

# Biomass allocation and carbon stock in Douglas fir and Norway spruce at the tree and stand level

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## Abstract

The effect of changing tree species composition in favor of a greater representation of Douglas fir at the expense of Norway spruce on the carbon pool of Central European forests has not yet been investigated. Here, we compare the allocation of aboveground biomass and carbon stock in Douglas fir and spruce at the tree and stand level. At the tree level, Douglas fir accumulated, on average, 16.9% more aboveground biomass than Norway spruce. A greater amount of biomass was allocated mainly in the wood and bark of Douglas fir stem. For these biomass compartments, the difference between Douglas fir and Norway spruce was 21.1% and 60.3%, respectively. Spruce allocated more biomass in the crown, where the difference was 25.6% compared to Douglas fir. In needle biomass, Norway spruce exceeded Douglas fir by 84%. At the stand level, the analysis of model stands revealed that pure Norway spruce stands accumulated more carbon in the high and medium quality sites. As the site quality decreased, so did the differences in the amount of stored carbon. The higher carbon sink in Norway spruce stands was also confirmed in the analysis of real Norway spruce and Douglas fir stands. The difference in the carbon stock of young, medium-aged, and mature stands was 11.5%, 14.8%, and 1%, respectively. The positive balance in favor of spruce is mainly due to significantly higher numbers of trees per ha in Norway spruce stands. A positive effect of a greater representation of Douglas fir on the carbon budget of forest stands was not confirmed.

**Key words:** aboveground biomass; biomass model; carbon sequestration; *Pseudotsuga menziesii*; *Picea abies*

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## 1. Introduction

Despite the widespread dieback in recent years, Norway spruce (*Picea abies* [L.] Karst.) still has a high representation of  $43 \pm 1\%$  in forests of the Czech Republic (Kučera et al. 2019). However, the natural representation of Norway spruce is stated to be around 11% and the recommended 36% (MZe 2020). In the Czech Republic, Norway spruce originally occurred naturally mainly at an altitude above 800 m a. s. l. (6<sup>th</sup>–8<sup>th</sup> forest vegetation zone), and in lower altitudes, it was represented only to a lesser extent on sites with permanent high soil moisture content and even on sites characterized by a high degree of waterlogging or on peat soils (Plíva 2000). Planting at unfavorable sites, declining biodiversity, and the use of unsuitable provenances have made Norway spruce stands more susceptible to fungal diseases and insect pests as well as abiotic disturbances (Klimo et al. 2000).

The extensive decline of Norway spruce stands raises the question in forestry practice of which tree species might replace Norway spruce at lower altitudes. In

addition to deciduous tree species, alternatives are also sought among conifers. Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) seems to be one of the suitable substitutes. In Europe, it is an introduced tree species whose natural range is located in the Pacific Northwest of the U.S. It has been grown in Europe since 1827. The first attempts to plant Douglas fir in the Czech forests can be dated to the middle of the 19<sup>th</sup> century (Beran 2018). Its current representation in the Czech forests is only 0.26% (ÚHÚL 2020), while in Germany, for example, Douglas fir occupies 3.3% of the forest land, i.e., an area of 300,000 ha, and is expected to increase to 5% (Podrázský et al. 2014). Owing to its massive root system (Mauer & Palátová 2012), it is more resistant to drought than Norway spruce (Eilmann & Rigling 2012; Nadezhdina et al. 2014). Douglas fir is also characterized by high volume production (Vinš & Šika 1981; Kantor 2008; Kantor & Mareš 2009; Podrázský et al. 2013) and good wood quality (Remeš & Zeidler 2014). It has a positive ameliorative effect on the forest soil (Menšík et al. 2009; Podrázský

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& Kupka 2018). Due to these favorable properties, the share of Douglas fir can be expected to increase in the Czech Republic and Central Europe in the coming years (Kubeček et al. 2014).

High volume production is undoubtedly an important parameter from an economic point of view, but it is no less important in terms of carbon sequestration in forest ecosystems (Petersson et al. 2012). In the Czech Republic, Douglas fir reaches higher hectare stocks of merchantable wood volume than Norway spruce (Kantor 2008; Remeš & Zeidler 2014). However, when assessing carbon sequestration, it is necessary to deal not only with the stem but with total above- and below-ground biomass. An important parameter in the evaluation of carbon stock is the biomass allocation in individual compartments (stem, branches, assimilation organs, roots). A number of models are currently available for the quantification of Douglas fir biomass either from North America (Harrison et al. 2009; Poudel & Temesgen 2016; Poudel et al. 2019) or from Western European countries (Nord-Larsen & Nielsen 2015; Forrester et al. 2017; Vonderach et al. 2018). The set of allometric equations for the calculation of Douglas fir biomass in the conditions of the Czech Republic was parameterized by Vejpustková & Čihák (2019). For Norway spruce in the territory of Central Europe, a set of general biomass models was parameterized by Wirth et al. (2004). However, a wide range of extensive studies that are applicable to larger geographic units can be found both in Europe (Muukkonen 2007; Repola 2009) and worldwide (Jenkins et al. 2003; Ung et al. 2008; Henry et al. 2011; Chojnacký et al. 2014). National allometric equations for the estimation of main biomass compartments of Norway spruce is recently available for the Czech Republic (Čihák & Vejpustková 2018).

