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Above-ground biomass allocation and potential carbon sink of black pine – a case study from southern Poland

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Abstract Biomass allocation is a key factor for understanding the forest carbon balance and reflects plants' ecological strategies in different environmental conditions. Allocation patterns and biomass models outside of the native range of black pine have not been analyzed in the context of the observed climate changes. The study's goals were to develop biomass equations for mature black pine from southern Poland and assess biomass and carbon allocation patterns and the potential of trees of different social statuses for carbon sequestration. A total of 129 felled black pine trees were measured, among which 14 were destructively sampled to determine biomass and carbon content in tree components. The developed set of biomass equations provided allocation patterns and accumulation of trees of different social statuses.

Biomass and carbon allocation patterns were different but related to tree social status. The introduction of diameter at crown base significantly improved the accuracy of the developed models. The analyzed trees allocated relatively more in stem than in crown in comparison with that observed in other studies.

Biomass and carbon allocation patterns of the analyzed black pines differ from those of the native range. They should be considered in biomass modeling with factors influencing social status structure.

Keywords: *Pinus nigra*; allometric biomass model; carbon sequestration; biomass expansion factor; tree social status; biomass accumulation.

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Introduction

Intensive biomass research has comparatively short history; nevertheless, the need to determine not only the trees dimensions but also their dry weight was indicated by Hartig in 1888 in his work "Das Holz der Totbuche" (Pardé 1980). There were no scientific reports on this subject in the literature almost until the end of the second decade of the last century.

Pardé (1980) undertook intensive research on biomass in the second half of the 20th century for three main reasons: (a) focusing of chemical industry on weight units opposed to volume units for wood transactions; (b) need for the development of scientific methods for estimating primary production in forest ecosystems; and (c) problem of increasing demands for energy with simultaneous depletion of sources of fossil fuels, for which the use of renewable energy sources, including forest biomass, was considered as a solution.

Another important reason for the development of biomass research was the recognition of forests as a natural carbon sink by the Intergovernmental Panel on Climate Change (IPCC), which significantly influenced the mitigation of climate change (Nabuurs et al. 2007).

Increasing forest cover and intensification of forest management are considered to be the most effective approaches to compensate for the increase in CO_2 emissions caused by increasing use of fossil fuels. Buotte et al. (2020) indicated that sustainable forest management can serve as a tool for carbon sequestration and constitutes a viable strategy in mitigating climate change. Moreover, many countries are obliged to assess and report CO_2 balance according to United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol, and presently, it has become important economically as greenhouse gases have become the subject of trade. Because CO_2 balance in practice relies on the determination of forest ecosystem biomass, its accuracy is strictly linked with biomass structure of different tree organs. While all tree organs play their own important ecological and physiological roles, they differ substantially in terms of water content, carbon content, and element content (Tolunay 2009, Thomas & Martin 2012).

The assimilates are distributed within a tree to achieve ecological success and results in different biomass of specific tree organs. The relative biomass of tree organs is defined as allocation (Poorter & Sack 2012). Among many different drivers playing important role in biomass allocation pattern, the most important ones are tree species (Schall et al. 2012, Poorter et al. 2015), age (Peichl & Arain 2007), geographic location (Cairns et al. 1997, Gill & Jackson 2000, Zhang et al. 2015, Jiang & Wang 2017, Qi et al. 2019), site fertility and moisture (Vanninen et al. 1996, Ioan Dutcă et al. 2014), stand density (Jagodzinski & Oleksyn 2009), and tree competitive status (Vanninen 2004, Gargaglione et al. 2010, Ochał et al. 2013, Konôpka et al. 2020, Wertz et al. 2020). Knowledge of the influence of these factors on allocation pattern can not only improve CO_2 balance but also contribute to design optimal silviculture routines in the context of production of desired wood assortments and to intensify carbon sequestration.

Because many abovementioned factors simultaneously affect biomass allocation, it is very important to collect data from a variety of local growth conditions; in particular, it is crucial to assess peripheral, marginal populations outside of the species native range, where influence of many external factors is more clear (Tigerstedt 1994, Abeli et al. 2014, de Medeiros et al. 2018). The additional requirement for the real biomass allocation assessment is an adequate number of tree samples collected by direct, destructive, and very laborious field measurements, which can enable to develop site-specific allometric models.

