



# Aboveground carbon and nutrient distributions are hardly associated with canopy position for trees in temperate forests on poor and acidified sandy soils

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## ARTICLE INFO

### Keywords:

Biomass  
Carbon  
Macronutrients  
Micronutrients  
Mass distribution  
Tree compartments  
Canopy position  
Nutrient imbalance  
N-deposition loads  
Nutrient poor soil

## ABSTRACT

High demands on forest for carbon storage and provision of timber and biofuel require precise and reliable estimates of the biomass, carbon and nutrient stocks in different tree compartments. Whether the fraction of biomass distributed in aboveground tree compartments and the carbon and nutrient concentrations varies systematically across trees in different canopy positions remains unclear despite its importance for understanding forest ecology. Here, we compared the distribution of biomass, carbon and nutrients from underlying carbon and nutrient concentrations between different aboveground tree compartments for 15 mature trees of European beech (*Fagus sylvatica*), Douglas fir (*Pseudotsuga menziesii*) and Scots pine (*Pinus sylvestris*) with dominant, intermediate and suppressed canopy position.

We show that carbon concentrations were relatively constant across tree compartments while nutrient concentrations increased from stem, bark, branches towards needles. Canopy position had only minor effects on carbon and nutrient concentrations and on the distribution of biomass, carbon and nutrients between aboveground tree components. Nutrient concentrations and stoichiometric results confirm that the forests were affected by high N deposition and low availability of P and base cations.

Our results imply that predictions from allometric scaling theory better apply to aboveground tree components than from functional equilibrium theory. Models aiming for estimating tree and forest biomass and carbon and nutrient stocks can apply equal biomass, carbon and nutrient stocks for trees independent of canopy position as a valid assumption but testing this assumption for a broader range of species and site conditions remains recommended.

## 1. Introduction

Forests cover approximately 31 % of the global land area and provide many ecosystem services including carbon sequestration, nutrient and water cycling, and the production of timber and biomass (UNEP, 2020). At global scale, forests sequester approximately 30 % of the anthropogenic CO<sub>2</sub> emissions (Pan et al., 2011; Quéré et al., 2018) and thus act as a net carbon sink. However, a growing demand for commodities (timber, biofuel and fibre) have intensified forest harvesting (Mantau et al., 2010; Nabuurs et al., 2015), with uncertain implications for future carbon sequestration and nutrient cycling by forests.

Forest models are used to estimate the stocks and fluxes of carbon (Liski et al., 2006; Akselsson et al., 2007; Franklin et al., 2012) and

nutrients (Akselsson et al., 2007; Vangansbeke et al., 2015; Pare and Thiffault, 2016; de Vries et al., 2020). Good estimates of carbon and nutrient stocks in forests require data on forest biomass, and the distribution of carbon and nutrients over the different tree compartments (Poorter and Sack, 2012; Wertz et al., 2020). Such information is still poorly quantified for large adult forest trees (Schippers et al., 2015), particularly for tree compartments other than foliage. Another caveat in such estimates is the role of canopy position of trees, ranging from fully exposed, large, dominant trees in the upper canopy to shaded, small, suppressed trees in the understory. Canopy position differences involve large differences in access to light, tree metabolism, carbon gain and transpiration across trees in the same forest, and potentially inflates the uncertainty in estimating nutrient and carbon stocks in forest models

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<https://doi.org/10.1016/j.foreco.2022.120731>

Received 2 November 2022; Received in revised form 8 December 2022; Accepted 10 December 2022

Available online 20 December 2022

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(Franklin et al., 2012) but this has hardly been quantified.

Two theories dominating the literature come with different predictions for resource distribution within plants. The functional equilibrium theory (Brouwer, 1962), also called the optimal partitioning theory (McCarthy and Enquist, 2007), predicts that the resource allocation in trees is driven by priority and demand, whereby resources are allocated to the organ that acquires the most limiting resource. Contrastingly, the theory of allometric scaling, predicts that resource allocation is driven by scaling relationships between organs that vary with individual size, and not with the environment (Shinozaki et al., 1964; Enquist and Niklas, 2002; McCarthy and Enquist, 2007). In most forest models, the distribution of biomass within trees is predicted based on allometric scaling from DBH or tree height (Bartelink, 1997; Li and Zhao, 2013; Pretzsch et al., 2014). Models based on the functional equilibrium theory are hardly used, although sometimes stem density measures, pointing towards effects of competition on biomass allocation, are included in the models (Xue et al., 2012; Schepaschenko et al., 2018). In this study the predictions of both theories will be tested for the above-ground biomass distribution in trees differing in canopy positions, creating a framework for including the effects of competition on resource allocation.

Trees with a dominant canopy position grow faster (D'Amato and Puettmann, 2004; Reid et al., 2004; Castagneri et al., 2008) and may increase the share of branches over the stem (Krejza et al., 2017; Wertz et al., 2020) in response to high light levels. Suppressed trees growing at lower light availability may increase height growth over radial growth (Naidu et al., 1998; Zhou et al., 2018; Yang et al., 2019), and invest more in stem wood (Wertz et al., 2020) at the costs of investment in the crown (Naidu et al., 1998; Reid et al., 2004; Vanninen and Mäkelä, 2005; Sterck and Schieving, 2007; Krejza et al., 2017). Such responses nevertheless differ between species differing in shade tolerance (Van de Peer et al., 2017; del Río et al., 2019), or environment (Lines et al., 2012). Despite the differences in biomass allocation between dominant and suppressed trees, there is no consensus on the magnitude of this effect. Trees can adjust their allocation to maintain remarkable constant biomass distributions between different components (e.g. crown versus stem) to maintain major functions in very different environments (Anfodillo et al., 2016; Petit et al., 2018). Yet, whether such relative biomass distributions also hold for trees in different canopy positions amongst different environments remains, as far as we know, poorly quantified.

Canopy position may also affect tree carbon concentrations, but in most forest, carbon models, tree carbon concentrations are assumed to be constant and approximately 50 % of the biomass (Litton et al., 2007; Zhang et al., 2009; Thomas and Martin, 2012). Such strong assumptions potentially add uncertainty in carbon stock estimates since carbon concentrations differ across compartments and organs (Bert and Danjon, 2006; Zhang et al., 2009; Thomas and Martin, 2012). Some studies showed that intraspecific competition alters carbon concentrations (Peri et al., 2010), but other imply that this is not the case (Zhang et al., 2009). It has been suggested that trees invest more in structural carbohydrates and lignin compounds under less favourable conditions, but more in lipid and protein compounds under favourable conditions (Lambers et al., 2008). In this study, we will test whether carbon concentrations can indeed be assumed constant across tree compartments for trees in different canopy positions.

For nutrient concentrations, the biogeochemical niche hypothesis (Peñuelas et al., 2008; Peñuelas et al., 2010) predicts that species maintain a constant nutrient stoichiometry in their compartments. Nevertheless, species retain a certain degree of plasticity in nutrient concentration and allocation to a change in competitive conditions (Peñuelas et al., 2008; Sardans et al., 2015), both belowground (Peri et al., 2006; Yang et al., 2009) and aboveground (Reid et al., 2004). Dominant, rapidly growing trees may maintain higher metabolic rates (D'Amato and Puettmann, 2004; Reid et al., 2004; Castagneri et al., 2008), and acquire water and nutrients more rapidly than suppressed

trees (Martin et al., 1997; Granier et al., 2000; Aranda et al., 2012). This is in line with higher nutrient concentrations observed for more dominant relative to suppressed trees (Peri et al., 2006; Peri et al., 2010; Wu et al., 2020) but, ambiguously, reverse patterns have also been reported (Reid et al., 2004; Peri et al., 2006; Couto-Vazquez and Gonzalez-Prieto, 2010). An additional complication is that higher nutrient concentrations in dominant trees were reported for N, P (Peri et al., 2006; Wu et al., 2020), K, Mg, and S (Peri et al., 2006), while Ca concentrations were found to be higher in suppressed trees (Peri et al., 2006). Furthermore, nutrient concentrations depend also on the compartment, with higher concentrations of N (Reid et al., 2004; Couto-Vazquez and Gonzalez-Prieto, 2010) and P (Reid et al., 2004) reported for foliage of suppressed trees relative to dominant trees. Data regarding the effects of canopy position on nutrient concentrations in other tree compartments (e.g., stem wood, stem bark, or branches of different size) are however very limited and, to our best knowledge, almost absent in combination with real measures of total biomasses of these compartments within mature trees. This means that possible effects of canopy position on the biomass, carbon and nutrient stocks within trees cannot yet be generalized, which is required for reducing the uncertainty of forest model predictions on carbon and nutrient stocks in forests.