Reliable quantification of forest tree biomass and carbon stock is required for the purposes of greenhouse

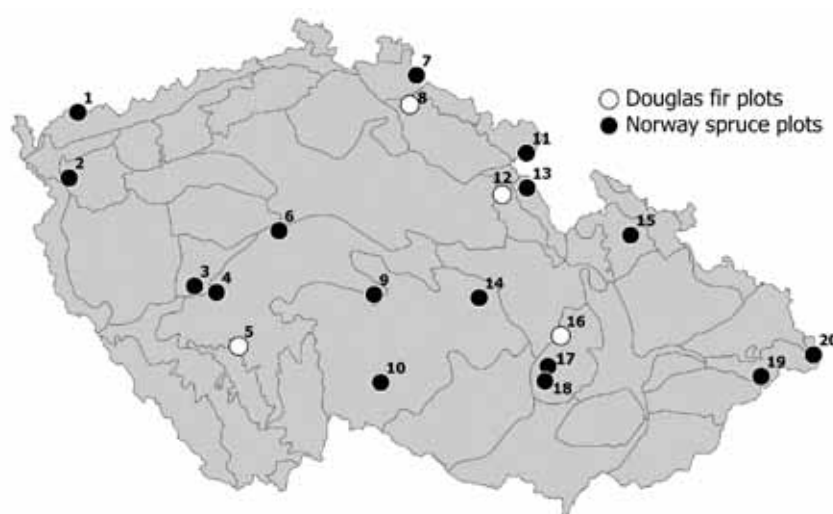
gas inventory reports (IPCC 2006; Krtková 2020), the processing of which is part of the international commitments under the Kyoto Protocol (UNFCCC, 1997). The rate of tree biomass production indicates the mitigation potential of a tree species. In the case of Douglas fir and Norway spruce, the effect of changing the tree species composition in favor of a greater representation of Douglas fir at the expense of Norway spruce on the carbon pool in forest biomass in Central European conditions has not yet been investigated.

In this study, we analyzed the allocation of biomass in individual compartments and the carbon stock in the biomass of Douglas fir and Norway spruce both at the tree and stand level. At the stand level, a comparison was made for both model and real Douglas fir and Norway spruce stands at different quality sites. We dealt only with aboveground biomass, for which empirical data from the territory of the Czech Republic were available for both tree species and national allometric equations were parameterized. We expected higher Douglas fir biomass production at the tree level and, thus, a positive effect of higher representation of Douglas fir on the carbon budget of forest stands.

## 2. Material and methods

Tree data for Douglas fir analyzed in this study were taken from Vejpustková & Čihák (2019). In the case of Norway spruce, the data presented in Čihák & Vejpustková (2018) were used, supplemented by a dataset from selected plots of the ICP Forest intensive monitoring programme in the Czech Republic (Fig. 1).

In the above-cited works, allometric models for the calculation of aboveground biomass and its compartments of both tree species were also published. In the case of Douglas fir, biomass models were derived by the nonlinear regression method, while in the case of Nor-



**Fig. 1.** Location of Douglas fir and Norway spruce study sites on the background of the map of natural forest areas in the Czech Republic.

way spruce, the data were first linearized by logarithmic transformation and then the models were parameterized by the linear regression method. For the purpose of this study, we adopted only the models for Norway spruce (Čihák & Vejpustková 2018), which were additionally supplemented by a new model for calculating the stem bark biomass.

For Douglas fir, new models, parameterized by the same procedure as the Norway spruce models and using the same independent variables, were derived to improve the comparability of the results. The parameterization set was identical to the data used in Vejpustková & Čihák (2019) and included 33 Douglas fir sample trees comprised of a wide range of diameters at breast height (6.6–66.4 cm) and tree heights (7.9–44.9 m). The biomass in dry matter was modelled using a linear regression model with two explanatory variables (diameter at breast height  $D$  and slenderness ratio  $H/D$ ). The form of the allometric model is provided by Equation 1. The reverse transformation of the results is carried out using Equation 2. The factor  $\lambda$  [Equation 3] is used for correction of bias caused by the reverse transformation of logarithmic values (Baskerville 1972). However, according to the findings of Shmueli (2010), this correction factor is equal to 1, and it is not necessary to use it in the calculation.

$$\ln(\widehat{B}_i) = \ln(b_0) + b_1 \ln(D_i) + b_2 \ln\left(\frac{H_i}{D_i}\right) + \varepsilon \quad [1]$$

$$\widehat{B}_i = e^{(b_0 + b_1 \ln(D_i) + b_2 \ln(H_i/D_i))} \lambda \quad [2]$$

$$\lambda = \frac{1}{n} \sum_{i=1}^n \frac{Y_i}{e^{\ln \widehat{Y}_i}} \quad [3]$$

$\widehat{B}_i$  – predicted biomass of  $i^{\text{th}}$  sample tree;  $b_0, b_1, b_2$  – regression parameters;  $D_i$  – diameter at breast height (cm) of  $i^{\text{th}}$  sample tree;  $H_i$  – tree height (m) of  $i^{\text{th}}$  sample tree;  $\varepsilon$  – random error;  $\lambda$  – correction factor;  $B_i$  – empirical biomass of  $i^{\text{th}}$  sample tree

For Douglas fir, models for calculating the dry weight of the total aboveground biomass (AGB), stem (ST), crown (CR), stem bark (STBR), and needle biomass (FL) were derived. Based on the outputs of the models, the biomass of branches (BR) was calculated by subtracting the needle biomass from the crown biomass; similarly, the stem wood biomass (STW) was computed by subtracting the stem bark biomass from the stem biomass. For each model, the significance of the regression parameters and normality and homoscedasticity of the residuals were assessed. The developed models were evaluated using the coefficient of determination ( $R^2$ ) and the Akaike information criterion (AIC). As no explicit validation data set was available, cross-validation was used to predict the model fit to a hypothetical validation set. The leave-one-out method of cross-validation was employed (Arlot & Celisse 2010), and the root mean square error of cross-validation (RMSECV) was calculated as a measure of the anticipated level of the model fit.

