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Comparison of nutrient and carbon stocks in the aboveground biomass of mature silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* L. Karst) stands

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Abstract: The aim of the study was to compare the stock of essential nutrients and carbon in the aboveground biomass of mature stands of silver fir and Norway spruce. A comparison was carried out for 14 mixed stands of spruce and fir. The tree-level dendrometric characteristics were taken from experimental measurements or were generated using the SIBYLA growth simulator. The amount of biomass was calculated using allometric equations. Samples of stem wood, stem bark, and needles were taken and analysed for carbon, nitrogen, calcium, magnesium, potassium, phosphorus, and sulphur concentrations. Using biomass data, the concentrations of the elements were converted into the stock at the stand level. Overall, spruce fixes a greater amount of carbon. The difference is in the carbon allocation, where fir allocates more carbon in the crown and spruce in the stem. Fir needles contain a greater amount of nutrients than spruce needles. A higher supply of phosphorus, nitrogen, and especially potassium was found in the stem wood and bark of fir, the amount of which is more than twice that of spruce. The stem wood of spruce, on the other hand, fixes more calcium and magnesium. As part of the study, linear regression models predicting the stock of nutrients and carbon depending on the stand basal area were parameterised.

Keywords: allometric models; needle biomass; nutrient content; stem bark biomass; stem wood biomass

Forest biomass estimation is used for the quantification of carbon stock (Litton et al. 2007; Domke et al. 2012; Neumann et al. 2016), calibration of remote sensing or laser scanning data (Novotny et al. 2021), and decision-making processes focused on sustainable forest management (Pan et al. 2016; Lindeskog et al. 2021). Information on the amount of biomass in forest stands can also be used to calculate nutrient stock (Eriksson, Rosen 1994; Šrámek et al. 2009; de Jong et al. 2022)

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or the energy accumulated in forest stands (Verkerk et al. 2019).

The silver fir representation (*Abies alba* Mill.) in the forests of the Czech Republic is 1.2% (31.429 ha), and its share has been increasing in recent years (Ministry of Agriculture 2020). The current economic use of fir wood is minimal due to the historically higher promotion of the Norway spruce (*Picea abies* L. Karst) (Málek 1983; Novák, Dušek 2021). However, in terms of wood properties and production capabilities, fir is fully comparable to spruce. In addition, fir has a positive effect on forest soils (Podrázský et al. 2018) and, due to a deeper root system, higher stability.

The Norway spruce is the main economic tree species in the Czech Republic and grows on 48.8% of the forest area. Although it is a tree with a wide ecological valence, it is currently dying off rapidly in many regions. The main predisposing factors are cultivation of spruce on unsuitable sites outside its ecological optimum, inappropriate management, neglected forest protection measures, and the influence of climatic factors, the most important of which are recurrent drought episodes. However, the main mortality factor in recent years (2018–2021) is the overpopulation of the bark beetle (Hlásny et al. 2021). Since 2014, salvage loggings caused by the bark beetle outbreaks have been gradually increasing. Their share in total cuttings culminated in 2019 and 2020 at 69.9% and 73.4%, respectively (Czech Statistical Office 2022). One of the tree species suitable as a substitute for the Norway spruce is the silver fir.

Most of the available studies aimed at nutrients in fir biomass focus on the evaluation of nutrient concentrations in the assimilation apparatus (Maňkovská et al. 2004; Novotný et al. 2010; Dušek et al. 2020). In order to estimate the stock of nutrients in the biomass, it is necessary to know, in addition to the nutrient concentrations, the weight of the individual biomass compartments.

The basic method for determining the amount of biomass and carbon sequestered in forest stands are allometric models. These are available both for economically important tree species (Wirth et al. 2004; Wutzler et al. 2008) and for trees where other qualitative characteristics prevail (Čihák et al. 2014). There are local studies as well as models applicable to larger territorial units (Jenkins et al. 2003; Chojnacky et al. 2014). The models of Wirth et al. (2004) and Čihák and Vejpustková (2018) are available for quantification of aboveground spruce biomass in the Czech Republic. Models for quantifying fir biomass have only recently been published. In the review study of Zianis et al. (2005), no model specifically parameterised for the silver fir is reported. Recently, the situation has significantly improved, and there are several models for calculating fir biomass in the European area.

A summary of published models for fir trees was compiled by Forrester et al. (2017), and the outputs of these models were used to parameterise their own models. Another set of models is presented by Vonderach et al. (2018). A local model for quantifying fir biomass growing in natural forest conditions was compiled by Dutcă et al. (2020). Tabacchi et al. (2011) also presented a model for the silver fir within a group of models for common species growing in Italy.

In the Czech Republic, a local model for the calculation of fir biomass is missing. In Central Europe, the models of Vonderach et al. (2018), Forrester et al. (2017), and Jagodziński et al. (2019) are usable. In terms of localisation, the number of sample trees, and biomass compartments that can be quantified using these models, the models of Jagodziński et al. (2019) seem to be the most suitable for the purposes of the present study.

When using allometric equations, it is possible to use tree-level data either from experimental plots or from growth tables (Černý, Pařez 1998). An alternative way to obtain basic dendrometric characteristics of sample trees is to use the outputs of growth simulators (Fabrika et al. 2019). Quantification of nutrient and carbon stocks at the stand level can be carried out in several ways. Ericsson and Rossen (1994) recalculate stocks from tree level to stand level based on stand basal area. Balboa-Murias et al. (2006), similarly to André and Ponnete (2003), present the calculation of nutrient stock at the stand level using information on element concentrations and biomass weight obtained as an output of an allometric model.

Information on the amount of nutrients and carbon fixed at the stand level in the fir and spruce growing in the same site is still missing. The present study aims to compare the Norway spruce and the silver fir in terms of the content of essential nutrients and carbon stock in the aboveground biomass of mature stands in the conditions of the Czech Republic.

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MATERIAL AND METHODS

Samples of stem wood, stem bark, and needles were taken in selected mixed stands of Norway spruce and silver fir (Figure 1, Table 1). Samples of wood and bark were taken at a height of 1.3 m above the ground by a Haglöf increment borer (Haglöf, Sweden). A pooled sample of wood and bark from at least 15 sample trees was prepared for each plot. Needles were taken from 5 trees, always from two branches located in the sunny part of the crown. The samples were analysed in the testing laboratories of the Forestry and Game Management Research Institute (FGMRI) according to the valid methodologies of the ICP Forests programme (UNECE 2010). Concentrations of carbon (C), nitrogen (N), sulphur (S), calcium (Ca), potassium (K), magnesium (Mg), and phosphorus (P) were determined.

