1. INTRODUCTION

Nutrient concentrations in different compartments of tree biomass are commonly used for evaluation of plant nutrient status, soil nutrient availability and as indicators of forest health [14, 26, 47, 53]. Biomass and nutrient concentrations in different tree compartments are used for estimation of tree nutrient uptake and nutrient removal by harvest, and are thus crucial for understanding of nutrient circulation in forest ecosystems and in the assessment of the sustainability of forest management [23, 50].

Review studies and large-scale foliar chemistry surveys show wide ranges of foliar nutrient concentrations and nutrient ratios in forest trees [11, 47, 51]. The wide ranges of nutrient concentrations hardly reveal particular differences between species, as the nutrient concentrations presented in those studies are the result of empirical generalisation of many investigations regardless of the time of sampling, climate conditions, soil type etc. Additionally, factors that influence species distribution may influence the results of inter-species comparisons, if some species are more frequently found on more fertile soils than the others.

Comparative studies of several species growing on the same soils allow a better understanding of differences between species under similar nutrient conditions. Studies of this kind have most often dealt with coniferous species, including one or, at most, two deciduous species [2, 3, 12, 19, 33, 38, 46]. While nutrient concentrations in coniferous species, and Norway

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**Table I.** Plantation year and wood production on each plot.

| Site | Plantation year | Stem wood production[3], $m^3$/ha | | | | | |
|---|---|---|---|---|---|---|---|
| | | Ash | Beech | Birch | Lime | Oak | Spruce |
| DK-1 | 1960 | 49 | 327 | 142 | 302 | 203 | 450 |
| DK-2 | 1973–1974 | 222 | –[2] | 186 | 231 | 197 | –[2] |
| LT-1 | 1958–1959 | 194 | –[2] | 515 | 353[1] | 275 | 306 |
| LT-2 | 1958–1959 | 313 | –[2] | –[2] | 426[1] | 332 | –[2] |
| LT-3 | 1960 | 214 | 497 | 326 | 403 | 207 | 337 |
| SE-1 | 1967 | –[2] | 216 | –[2] | 325 | 349 | –[2] |

[1] At these sites lime was growing with a 30% admixture of oak (*Q. robur.* L). Values in the table give the total wood volume on the site, for both species together.
[2] "–" Indicates that there was no suitable plot with this species at the site.
[3] Includes last 10 years' thinnings.

spruce in particular, have been extensively studied, European deciduous temperate forest species have received considerably less attention in this respect.

The aim of this study was to compare foliar and wood nutrient concentrations in common European tree species (*Quercus robur* L., *Tilia cordata* Mill., *Betula pendula* Roth., *Fraxinus excelsior* L., *Fagus sylvatica* L. and *Picea abies* (L.) Karst.) planted in adjacent stands on the same soils. The study was focused on deciduous species, but Norway spruce was also included for comparison due to the fact that nutritional aspects of this species in relation to soil condition have been well studied [25, 29, 42, 48, 49].

Nutrient concentration in plant biomass is the result of the balance between nutrient uptake, plant growth and nutrient retranslocation and loss. These processes are likely to be influenced both by plant genomes and soil fertility, as well as other environmental conditions. The relative importance of site and species as factors determining nutrient concentrations in plant biomass may differ depending on nutrient element and biomass fraction. Foliar nutrient concentrations are most often used for the evaluation of plant nutrient status and, according to Augusto et al. [6], are more sensitive to soil nutrient conditions than nutrient concentrations in stem biomass. Despite the fact that good correlations are rarely observed between nutrient concentrations in plant biomass and non-fertilized forest soils, most often Ca, and sometimes also Mg and N, are the macroelements that show a consistent relationship [4, 7, 34, 35].

Nutrient concentrations and nutrient allocation between different plant tissues and biomass compartments are primarily determined by their functions, as various physiological processes require nutrient elements to different extents [30]. Stem biomass usually has the lowest concentrations of elements compared with other aboveground biomass compartments [6, 38, 44, 52]. The distribution of nutrients between different compartments can, however, also be species dependent, reflecting ecological differences between species. The differences between species regarding nutrient concentrations in foliage may not correspond to the differences in stem wood nutrient concentrations [3, 46].

Thus, the following specific hypotheses were tested in our study: (i) foliar nutrient concentrations differ between species, not only between Norway spruce and deciduous species, but also within the deciduous species group; (ii) stem wood nutrient concentrations also differ between species, but not necessarily in the same way as foliar nutrient concentrations. We also hypothesised that, within the gradient of soil conditions included in our study, the nutrient concentrations in plant biomass would be more dependent on species than on site.