The comparison of the amount of Norway spruce and Douglas fir biomass at the tree level was performed based

on dendrometric data for 409 Douglas fir and 964 Norway spruce trees from 20 localities in the Czech Republic (Fig. 1). The biomass of individual compartments was calculated for all trees using the two-parameter allometric equations described above. Only sample trees with  $D$  over 7 cm (merchantable wood) were included in the analyses.

The calculated biomass for each compartment was fitted to a regression model describing the dependence of the biomass weight on  $D$  [Equation 4]. The reason for this procedure was to eliminate the variability caused by the application of the two-parameter model. Using model values, relative differences [Equation 5] in the biomass weight of individual Douglas fir and Norway spruce compartments were then computed and plotted as a function of  $D$ .

$$\widehat{B}_i = e^{(b_0 + b_1 \ln(D_i))} \quad [4]$$

$$DIF_i = 100 (\widehat{B}_{i_{Df}} - \widehat{B}_{i_{Ns}}) / \widehat{B}_{i_{Df}} \quad [5]$$

$DIF_i$  – difference in biomass weight of the individual compartments;  $\widehat{B}_{i_{Df}}$  – predicted biomass of a given compartment for Douglas fir (kg in dry matter);  $\widehat{B}_{i_{Ns}}$  – predicted biomass of a given compartment for Norway spruce (kg in dry matter).

Furthermore, the dependence of the proportions of individual biomass compartments on  $D$  was analyzed. The ratios of stem biomass to AGB, needle biomass to crown biomass, stem bark biomass to stem biomass, and crown biomass to AGB were expressed. In order to compare the values of the ratios of individual biomass compartments, the linear model [Equation 6] describing the biomass ratio as a function of  $D$  was parameterized for each of these ratios and tree species.

$$R_i = b_0 + b_1 \ln D_i \quad [6]$$

$R_i$  – ratio of biomass compartments (%);  $b_0, b_1$  – regression parameters;  $D_i$  – diameter at breast height (cm).

The weight of the individual compartments in dry matter was converted to carbon mass using the carbon percentage given in Table 1 (Čihák, unpublished data). Then, the dependence of the carbon allocation to the individual biomass compartments of Douglas fir and Norway spruce on  $D$  was compared.

**Table 1.** Carbon concentration in Douglas fir and Norway spruce biomass compartments.

Biomass compartment	C concentration [%]	
	Norway spruce	Douglas fir
Needles	51.5	52.1
Branches	51.3	52.2
Stem wood	50.0	49.7
Stem bark	51.2	52.4

A comparison of carbon stock in the AGB of Norway spruce and Douglas fir was also performed at the stand level. Using valid yield tables for Norway spruce (Černý

et al. 1996) and Douglas fir (Černý & Pařez 1998), the parameters of model pure, even-aged, and fully-stocked Douglas fir and Norway spruce stands were defined. Based on the data on the mean diameter at the breast height and the mean height of the model stands, the dry weight of aboveground biomass of the mean tree was calculated according to Equation 2 (parameters are given in Table 2) and subsequently converted to carbon mass. Using the values of number of trees per ha in the yield tables, the carbon stock in the model pure stand at a given age was then computed [Equation 7]. The calculation was performed for different quality sites corresponding to the relative site index 1, 5, and 9.

$$C_{t/ha} = \frac{(0.5 (B \times N))}{1000} \quad [7]$$

$C_{t/ha}$  – carbon stock (t/ha);  $B$  – aboveground biomass of mean tree (kg in dry matter);  $N$  – number of trees per ha

Finally, the amount of sequestered carbon in the real Douglas fir and Norway spruce stands was compared. The calculation was performed on the basis of dendrometric data obtained by field measurement of established research plots for biomass assessment (Table 3). The AGB of individual trees was calculated using the allometric model described by Equation 2 (parameters are given in Table 2). The estimated AGB of Douglas fir and Norway spruce was converted to AGB of fully-stocked pure stand of the respective tree species, and the total weight of sequestered carbon was subsequently computed.

### 3. Results

#### 3.1. Allometric models for biomass calculation

The allometric models for the calculation of Norway spruce biomass were taken from the publication by Čihák & Vejpustková (2018). For Douglas fir, new models are presented (Table 2). The coefficient of determination ( $R^2$ ) for all Douglas fir models ranged from 0.92 to 0.99, which were higher than for the Norway spruce models. The models for AGB and stem bark biomass reached the highest share of explained variability (99%). The best models for stem and crown biomass explained 97% and 96% of the variability, respectively. A weaker fit was recorded for foliage biomass ( $R^2 = 0.92$ ). Except for parameter  $b_2$  of the models for needle and crown biomass, all parameters were statistically significant. However, these models were also included in the analyses due to the maintenance of consistent calculation procedures. The basic characteristics of the models are shown in Table 2.

#### 3.2. Biomass accumulation at the tree level

In young trees with  $D$  up to 11 cm, AGB is higher in Norway spruce than in Douglas fir. For trees with  $D$  equal to 11 cm, the weight of AGB is 41.5 kg, on average. From this value, the AGB of Douglas fir begins to increase compared to Norway spruce, and for large trees with  $D$  equal to 70 cm, it reaches 3,925.1 kg for Douglas fir compared to 2,893.1 kg for Norway spruce. On average, 16.9% more biomass is accumulated in the AGB of Douglas fir than in the AGB of Norway spruce (Fig. 2A).