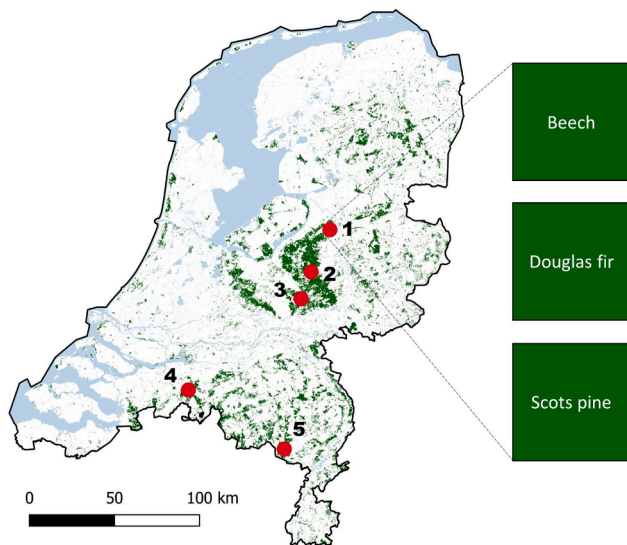
In this study, we aim at assessing the impact of canopy position on the distributions of tree biomass, carbon and nutrients amongst different tree compartments. We therefore quantified the biomass and the carbon and nutrient concentrations within tree compartments in dominant, intermediate and suppressed trees of European beech (*Fagus sylvatica*), Douglas fir (*Pseudotsuga menziesii*), and Scots pine (*Pinus sylvestris* L.) growing in forests on poor sandy soils in the Netherlands. The above-ground compartments that were considered include needles, small branches, coarse branches and stem bark, stem sapwood and stem heartwood. The nutrients considered involve macronutrients (N, P, K, Ca, S, Mg) and micronutrients (Cu, Fe, Mn, Zn). We specifically addressed the following questions:

- (1) Is carbon concentration indeed rather constant across tree compartments?
- (2) Do nutrient concentrations within trees reflect the low cation and phosphorous availability of acidified sandy soils and the relatively levels of nitrogen deposition over the past decades?
- (3) What is the distribution of biomass, carbon and nutrients among different tree compartments?
- (4) What is the effect of canopy position on total amounts and the distribution of biomass, carbon and nutrient stocks among different tree compartments?

## 2. Method

### 2.1. Study area

In 2018, we selected one 1-ha forest plot dominated by European beech (*Fagus sylvatica*), one by Douglas fir (*Pseudotsuga menziesii*) and one by Scots pine (*Pinus sylvestris* L.) in five study areas (Fig. 1), resulting in 15 forest plots in total. These three species represent important timber species in the Netherlands and other parts of Western and Central Europe. The selected forest plots were located on acidic sandy soils classified as Albic or Entic Podzols or Dystric Cambisols (WRB, 2015) (Table S1). These soils are characterized by high nitrogen stocks, ranging between 42 and 54 kg ha<sup>-1</sup> in the top 30 cm of the mineral soil and between 1000 and 1100 kg ha<sup>-1</sup> in the organic layers. Dissolved organic carbon in the top 30 cm of the mineral soil ranged between 1000 and 1100 kg ha<sup>-1</sup> (Vos et al., Under review). The plots were characterized by a similar temperate, maritime climate with an interpolated 30-year average annual rainfall and temperature of 850 mm and 10.6 °C respectively (KNMI, 2021). The forest in the plots consisted of relatively homogeneous, even-aged, single-tree species, planted forests between 50 and 120 year old. The dominant species within a stand took up more



**Fig. 1.** Locations of sites selected for biomass, carbon and nutrient measurements in this study. The numbers denote the locations of the study sites. The nationwide forest cover (in total 10% of the land area of the Netherlands) is shown in green (PDOK, 2015).

than 80 % of the total crown cover and basal area. All plots had previously been managed following common silvicultural methods in the Netherlands. Thinning regimes started with thinning from below (removal of suppressed trees) and, in the last three decades, all stands were treated using high-thinning (removal of trees directly competing with future crop trees). All study sites are subject to moderately high to high levels of *N*-deposition with annual atmospheric input ranging between 1200 and 2150 mol N/ha (RIVM, 2020), resulting in accelerated soil acidification, reducing nutrient availability (De Vries et al., 1995; de Vries et al., 2014).

In October 2018, forest stand properties were measured in each of the 15 plots before harvest of the trees in February–March 2019. The stem diameters at breast height (DBH) were measured for all trees in the 1-ha plot (Table 1). For 16 sampling points, dominant tree height was measured for 5 dominant trees using a digital measuring device (Nikon Forestry Pro laser, Japan). Each sampling point was in a 4 by 4 grid across the plot with 20 m distance between the points. Forest biomass stock was calculated based on the dry weight of the trees and the DBH of

all trees using plot-specific biomass expansion factors (Vos et al., Under review). We cored 20 bulked soil samples from the mineral layer (0–30 cm depth) separately via systematic sampling, with equal distances between sampling points covering the whole plot. Samples were dried at 40 °C to a constant weight and sieved (<2 mm). Unbuffered cation exchange capacity (CEC) was measured according to Varian Vista with ICP-AES (Thermo-Scientific iCAP 6500 DUO, USA) (Houba, 1997). The unbuffered cation exchange capacity in the mineral soil for all sites was dominated by exchangeable aluminium. Concentrations of exchangeable base cations (Ca, K and Mg) were below detection limit indicating almost an absence of any base saturation (Table 1).

## 2.2. Biomass, carbon and nutrient measurements

To estimate the aboveground biomass, carbon and nutrient stocks for trees differing in canopy position, one dominant, one intermediate and one suppressed tree was selected in each plot (Table 2). Those trees were picked from three equally-spaced DBH classes, covering the entire observed DBH range in each plot (Figure S1). The total of three trees per plot in five study areas resulted in 15 sampled trees per species. Tree compartments included were needles (no leaves for beech, since trees were harvested in winter, February/March 2019), small branches (<2 cm diameter) and coarse branches (2–10 cm diameter), and for the stem

**Table 2**

Mean  $\pm$  standard error ( $n = 5$ ) of DBH (cm), tree height (m) and stem length (m) for the sampled dominant, intermediate and suppressed trees per species. Tree height is defined as the vertical distance between stem base to highest crown part, and stem length as the distance from stem base to the point along the stem with a stem diameter < 10 cm. This latter point was a cutoff point, where we distinguished between stem and crown.

Species	Canopy position	DBH (cm)	Tree height (m)	Stem length (m)
Beech	Dominant	48.4 $\pm$ 5.5	23.9 $\pm$ 1.2	18.6 $\pm$ 1.4
	Intermediate	34.5 $\pm$ 4.9	22.6 $\pm$ 1.6	16.3 $\pm$ 2.0
	Suppressed	26.6 $\pm$ 4.2	20.8 $\pm$ 1.1	13.7 $\pm$ 2.4
Douglas fir	Dominant	62.8 $\pm$ 2.4	34.7 $\pm$ 1.9	29.9 $\pm$ 1.9
	Intermediate	48.3 $\pm$ 2.0	33.8 $\pm$ 2.9	29.1 $\pm$ 2.6
	Suppressed	34.7 $\pm$ 3.4	27.0 $\pm$ 3.0	22.0 $\pm$ 0.9
Scots pine	Dominant	33.7 $\pm$ 2.6	20.2 $\pm$ 1.2	15.6 $\pm$ 0.6
	Intermediate	25.2 $\pm$ 2.4	18.0 $\pm$ 0.5	13.4 $\pm$ 0.7
	Suppressed	16.6 $\pm$ 1.1	14.9 $\pm$ 0.7	8.2 $\pm$ 0.9

**Table 1**

Overview of stand and soil characteristics of the selected European beech, Douglas fir and Scots pine forests of this study.