## 2. MATERIALS AND METHODS

### 2.1. Site description

Plots with six different tree species: *Quercus robur* L., *Tilia cordata* Mill., *Fraxinus excelsior* L., *Betula pendula* Roth., *Fagus sylvatica* L. and *Picea abies* L. Karst, at six sites in three European countries were studied. At each site, three to six plots (of about 400 $m^2$) containing different species planted at the same time, in adjacent or closely situated stands, were investigated (Tab. I). Three Lithuanian sites were situated along the shores of the artificial lake "Kauno marios" in southern Lithuania (54° 45'–54° 53' N, 24° 04'–24° 09' E). The soils at these sites have developed on limnoglacial deposits with soil types ranging from Haplic Arenosols (site LT-1) to types intermediate between Eutric Cambisols and Dystric or Eutric Planosols (sites LT-2 and LT-3) [20]. On the Swedish site (SE-1) at Snapparp (56° 32' N, 12° 58' E), soils had developed on sand deposits of presumably aeolian origin and were classified as Haplic Arenosols [20].

The two Danish sites differed considerably in soil characteristics (Tab. II). The soil at the first site (DK-1), which was situated in Jutland, near Kragelund (56° 10' N, 9° 23' E), had developed on medium sandy till and was classified as Haplic Alisol [20]. The soil at the other Danish site (DK-2) at Odsherred (55° 51' N, 11° 41' E) had developed on a nutrient-rich loamy Weichsel till and was classified as Haplic Luvisol [20]. This site has been forested for at least 200 years, in contrast to the other five sites, which were previously used for agricultural purposes prior to forest planting in 1958–1967 (Tab. I).

### 2.2. Sampling, analysis and data treatment

Sampling at each site was preceded by visual evaluation of homogeneity of relief and soil conditions, which were further confirmed by analysis of soil chemistry and texture. Mineral soils down to 30 cm depth were sampled within each plot at 20 systematically distributed points and separated into three 10 cm thick layers. The samples were

**Table II.** Mean (± SE) topsoil characteristics at each site. Soil texture was determined at 10–20 cm depth. Other parameters of mineral soil were analyzed both at 0–10 cm and 20–30 cm depth and average values between these two layers were calculated for each plot.

| Site | Clay % | Silt % | Sand % | CEC[a] mmol(+)/kg | pH ($BaCl_2$) | Base[b] saturation, % | N mg/g | C mg/g | P µg/g | K µg/g | Ca µg/g | Mg µg/g |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DK-1 | 3.2 (0.2) | 11.8 (1.7) | 85.0 (1.7) | 15.9 (1.8) | 3.9 (0.0) | 37.2 (6.7) | 0.80 (0.08) | 13.5 (1.5) | 13.3 (1.5) | 16.9 (2.4) | 96 (28) | 16.6 (4.1) |
| DK-2 | 8.7 (0.9) | 26.2 (6.2) | 65.1 (7.0) | 45.4 (2.2) | 3.6 (0.1) | 49.4 (5.8) | 2.43 (0.24) | 36.5 (3.0) | 32.9 (3.2) | 51.6 (4.8) | 383 (66) | 48.7 (6.2) |
| LT-1 | 4.7 (0.4) | 17.8 (2.9) | 77.5 (3.3) | 22.0 (1.9) | 4.0 (0.1) | 55.8 (7.9) | 0.93 (0.11) | 14.7 (2.0) | 19.7 (5.4) | 27.7 (4.7) | 225 (40) | 26.3 (5.2) |
| LT- 2 | 10.1 (1.6) | 44.7 (0.5) | 45.2 (1.2) | 43.5 (7.0) | 4.0 (0.0) | 84.2 (4.4) | 1.21 (0.16) | 17.4 (1.7) | 11.7 (0.9) | 61.5 (9.8) | 582 (119) | 86.5 (21.6) |
| LT-3 | 7.8 (0.7) | 39.2 (1.6) | 52.9 (1.6) | 33.7 (2.5) | 4.1 (0.1) | 69.9 (7.3) | 1.09 (0.05) | 16.9 (1.0) | 14.1 (1.8) | 44.3 (5.8) | 406 (64) | 48.8 (8.3) |
| SE-1 | 5.3 (0.4) | 14.9 (1.9) | 79.8 (2.3) | 39.9 (1.8) | 3.9 (0.0) | 73.0 (1.9) | 1.90 (0.19) | 29.7 (3.9) | 34.8 (1.9) | 46.6 (1.3) | 459 (14) | 51.0 (1.0) |

[a] Cation exchange capacity was determined as the sum of the extractable amounts of $H^+$, $Na^+$, $K^+$, $Ca^+$, $Mg^{2+}$, $Al^{3+}$, $Fe^{3+}$ and $Mn^{2+}$ from the $BaCl_2$ extraction. [b] Base saturation was calculated as the ratio between the sum of extractable amount of base cations and the total cation exchange capacity of a soil sample.

mixed in the field to make one combined sample per plot for each layer. The samples from the 10–20 cm layer were used for texture analyses [29], while the samples from 0–10 and 20–30 cm layers were used for assessment of soil chemistry. Total nitrogen was determined using the Kjeldahl method, and a CR 12; Leco carbon determinator instrument was used for the measurement of total soil carbon. Concentrations of extractable nutrients were determined using ICP-AES (Optima) after equilibrium extraction of a 20 g (dry weight) soil sample in 100 mL 0.1 M acid Na-EDTA (pH 4.6) for P, and in 100 mL of a 0.1 M solution of $BaCl_2$ for all other elements. General characteristics of the soil nutrient conditions in topsoil at each site are presented in Table II.