The study sites are situated in mixed stands of spruce and fir in commercial forests where standard forest management is applied, with the exception of MA5, which is located in a nature reserve. The managed stands are single-layered, even-aged, established mainly by artificial regeneration. The two oldest managed stands, RO2 and MA4, probably originated from natural regeneration. Site MA4 was the only one recorded with an age difference between tree species, where fir was about 50 years older than spruce. However, despite the age difference the stand is now mono-layered with both tree species reaching the main canopy.

The circular plots were established using Field-Map technology (IFER, Czech Republic) to determine the stand characteristics. In the case of stands recently disturbed by bark beetle outbreaks or wind storms, virtual stands were created in the SIBYLA growth simulator (Technical University Zvolen, Slovakia) (Fabrika, Ďurský 2005) based on the original stand description in forest management plans (mean diameter at breast height, mean height and standing volume for individual tree species). The virtual stands were simulated as mono-layered stands, which corresponds to the original structure of the real stands. For the purpose of comparison, the stand characteristics of fir and spruce were recalculated to full stocking and 100% representation of given tree species. This resulted in 14 pairs of model homogeneous spruce and fir stands. For each stand, dendrometric characteristics of individual trees were available. Hence, it was possible to calculate the weight of biomass compartments in dry matter using allometric models. Spruce biomass was quantified by the models of Čihák and Vejpustková (2018), and fir biomass

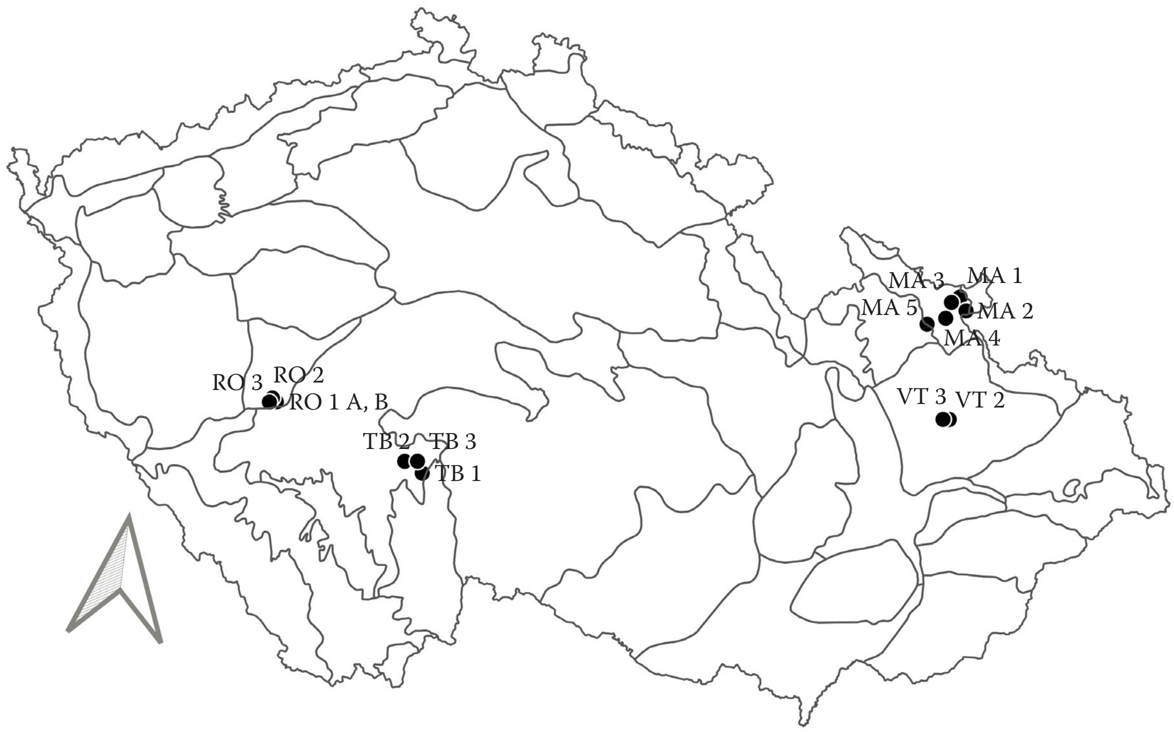

Figure 1. Location of study sites on the background of the map of natural forest areas in the Czech Republic

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Table 1. Basic characteristics of experimental plots and trees

Plot	Latitude (°)	Longitude (°)	Plot type	Plot area (m^2)	Forest type	Age (years)	Species	*DBH* (cm)	*H* (m)	*G* ($m \cdot ha^{-1}$)	*N* ($trees \cdot ha^{-1}$)
TB1	49.370310	14.67157	FM	1 000	4H	130	SF	38.49	31.5	55.38	477
							NS	36.29	32.2	54.69	531
TB2	49.404680	14.56528	FM	1 000	3S	140	SF	49.51	37.2	74.23	386
							NS	44.81	38.7	73.03	464
TB3	49.411240	14.63623	FM	1 257	4A	100	SF	40.81	38.5	49.97	383
							NS	51.69	42.7	50.85	243
RO1A	49.554650	13.80564	FM	707	5O	127	SF	42.90	36.9	68.12	471
							NS	44.72	36.0	68.50	437
RO1B	49.554650	13.80564	FM	707	5O	127	SF	43.55	31.9	54.48	367
							NS	62.45	36.7	54.86	184
RO2	49.566540	13.78048	VR	2 500	6S	170	SF	39.72	30.7	47.02	380
							NS	54.24	32.6	48.89	212
RO3	49.550214	13.76718	VR	2 500	5K	127	SF	38.91	25.8	50.83	428
							NS	33.05	24.1	47.29	552
MA1	50.234280	17.57684	VR	2 500	4B	120	SF	36.82	27.8	36.14	340
							NS	30.89	27.0	40.12	536
MA2	50.185840	17.61807	VR	2 500	4S	141	SF	33.02	25.9	39.69	464
							NS	35.99	29.0	42.67	420
MA3	50.211880	17.53056	VR	2 500	4S	128	SF	34.59	22.9	39.40	420
							NS	33.11	26.1	36.47	424
MA4	50.151900	17.50676	VR	2 500	4A	173	SF	35.71	24.9	46.80	468
							NS	37.02	26.1	49.03	456
MA5	50.123800	17.40442	VR	2 500	5B	189	SF	49.02	35.5	49.73	264
							NS	43.86	32.9	56.74	376
VT2	49.784692	17.58132	VR	2 500	5S	125	SF	34.87	23.9	48.06	504
							NS	34.96	27.1	43.71	456
VT3	49.782948	17.54618	VR	500	5S	85	SF	38.03	28.8	54.46	480
							NS	41.69	31.9	52.89	388