Many local empirical models for determining biomass and carbon sequestration of individual tree fractions were developed across Europe (Zianis et al. 2005). Usually, these models focused on tree species with the largest share and economic importance in European forests. In Poland, where Scots pine stands occupy 58.2% of forest area (Zajączkowski et al. 2019), local biomass models were developed for pure Scots pine stands (Bijak & Zasada 2007, Socha & Wezyk 2007, Bronisz et al. 2009, Orzeł 2015, Jagodziński et al. 2018, 2019a). For other tree species, biomass models are rare and include young stands of silver birch on abandoned farmland as a result of natural succession (Jagodziński et al. 2017), young black alder stands (Ochał 2013), European larch stands (Jagodziński et al. 2018), and silver fir stands (Jagodziński et al. 2019b).

The advantage of local models is not only to provide unbiased estimation of biomass allocation for specific growth conditions, but they are also suitable to compare biomass allocation in different locations and can be incorporated into more general models designed for the estimation of biomass on regional or national scale. One of the most promising ways to achieve this goal seems to be area base approach (ABA) (Socha et al. 2020) for biomass estimation, where local allometric models are combined with data stand features acquired by using remote sensing techniques.

In Polish forests, many non-native species exist, which have been introduced not only to enhance biodiversity but mainly as a substitute for native species; they are potentially more productive and more resistant to unfavorable factors, i.e., industrial pollution.

One of the most promising non-native species among them is black pine (*Pinus nigra* Arn.) whose native range extends from the northwest part of Africa through the southern part of Europe to Asia Minor (Isajev et al. 2004). This species frequently occurs in Turkey (Isajev et al. 2004, Sevgi & Akkemik 2007), where together with Turkish pine (*Pinus nigra* subsp. *nigra* var. *caramanica*), it covers 4.2 million ha (Janssen et al. 2018).

The taxonomy of black pine is still a subject of research; Isajev et al. (2004) listed six of its subspecies, whereas Enescu et al. (2016) distinguished only two main subspecies of black pine: Corsican pine (*Pinus nigra* subsp. *salzmannii*) occurring from Morocco through Spain to southern France and Corsica, and Austrian pine (*Pinus nigra* subsp. *nigra*) found in Austria, northeastern and central Italy through the Balkans to Turkey and Crimea.

In Poland grows mainly a subspecies of black pine, which was introduced by German foresters at the end of the 19th century and initially planted on the coast and in the western part of the country (Bellon & Tumiłowicz 1977).

Although black pine was introduced as a promising foreign species, it can be actually found mainly as a small admixture in Scots pine (*Pinus sylvestris* L.) stands, while pure black pine stands, especially those older than 60 years, can be treated as unique.

Unfortunately, no studies on black pine productivity and its potential to carbon sequestration in Poland have been reported. Recognizing this potential can be useful not only for local forest management purposes, but it will also provide valuable inputs to compare the performance of black pine under a wide range of European growth conditions; this is especially important as this species can be considered as a possible beneficent of observed climate changes and may positively influence biodiversity and local environmental conditions (Mikulová et al. 2019).

The main goal of the present study was to determine the above-ground biomass allocation and carbon content of specified components of black pine trees of different social status, based on the case-study of the mature stand from southern Poland, located outside of the species native range. The specific goals were as follows: (a) development of the set of local allometric biomass equations, with commonly used explanatory variables, i.e., tree diameter at breast height (DBH) and height as well as other variables that are expected to be more correlated with tree biomass, i.e., tree volume, selected taper quotients, or tree crown parameters; (b) comparison of biomass allocation for trees of different social status, which is considered as a key factor for modifying biomass allocation pattern; and (c) assessment of the annual biomass and carbon accumulation in the stem wood, the most important tree component in terms of carbon sequestration and carbon sink.

Materials and Methods

Study area

The research was conducted in an 85-year-old black pine (*Pinus nigra*) stand, growing outside of the species' native range, in southern Poland, Central Europe (Figure 1). The stand with a total area of 1.38 ha was situated within the Pińczów Forest District (50.4565°N, 20.2791°E) at altitude 325 m a.s.l. and was growing on relatively plain terrain with slope lower than 5°.