Tree heights and diameters at breast height (DBH) were measured and used for calculation of the basal area and standing tree volume at each plot. Four trees with diameters approaching the mean stand DBH were randomly chosen for biomass sampling. The samples from these trees were mixed in the field to provide a composite sample for each biomass fraction for each plot. Leaves and needles were sampled in the second half of August 2000 in Sweden and Lithuania and at the beginning of September 2000 in Denmark at the DK-2 site. At the other Danish site (DK-1) leaves were sampled at the end of August 2001. Leaf samples were collected from the upper third of the crown. Current year and 1-year-old spruce needles were sampled from the 7th branch from the top. Wood cores (including bark) were taken from the same trees at DBH from four different sides of the trunk on Lithuanian sites and from two opposite sides at the Danish and Swedish sites.

Leave samples and wood core samples, including bark, were dried to constant weight at 40 °C, homogenised and analysed for nutrient elements. For ash leaves the leaflets were separated from the other leaf parts and the two fractions were weighed and analysed separately. Nutrient concentrations in the whole ash leaves were calculated based on nutrient concentrations of these two fractions and weight relation between them on each plot. Nitrogen in plant samples was analysed by the Kjeldahl method. Other macronutrients were analysed using ICP-AES after 1 g plant material was digested in 25 mL concentrated $HNO_3$ on hot plates. The results of soil and plant material analysis were corrected for the difference in water content between 40 °C and 80 °C.

Nutrient concentrations in leaves and wood biomass were analysed by analysis of the variances (ANOVA) with species and site as factors. Only the main effects were analysed. The Tukey – Kramer procedure (a variant of Tukey HSD for unbalanced models [32]) was used in order to determine significant differences between species. For those elements that showed statistically unequal variances between species (N, K in stem wood and Ca-to-N ratio in the foliage), Tamhane 2T test was used instead (SPSS software, version 11).

All nutrient ratios, with the exception of Ca-to-N ratio, were subjected to arcsine transformation [45] in order to fit the ANOVA assumption of normally distributed residuals. All statistical analysis was performed with SPSS, v.11 software.

## 3. RESULTS

The differences between species regarding nutrient concentrations were not the same in different parts of the biomass for most of the elements and species studied. For N and S, however, the differences between the species in foliar and stemwood biomass were rather similar with the exception of ash, which had the highest N concentration in stemwood, but not in the leaves (Tab. IV).

Species proved to be a more important factor than site in determining nutrient concentrations in both leaf and stem wood biomass (Tab. III). Site was significant only for foliar concentrations of N and Ca (only when spruce was included in the analysis), and for stem wood concentrations of P and N.

Nutrient concentrations in mineral topsoils (0–30 cm depth) were, in contrast to nutrient concentrations in the biomass, significantly different at the studied sites, but not between species. Only for nitrogen was species of importance in influencing the soil nutrient concentration (Tab. III).

### 3.1. Foliar nutrient concentrations

Concentrations of macronutrients in leaves differed depending on species and element (Tab. IV). N concentrations in spruce needles were about half those in deciduous species. Foliar N concentrations in lime, oak and beech were not significantly different but lime leaves showed the highest N concentration of all species at all sites, with the exception of DK-1 where oak showed the highest concentration (Fig. 1A). Birch leaves showed a significantly lower N concentration than lime, but higher than ash. Ash leaves had the lowest N concentration among the deciduous species, mainly due to the fact that N concentrations in its petioles and rachides were less than one third of that in the leaflets. The nitrogen concentration in ash leaflets was, on average, similar to the N concentration in other deciduous species, but showed a higher variation between the sites. There was no significant difference in foliar P concentrations between the species. However, the P/N ratio, was significantly

**Table III.** P-values for the factors site and species in two-way ANOVAs. "ns" indicates that the values were not significant at 0.05 level, "–" means no chemical analysis was performed for this element.