Location	Species	Age (yr.)	Density (tree ha <sup>-1</sup> )	Dg (cm)	BA (m <sup>2</sup> ha <sup>-1</sup> )	Stock (t ha <sup>-1</sup> )	Hdom (m)	Soil pH	Al-CEC (%)	Soil BS (%)
1	Beech	94	248	34	22.8	195	22.1	4.3	91	2.1
2	Beech	101	140	47	24.8	194	25.6	4.3	97	0
3	Beech	82	197	37	21.6	194	24.5	4.2	94	1.3
4	Beech	98	219	34	21.2	201	24.3	4.5	83	10
5	Beech	46	840	17	21.5	129	19.4	4.1	77	1.3
1	Douglas fir	74	119	54	28.0	203	41.0	4.2	68	3.3
2	Douglas fir	59	170	50	32.8	233	36.5	4.0	75	2.0
3	Douglas fir	60	138	52	29.7	216	37.3	4.2	96	3.8
4	Douglas fir	66	127	52	27.0	197	36.0	4.0	74	4.0
5	Douglas fir	60	239	44	37.1	247	28.3	4.2	88	7.1
1	Scots pine	55	406	25	21.0	83	18.8	4.3	79	1.3
2	Scots pine	48	425	24	19.8	87	18.3	4.1	88	3.2
3	Scots pine	47	835	17	20.3	77	18.7	4.4	88	5.0
4	Scots pine	62	400	26	22.4	97	20.9	4.0	69	4.3
5	Scots pine	73	466	27	26.6	118	15.8	4.2	91	5.0

Notes: Density includes all trees with DBH > 10 cm; Dg is the average arithmetic DBH; BA is the forest basal area; Stock is the biomass stock per hectare based on plot specific biomass expansion factors (Vos et al., Under review); Hdom the dominant height based on height of 16 dominant trees per hectare; Soil pH is pH H<sub>2</sub>O of mineral soil 0–30 cm depth; Al-CEC is the percentage of the unbuffered CEC occupied by Al; Soil BS is the base saturation of the mineral soil based on the percentage of the unbuffered CEC occupied by the sum of Ca, K, Mg and Na (all under detection limit).



(>10 cm diameter), bark and sapwood and, if present, heartwood. The stem was defined as the main axis from the stem base upwards until the point where the stem diameter became smaller than 10 cm. The crown was defined as branches < 10 cm diameter, including needles. To estimate the total stem and branch volume of the tree, the total tree height, stem length and the branch base diameters and lengths for all living branches (>1 cm diameter) were measured. Whole tree fresh weight and stem fresh weight were measured directly after harvest in the field, using a tractive scale (Allscales Europe, cap. 3000 kg  $\pm$  2 kg) attached to an excavator (Fig. 2). Difference between whole tree fresh weight and stem fresh weight resulted in the crown fresh weight. To estimate the biomass of needles, small branches and coarse branches 4 representative branches (not severely damaged due to the felling) per tree were selected covering the observed range of measured branch diameters. For each of those branches, the diameter, the total length and the length of the coarse branch were measured. Total fresh weight and fresh weight of the coarse branch were measured by weighing the whole branch and the coarse branch with a tractive scale (crane scale SF-918, cap. 150 kg  $\pm$  0.1 kg, Fig. 2). All small branches per sampled branch were collected in sealed plastic bags, labelled and stored at 4 °C until measurement of: 1) total fresh weight; 2) dry weight of branch wood; 3) dry weight of needles (except for beech); and 4) dry weight of cones (except for beech), with dry weight defined as the constant weight after drying samples at 70 °C. Fresh and dry weights were also determined separately for a subsample of needles to calculate moisture loss allowing the calculation of fresh needle mass.

To estimate the biomass of the stem bark, stem sapwood and stem heartwood and the coarse branches, various disk samples were taken from each stem: close to the stem base, at the cut-off point of 10 cm stem diameter, and at 1/4th, 2/4th and 3/4th of the stem length, and for the branches at 2 cm stem diameter cut-off point, and halfway the 10-cm a 2-cm cut-off point. All disks were labelled, stored in plastic bags at 4 °C to prevent drying until further processing. Prior to destructive subsampling, the diameter, thickness and perimeter of the disks were measured. Subsequently, the whole disk was separated into bark, sapwood and, if present, heartwood (Fig. 2). Measurements conducted on separated compartments included measurements of 1) diameter; 2) perimeter; 3) fresh weight; 4) fresh weight density; 5) dry weight; and 6)

dry weight density.

Samples for chemical analysis were based on a mass weighted sample along the tree compartments (Supplement 1, Formulas S1-S11). The material was ground in a mill containing 1.5 mm stainless steel screen for nutrient analysis and analysed for N and carbon content by using a CN-analyzer (LECO TruSpec CHN, USA). Concentrations of P, S, K, Ca, Mg, Mn, Cu, Fe and Zn were analysed following 0.43 M HNO<sub>3</sub> extraction and by using an ICP-AES (Thermo-Scientific iCAP 6500 DUO, USA) (Houba, 1997). Details on the method are in Supplement 1.

### 2.3. Biomass quantification models

The biomass of the stem bark, stem sapwood and stem heartwood were calculated based on the volume and density of the tissues along different segments of the stem. Stem length was divided into four segments, and for each segment the volume was calculated based on the means of the stem disks at the top and bottom of the segment, treating the stem segment as a truncated cone. Accuracy of the calculation was evaluated based on the calculated and measured fresh aboveground biomass (Figure S5 - S6). Highest accuracy for volume calculations of the stem wood was achieved by calculating the radius of the stem wood and heartwood as a function of the perimeter of the disk, instead of calculations based on measured disk diameter. Bark volume was calculated as a function of the dry weight, density and thickness of the bark per disk to correct for the heterogenous nature of the bark. Volume corrections for bark, sapwood and heartwood were executed for beech and Scots pine, based on the number of ramifications within the stem (formula S18). The specific density of the bark, sapwood and heartwood per stem disk was used to calculate the fresh and dry biomass per compartment. A stepwise overview of the calculations to derive stem volume, stem dry weight and stem fresh weight and the validation of the calculations are in Supplement 1.

The dry and fresh biomass of needles, small branches and coarse branches was estimated for the entire crown based on the four sampled branches per crown. To derive whole crown estimates, linear mixed effect models were fitted per species using the restricted maximum likelihood method and nested within the tree following the procedure as described by (Zuur et al., 2009). Branch models were formulated as a



**Fig. 2.** Pictures of measurements in the field (top) and in the laboratory (bottom). Fieldwork included measurement of the fresh weight of the entire tree (top left), fresh weight of the stem (top middle left), fresh weight of branches (top middle right) and fresh weight of the coarse branch (top left). Laboratory work included separation of the stem disk into bark, sapwood and, if present, heartwood (bottom left), extracting slices for determination of the dry weight density (bottom middle) and separation of the dried branch material into needles (bottom middle right) and small branches (bottom right).



compromise between the best possible estimates and the simplicity of the model. Therefore, models were based on the volume of branches as this proved to be a better estimate than length and diameter separately. Overview of the fitted regression models is in Table S2 – S3.