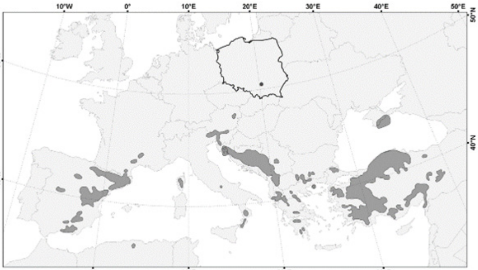

Figure 1 Localization of the study area (black dot) and continuous areas of occupancy of the black pine (*Pinus nigra* Arnd.) in Europe (dark grey area) according to Eufrogen (www.euforgen.org).

The climate of the area can be characterized as continental (Cervellini et al. 2020) with relatively high variability of weather conditions, which results from the alternating influence of humid air masses from the Atlantic Ocean and continental dry air masses from the east. The average annual temperature is +8 °C; the warmest month is July with an average temperature of +18 °C and the coldest month is January with an average temperature of −3 °C. Total annual precipitation is approximately 600 mm; most rainfall occurs in July (95 mm), and the least is in February (30 mm). The length of the vegetation period varies from 200 to 210 days, while the period of the snow cover lasts 80-90 days. The study area has relatively frequent frost occurrences; there are usually 50-60 frosty days from March to November, and the period with frosts lasts for 110-140 days (Bureau for Forest Management And Geodesy 2013). The soil is classified as typical brown rendzina, and the forest community is classified as *Tilio-Carpinetum*.

The stand canopy layer was composed mainly of black pine (*Pinus nigra*) and a small admixture of Scots pine (*Pinus sylvestris*) with the basal area share of 96.5% and 3.5%, respectively. The understory layer was composed mainly of deciduous trees, i.e., common hornbeam (*Carpinus betulus* L.), wild cherry (*Prunus avium* L.), common oak (*Quercus robur* L.), Norway maple (*Acer platanoides* L.), and a single Norway spruce (*Picea abies* (L.) H. Karst.).

Dry above-ground biomass of destructively sampled black pine trees used for the development of allometric models is summarized in Table 2. The total mean above-ground biomass was 533.03 ± 76.25 kg, ranging from 168.45 kg to 960.63 kg. Most of the biomass of sampled trees (average: 433.29 kg) was stored in the stem components (wood and bark), while the mass of living crown components (branches, shoots, and foliage) was lower (average: 85.74 kg). The weight of the components that could be classified as a litter fallout (dead branches and cones) was relatively small (average: 14.00 kg), and their variability was highest.

Field measurements

A sample plot of 0.3 ha area was established in a stand, and DBH of all trees thicker than 7 cm was measured in two perpendicular directions, namely NS and WE, with an accuracy of 0.1 cm. Additionally, the social status of all trees was determined according to the Kraft classification (Kraft 1884) and named as follows: I – predominant, II – dominant, III – codominant, IV – dominated, and V – entirely overtopped. All black pine trees (n=129) on the sample plot were felled, and tree length (H), crown width (CW), and crown length (CL) were measured with an accuracy of 0.01 m. For all sample trees the stem part was distinguished, extending from the lowest above-ground point of the tree up to top of the tree. According to Huber's sectional formula, two perpendicular diameters over bark and bark thickness at intervals of 1 m were measured to the nearest 0.1 cm, and stem volume over bark (VOB) and stem volume under bark (VUB) of all trees on the sample plot were calculated. Additionally, the diameter at half of the stem length (D05) and diameter at the crown base (DCB) were recorded (Table 1).

Table 1 Basic characteristics of selected biometric variables for the sampled black pine trees (n=129); arithmetic mean ± standard error (SE), range (min - max), standard deviation (SD), and coefficient of variation (CV).