| | Concentrations in foliar biomass | | | | Concentrations in stem wood biomass | | | | Concentrations in mineral soil (0–30 cm) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | All species | | Deciduous species only | | All species | | Deciduous species only | | All species | | Deciduous species only | |
| Factor | Species | Site | Species | Site | Species | Site | Species | Site | Species | Site | Species | Site |
| N | 0.000 | 0.013 | 0.000 | 0.023 | 0.000 | 0.050 | 0.032 | ns | ns | 0.000 | 0.047 | 0.000 |
| P | 0.012 | ns | 0.018 | ns | 0.000 | 0.000 | 0.000 | 0.001 | ns | 0.000 | ns | 0.000 |
| K | 0.000 | ns | 0.001 | ns | 0.000 | ns | 0.000 | ns | ns | 0.000 | ns | 0.001 |
| Ca | 0.000 | 0.035 | 0.001 | ns | 0.000 | ns | 0.000 | ns | ns | 0.000 | ns | 0.003 |
| Mg | 0.001 | ns | 0.003 | ns | 0.000 | ns | 0.000 | ns | ns | 0.000 | ns | 0.003 |
| S | 0.000 | ns | 0.000 | ns | 0.000 | ns | 0.000 | ns | – | – | – | – |

**Table IV.** Nutrient concentrations in foliage and stem wood of different species. Means which differ significantly at 0.05 level are indicated by different letters. Standard deviations of means are given in parentheses.

| Species | Foliar concentrations, mg/g | | | | | | Stem wood (including bark) concentrations, mg/g | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | P | K | Ca | Mg | S | N | P | K | Ca | Mg | S |
| Ash | 21.60 (4.17) b | 1.80 (0.61) ns | 11.44 (2.83) b | 15.10 (2.34) bc | 3.54 (1.03) c | 2.85 (0.40) c | 1.29 (0.06) c | 0.11 (0.03) bc | 1.73 (0.29) c | 1.29 (0.19) a | 0.25 (0.03) cd | 0.15 (0.01) d |
| Beech | 27.37 (2.27) cd | 1.63 (0.06) ns | 9.42 (1.39) ab | 10.14 (4.41) ab | 1.64 (0.37) ab | 1.75 (0.16) b | 1.13 (0.00) b | 0.13 (0.04) cd | 1.07 (0.12) bc | 1.01 (0.05) a | 0.32 (0.06) d | 0.10 (0.00) b |
| Birch | 26.15 (2.62) c | 2.51 (0.56) ns | 9.01 (0.95) ab | 9.46 (1.73) ab | 2.64 (0.42) bc | 1.79 (0.18) b | 1.10 (0.13) bc | 0.09 (0.01) bc | 0.56 (0.08) a | 1.24 (0.34) a | 0.21 (0.06) bc | 0.09 (0.01) b |
| Lime | 30.74 (2.24) d | 2.49 (0.51) ns | 16.72 (2.98) c | 17.29 (5.12) c | 2.09 (0.51) ab | 2.77 (0.23) c | 1.31 (0.22) bc | 0.16 (0.03) d | 1.27 (0.17) bc | 2.00 (0.24) b | 0.24 (0.04) cd | 0.15 (0.01) d |
| Oak | 29.17 (1.81) cd | 2.40 (0.46) ns | 11.63 (2.15) b | 8.48 (1.36) a | 1.71 (0.31) ab | 1.70 (0.04) b | 1.27 (0.08) bc | 0.09 (0.03) b | 1.00 (0.13) b | 1.45 (0.22) a | 0.12 (0.02) ab | 0.12 (0.01) c |
| Spruce | 13.78 (1.21) a | 1.80 (0.07) ns | 6.35 (1.04) a | 8.89 (4.96) a | 1.20 (0.39) a | 1.00 (0.13) a | 0.58 (0.06) a | 0.04 (0.01) a | 0.40 (0.13) a | 1.12 (0.24) a | 0.12 (0.01) a | 0.06 (0.01) a |

higher in spruce than in beech, with other species being somewhere between (Fig. 2).

Lime showed higher K concentration in leaves than all other species. Ash and oak had lower concentrations than lime, but almost twice that of spruce. Beech and oak also had higher concentrations than spruce, but the differences were not significant at 0.05 level (Tab. IV and Fig. 1C). In ash leaves, K was the only element that showed a higher concentration in petioles and rachides than in leaflets.

Foliar concentrations of Ca were highest in lime and ash. Lime differed significantly from all other species but ash. Oak and spruce exhibited the lowest foliar Ca concentrations. Spruce, however, had much higher, and similar to beech and ash, Ca concentration at the site LT-3 where the Ca concentration in the soil was high.

Leaf concentrations of Mg were highest in ash and lowest in spruce. Ash differed significantly from all the other tree species with the exception of birch, which also showed a relatively high concentration of Mg. Mg/N ratios in ash leaves were higher than in leaves of all other species (Fig. 2).