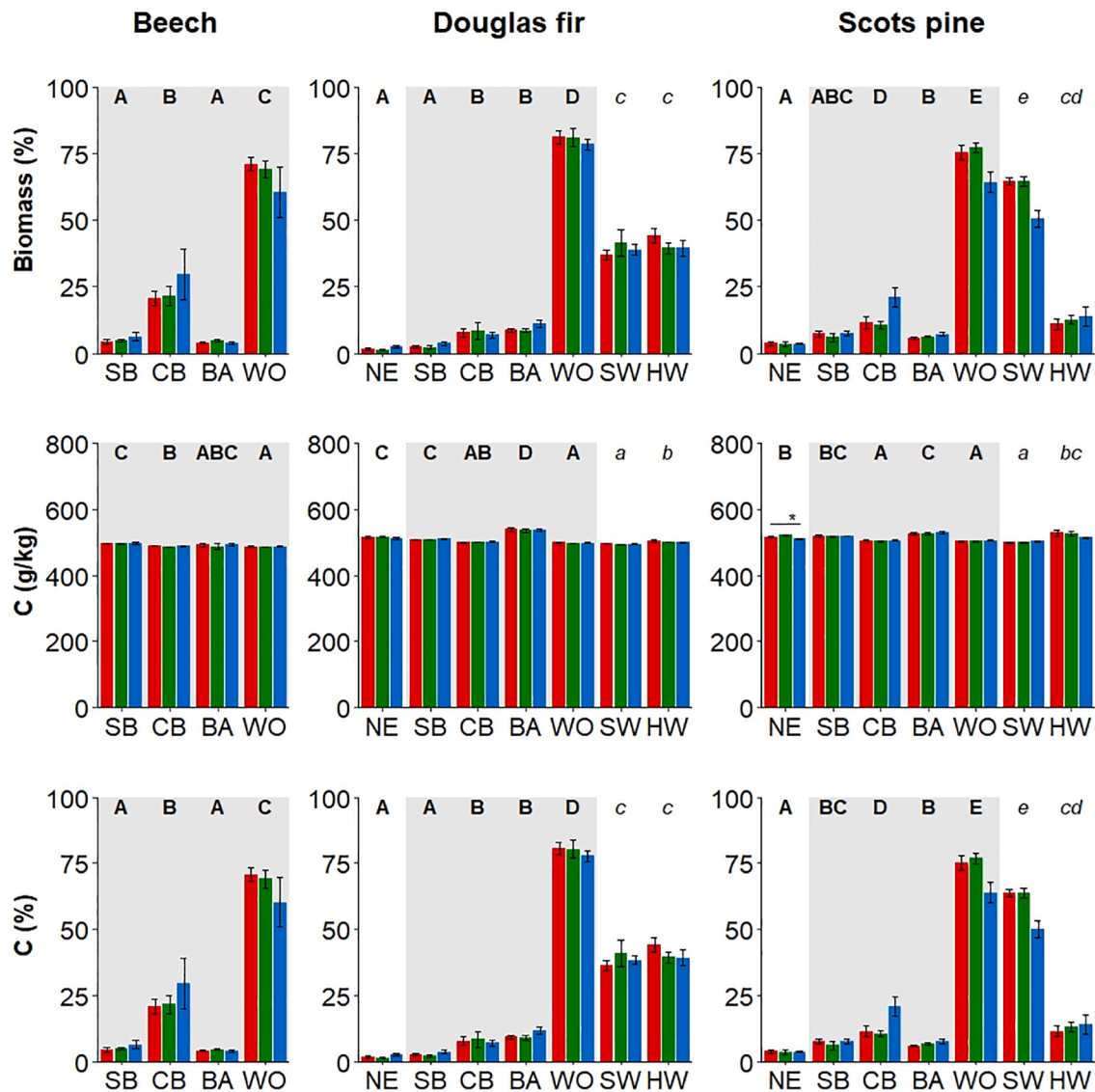
#### 2.4. Statistical analysis

Biomass, carbon and nutrient distributions between the different tree compartments were expressed as the mass fraction (%) of the total aboveground biomass, carbon stock and nutrient stock, respectively. The aboveground biomass excluded the foliage mass to harmonize the biomass fractions of the coniferous trees (Douglas fir and Scots pine) with the deciduous European beech. Differences in the biomass, carbon and nutrient distributions and carbon and nutrient concentrations between canopy positions and tree compartments were analysed by using a two-factor nested ANOVA. Nesting was carried out to correct for the

dependency between compartments within the tree and site. The used statistical was:

$$Y_{it} = \mu + \alpha_i + B_{t(i)} + \varepsilon_{iz}$$

Where Y is the biomass distribution, carbon or nutrient concentration or mass distribution per tree (i),  $\alpha$  is the fixed effect of canopy position,  $\beta$  is the fixed effect of the tree compartment (t) and  $\varepsilon$  is the residual error within tree (i) and study site (z). All data were checked for normality and homogeneity of variances. The constant variant function varIdent (nlme package) was used when variances were heterogenous. All statistical analyses were performed with R version 3.6.1. based on the nlme package followed by pairwise comparison with Tukey's *posthoc* test (Emmeans package). To reduce the number of type-I error results in the multiple test comparison, statistical tests were considered significant at  $P < 0.01$ .



**Fig. 3.** Biomass distribution (%), carbon (C) concentrations ( $\text{g kg}^{-1}$ ) and carbon mass distribution (%) in needles (NE), small branches (SB), coarse branches (CB), stem bark (BA), stem wood (WO), and for both conifers separately stem sapwood (SW) and stem heartwood (HW), for trees of European beech, Douglas fir and Scots pine in dominant position (red bars), intermediate position (green bars) and suppressed position (blue bars). Error bars indicate standard error from the mean value ( $n = 5$ ). Different capital letters indicate significant differences ( $p < 0.01$ ) among NE, SB, CB, BA and WO, and small letters between sapwood (SW) and heartwood (HW) for Douglas fir and Scots pine. We did not find significant differences for between canopy positions although canopy position did influence specific tree compartments within Scots pine ( $p < 0.01$ ). The within compartment interaction with canopy position is marked with \* when  $p < 0.01$ . Without an \* the main effects of canopy position and interactions with compartments were insignificant.

### 3. Results

#### 3.1. Biomass distribution, carbon concentration and mass distribution

The total aboveground dry biomass per tree ranged between 108 and 3117 kg for beech, 255–2913 kg for Douglas fir and 54–698 kg for Scots pine. Average mass-based total tree carbon concentrations were 487 g kg<sup>-1</sup> biomass for beech, 503 g kg<sup>-1</sup> for Douglas fir and 507 g kg<sup>-1</sup> for Scots pine. Trees from different canopy positions varied substantially in total biomass; relative to suppressed trees, intermediate and dominant trees had 59–204 % and 255–441 % more biomass, respectively.

Biomass and carbon mass fractions differed strongly between tree compartments, with highest (up to 75 %) values for stem wood, followed by coarse branches, small branches and bark for beech and Scots pine, and by bark, coarse branches and small branches for Douglas fir (Fig. 3). Carbon concentrations varied little between tree compartments. However, carbon concentrations were slightly lower in stem wood and higher in small branches for beech, and lower in stem wood and coarse branches but higher in stem bark for both conifers (Fig. 3).

Trees from different canopy positions were remarkably similar in biomass distribution, carbon concentration, and carbon distribution, despite few significant trends for Scots pine (Table S4). Canopy position influenced biomass distribution and carbon mass distribution in the sapwood of Scots pine (ANOVA test,  $P < 0.01$ ), but the differences between tree components were not significant probably because the canopy position effects were relatively inferior (Fig. 3). Overall, suppressed Scots pine trees had a lower, but insignificant, biomass (and carbon) fraction in the sapwood, which was mainly compensated by higher, but insignificant, mass fractions in coarse branches. On tissue level, canopy position caused a higher needle carbon concentration in intermediate trees compared to suppressed trees, but effect sizes were small (Fig. 3).

#### 3.2. Nutrient concentrations

Nutrient concentrations differed between tree compartments. Overall, nutrient concentrations increased from stem wood < coarse branches < stem bark < small branches < needles (Fig. 4). Calcium, however, showed the highest concentrations in the stem bark for both beech and Scots pine (Fig. 4). Patterns were less obvious for micronutrients, such as Mn, Cu, Zn and Fe (Figure S8).

Significant effects of canopy position on macronutrient concentrations were absent in European beech and Douglas fir and hardly observed in Scots pine. Suppressed Scots pine trees had higher Ca concentrations compared to dominant trees with strongest effects in the stem wood (Fig. 4). Micronutrient concentration in Douglas fir was hardly influenced, effects were absent in both beech and Scots pine (Table 3, Figure S8). Significant interactions between tree compartments and canopy positions were scarce, only in Scots pine weak significances were found.