The stem biomass is the largest contributor to the

**Table 2.** Parameters of the two-variable biomass models [Equation 2] for Douglas fir (Df) and Norway spruce (Ns); the statistically significant coefficients ( $\alpha = 0.05$ ) are indicated in bold.

Model	Species	AIC	$R^2$	RMSECV	Parameter (standard error)			$\lambda$
					$b_0$	$b_1$	$b_2$	
AGB	Df	445.7	0.99	183.44	<b>-3.11844</b> (0.27256)	<b>2.75263</b> (0.08593)	<b>0.86866</b> (0.25075)	1.020
AGB	Ns	1012.96	0.96	80.51	<b>-2.0323</b> (0.06075)	<b>2.40781</b> (0.02131)	<b>0.48803</b> (0.06938)	
ST	Df	435.58	0.97	157.52	<b>-3.74627</b> (0.28846)	<b>2.90285</b> (0.09094)	<b>1.14552</b> (0.26537)	1.020
ST	Ns	907.65	0.96	68.07	<b>-3.62155</b> (0.05227)	<b>2.84648</b> (0.01793)	<b>1.08860</b> (0.05971)	
CR	Df	354.46	0.96	46.08	<b>-3.06006</b> (0.51323)	<b>2.08825</b> (0.16181)	<b>-0.34004</b> (0.472153)	1.074
CR	Ns	887.64	0.84	27.68	<b>-1.32840</b> (0.12263)	<b>1.64827</b> (0.04288)	<b>-0.36054</b> (0.13075)	
FL	Df	253.41	0.92	9.97	<b>-4.53796</b> (0.64984)	<b>2.12709</b> (0.20488)	<b>0.72990</b> (0.59783)	1.032
FL	Ns	546.55	0.79	9.54	<b>-1.98720</b> (0.12753)	<b>1.49555</b> (0.04471)	<b>-0.72780</b> (0.13989)	
STBR	Df	310.93	0.99	23.83	<b>-6.72132</b> (0.38349)	<b>3.12037</b> (0.12090)	<b>1.51964</b> (0.35280)	
STBR	Ns	270.02	0.85	12.82	<b>-6.22472</b> (0.57612)	<b>2.78171</b> (0.17757)	<b>1.05917</b> (0.27553)	

AGB – total aboveground biomass; ST – stem biomass; CR – crown biomass (branches + foliage); FL – foliage biomass; STBR – stem bark biomass; Species: Df – Douglas fir; Ns – Norway spruce; AIC – Akaike information criterion;  $R^2$  – coefficient of determination; RMSECV – root mean square error of cross validation;  $b_0, b_1, b_2$ : parameters, in bold: statistically significant parameters ( $\alpha = 0.05$ );  $\lambda$  – correction factor.

AGB. The difference in stem biomass between Douglas fir and Norway spruce ranges from 35.7% for trees with  $D$  equal to 7 cm to 23.4% for the thickest trees with  $D$  equal to 70 cm. On average, 25.1% more biomass is accumulated in the Douglas fir stem than in the Norway spruce stem (Fig. 2B).

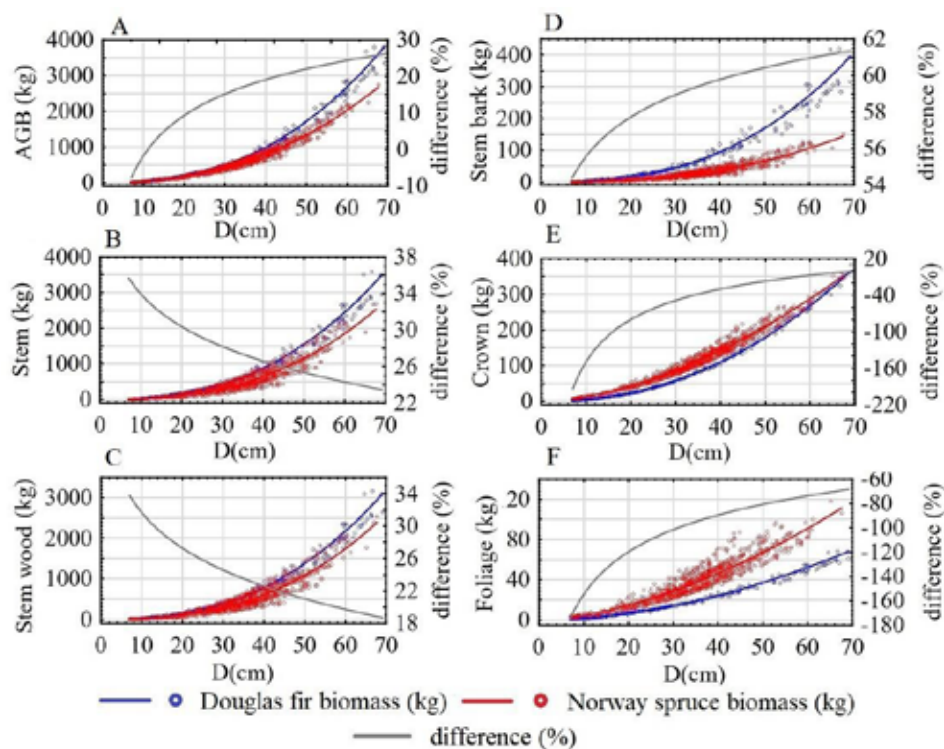
Douglas fir has a significantly higher weight of the stem bark biomass. On average, it is 60.3% (54.4–61.6%) higher in Douglas fir than in Norway spruce (Fig. 2D). In the case of stem wood, an average difference of 21.1% (15.2–33.8%) in favor of Douglas fir was found (Fig. 2C). The difference in the amount of accumulated stem bark biomass between Douglas fir and Norway spruce increases with increasing  $D$ . In contrast, the opposite trend was observed for stem wood biomass, where the difference between Douglas fir and Norway spruce decreases slightly with increasing  $D$ . Compared to Douglas fir, Norway spruce accumulates significantly higher amounts of biomass in assimilation organs (Fig. 2F). The difference decreases with increasing  $D$ ; however, it reaches a high average value of 84% (52.7–175.2%). The same is true for crown biomass (Fig. 2E). However, for the thickest trees with  $D$  around 70 cm, the crown biomass of Douglas fir and Norway spruce is already balanced.