S concentrations were highest in ash and lime leaves, intermediate and very similar in beech, oak and birch, and lowest in spruce. The high concentration of S in ash leaves was due to high concentration in the leaflets, as the concentrations in leaf petioles and rachides were about four times lower and about the same as S concentrations in spruce needles. S/N ratios in different

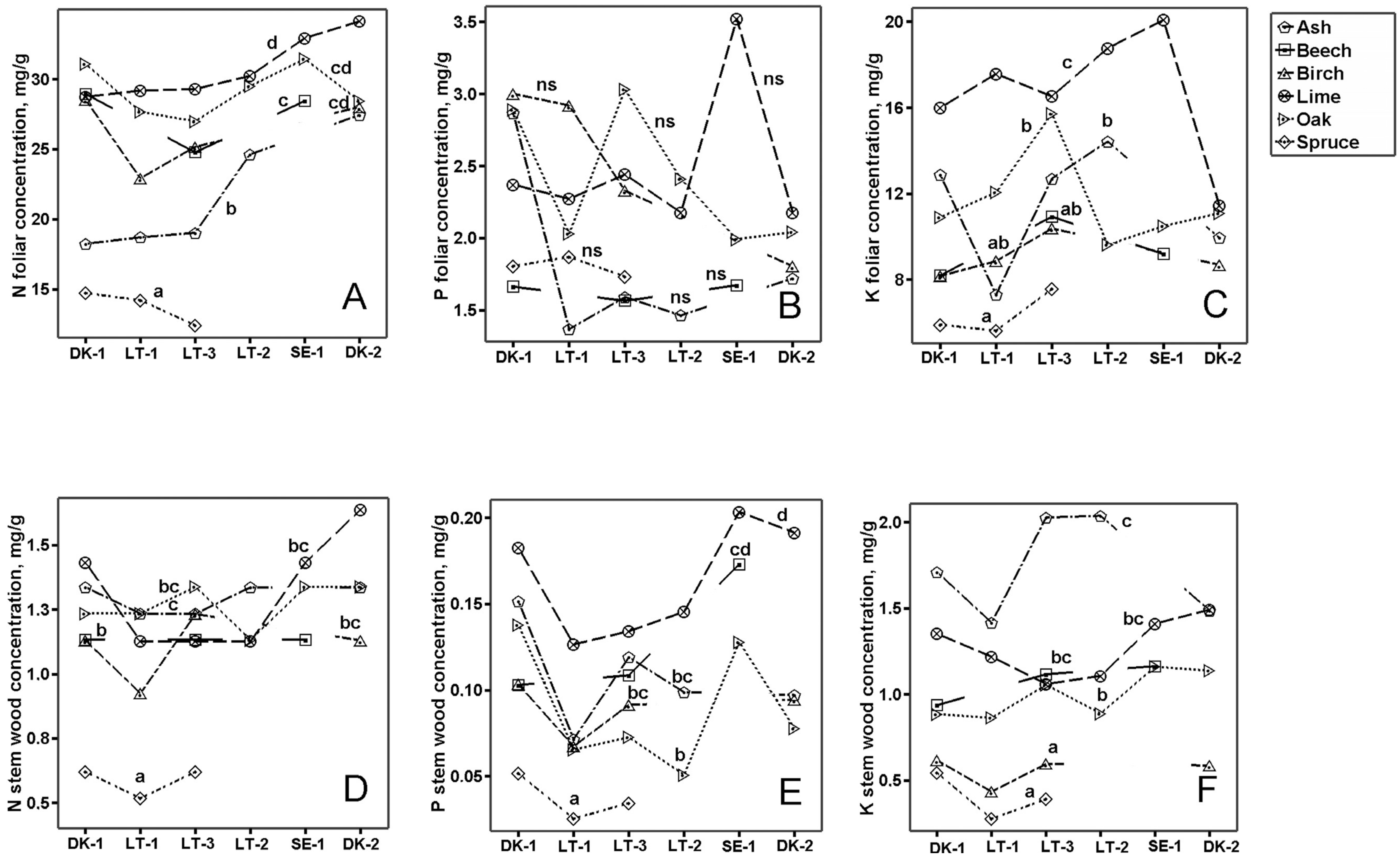


**Figure 1.** Foliar (A–C) and stem wood (D–F) concentrations of N, P and K in different species across the sites. The sites are arranged in order of increasing N concentration in the soil. Different letters indicate significance at the 0.05 level in two-way ANOVA (as also shown in Tab. IV).