DBH – average diameter at breast height; FM – FieldMap plot; VR – virtual plot; *G* – stand basal area; *H* – average tree height; *N* – number of trees per ha; NS – Norway spruce; SF – silver fir; forest type – forest type according to Viewegh et al. (2003)

was quantified by the models of Jagodzinsky et al. (2019). The stocks of essential nutrients and carbon were calculated for stem wood, stem bark, and needle biomass. For the other compartments of aboveground biomass, only carbon stock was determined. Where chemical analyses were not available, a carbon concentration of 50% was applied. To calculate the supply of nutrients in assimilation organs, average concentrations of elements from three analysed needle sets were used. The weight of biomass compartments was employed to estimate the nutrient and carbon stocks at the stand level [Equation (1)].

$$M_e = B_c \times C_e \quad (1)$$

where:

M_e – weight of the chemical element in the biomass compartment ($kg \cdot ha^{-1}$);

B_c – weight of the biomass compartment in ($kg \cdot ha^{-1}$);

C_e – the chemical element concentration in kg to 1 kg of dry matter of a biomass compartment.

Concentrations and contents of the examined nutrients and carbon in needles, stem wood, and stem bark of spruce and fir were compared using a paired *t*-test. Furthermore, the amount of accu-

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mulated carbon in the biomass of the stem, crown, and in the total aboveground biomass was compared by paired *t*-test.

The element content in the individual biomass compartments was modelled using a linear regression equation with stand basal area as the explanatory variable [Equation (2)]. In addition, models describing the relationship between stand basal area and the weight of carbon fixed in the stem, crown, and total aboveground biomass were also parameterised. For all models, the values of the coefficient of determination (R^2) and the root mean square error (*RMSE*) were calculated to evaluate the quality of model fit.

$$Y_i = b_0 + b_1 X_i + \varepsilon \quad (2)$$

where:

Y_i – the predicted weight of the chemical element in the biomass compartment in kg·ha^{-1} (resp. in t·ha^{-1} for carbon);

b_0, b_1 – regression parameters;

X_i – predictor (stand basal area in m^2·ha^{-1});

ε – random error.

RESULTS

The number of trees per ha ranged from 184 to 552 with an average value of 406 in model homogeneous spruce stands and from 264 to 504 with an average of 417 in fir stands. The stand basal area reached an average value of 51.41 m^2·ha^{-1} in spruce stands and 51.02 m^2·ha^{-1} in fir stands. The diameter at breast height (*DBH*) and tree height (*H*) of the mean stem were 39.71 cm and 30.15 m, respectively, for fir stands and 41.77 cm and 31.6 m, respectively, for spruce stands (Table 1).

The nutrient concentrations in needles are higher in fir than in spruce for all analysed elements. Due to the fact that fir stands accumulate a larger amount of biomass in needles, the stock of all investigated elements is higher in fir stands. The differences between tree species are statistically significant ($P < 0.05$) with the exception of potassium and phosphorus concentrations (Table 2). In the bark, similar concentrations of phosphorus and carbon were found. The concentrations of all other elements are significantly different ($P < 0.05$), with fir bark having higher concentrations of potassium, nitrogen, and sulphur, while spruce bark has higher concentrations of calcium and magnesium. Differences in chemical composition were also found in the stem wood. The concentration of potassium, phosphorus, carbon, and nitrogen are significantly higher in fir stem wood. Higher concentrations, although not statistically significant, were also observed for magnesium (Tables 3 and 4).

Statistically significant ($P < 0.05$) differences in the stock of accumulated nutrients and car-

Table 2. Nutrients (mg·kg^{-1}), nitrogen (%), and carbon (%) average concentration in silver fir and Norway spruce needles

Chemical element	Species	Average	Median	Min.	Max.	Standard deviation
C	**SF**	**53.2**	**53.8**	**51.1**	**54.5**	**1.23**
	NS	**52.6**	**52.8**	**51.0**	**53.7**	**0.88**
Ca	**SF**	**9 466.0**	**8 644.5**	**4 730.4**	**15 414.7**	**3 101.50**
	NS	**6 305.0**	**5 430.7**	**2 679.6**	**10 263.1**	**2 437.90**
K	SF	5 749.4	6 057.1	4 396.4	6 394.5	695.00
	NS	5 422.3	5 782.2	3 515.6	6 192.4	846.90
Mg	**SF**	**1 654.5**	**1 522.8**	**1 057.5**	**2 660.6**	**521.00**
	NS	**1 118.0**	**993.0**	**734.9**	**1 836.0**	**316.90**
N	**SF**	**1.4**	**1.4**	**1.3**	**1.7**	**0.10**
	NS	**1.2**	**1.2**	**1.1**	**1.3**	**0.10**
P	SF	1 334.3	1 180.0	1 024.5	2 102.3	318.70
	NS	1 245.9	1 210.9	920.4	1 612.5	177.70
S	**SF**	1 364.8	1 286.3	1 136.0	1 840.0	228.70
	NS	1 021.4	966.7	894.0	1 390.0	159.10

Bold – statistically significant differences ($P < 0.05$); NS – Norway spruce; SF – silver fir

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Table 3. Nutrients (mg·kg^{-1}), nitrogen (%), and carbon (%) average concentration in silver fir and Norway spruce stem wood

Chemical element	Species	Average	Median	Min.	Max.	Standard deviation
Ca	SF	705.59	706.65	450.45	931.35	145.58
	NS	776.84	796.78	551.25	921.90	110.89
C	SF	**51.10**	**51.07**	**50.90**	**51.47**	**0.17**
	NS	**50.90**	**50.85**	**50.64**	**51.77**	**0.31**
K	SF	**1 373.19**	**1 386.44**	**1 168.86**	**1 658.30**	**133.10**
	NS	**462.40**	**441.66**	**390.63**	**554.88**	**57.98**
Mg	SF	109.57	113.63	94.57	124.35	10.17
	NS	106.42	100.12	83.29	132.09	16.36
N	SF	**0.08**	**0.08**	**0.07**	**0.10**	**0.01**
	NS	**0.06**	**0.06**	**0.05**	**0.07**	**0.01**
P	SF	**36.23**	**33.71**	**24.81**	**60.73**	**11.17**
	NS	**22.89**	**21.32**	**17.59**	**37.24**	**5.61**
S	SF	276.59	243.99	155.00	480.00	121.23
	NS	233.52	155.00	155.00	430.00	105.77