For Douglas fir, the share of stem biomass in AGB is relatively stable and varies in the range of 80.7–91.9% (88.3% on average) depending on  $D$ . In contrast, for

Norway spruce, the proportion of stem biomass in AGB is more variable and ranges from 46.9 to 93.7% (Fig. 3A). The ratio of crown biomass to AGB of Douglas fir ranges from 8.8 to 17.5%. For Norway spruce, this ratio varies distinctly, reaching values from 7.9 to 45.2% (Fig. 3B). The difference is also in the development of the ratio of needle biomass to the biomass of the crown. It decreases in both tree species with increasing  $D$ . However, while it does not change much in Norway spruce and ranges between 31.1–36.8%, in the case of Douglas fir, it significantly decreases from 37.7% in trees with  $D$  equal to 7 cm to 17.5% in trees with  $D$  equal to 75 cm (Fig. 3C). The proportion of stem bark in the total stem biomass also differs. While it decreases slightly from 6.5 to 5.7% in Norway spruce, in Douglas fir, the share of bark in the stem biomass is higher and exhibits an increasing trend from 9.2 to 11.3% (Fig. 3D).

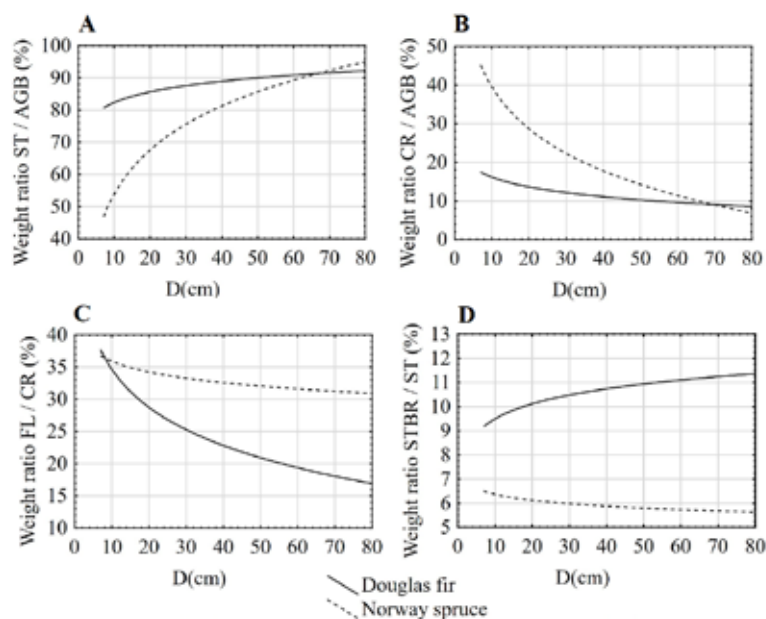
### 3.3. Carbon sequestration at the tree level

On average, 729.5 kg of carbon (22.2–2,188.8 kg) is stored in the Douglas fir AGB. This is significantly more than in Norway spruce AGB, with an average value of 600.3 kg (33.5–1,808.5 kg). Most carbon is sequestered in the biomass of the stem. For Douglas fir, it is 649.2 kg (19.6–1,956.8 kg), and for Norway spruce, it is 512.3 kg (26.0–1,590.3 kg). Douglas fir also accumulates more

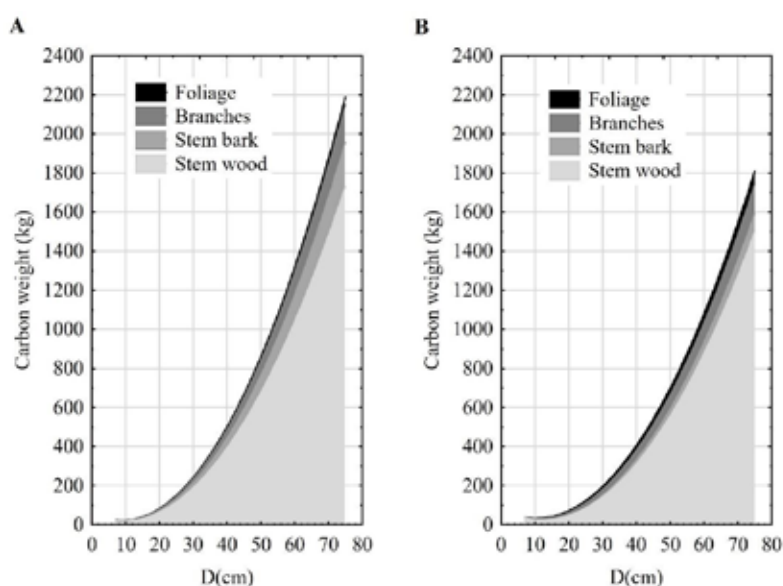


**Fig. 2.** Observed (A) total aboveground biomass, (B) stem biomass, (C) stem wood biomass, (D) stem bark biomass, (E) crown biomass, and (F) foliage biomass of Douglas fir and Norway spruce plotted against diameter at breast height (scatter graph); derived biomass data according to Eq. 4 displayed as blue (Douglas fir) and red (Norway spruce) lines. The differences (%) are plotted on the right axis and displayed as a gray line.