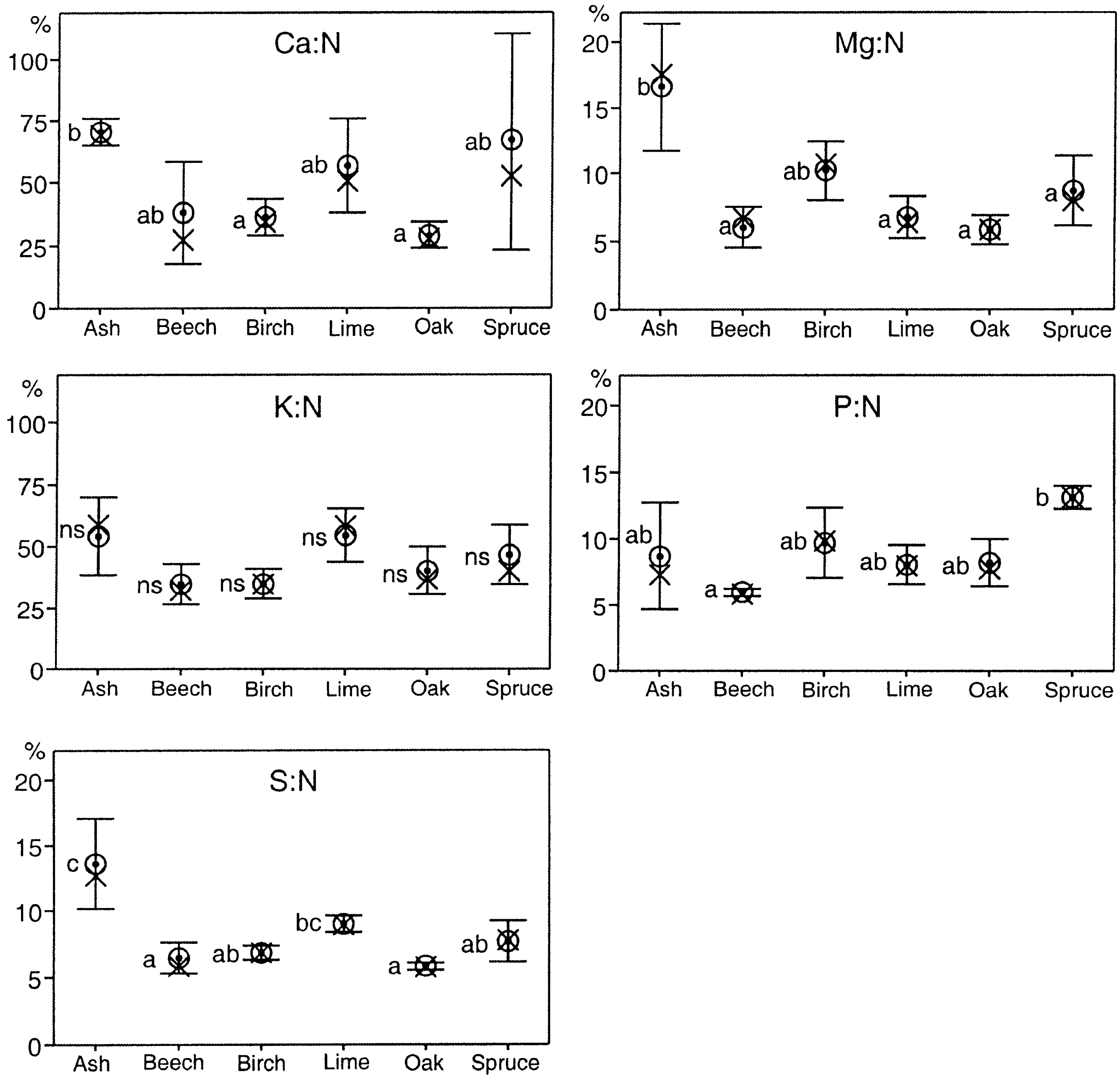


**Figure 2.** Nutrient-to-nitrogen ratios in foliage of different species. Means (± 1SD) are shown by dots in circles, crosses show medians. The figure shows non-transformed ratios. Different letters indicate significant difference between means in two-way ANOVA after arcsine transformation. Note the different scale on the Y-axes.

parts of ash leaves were, however, higher than in all other species. Lime foliage also had a relatively high S/N ratio, whereas oak leaves had the lowest (Fig. 2).

### 3.2. Stem wood concentrations

The concentration of N in spruce stem wood was about half that in the stem wood of deciduous species, and corresponded to differences between needles and leaves. Unlike foliar N concentrations, ash stem wood had N concentrations similar to those in other deciduous species. Beech had a slightly lower stem wood N concentration than other deciduous species, and was different from ash but not from other deciduous species (Tab. IV and Fig. 1E).

In contrast to foliar P, stem wood P varied significantly between the species. Lime had the highest P stem wood concentration at all sites, and the value was significantly different from those of other species except beech. At the least fertile site (DK-1) beech had, however, a lower concentration than ash and oak, indicating an interaction between species and site factors for this element and species. Spruce exhibited the lowest stem wood P concentration across all sites (Fig. 1E and Tab. IV).

The concentration of K was highest in ash wood, followed by lime, beech and oak. Birch stem wood showed a significantly lower K concentration than other deciduous species, and was not different from spruce in this respect. Mg concentrations in stem wood samples of the deciduous species did not reflect the foliar Mg concentrations. Ash, which showed much higher Mg concentrations in leaves than other species, had the same Mg concentration in stem wood samples as beech and lime. The Mg concentration in oak stem wood was lower than in other deciduous species and was similar to that in spruce stem wood (Tab. IV). Lime stem wood exhibited the highest Ca concentration of all the species at all sites. The differences between other species were not significant.