#### 3.3. Nutrient mass fractions

All tree compartments contributed substantially (> 10 %) to nutrient stocks in trees, regardless of low biomass fractions or low nutrient concentrations (Fig. 5, Figure S10). Stem wood in general contained the highest stocks, up to 50 %, but not in all cases. For example, beech trees stored up to 40 % of the Ca mass in the stem bark and only 30 % in the stem wood. Douglas fir trees stored relatively similar nutrient amounts in stem wood and stem bark, except for N. Scots pine trees stored 40 % of the total P mass in needles, while for other macronutrients the highest stocks were present in the sapwood. On average, woody branches hold 42 % of the nutrient mass in beech, 30 % of the nutrient mass in Douglas fir and 40 % of the nutrient mass in Scots pine. Overall, the analyses imply that all tree components contribute substantially to overall nutrient stocks, but that nutrient stocks per tree compartment differ largely between species.

Effects of canopy position on the nutrient mass distributions were non-significant (Table 3). Significant interactions between tree compartments and canopy positions were scarce, only in Scots pine weak significances were found (Table S6). Overall, canopy position effects were thus marginal or absent.

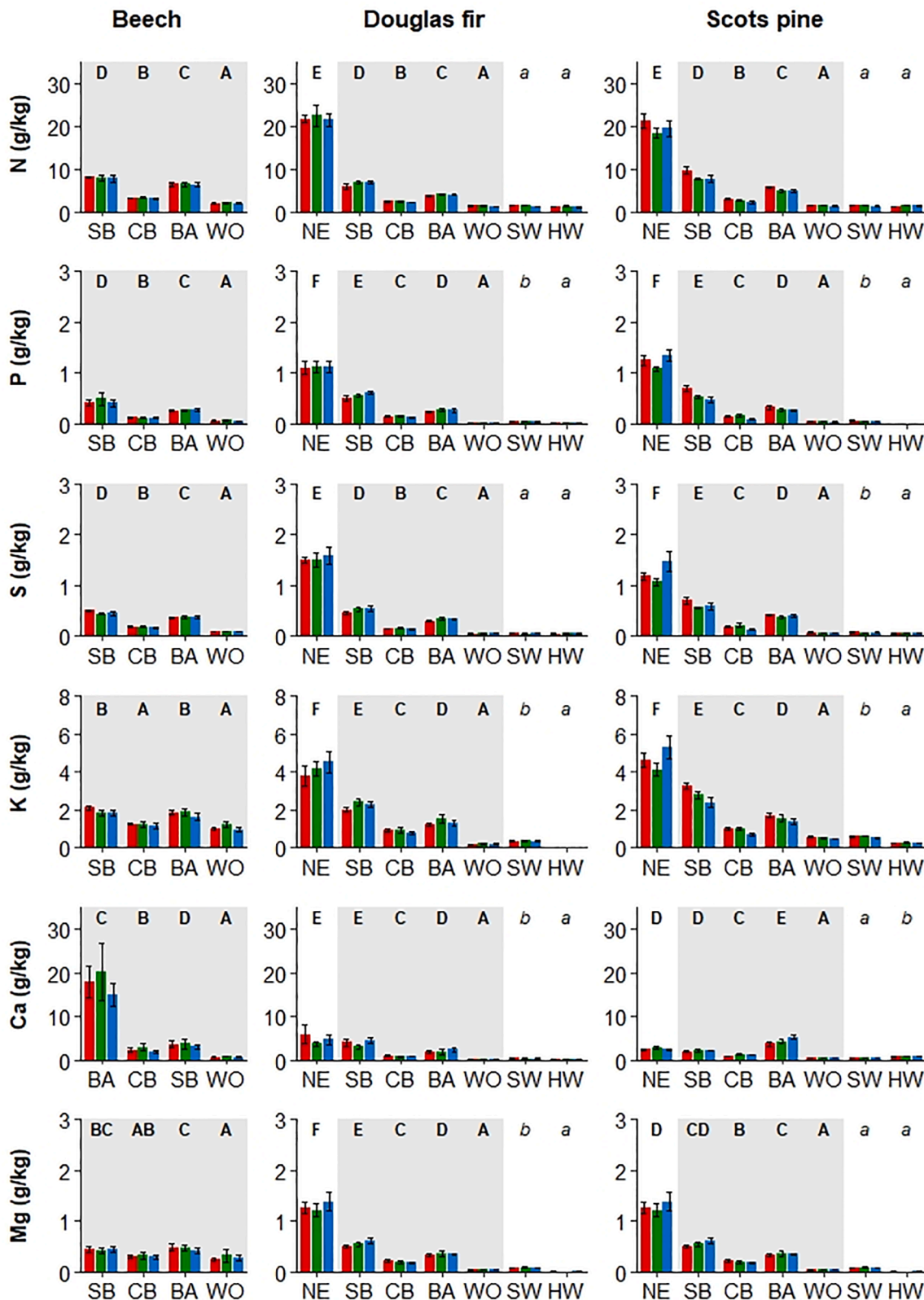
### 4. Discussion

In this study, we compared the biomass stocks and the carbon and nutrient concentrations within tree compartments between dominant, intermediate and suppressed trees of European beech, Douglas fir and Scots pine growing in forests on poor sandy soils in the Netherlands. We show that the effects of canopy position on the carbon and nutrient concentrations and on the distributions of biomass, carbon and nutrients between compartments are often not significant. In line with our questions, we put this major result in context by discussing the carbon concentrations within tree compartments, the nutrient concentrations within tree compartments and the distribution of biomass, carbon and nutrients among different tree compartments. Ultimately, the implications for the effect of canopy position on total amounts and distribution of biomass, carbon and nutrient stocks are discussed.

#### 4.1. Carbon concentrations slightly deviated from 50 %

Our study results confirm that carbon concentrations are indeed relatively constant and close to 50 % but highlights nevertheless subtle differences across species and tree compartments. Averaged carbon concentrations in this study were above 50 % in both conifers (Douglas fir: 50.3 %, Scots pine 50.7 %) and below 50 % in beech (48.8 %). These values are similar to those reported in the literature for beech (Joosten et al., 2004), Douglas fir (Canary et al., 2000; Jain et al., 2010) and Scots pine (Janssens et al., 1999; de Aza et al., 2011). Our study thus confirms that carbon concentrations are close to the 50 % estimate, but that angiosperms may have slightly lower carbon concentrations in plant tissues than gymnosperms (Thomas and Martin, 2012).

For all three species, a subtle increase in carbon concentrations was observed from stem wood, coarse branches, small branches towards needles. This slight increase can be explained by the proximity towards foliage where sugars are produced (Woodruff and Meinzer, 2011) and, in case of beech, related to the storage of non-structural carbohydrates for spring growth (Barbaroux et al., 2003). The observed carbon concentrations per tree compartment were similar to those reported by others (Laiho and Laine, 1997; Tolunay, 2009; Armolaitis et al., 2013; Hernández-Vera et al., 2017; Beets and Garrett, 2018; Husmann et al., 2018; Węgiel and Polowy, 2020). Subtle differences were found between different tree compartments with relatively low carbon concentrations in the sapwood and, for both conifers, high carbon concentrations in the bark (Fig. 3). High carbon concentrations in the bark have also been observed among other species (Bert and Danjon, 2006; Tolunay, 2009; Martin et al., 2015; Pompa-Garcia et al., 2017), and might be related to high levels of lignin (Franceschi et al., 2005; Bert and Danjon, 2006), non-structural carbohydrates (Zhang et al., 2014), and defence chemicals (Franceschi et al., 2005; Graça, 2015). In contrast, the carbon concentration in the thin bark of beech was similar to the carbon concentrations of other tree compartments (Fig. 3). The higher carbon concentration in the heartwood compared to the sapwood of both conifers, most strikingly for Scots pine, has also been observed in other coniferous tree species (Jain et al., 2010; de Aza et al., 2011), and may be attributed to higher concentrations of lignin (Scheffer, 1966; Bertaud and Holmbom, 2004; Benouadah et al., 2019), cellulose (Bertaud and Holmbom, 2004; Campbell et al., 2007; Benouadah et al., 2019), resin acids (Piispanen and Saranpää, 2002; Bergström, 2003), and various kinds of lipophilic and hydrophilic extractives (Bertaud and Holmbom, 2004; Benouadah et al., 2019) all with different carbon concentrations. These results imply that the presence of heartwood affects the observed carbon concentrations within stems. Overall, our study confirms that



**Fig. 4.** Concentrations of macronutrients in needles (NE), small branches (SB), coarse branches (CB), stem bark (BA), stem wood (WO), and for both conifers separately stem sapwood (SW) and stem heartwood (HW) for trees in dominant position (red bars), intermediate position (green bars) and suppressed position (blue bars). Error bars indicate standard error from the mean value ( $n = 5$ ). Different capital letters indicate significant differences ( $p < 0.01$ ) among NE, SB, CB, BA and WO, and small letters between sapwood (SW) and heartwood (HW) for Douglas fir and Scots pine. All interactions between canopy position and tree compartments were insignificant ( $p > 0.01$ ).