**Fig. 3.** Weight ratio of (A) stem (ST) to total aboveground biomass (AGB), (B) crown (CR) to total aboveground biomass, (C) foliage (FL) to crown biomass, and (D) stem bark (STBR) to stem biomass of Douglas fir and Norway spruce plotted against diameter at breast height.



**Fig. 4.** Carbon accumulation at the tree level in (A) Douglas fir and (B) Norway spruce biomass compartments.

than twice the amount of carbon in the stem bark, averaging 74.5 kg (2.2–227.6 kg). In the stem bark of Norway spruce, it is only 30.3 kg (1.6–93.1 kg) of carbon. An average of 80.4 kg of carbon (2.2–232.0 kg) is sequestered in the crown biomass of Douglas fir; in the Norway spruce crown, it is 88.0 kg (1.6–218.2 kg). Norway spruce shows a higher carbon accumulation in the needles, averaging 28.2 kg (0.3–67.6 kg), while in Douglas fir, it is 15.5 kg (0.4–39.5 kg) (Fig. 4).

### 3.3. Carbon sequestration at the stand level

Analysis of carbon sequestration at the tree level has shown that when comparing trees of similar dimensions, more carbon is accumulated in Douglas fir biomass. However, when analyzing the carbon stocks of model stands, it was found that this finding may not always apply at the stand level. Figure 5 shows the carbon stocks in model stands of Douglas fir and Norway spruce at high-quality.

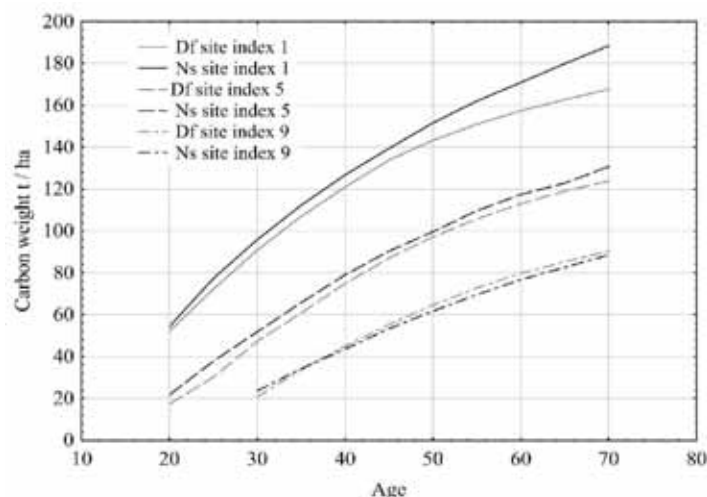


Fig. 5. Carbon sequestration by model stands. Df – Douglas fir, Ns – Norway spruce.

ity (relative site index 1), medium-quality (relative site index 5), and poor-quality sites (relative site index 9). In the best sites, more carbon is accumulated in Norway spruce than in Douglas fir stands. As the quality of the site decreases, so do the differences in the amount of stored carbon. In the poor-quality sites, a higher carbon stock was recorded in Douglas fir stands from the age of about 40 years (Fig. 5).

The comparison of carbon stock in Douglas fir and Norway spruce stands was also performed for real stands using measured dendrometric characteristics. The summary results are shown in Table 3. The highest carbon stock was recorded in the old Douglas fir stand at the NV 1 site. This is a high-quality homogeneous Douglas fir stand, which is exceptional in terms of production throughout the Czech Republic. In all mixed stands where the carbon stock has been converted to full-stock and 100% representation of both tree species, there was a higher carbon pool in the Norway spruce biomass. This

finding is consistent with the results obtained from the analysis of model stands presented above. The average weight of carbon sequestered in old Douglas fir stands (excluding the plot NV 1), middle-aged stands, and young stands was 309.1 t per ha, 161.0 t per ha, and 77.7 t per ha, respectively. For Norway spruce, the average value for old stands middle-aged stands, and young stands was 313.2 t per ha, 184.8 t per ha, and 86.6 t per ha, respectively.

#### 4. Discussion

The estimation of biomass and carbon stock of Douglas fir as a commercially less important species has not yet received sufficient attention in Central Europe. Only models derived by Forrester et al. (2017), Vonderach et al. (2018), and recently parametrized allometric equations based on data from the Czech Republic (Vejpustková & Čihák 2019) are available for this region. However,

Table 3. Carbon stock in real Douglas fir and Norway spruce stands.