Bold – statistically significant differences (P < 0.05); NS – Norway spruce; SF – silver fir

Table 4. Nutrients (mg·kg^{-1}), nitrogen (%), and carbon (%) average concentration in silver fir and Norway spruce stem bark

Chemical element	Species	Average	Median	Min.	Max.	Standard deviation
Ca	SF	**7 911.30**	**8 120.00**	**3 795.75**	**10 867.50**	**2 127.54**
	NS	**10 312.35**	**10 657.50**	**5 533.50**	**15 225.00**	**3 257.48**
C	SF	51.62	51.66	50.97	52.08	0.35
	NS	52.02	51.59	51.05	53.85	0.96
K	SF	**2 574.49**	**2 621.08**	**1 887.00**	**3 025.88**	**256.48**
	NS	**1 703.97**	**1 700.16**	**1 277.20**	**1 983.52**	**209.42**
Mg	SF	**437.11**	**415.94**	**289.80**	**671.72**	**107.92**
	NS	**559.58**	**521.64**	**449.17**	**909.09**	**129.74**
N	SF	**0.43**	**0.42**	**0.37**	**0.51**	**0.04**
	NS	**0.36**	**0.37**	**0.30**	**0.41**	**0.04**
P	SF	324.35	318.61	274.58	420.89	43.95
	NS	319.60	290.13	253.05	471.87	60.11
S	SF	**569.62**	**577.02**	**452.40**	**660.00**	**66.49**
	NS	**446.43**	**450.79**	**370.00**	**590.00**	**68.07**

Bold – statistically significant differences (P < 0.05); NS – Norway spruce; SF – silver fir

bon in spruce and fir stands were recorded for all elements, with the exception of calcium in the stem bark and sulphur in the stem wood (Tables 5 and 6). A higher stock of nitrogen was found in needles and bark of fir stands (Figure 2A–C). The concentration of calcium, as well as its supply, is higher in the wood of the spruce stem. On the other hand, in spruce needles, the calcium content is lower than in fir stands (Figure 2E–F). Potassium supply in fir stands exceeded those in spruce stands in all examined biomass compartments (Figure 3A–C). In particular, in fir wood, the supply of potassium is almost three times higher than in spruce wood. A significantly higher magnesium content was recorded in the needles of fir stands. More magnesium is also bound in the bark of the stem (Figure 3D–F). Higher phosphorus and sulphur stocks were found in the bark and nee-

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Table 5. Stock of nutrients (kg·ha^{-1}) in silver fir and Norway spruce stands

Compartment	Chemical element	Average SF	Average NS	Standard deviation SF	Standard deviation NS	t	P
Stem bark	N	**114.662**	**66.460**	**38.603**	**23.907**	**11.699**	**0.000**
Stem wood		**204.053**	**194.131**	**75.012**	**67.442**	**2.226**	**0.044**
Needles		**335.053**	**200.887**	**65.184**	**36.258**	**13.334**	**0.000**
Stem bark	Ca	220.706	197.111	98.431	93.436	1.561	0.143
Stem wood		**173.219**	**239.590**	**75.757**	**90.465**	**–9.127**	**0.000**
Needles		**225.418**	**105.824**	**101.769**	**49.763**	**6.861**	**0.000**
Stem bark	K	**66.130**	**31.535**	**21.425**	**10.364**	**10.311**	**0.000**
Stem wood		**325.624**	**143.191**	**124.313**	**56.204**	**8.827**	**0.000**
Needles		**135.326**	**88.562**	**29.173**	**17.900**	**6.376**	**0.000**
Stem bark	Mg	**11.584**	**9.701**	**4.353**	**2.456**	**2.273**	**0.041**
Stem wood		**26.332**	**32.402**	**8.465**	**11.339**	**–4.210**	**0.001**
Needles		**39.329**	**18.435**	**15.476**	**6.173**	**7.308**	**0.000**
Stem bark	P	**8.281**	**5.655**	**2.788**	**1.797**	**8.827**	**0.000**
Stem wood		**8.513**	**6.487**	**3.282**	**2.257**	**3.058**	**0.009**
Needles		**31.494**	**20.461**	**9.384**	**4.503**	**5.712**	**0.000**
Stem bark	S	**15.367**	**8.572**	**5.023**	**2.786**	**10.396**	**0.000**
Stem wood		58.628	61.934	20.653	25.649	–0.739	0.473
Needles		**32.499**	**16.881**	**9.623**	**4.364**	**10.316**	**0.000**

Bold – statistically significant differences (P < 0.05); NS – Norway spruce; SF – silver fir; t – test statistics value

dle biomass of fir stands (Figures 4A–C and 4D–F, respectively).

Overall, spruce stands sequester more carbon in aboveground biomass than fir stands. This is due to the higher accumulation of carbon in the stem, which in spruce trees accounts for up to 90% of the total biomass. Fir stands store a larger amount of carbon in the crown (Table 6, Figure 5A–F). Fir stands also have a larger supply of carbon in the stem bark, but the share of the bark in the total aboveground biomass is small, accounting for less than 10%.