**Table 3**

Significance levels (P-values) of the analysis of variance for the effect of canopy position on nutrient concentrations and nutrient mass fractions. Mean values, S.E. and test statistics of Anova are in Table S5 and Table S6. To reduce the number of type-I error results in our multiple test comparison, we only highlight (in bold) the significant results with  $P < 0.01$ .

Species	N	P	S	K	Ca	Mg	Mn	Cu	Zn	Fe
Concentration										
Beech	0.87	0.67	0.32	0.45	0.67	0.90	0.099	0.22	0.30	0.14
Douglas fir	0.31	0.90	0.12	0.69	0.78	0.39	<b>&lt;.001<sup>a</sup></b>	0.34	0.65	0.12
Scots pine	0.21	0.083	0.88	0.84	<b>&lt;.001<sup>a</sup></b>	0.063	0.18	0.34	0.32	0.049
Mass fraction										
Beech	0.70	0.81	0.69	0.89	0.60	0.63	0.93	0.51	0.38	0.41
Douglas fir	0.15	0.85	0.76	0.31	0.55	0.50	0.60	0.14	0.70	0.028
Scots pine	0.29	0.70	0.73	0.84	0.97	0.67	0.94	0.96	0.078	0.44

Notes: Significant P-values are given in bold. To reduce the number of type-I error results in our multiple test comparison, statistical tests were considered significant at  $p < 0.01$ . <sup>a</sup> not different in post-hoc test.

small differences exist in carbon concentrations between aboveground tree compartments whereby variation within conifers was higher compared to beech, and that assumption of 50 % carbon concentrations would lead to an overestimation of the carbon stock of 3.6 % in European beech and an underestimation of 1.2 % in Scots pine.

#### 4.2. Nutrient concentrations indicate N surplus and P limitation

We compared nutrient concentrations within different aboveground tree compartments with other studies to show possible effects of the nutrient availability in the acidified sandy soils, and the relatively high levels of nitrogen deposition. Nutrient concentrations differed between tree compartments: macronutrients were highest in the needles and lowest in the stem wood, as was expected based on the different physiological demands of tree compartments and shown by multiple other studies (Clayton and Kennedy, 1980; Ranger et al., 1995; Mussche et al., 1998; Knust et al., 2016; Husmann et al., 2018; Węgiel et al., 2018; de Vries et al., 2019). For micronutrient concentrations we did however not observe such trends amongst tree compartments (Table S8) suggesting that physiological demands are of limited importance and possibly overruled by age related nutrient accumulation (Caritat and Terradas, 1990; Li et al., 2020), and the relative mobility of micro-nutrients (Ots and Mandre, 2012) which can be influenced by a surplus of N as well as P-limitation (Wu et al., 2021).

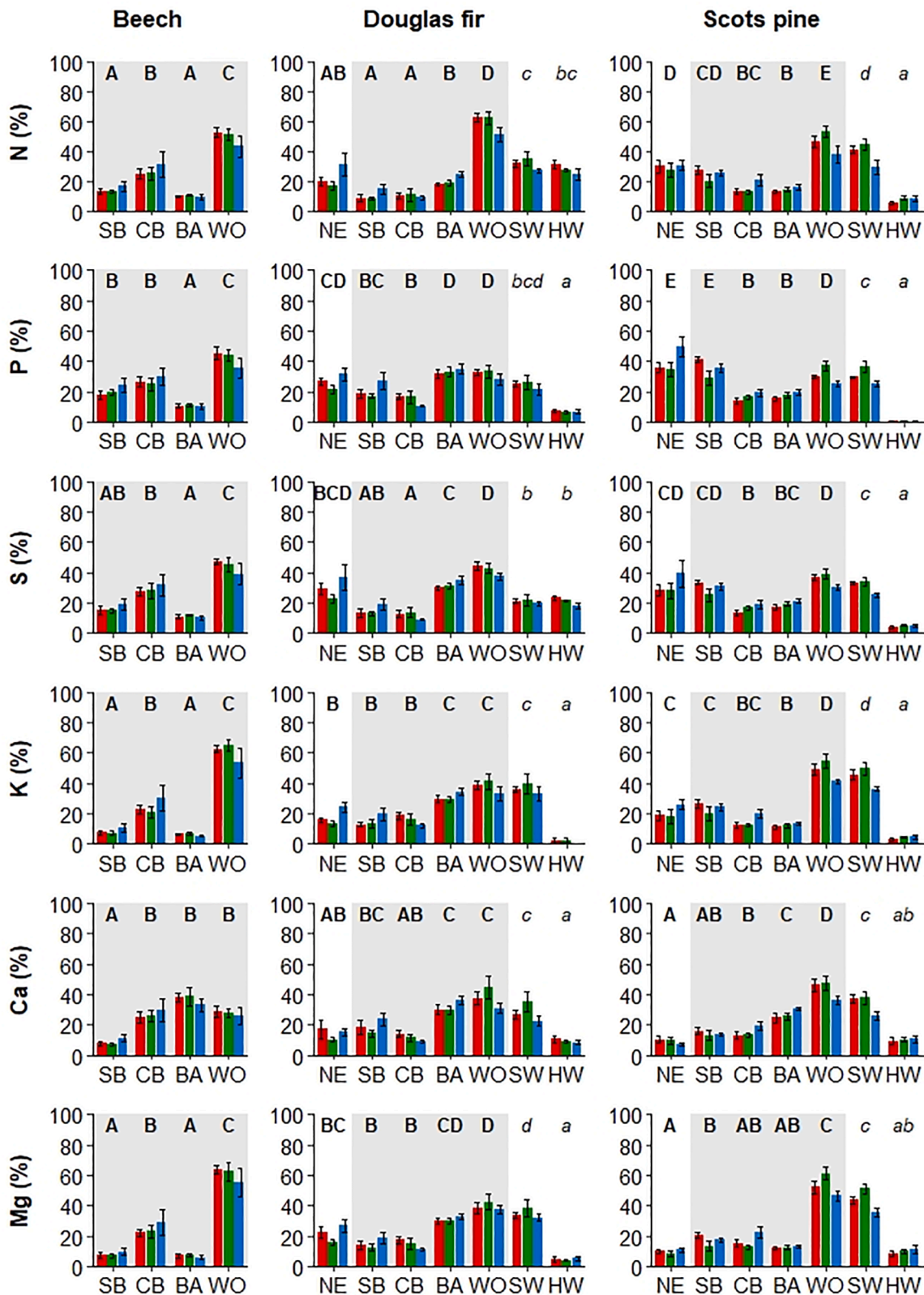
The nutrient concentrations of our study trees differed from the values reported in literature, with low concentrations of P, K, Ca, Mg and Mn, especially in both conifer species (Table 4). The N concentrations were high, which agrees with the high levels of nitrogen deposition for our study sites. These high N concentrations were also reflected by low foliar C:N ratios in Douglas fir and Scots pine, with values (resp. 24 and 27 %) only half the ratios reported for other temperate conifers (McGroddy et al., 2004; Sardans et al., 2011). Foliar concentrations indicated low nutritional status of P and K in Douglas fir while P only was latent deficient in Scots pine (Van den Burg and Schaap, 1995; Mellert and Gottlein, 2012). The observed foliar N:P ratios (17–20 %) exceeded the N:P thresholds of 14.1 (Scots pine) and 16 (general threshold), which is indicative of P limitation (Koerselman and Meuleman, 1996; Aerts and Chapin III, 1999; Mellert and Gottlein, 2012). Such P limitation is also echoed by the very low foliar C:P ratios of Douglas fir and Scots pine, which was only 1/3th of the average foliar C:P ratio reported for a set of temperate conifers (McGroddy et al., 2004). The observed differences in nutrient concentrations are probably driven by surplus of N and limitation of P and base-cations, reflecting the soil acidity (pH between 4.0 and 4.5) of the studied forests.