Plot	No.*	Species	Age	Forest type**	D [cm]	H [m]	N per ha	G [m <sup>2</sup> ha <sup>-1</sup> ]	V [m <sup>3</sup> ha <sup>-1</sup> ]	C [t ha <sup>-1</sup> ]
NV 1	8	Df	144	5S	76.7	52.6	284	131.3	3065.7	697.3
NV 2	8	Df	51	5K	21.3	25.2	1000	35.8	475.0	116.0
NV 2	8	Ns	51	5K	16.8	21.9	2000	44.2	484.7	135.7
NV 3	8	Df	36	5S	10.1	13.1	2488	20.1	144.0	40.1
NV 3	8	Ns	36	5S	6.6	8.3	8367	29.0	90.6	58.8
PI 1	5	Df	101	3K	41.7	33.6	438	62.4	1000.5	231.5
PI 1	5	Ns	101	3K	37.2	30.6	666	72.2	998.5	244.5
PI 2	5	Df	49	4S	34.8	30.5	519	49.2	743.7	179.3
PI 2	5	Ns	49	4S	22.4	24.0	1616	63.8	734.5	199.1
PI 3	5	Df	13	3K	6.7	8.9	4845	16.9	50.7	25.6
PR 1	16	Df	97	5K	54	41.6	312	71.4	1374.4	322.5
PR 2	16	Df	59	5K	41	34.2	345	45.7	749.6	179.5
PR 2	16	Ns	59	5K	29.3	28.0	842	56.7	732.4	187.3
PR 3	16	Df	34	5K	23.6	26.2	1061	46.4	633.3	154.5
OP 1	11	Df	140	2H	66.8	43.5	233	81.7	1592.5	373.4
OP 2	11	Df	50	3H	32.1	27.6	622	50.3	682.4	169.2
OP 2	11	Ns	20	3H	18.6	22.7	2588	70.6	695.7	217.2
OP 3	11	Df	20	2K	11.6	15.0	3849	40.5	330.3	90.6
OP 3	11	Ns	30	1M, 1P	13.1	15.5	3217	43.6	333.4	114.4

\* Identification of plots in Figure no. 1, \*\* Forest type 4S: Nutrient – medium Beech; 5S: Nutrient – medium Fir – Beech; 2K: Acidic Beech – Oak; 3K: Acidic Oak – Beech; 5K: Acidic Fir – Beech; 2H: Lomy Beech – Oak; 3H: Loamy Oak – Beech; 1M: Nutrient – very poor Pine – Oak; 1P: Acidic Birch – Oak (Viewegh et al. 2003).

Plot NV: Navarov; PI: Pisek; PR: Prostějov; OP: Opočno (see localities 8, 5, 16, and 12 in Figure 1); Species Df: Douglas fir, Ns: Norway spruce; D, H – diameter at breast height and tree height of mean tree; N: number of trees per ha; G: stand basal area (m<sup>2</sup>/ha); V: volume of merchantable wood with bark (m<sup>3</sup>/ha); C: carbon weight (t/ha).

the importance of carbon accumulation and biomass production of this species will increase due to the wider use of Douglas fir as a suitable alternative to declining Norway spruce in European forests (Kubeček et al. 2014; Podrázský et al. 2014).

Here, we parameterized new biomass models for Douglas fir based on the data used in Vějpustková & Čihák (2019). The data set consists of 33 sample trees from 4 localities. The pooled data set represented a wide range of tree dimensions and stand ages, and the selected localities cover well the main areas of Douglas fir planting in the Czech Republic. Also, due to the low representation of Douglas fir in the forests of the Czech Republic (only 0.26%) (ÚHÚL 2020), this data set can be considered sufficiently representative.

When deriving the models, logarithmic linearization of the data was applied, which stabilizes the variance and allows the application of the standard linear regression procedure (e.g., Wirth et al. 2004). On the other hand, this approach requires the application of a correction factor in the reverse transformation of logarithmic values (Baskerville 1972; Marklund 1987; Zianis & Mencuccini 2003). However, as more recent work shows, this factor is often close to 1 and does not need to be incorporated into the model (Shmueli 2010). A model with two independent variables (D and H/D) was chosen to calculate the biomass. It usually gives better results than the one-parameter model (Cienciala et al. 2006). The slenderness ratio was prioritised over tree height in order to eliminate multicollinearity between explanatory variables. An overall strong fit of the biomass models was found for AGB and also for the biomass components, such as stem, stem bark, and crown. A weaker fit was recorded for the foliage biomass. It suggests that a two-parameter model might not be sufficient for estimating needle biomass of Douglas fir. This is in line with the analysis performed for Norway spruce by Wirth et al. (2004), who demonstrated that this component was predicted best by the most complex model.

Biomass partitioning in Douglas fir is different than that in Norway spruce. In Douglas fir, the share of stem and crown biomass in AGB changes significantly in young trees with D up to 30 cm and then stabilizes. The stem to AGB ratio is 88% for trees with D equal to 30 cm, which corresponds to the findings of Bartelink (1996), who reported a stem to AGB ratio of 80–84% for Douglas fir with these dimensions. Similarly, Vonderach et al. (2018) stated a ratio of coarse wood with bark to AGB of 85%. The supplement up to 100% expresses the share of the crown biomass in AGB. It means that in the study by Vonderach et al. (2018), the crown biomass represents 15% of AGB, and in the work of Bartelink (1996), it is 16–20%. In both cases, it is slightly above the value of 12% that we found in our study.

We observed a different development of biomass allocation for Norway spruce. The percentage of stem biomass increased rapidly up to D of 30 cm when it reached

the value of 75%, and then it slowed down. This is consistent with the work of Wirth et al. (2004), which stated the stable percentage of aboveground biomass allocated to stem of about 75% at a stand age of 70 years. Vonderach et al. (2018) indicated a stable share of stem biomass of about 80% for Norway spruce with a stem diameter over 30 cm. In contrast, in our study, the share of stem biomass in trees over 30 cm in diameter is not stable but continues to grow slowly.