Single-parameter linear regression models were parameterised, describing the relationship between the stocks of nutrients and carbon in the biomass compartments and stand basal area. The reliability of the nutrient models is not very high due to the large variability of input data, but it provides a general overview of the nutrient balance in the examined stands. The weak-

Table 6. Carbon stock (kg·ha^{-1}) in silver fir and Norway spruce stands (N = 14)

Compartment	Average SF	Average NS	Standard deviation SF	Standard deviation NS	t	P
AGB	**165.517**	**178.631**	**45.006**	**44.153**	**–6.288**	**0.000028**
Whole stem	**135.764**	**162.933**	**45.252**	**50.812**	**–10.572**	**0.000000**
Stem bark	**13.474**	**9.316**	**4.384**	**2.835**	**9.616**	**0.000000**
Stem wood	**123.061**	**153.617**	**41.364**	**47.978**	**–11.704**	**0.000000**
Whole crown	**29.810**	**25.394**	**5.748**	**4.047**	**5.480**	**0.000106**
Needles	**11.818**	**8.209**	**2.149**	**1.208**	**10.661**	**0.000000**

Bold – statistically significant differences (P < 0.05); *AGB* – aboveground biomass; N – number of plots; NS – Norway spruce; SF – silver fir; t – test statistics value

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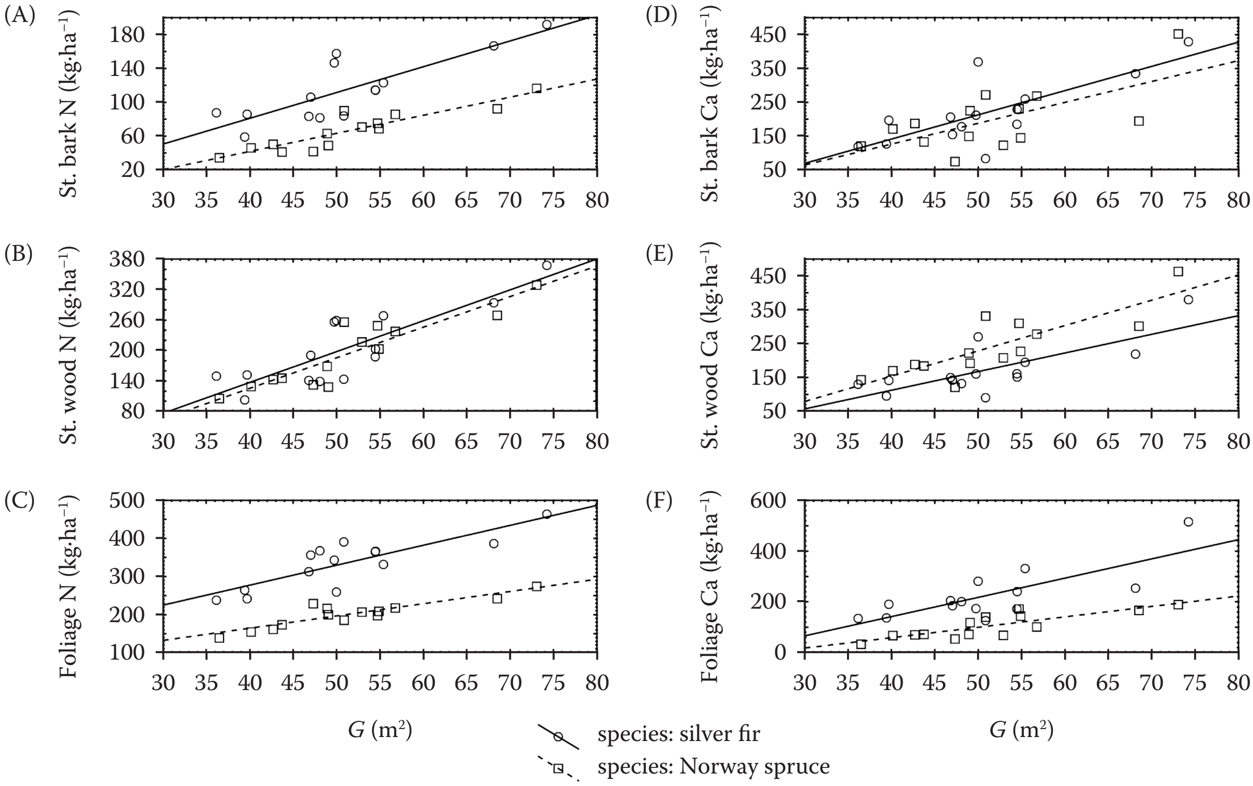

Figure 2. Stock of (A–C) nitrogen and (D–F) calcium in stem wood, stem bark, and needles, respectively, of the silver fir and Norway spruce stands plotted against stand basal area G (m^2)

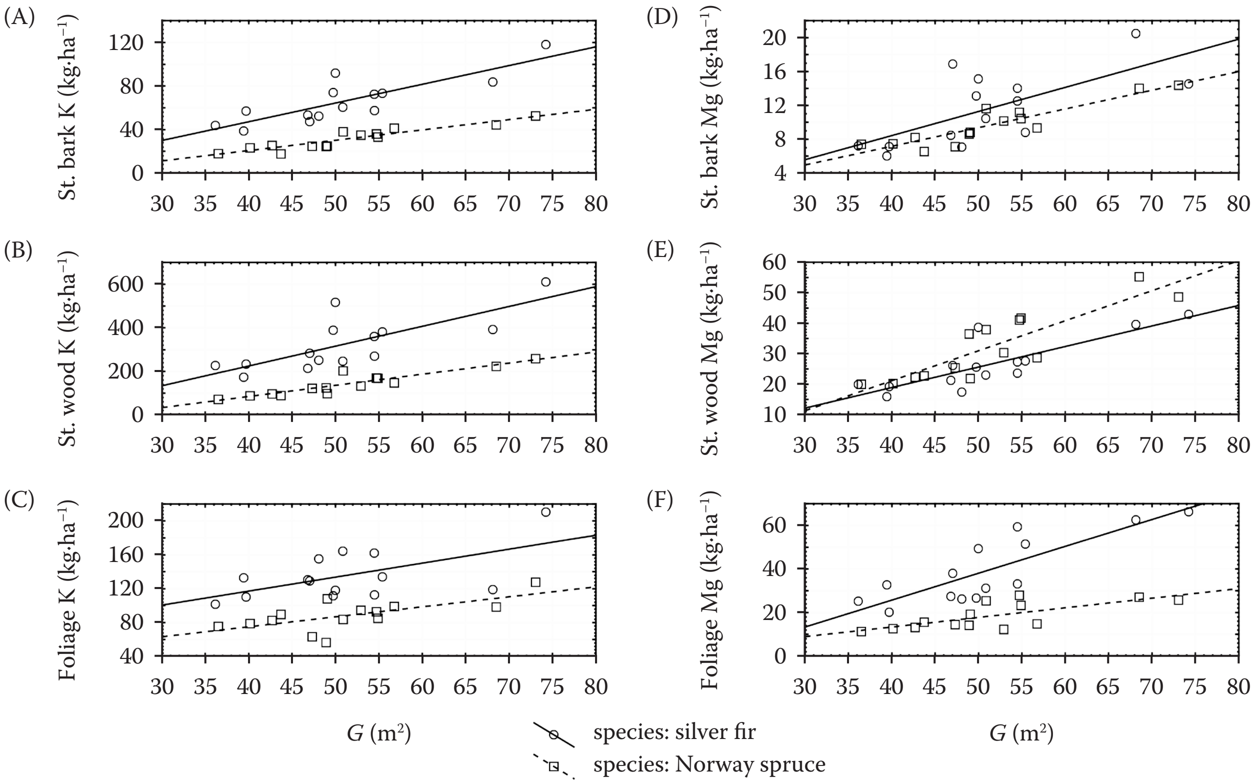

Figure 3. Stock of (A–C) potassium and (D–F) magnesium in stem wood, stem bark, and needles, respectively, of the silver fir and Norway spruce stands plotted against stand basal area G (m^2)