Our study trees are representative of forest with low tree nutritional status. Tree nutritional status is decreasing over Europe with N deposition as the hypothesized trigger (Jonard et al., 2015). Surplus of N and the related soil acidification causes leaching of base cations and releases of aluminum from the soil (Bowman et al., 2008). The average occupation of aluminum on the cation exchange complex in this study is 84

± 2.5 % (Table 1) indicating a nutrient poor and strongly acidified soil. High soil N and soil acidification can impair the uptake of P, K and Mg (Braun et al., 2020) but still increases tree productivity (de Vries et al., 2014; Jonard et al., 2015; Sardans et al., 2016), which results in limitation of nutrients like P (Braun et al., 2010; Sardans et al., 2016; Du et al., 2021). Signs of deficiencies of P in Douglas fir stands and shortages of Mg and Ca in Scots pine stands was already detected in 1986 in forests in the Netherlands and related to high levels of N deposition (Mohren et al., 1986; Houdijk and Roelofs, 1993). Low K concentrations, especially in Douglas fir, is known to be negatively correlated with increasing levels of ammonium (Van Dijk et al., 1990). Also, this study confirms low macro nutrient concentrations in the aboveground tree compartments indicating the persistent effects of N deposition on the forest ecosystem.

#### 4.3. Distributions were similar for biomass and carbon, but differed for nutrients

The distribution of biomass and carbon amongst tree compartments was – as expected from the relatively constant carbon concentrations – highly similar (and hence we focus on only biomass in this discussion) but differed from the distributions of nutrients. As expected, most biomass is stored in stem wood (range: 67 % – 80 %) and these observed stem wood mass fractions fell within the range of reported values in earlier studies (Nihlgård, 1972; Grier and Logan, 1977; Pellinen, 1986; Ranger et al., 1995; Vanninen et al., 1996; Andre et al., 2010; Husmann et al., 2018). The sapwood fraction (Douglas fir 39 %, Scots pine 60 %) was relatively close to the heartwood fraction (41 %) in Douglas fir, while the heartwood fraction (12 %) was lower in Scots pine, but such fractions are typically age dependent (Vanninen et al., 1996; Gjerdrum, 2003). Stem bark biomass fractions in beech (4.2 %) and Douglas fir (9.3 %) were close to those reported by earlier studies for beech (Nihlgård, 1972; Husmann et al., 2018) and Douglas fir (Ranger et al., 1995), but lower for Scots pine (6.4 %) compared to an earlier study on 40–80 year old trees (DBH 16–33 cm) in southern Finland (Vanninen et al., 1996). The lower stem bark fraction was probably caused by a lower volume of the bark since the density of the bark ( $0.32 \text{ g cm}^{-3}$ ) was within the normal range ( $0.27\text{--}0.36 \text{ g cm}^{-3}$ ) (Dibdiakova and Wang, 2015). The observed biomass fractions in branches (range: 10 % – 29 %) were consistent with branch mass fractions reported by previous studies (Nihlgård, 1972; Ranger et al., 1995; Skovsgaard and Nord-Larsen, 2012; Wertz et al., 2020). The observed needle mass fractions in both Douglas fir (1.8 %) and Scots pine (3.6 %) were low, only half the needle mass percentages reported in literature (Ranger et al., 1995; Vanninen et al., 1996). Since our study trees were harvested in the winter of 2019, we speculate that these low needle masses were caused the severe 2018 summer drought, causing defoliation both in Douglas fir and Scots pine (Rebetez and Dobbertin, 2004; Galiano et al., 2010; Sergeant et al., 2014). We thus conclude that biomass and carbon distributions were rather similar to values reported from other sites, expect for some



**Fig. 5.** Mass distribution expressed as 100 % of total above ground woody mass for macronutrients in needles (NE), small branches (SB), coarse branches (CB), stem bark (BA), stem wood (WO), and for both conifers separately stem for sapwood (SW) and stem heartwood (HW), for trees in dominant position (red bars), intermediate position (green bars) and suppressed position (blue bars). Error bars indicate standard error from the mean value ( $n = 5$ ). Different capital letters indicate significant differences ( $p < 0.01$ ) among NE, SB, CB, BA and WO, and small letters between sapwood (SW) and heartwood (HW) for Douglas fir and Scots pine. All interactions between canopy position and tree compartments were insignificant ( $p > 0.01$ ).

**Table 4**

Average nutrient concentrations of N, P, S, K, Ca and Mg (g/kg) in literature and the difference (%) with values observed in this study. Percentage of difference (Diff) is calculated as the mean concentration of this study divided by the mean concentration in literature minus 100 %. Difference of  $\geq 20$  % are highlighted. The reference studies used (n: number of studies) are in table S7.

		Beech			Douglas fir			Scots pine		
		Mean		Diff	Mean		Diff	Mean		Diff
		n	g/kg		n	g/kg		n	g/kg	
N	NE				7	13	<b>63</b>	4	13	<b>50</b>
	SB	3	7.4	−3.0	4	6.7	−2.1	2	6.2	<b>35</b>
	CB	2	2.8	15	2	4.1	−43	2	2.3	16
	BA	6	7.8	−18	6	3.6	10	4	4.1	<b>27</b>
	SW	5	2.0	2.6	3	1.7	−18	4	0.93	<b>57</b>
P	HW				3	1.5	−20	4	0.72	<b>87</b>
	NE				7	1.8	−37	4	1.3	−5.8
	SB	4	0.59	−25	4	0.71	−21	2	0.56	1.3
	CB	3	0.25	−52	2	0.35	−59	2	0.25	−46
	BA	7	0.37	−29	6	0.34	−23	6	0.44	−33
S	SW	6	0.09	−33	2	0.06	−31	4	0.07	−28
	HW				2	0.01	2.9	4	0.02	−75
	NE				2	0.99	55	2	1.1	11
	SB	1	0.48	−4.0	0	n.d.	n.d.	1	0.73	−16
	CB	1	0.15	22	1	0.12	26	1	0.25	−31
K	BA	3	0.51	−27	3	0.19	64	4	0.55	−27
	SW	2	0.10	−7.6	2	0.07	−35	0	n.d.	n.d.
	HW				2	0.06	−23	0	n.d.	n.d.
	NE				7	6.1	−32	5	4.6	1.0
	SB	4	2.2	−12	4	2.6	−13	3	2.7	4.9
Ca	CB	3	1.4	−14	2	1.4	−37	2	1.0	−13
	BA	7	2.3	−23	6	1.6	−17	6	1.6	−2.5
	SW	6	1.1	−1.4	3	0.42	−14	5	0.44	<b>32</b>
	HW				3	0.14	−90	5	0.17	<b>55</b>
	NE				7	6.2	−23	5	3.1	−18
Mg	SB	4	4.3	−21	4	6.1	−37	3	2.2	−3.4
	CB	3	2.5	−5.0	2	5.3	−84	2	1.7	−32
	BA	7	18	0.28	6	4.3	−52	6	7.3	−39
	SW	6	0.97	−24	3	0.43	−14	5	0.61	−7.3
	HW				3	0.22	−47	5	0.77	7.6
	NE				6	1.3	−0.5	5	0.75	−9.3
	SB	4	0.44	−2.3	3	0.73	−23	3	0.60	1.9
	CB	3	0.32	−2.8	2	0.33	−38	2	0.39	−22
	BA	6	0.51	−11	6	0.33	4.9	4	0.57	−15
	SW	6	0.25	14	3	0.09	3.7	5	0.16	8.3
	HW				3	0.03	−61	5	0.16	14

differences caused by age (heartwood – sapwood) or recent weather conditions (needle mass).