The differences in stem wood concentrations of S were rather similar to the differences in foliar S concentrations. Ash and lime showed the highest S concentrations in stem wood, oak had a lower concentration, and birch and beech showed the lowest concentrations among the deciduous species. Spruce had lower stem wood concentration of S than all deciduous species.

## 4. DISCUSSION

Our data indicated that nutrient concentrations in the plant biomass of the tree species studied were affected to a greater extent by genetic differences between the species than by site conditions. This is in correspondence with the previous investigations of forests in southern Sweden. In spruce forests in the province of Scania, Ca was the only macroelement that showed a good correlation between nutrient concentration in needles and in soil [34, 35]. Studies of the southern Swedish beech forests [4, 7] have shown that for Ca, Mg, Mn and N the nutrient concentrations in buds and leaves were related to nutrient concentrations in the soil, but soil alone did not account for the major part of the variation in leaf nutrient concentrations.

For a given species at a particular site, the methods of soil analysis give only approximate estimates of actual nutrient availability, which depends on many factors such as soil moisture [8, 17] or mycorrhizal association [21]. The absence of good correlations between nutrient concentrations in the soil and in plant biomass for the majority of nutrient elements is also a strong indication of species' ability to keep nutrient concentrations in the biomass within a certain range, even on less fertile soils.

In a review study on nutrient concentrations in Douglas fir, Scots pine, Norway spruce and European beech, Augusto et al. [6] drew a similar conclusion concerning nutrient concentrations in above-ground biomass, which were found to be fairly constant for adult stands of these species. This was especially pronounced for stem wood biomass concentrations, while foliar nutrient concentrations were more affected by environmental conditions.

In our study, foliar concentrations of N in deciduous species, have showed a positive dependency on N concentration in soil, which was most pronounced for ash (Fig. 1), which showed the lowest N concentrations at the least fertile Danish site (DK-1) and two Lithuanian sites. At the Danish site the growth rate, was also probably affected (Tab. I) although the other elements could also have been limiting.

For those elements and species that showed significant differences (Tab. IV), the possible interactions between site and species were presumably much weaker than the effects of the main factors. In cases when the differences were not consistent across the sites no significant differences were found at the $p = 0.05$ level (Fig. 1). Two particular cases must, however, be mentioned. Oak, which showed a significantly lower P concentration in the stem wood than beech, had a higher P concentration at the least fertile site, and spruce, which showed a significantly lower Ca concentration in the foliage than ash had a similar Ca concentration to ash at the Ca-rich site. In these two cases the lower number of plots for spruce and beech ($n = 3$) may have influenced the statistical results.

### 4.1. Foliar nutrient concentrations

The differences in foliar nutrient concentrations between Norway spruce and the deciduous species were expected as differences between deciduous and evergreen species have been reported previously [1, 3, 46, 54]. The N concentrations in Norway spruce needles are often 40–50% lower than N concentrations in leaves of temperate deciduous species [3, 9, 10, 33, 43]. A review of the variation of foliar nutrient concentrations in spruce, birch, beech and oak in Europe [43], demonstrated that the same differences existed for K, Mg and Ca, resulting in similar ratios of these elements to N for all four species, with the exception of a higher Mg/N ratio in birch. The P/N ratio in spruce foliage in the same study was, however, higher than that in foliage of other species as the N concentration in spruce needles was lower, while the P concentration was roughly the same as in the foliage of deciduous species. The same tendency regarding the P/N ratio in spruce foliage compared with other species was observed in our study and in a study on nutrient concentrations in spruce and beech along the European transect [10].

The Ca/N ratio in spruce needles was relatively high in our study and also showed the biggest variation between the sites. The concentration of Ca in forest trees can vary over a very wide range [11, 47] depending on soil conditions [4, 7, 34, 35] as well as plant water consumption [5, 24]. High concentration of Ca in Norway spruce needles compared to the foliage of other coniferous species and silver birch have been previously reported for plantations on productive soils [3]. Our study demonstrated that for some elements and species the nutrient concentrations in the foliar biomass were also different within the deciduous species group. Lime leaves had the highest average N concentration (30.7 mg/g) among deciduous species, though the difference was significant only in comparison to birch and ash leaves (Tab. IV). Kazda et al. [28] also reported a high (33.2 mg/g) N concentration in lime leaves growing in a 120-year-old nutrient-rich flood-plain forest in the Czech Republic, while foliar N concentrations in oak were lower (24.7–28.5 mg/g). The differences between foliar N concentrations in ash and other species were mainly due to lower N concentrations in the ash leaf petioles and rachides.