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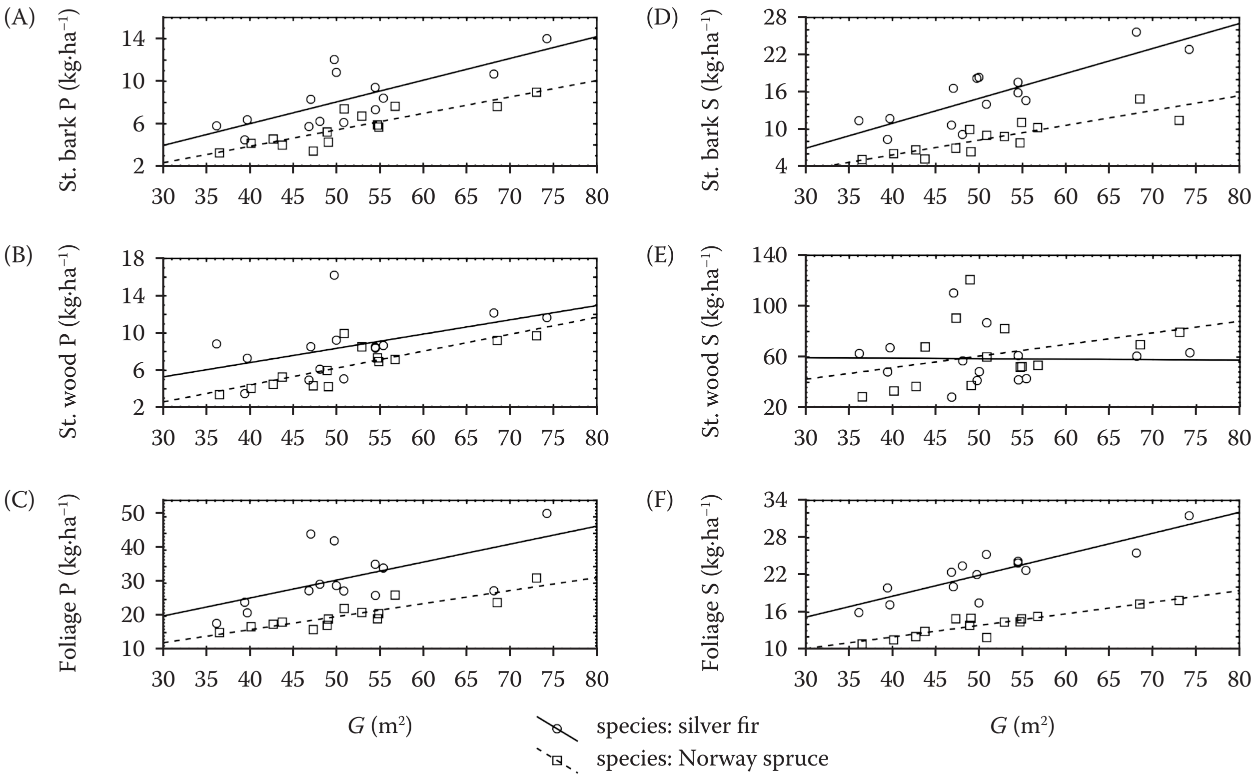

Figure 4. Stock of (A–C) phosphorus and (D–F) sulphur in stem wood, stem bark, and needles, respectively, of the silver fir and Norway spruce stands plotted against stand basal area G (m^2)