Although Douglas fir at the tree level clearly outperforms Norway spruce in carbon accumulation, this may not be the case at the stand level. In model stands, we found lower carbon sequestration in Douglas fir in sites of high (relative site index 1) and medium quality (relative site index 5). If we compare Norway spruce and Douglas fir stands according to the absolute site index derived from the mean stand height at the age of 100 years, this difference is even more pronounced. For Norway spruce and Douglas fir stands with an absolute site index of 34, which corresponds to relative site index 1 for Norway spruce and relative site index 5 for Douglas fir, the amount of accumulated carbon in a 20-year-old Norway spruce stand is 214.8% higher than for Douglas fir. The difference decreases with age, but even in the 70-year-old stand, the difference is 52.2% in favor of Norway spruce. Our analyses of model stands were limited to stands up to 70 years of age, as the current yield tables for Douglas fir in the Czech Republic (Černý & Pařez 1998) do not contain data on older stands.

Petráš & Mecko (2008) pointed out the lower number of Douglas fir trees per ha compared to Norway spruce. It is likely that with increasing age and the declining number of trees per ha, the difference in stored carbon will decrease in favor of Douglas fir. The results of the analyses of real Douglas fir and Norway spruce stands presented in this study also support the fact that the number of trees per ha can significantly affect the amount of accumulated biomass and carbon. In all examined real stands, the carbon stock was higher in Norway spruce stands. At the same time, there were significantly higher numbers of individuals per hectare in Norway spruce stands, in some cases more than three times. For stands with a basal area of 31.5–49.0 m<sup>2</sup>/ha, the difference in the amount of stored carbon ranged from 2.2 to 8.3% in favor of Norway spruce, whereas the difference decreased with increasing basal area.

It is interesting that the volume of merchantable wood was higher for Douglas fir in most of the analyzed real stands despite the significantly lower number of individuals per ha compared to Norway spruce. This is due to the predominance of Douglas fir in the production of stem biomass. Similarly, Kantor (2008) and Remeš & Zeidler (2014) found higher hectare stocks of merchantable wood volume of Douglas fir compared to Norway spruce. In contrast, Petráš & Mecko (2008), based on a comparison of pure Douglas fir and Norway spruce stands according to the yield tables, reported a lower volume production of Douglas fir by 26–35%.



Ponette et al. (2001) quantified AGB in five Douglas fir stands growing in France. The age of the analyzed stands ranged from 26 to 54 years. For stands aged 26, 28, 29, and 36 years, the amount of AGB corresponds to our model stands in high-quality sites (relative site index 1). In the oldest stand (54 years), 20% more AGB is accumulated here compared to the data for our model stand of highest quality. The stands analyzed in the study by Ponette et al. (2001) have a significantly lower density of individuals per ha than our model stands. The difference in the number of trees per ha is around 44%, on average. Obviously, these are stands where the dimensions of the trees significantly exceed the dimensions of the mean stem given by our yield tables.

However, the focus of Douglas fir planting in the Central European forests is not in pure stands but clearly in mixtures. The analysis of Remeš & Zeidler (2014) includes stands with Douglas fir representation from 5 to 100%, and in terms of the merchantable wood volume, Douglas fir clearly surpasses Norway spruce. In addition, mixtures of Douglas fir with Norway spruce seem to be particularly effective in sequestering C and N in the soil, which emphasizes the benefit of mixed stands not only with regard to production and ecosystem stability but also with regard to mitigation of atmospheric CO<sub>2</sub> enrichment and minimization of N exports into groundwater aquifers (Prietz & Bachmann 2012).

## 5. Conclusion

The aim of the study was to compare the allocation of aboveground biomass and the carbon stock of Douglas fir and Norway spruce at the tree and stand level. We hypothesized that Douglas fir accumulates more carbon than Norway spruce.

At the tree level, when comparing sample trees of Norway spruce and Douglas fir of the same D, the above hypothesis was confirmed. Douglas fir accumulates significantly more biomass and, thus, carbon in AGB than Norway spruce. The studied tree species also differ in biomass partitioning. Douglas fir produces a significantly higher amount of biomass in the stem wood and bark. In contrast, Norway spruce accumulates more biomass in the branches and assimilative organs. Needle biomass has a much higher proportion of crown biomass in Norway spruce than in Douglas fir. The share of crown biomass in AGB with increasing D decreases in favor of the stem biomass. In Norway spruce, these changes are more pronounced than in Douglas fir. The differences in biomass allocation between Douglas fir and Norway spruce decrease with increasing D, but they even out only in large trees. Such findings suggest a different strategy in biomass allocation for Douglas fir and Norway spruce trees with D up to 60 cm.

Although Douglas fir at the tree level clearly outperforms Norway spruce in biomass and carbon accumula-

tion, this is not true at the stand level. The analyses of model and real Douglas fir and Norway spruce stands have shown that more carbon is accumulated in Norway spruce stands than in Douglas fir stands (Černý et al 1996, Černý & Pařez 1998.). In the analysis of model stands, we found that in high-quality sites, more carbon is accumulated in Norway spruce stands. As the quality of the site decreased, so did the differences in the amount of sequestered carbon. In poor-quality sites (relative site index 9), a higher carbon stock was recorded in Douglas fir from the age of about 40 years.

When comparing the two tree species, it is necessary to take into account that both model and real Norway spruce stands show significantly higher numbers of trees per ha. Due to the recently recommended reduction in the number of trees per ha in order to increase the mechanical stability of Norway spruce stands, Douglas fir stands may accumulate more or comparable amounts of carbon as Norway spruce stands in the future. The fact that Douglas fir has a high production and sequestration potential is also indicated by the analysis of the old NV 1 stand, which accumulates 697.3 t of carbon per ha in aboveground biomass.

Douglas fir is an equivalent alternative to Norway spruce in terms of wood production and also carbon accumulation.

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