Concentrations of foliar P did not differ significantly between species in our study. However, beech, ash and spruce tended to have lower P concentrations than lime, oak and birch (Tab. IV). In a review study [43] the range of P concentrations found in leaves of birch trees was wider than in foliage of beech and oak; birch often had a higher P concentration than other species and P/N ratios in birch were also higher, whereas beech had slightly lower P concentrations than other species. In our study the P/N ratio in beech leaves tended to be low compared to other species but the difference was significant for spruce only.

Foliar concentrations of K and Ca were high in lime compared to other deciduous species. Lime has previously been reported to have high concentrations of these elements in the litterfall [55] and to influence the soil base saturation in a positive way [22, 36, 39]. For Mg, however, it was not lime, but birch and especially ash that showed the highest elemental concentration in foliage, and higher Mg/N ratios. Rosengren et al. [43] also found a higher concentration of Mg in birch leaves than in the leaves of beech, oak and spruce, as well as higher Mg/N ratios.

Foliar nutrient concentrations at the same site can vary from year to year depending primarily on weather conditions. However, a long-term comparative study in Denmark [9] showed that the variation in foliar nutrient concentrations between years was lower than the variation between species and locations. As our sites were situated in different countries the variation in weather was one of the constituents of site as a factor. Moreover, most of the differences observed in the absolute concentrations were also reflected in nutrient-to-N ratios and nutrient ratios are considered to be less variable than absolute nutrient concentrations [29], although both should be taken into consideration when evaluating nutrient requirements and deficiencies in plant species [11].

### 4.2. Nutrients in the stem wood

Nutrient concentrations may vary within tree stems in both the vertical and horizontal directions in different ways, depending on element and tree species [13, 15, 37, 41]. Bark usually has higher nutrient concentrations than the rest of the stem [13, 40, 44, 52], while differences between heartwood and sapwood seem to be more variable depending on species and nutrient elements [31].

The stemwood concentrations observed in our study represent the integrated inter-specific differences across all stemwood compartments at DBH level. At this level the formation of heartwood and the possible differences between species in nutrient resorption from senescing sapwood may strongly influence the total nutrient content of the sampled stemwood core. Pedunculate oak is known to have a lower heartwood/sapwood ratio for Ca and especially Mg than European beech [37] and many other European tree species [31]. This is the most probable explanation of the considerably lower Mg concentrations in oak stemwood, than in other deciduous species, found in our study. A study of Canadian hardwoods [13] revealed similar low concentrations of Mg in the heartwood of red oak, as well as lower nutrient stem content, compared with other American hardwoods.

The concentration of Ca in oak stem wood in our study was not lower than in other species (with the exception of lime). The study of Canadian hardwoods referred to above [13] showed that while the Ca concentration in the heartwood of red oak was low; the concentration in bark was about twice that in beech. If the same is true for European species, this may partly explain why the Ca concentrations in oak and beech were similar in our study, as the bark was included in the analysed samples.

Concentrations of Ca in the stemwood may depend on water consumption [5], and the uptake of this element can be increased by increasing transpiration rate [8]. Among the species we have studied, lime had the highest Ca concentration in both foliar and stem wood biomass, which may be related to higher water consumption, due to the large area of lime foliage and high transpiration rate of this species [28].

The differences in nutrient concentrations between spruce and deciduous species were more prominent in stem wood than in foliage. With the exception of low Mg in stemwood of oak and low K in stemwood of birch, the concentrations of N, P, K, Mg and S in spruce stem wood were, on average, about half those in the deciduous species. Since Ca concentrations in spruce were similar to concentrations in ash, beech, birch and oak, but N concentrations in spruce were much lower than in deciduous species, the Ca/N ratio in spruce stemwood was high. Alriksson and Eriksson [3], on the other hand, found no differences in N stem wood concentrations between spruce and birch growing in the same soils, while another comparative study [46] reported N and P concentrations in the stem wood of spruce to be about half those in stem wood of red oak.

The differences in wood densities together with differences in nutrient concentrations must be taken into account when estimating the amount of nutrients in stem wood biomass. The density of ash, beech and oak wood is known to be rather similar, while the density of birch and lime is lower, and Norway spruce has the lowest wood density [16, 18]. The nutrient pools of Ca, calculated from the mean concentrations observed in our study and literature data on wood density [18], were, for instance, similar for lime, oak and beech, while the Ca concentration in lime stem wood was higher than in oak or beech.

Species-related differences in nutrient concentrations and amounts in different biomass compartments could be important in the long-term perspective. From the point of view of nutrient balance and the sustainability of forest management it would be of special interest to make further studies of species that exhibit higher nutrient concentrations in the leaves, and lower nutrient concentrations in the stem wood, together with a lower wood density. Higher foliar concentrations may lead to higher nutrient fluxes to the soil surface improving the nutrient status of the upper soil layer. At the same time, the wood harvesting of such a species may remove lower amounts of nutrients from the ecosystem.

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