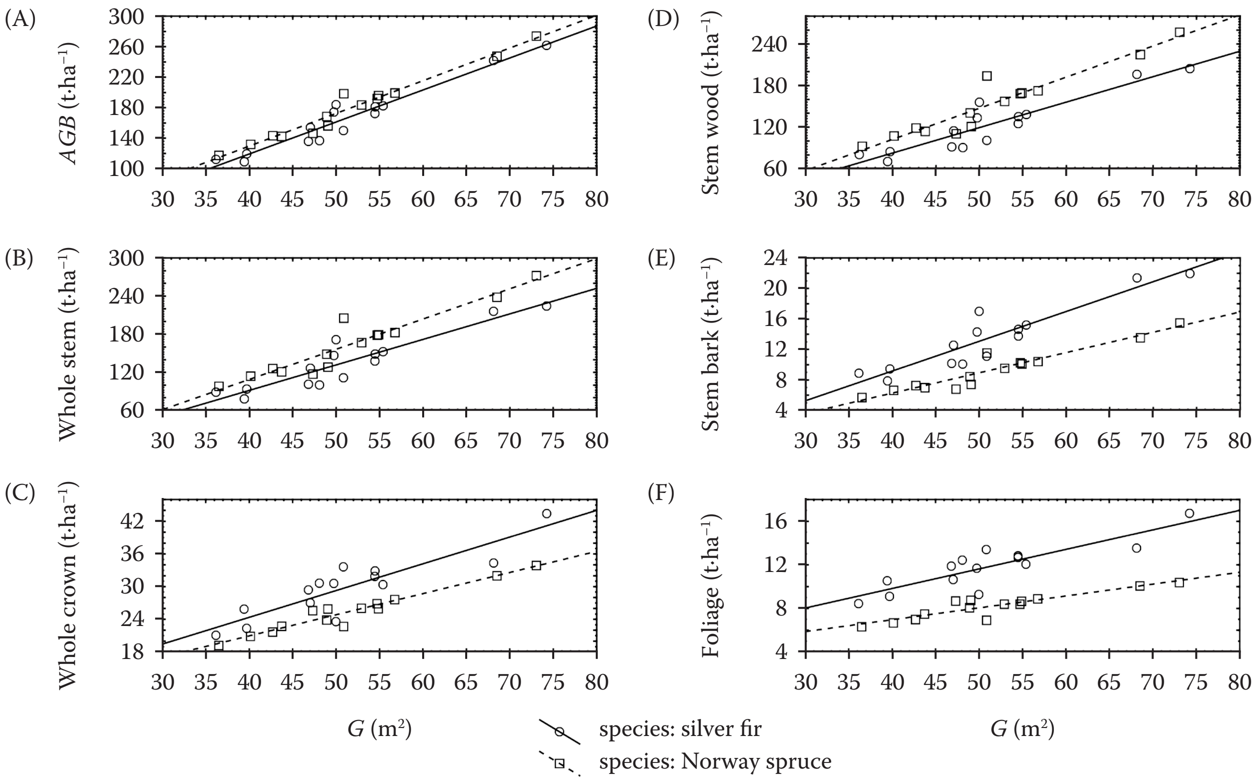

Figure 5. Carbon stock in (A) total aboveground biomass, (B) whole stem, (C) whole crown, (D) stem wood, (E) stem bark, and (F) needles biomass of the silver fir and Norway spruce stands plotted against stand basal area G (m^2)

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est fit exhibits the model for phosphorus stock in the wood of spruce stems (Table 7, model No. 21) and the models for sulphur stock in the stem wood of both tree species (Table 7, model No. 23 and 24). These models do not provide credible estimates. The reliability of carbon models is higher, with R^2 values ranging from 0.75 to 0.96 (Table 8).

Table 7. The results of parameterisation of the models for nutrient stock in stem bark, stem wood, and needles of the silver fir and Norway spruce stands

ID	Compartment	Element	Species	R^2	*RMSE*	b_0 (standard error)	b_1 (standard error)
1	stem bark	N	SF	**0.65**	22.086	−40.8018 (31.904)	**3.0470 (0.614)**
2			NS	**0.81**	10.137	−43.6536 (15.148)	**2.1419 (0.290)**
3		Ca	SF	**0.54**	64.510	−144.3433 (93.185)	**7.1547 (1.792)**
4			NS	**0.40**	69.614	−119.8580 (104.022)	**6.1655 (1.988)**
5		K	SF	**0.67**	11.809	−21.6534 (17.057)	**1.7205 (0.328)**
6			NS	**0.85**	3.857	**−17.3861 (5.763)**	**0.9516 (0.110)**
7		Mg	SF	**0.42**	3.192	−2.9472 (4.611)	**0.2848 (0.089)**
8			NS	**0.81**	1.037	−1.6188 (1.550)	**0.2202 (0.030)**
9		P	SF	**0.55**	1.803	−2.1590 (2.605)	**0.2046 (0.050)**
10			NS	**0.74**	0.882	−2.3087 (1.317)	**0.1549 (0.025)**
11		S	SF	**0.67**	2.777	−5.1844 (4.011)	**0.4028 (0.077)**
12			NS	**0.73**	1.400	−3.6775 (2.092)	**0.2383 (0.040)**
13	stem wood	N	SF	**0.67**	40.387	−106.3346 (58.388)	**6.0834 (1.122)**
14			NS	**0.80**	28.917	**−115.7377 (43.210)**	**6.0274 (0.826)**
15		Ca	SF	**0.54**	49.503	−108.3680 (71.508)	**5.5189 (1.375)**
16			NS	**0.67**	49.568	−145.2913 (74.067)	**7.4864 (1.416)**
17		K	SF	**0.55**	80.551	−139.3050 (116.356)	**9.1123 (2.238)**
18			NS	**0.83**	22.122	**−119.5803 (33.057)**	**5.1113 (0.632)**
19		Mg	SF	**0.66**	4.759	−8.0434 (6.875)	**0.6737 (0.132)**
20			NS	**0.75**	5.451	**−18.1647 (8.145)**	**0.9836 (0.156)**
21		P	SF	0.17	2.873	0.7209 (4.151)	0.1527 (0.080)
22			NS	**0.63**	1.313	−2.8467 (1.962)	**0.1816 (0.038)**
23		S	SF	0.00	20.649	60.6643 (29.828)	−0.0399 (0.574)
24			NS	0.06	23.911	14.7365 (35.73)	0.9181 (0.683)
25	needles	N	SF	**0.67**	35.769	67.4794 (51.668)	**5.2442 (0.994)**
26			NS	**0.79**	15.978	35.3566 (23.876)	**3.2198 (0.456)**
27		Ca	SF	**0.57**	64.266	−162.0503 (92.832)	**7.5941 (1.785)**
28			NS	**0.67**	27.414	**−105.3982 (40.964)**	**4.1086 (0.783)**
29		K	SF	**0.29**	23.628	51.3088 (34.131)	**1.6467 (0.656)**
30			NS	**0.40**	13.356	27.9508 (19.957)	**1.1790 (0.381)**
31		Mg	SF	**0.66**	8.666	−23.6315 (12.518)	**1.2340 (0.241)**
32			NS	**0.48**	4.269	−4.2413 (6.379)	**0.4411 (0.122)**
33		P	SF	**0.30**	7.498	3.7856 (10.813)	**0.5431 (0.208)**
34			NS	**0.76**	2.105	0.2140 (3.145)	**0.3938 (0.060)**
35		S	SF	**0.73**	2.017	5.0244 (2.913)	**0.3381 (0.056)**
36			NS	**0.83**	0.867	**4.5180 (1.296)**	**0.1868 (0.025)**

Bold – statistically significant values of R^2 ($P < 0.05$); b_0, b_1 – regression parameters; *RMSE* – root mean square error; NS – Norway spruce; SF – silver fir

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Table 8. The results of parameterisation of the models for carbon stock in biomass compartments of the silver fir and Norway spruce stands

ID	Compartment	Species	R^2	*RMSE*	b_0 (standard error)	b_1 (standard error)
1	*AGB*	SF	**0.93**	10.69	**–48.6581 (16.019)**	**4.1977 (0.308)**
2		NS	**0.96**	8.09	**–41.8221 (12.549)**	**4.2881 (0.240)**
3	whole stem	SF	**0.84**	16.72	–69.4621 (25.058)	4.0223 (0.482)
4		NS	**0.89**	15.80	**–81.6602 (24.505)**	**4.7577 (0.468)**
5	stem bark	SF	**0.84**	1.61	**–6.4273 (2.414)**	**0.3900 (0.046)**
6		NS	**0.89**	0.85	**–4.3771 (1.325)**	**0.2663 (0.025)**
7	stem wood	SF	**0.84**	15.37	**–64.3318 (23.045)**	**3.6728 (0.443)**
8		NS	**0.89**	14.95	**–77.2831 (23.183)**	**4.4913 (0.443)**
9	whole crown	SF	**0.77**	2.55	4.7590 (3.824)	**0.4910 (0.074)**
10		NS	**0.93**	0.96	**5.4391 (1.483)**	**0.3882 (0.028)**
11	needles	SF	**0.73**	1.03	2.6654 (1.545)	**0.1794 (0.030)**
12		NS	**0.81**	0.49	**2.6266 (0.753)**	**0.1086 (0.014)**