Whereas the highest stocks of biomass and carbon (>67 %) were within stems and much lower for the other tree compartments (range: 1.8 % – 24 %), stem stocks were relatively low for nutrients (range: 23 % – 60 %) while other tree compartment had stocks of 18 % – 19 %. These differences result from the (in most cases) much higher nutrient concentrations in bark, branches and needles, reflecting high physiological demands compared to the stem. The nutrient stocks in the stem wood are compared to the other components still higher (average: 44 %), which thus resulted from the large stem wood biomass fractions. The implications of these nutrient stocks in bark and crown should be considered in forestry practices, moving from stem only harvest to biomass harvest including crown.

#### 4.4. Canopy position had only minor effects on aboveground carbon and biomass distributions

Our results show that the aboveground distribution of carbon and biomass among different tree compartments was hardly affected by the canopy position of trees. First, canopy position had no effect on carbon concentrations except in Scots pine where the needles of suppressed trees had slightly lower carbon concentrations than the needles of dominant or intermediate trees (Fig. 3). Since trees were harvested in winter, it remains very speculative whether such differences in needle carbon concentrations between canopy positions result from a lower respiration: gross assimilation - ratio in trees with higher canopy

position (Lebaube et al., 2000). Earlier studies also find hardly any significant effect of canopy position on tree carbon concentrations (Naidu et al., 1998; Xing et al., 2005; Zhang et al., 2009; Zhou et al., 2018). We therefore conclude that carbon concentrations are not affected by the canopy position of trees.

Second, the distribution of biomass and carbon hardly differed between suppressed, intermediate and dominant trees, except for some minor effects observed for Scots pine. This result seems remarkable since it is well known that dominant trees grow much faster than suppressed trees (D'Amato and Puettmann, 2004; Reid et al., 2004; Castagneri et al., 2008) and develop wider crowns and thicker stems than more suppressed trees (Dieler and Pretzsch, 2013; Pretzsch, 2014). While such differences were also apparent for our study trees confirming that trees are plastic in crown shapes, our results show that trees can have be highly plastic in shape while controlling the distributed biomass amongst tree compartments within narrow ranges. This result is consistent with observations of similar biomass distributions between twigs and leaves for trees in temperate to boreal conditions (Petit et al., 2018), by the similar distributions of leaf versus stem biomass in trees of dry versus wet sites (Anfodillo et al., 2016) and by other studies on aboveground biomass distribution (Gargaglione et al., 2010; Skovsgaard and Nord-Larsen, 2012; Van de Peer et al., 2017). Our results thus imply that aboveground biomass distributions are more in line with the theory of fixed scaling relationships (Shinozaki et al., 1964; Enquist and Niklas, 2002), and less with the functional equilibrium theory (Brouwer, 1962; Reynolds and Thornley, 1982).

Remarkably, the functional equilibrium theory – predicting that



resource allocation is driven by priority and demand whereby trees adapt the biomass distribution in response to competition - was supported by other studies reporting a higher share of crown biomass for dominant trees (Bartelink, 1996; 1997; Naidu et al., 1998; Vanninen and Mäkelä, 2005; Krejza et al., 2017; Wertz et al., 2020) and increased height growth for suppressed trees (Naidu et al., 1998). The effects of canopy position on the biomass distribution in Scots pine did not involve an increase of crown biomass fraction for dominant trees (Fig. 3) nor increased height growth for suppressed trees (Figure S7) providing no support for the functional equilibrium theory. Absence of an effect of canopy position on the aboveground biomass distribution might be related to the environment (Lines et al., 2012) and the exposure to limited resources (Schall et al., 2012; Slot et al., 2012). For example, beech showed remarkable plasticity in response to competition (Dieler and Pretzsch, 2013; Pretzsch, 2014) although low site fertility weakened the effect (Dieler and Pretzsch, 2013). Also for Scots pine smaller effects of competition on biomass distribution were observed on poor sites (Vanninen and Mäkelä, 2005). We therefore hypothesize that the absence of an effect of canopy position on biomass distribution, nutrient concentrations and nutrient stocks is related to the nutrient poor and acidic site conditions resulting from the effects of N deposition.

#### 4.5. Canopy position is not the main driver of nutrient concentrations and stocks

Canopy position was hypothesized to alter nutrient concentration as dominant trees have higher metabolic rates and therefore acquire water and nutrients more rapidly (Martin et al., 1997; Granier et al., 2000; D'Amato and Puettmann, 2004; Reid et al., 2004; Castagneri et al., 2008; Aranda et al., 2012). Surprisingly, this study showed hardly any effect of canopy position on nutrient concentrations. Absence of an effect of canopy position on nutrient concentrations was observed by multiple studies (Höhne, 1964; Son and Gower, 1992; Naidu et al., 1998; Sette et al., 2013). The higher levels of Ca in Scots pine trees with a suppressed canopy position are in line with observations for *Nothofagus antarctica* (Peri et al., 2006). Remarkably there is no consistency in the nutrient concentrations between trees of different canopy position in Scots pine as lower concentrations of N, P, K and S were observed in dominant trees compared to suppressed trees (Wright and Will, 1958; Węgiel et al., 2018). The mechanisms behind these differences in nutrient concentrations remains speculative. Immobile nutrients, like Ca, can accumulate in older woody parts due to low translocation rates which could cause higher concentrations in suppressed trees (Finér and Kaunisto, 2000; Prasolova and Xu, 2003). The minor effects of canopy position on biomass distributions and nutrient concentrations explain the absence of strong effects of canopy position on nutrient stocks. While we cannot exclude a mitigating role of the poor soils in our study sites on divergent nutrient concentrations within trees, our results and those from the reported literature imply that canopy position does not act as the main driver of tree nutrient concentrations for supporting divergent metabolic rates between trees differing in canopy position.

#### 4.6. Conclusions

The distribution of biomass, carbon and nutrient differs among tree compartments and tree species. The canopy position does have no or minor effects on the aboveground distribution of biomass and carbon and on nutrient concentration and distributions between aboveground tree compartments. These results are better in line with the allometric scaling theory than the functional equilibrium theory.

Our study implies that models aiming for estimating tree and forest biomass and carbon and nutrient stocks should apply species specific biomass, carbon and nutrient stocks with equal biomass, carbon and nutrient stocks for trees independent of canopy position as a valid assumption, but we nevertheless recommend testing this assumption for a broader range of species and site conditions.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

#### Acknowledgements

This research is part of the Nutrient Balance project and was funded by the Dutch Research Council (NWO, No. ALWGS.2017.004). We acknowledge Henk van Roekel, Leo Goudzwaard and many other members of the harvest team for their valuable help with establishing the experiment, the harvest and the sample processing. We thank our partners, National Forest Service, Union of private Forest Owner Groups, Het Loo Royal Estate, Staro nature and countryside, Borgman management consultants, National Park de Hoge Veluwe and Blom Ecology for financial support, permission to work in their forest or other provided services.

#### Author contributions

Marleen A.E. Vos, Wim de Vries, Jan den Ouden and Frank J. Sterck conceptualized the ideas. The funding was acquitted by Marleen A.E. Vos supported by Wim de Vries, Jan den Ouden and Frank J. Sterck. Methodology was designed by Marleen A.E. Vos, Dieke de Boer and Jan den Ouden. Investigation and data curation were conducted by Marleen A.E. Vos and Dieke de Boer. The formal analysis and visualisations were performed by Marleen A.E. Vos. Marleen A.E. Vos led the writing of the manuscript of both the original draft as the review. All authors contributed critically to the drafts and gave final approval for publication.

#### Data availability statement

No data has been published yet.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120731>.

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