Bold – statistically significant values of R^2 ($P < 0.05$); *AGB* – aboveground biomass; b_0, b_1 – regression parameters; *RMSE* – root mean square error; NS – Norway spruce; SF – silver fir

DISCUSSION

The calculation of nutrient content and carbon stocks is burdened by several uncertainties. The first source of uncertainty is the accuracy of chemical analyses. This can be significantly reduced by choosing a well-established laboratory. The chemical analyses of the samples presented in this study were performed in the laboratory of FGMRI according to the valid ICP Forests protocols (UNECE 2010). The laboratory specialises in the analysis of plant material and regularly participates in interlaboratory comparison ringtests.

Another source of uncertainty is the modelling of tree and stand characteristics in the growth simulator. We employed the SIBYLA simulator (Fabrika, Ďurský 2005), which was parameterised for the conditions of Central Europe using datasets from the Czech Republic and Slovakia. This simulator is commonly used for modelling forest growth and stand characteristics, and its reliability has been verified in previous studies (Špulák, Souček 2010; Hlásny et al. 2011; Ambrož et al. 2015). A significant advantage of the simulator is primarily a better capture of the variability of dendrometric characteristics at the tree level. This cannot be achieved when modelling stand characteristics using yield tables.

The last major source of uncertainty is the estimate of the amount of biomass using allometric models. The models allowed us to calculate the weight of biomass in dry matter based on basic dendrometric characteristics (*DBH*, *H*) of the individual trees. Selected models should be parameterised on a dataset with a sufficient number of trees representing the widest possible range of dimensions and originating from similar site conditions. Spruce biomass models used in this study were parameterised on 177 sample trees from different regions of the Czech Republic (Čihák, Vejpustková 2018). For fir stands, biomass models created in the area of Poland were used (Jagodziński et al. 2019). Conditions in this area are close to the Czech Republic, and the models were parametrised on 96 sample trees. Jagodziński et al. (2019) made a comparison with other available fir biomass models and concluded that their own models achieved reliable predictions for small and medium-sized trees; however, for trees of larger dimensions, the models have tended to underestimate the actual amount of biomass.

Špulák (2012) draws attention to the different distribution of nutrients within one biomass compartment; for example, the concentration of nutrients in the trunk may have an increasing trend with increasing height of the sampling point. In our study, wood and stem bark were taken at the height of 1.3 m above the ground and, therefore, the nutrient content may be partially underestimated. Hence, the estimates of nutrient stocks in this study must be considered minimal.

Studies focused on quantification of nutrients in the above-ground biomass of tree species are still rare due to the complexity of sampling and analysis.

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Existing studies are usually focused on economically important tree species (André, Ponnete 2003; Balboa-Murias et al. 2006; Šrámek et al. 2009; Vos et al. 2023). In the case of silver fir, only the study of Ericsson and Rosen (1994) is available. The authors quantified the nutrient supply of fir in the biomass of young (35–36 years) mixed stands. Quantification of nutrients in needles is not included in this study. The total nutrient content in the fir stems is lower than in our study due to the tree age and mixing with other tree species. When comparing fir and spruce, higher level of nitrogen, calcium and magnesium was found in the biomass of spruce stems, which is in accordance with the results of our study. On the other hand, the potassium and phosphorus level in spruce stems was higher than in fir, which was not confirmed by our results.

Šrámek et al. (2009) presented average values and ranges of nutrient stocks in needles and stems of spruce trees. The average nutrient supply in needles found in this study differs from our results in the order of units of percent (0.36–8.08%). The exception is calcium, where the deviation is 40.37%. In the stem, we found higher average nitrogen, potassium, calcium, and magnesium contents. In the case of potassium and calcium, the values found by us exceeded the ranges indicated in the study of Šrámek et al. (2009) by 6.80% for potassium and 41.56% for calcium.

Fir accumulates a larger amount of biomass in needles and, at the same time, has higher concentrations of nutrients in this compartment. Therefore, the stock of all investigated elements in needles is higher in fir stands than in spruce stands. The supply of magnesium and phosphorus in the biomass of fir needles is even higher than in the biomass of the spruce stem.

CONCLUSION

Greater stock of carbon in aboveground biomass was found in spruce compared to fir. Differences were recorded in the carbon allocation between both examined tree species, where fir accumulates a significantly higher amount of carbon in the crown and spruce in the stem. While spruce accumulates more calcium and magnesium in the wood of the stem, fir fixes a significantly larger amount of potassium in this compartment. More calcium is stored in the stem bark of spruce stands, but the stocks of all other nutrients are higher in the bark of fir. Fir also accumulates more nutrients in needles. In the case of calcium, magnesium, and sulphur, the contents are on average more than twice as high as in spruce needles.

When whole-tree harvesting is used, in which the entire aboveground biomass, including the assimilation apparatus, is removed from the stand, there is an increased risk of impoverishing the site of the basic nutrients like calcium, magnesium, and potassium. Stem-only harvesting also represents a significant change in the nutrient balance, especially in the case of potassium in fir stands and calcium and magnesium in spruce stands. Fertilisation or liming with dolomitic limestone may be a suitable method to replenish the nutrients mentioned above in case of deficiency.

In this study, we looked at the nutrient content in the aboveground biomass of mature fir and spruce stands over 85 years of age. The topic for further research would certainly be the accumulation of nutrients in belowground biomass, which can make up to 25–30% of the aboveground biomass in coniferous trees (Levy et al. 2004) and can fix a significant amount of nutrients. The allometry of young stands up to 60 years of age differs from that of mature stands, e.g. young stands have a higher proportion of crown biomass and may differ from adults in concentrations and allocation of fixed nutrients. Therefore, it would be appropriate to focus follow-up studies on young trees for which the results of this study cannot be extrapolated without the risk of significant estimation error.

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