Var	Mean ± SE	Range	SD	CV
DBH	31.16±0.39	19.80-44.31	4.39	14.1
D05	21.50±0.29	13.81-30.70	3.32	15.5
DCB	15.87±0.33	4.10-26.66	3.72	23.4
H	21.45±0.12	14.15-24.08	1.34	6.3
CL	5.35±0.13	1.35-9.20	1.43	26.7
CW	4.54±0.10	1.50-8.00	1.13	24.9
VOB	0.8309±0.0243	0.3162-1.6951	0.2765	33.3
VUB	0.6560±0.0202	0.2302-1.3843	0.2298	35.0

Note: Var-variable; DBH: diameter at breast height (cm), D05: diameter at 0.5H, DCB: diameter at crown base (cm), H: tree height (m), CL: crown length (m), CW: crown width (m), VOB: stem volume over bark (m^3), VUB: stem volume under bark (m^3).are shown in bold

Following the stand diameter distribution, 14 even width diameter classes was distinguished and one sample biomass tree of undamaged crown, without visual defects in each class was randomly chosen. Among those 14 sample biomass trees, 4, 5, 3 and 2 represented I, II, III and IV Kraft social status class, respectively. The stem of each sample biomass tree was divided into parts and cut at distances of 0.5, 2.0, and 4.0 m and then every 2 m to the tree top. Next, all individual parts were directly weighed with an accuracy of 0.05 kg. At the thinner end of each part, a sample disc of approximately 15 cm thickness was cut. The sample discs were separated into wood and bark; their fresh mass was weighed with an accuracy of 0.5 g and packed separately for water and carbon content analysis. The crown was separated into the following parts: dead branches, cones, branches of diameters over 0.5 cm, and twigs under 0.5 cm with needles. The total fresh weight of these parts was directly weighed with an accuracy of 0.002 kg. To determine the water and carbon content, a sample of 0.5-1.0 kg for dead branches, a sample of 0.8-1.5 kg, and a sample of 0.8-1.2 kg for branches and cones were collected for each tree. The 2-3 kg sample of twigs was additionally separated into shoots and foliage components. All the collected samples were weighed to the nearest 0.5 g and packed separately.

Biomass and carbon content determination

For each biomass sample tree, the mass of every stem part was increased by the estimated mass of saw cuts and divided into fresh mass of wood and fresh mass of bark on the basis of average wood and bark share found in two stem discs collected from the bottom and top of the specific part. The total fresh mass of wood and bark was calculated as a sum of the masses of those components in all parts. The total mass of shoots and total mass of foliage of tree crown was calculated as a product of total weight of twigs with needles and share of shoots and foliage derived from the collected sample. The total fresh mass of branches, dead branches, and cones was weighed directly in the field.

All samples collected in the field were dried at 103 ± 2 °C in an oven with forced air circulation until a constant weight was obtained. The stem discs were weighed with an accuracy of 0.5 g, while all other samples were weighed with an accuracy of 0.01 g. The dry mass of each tree component was determined on the basis of its total fresh mass, and the dry-to-fresh mass ratio was estimated for the sample. By summing up the dry mass of individual components, namely stem wood, stem bark, branches, shoots, and foliage, the total dry above-ground biomass of trees (Total AB) was calculated. Dry above-ground biomass of destructively sampled black pine trees used for the development of allometric models is summarized in Table 2. Fractions of dead branches and cones were

Table 2 Characteristics of dry above-ground biomass for the distinguished components of the destructively sampled black pine trees (n=14).

Tree comp.	Mean ± SE	Range	SD	CV
Wood	375.20±50.18	129.10-650.17	187.76	50.04
Bark	58.09 ± 6.53	22.75 - 93.35	24.43	42.06
Dead br.	9.90 ± 2.80	0.77 - 29.91	10.47	105.70
Branches	55.48 ± 11.95	4.65-125.10	44.71	80.57
Shoots	6.74 ± 1.21	1.17 - 14.38	4.53	67.25
Foliage	23.52 ± 4.15	4.76 - 48.18	15.53	66.04
Cones	4.10 ± 0.84	0.65 - 9.80	3.12	76.29
Total AB	533.03±76.25	168.45-960.63	285.31	53.53

Note: Tree com: Tree component; Dead br: Dead branches; arithmetic mean ± standard error (SE), range (min - max), standard deviation (SD), and coefficient of variation (CV).

excluded from the analysis of carbon content and allometric biomass modeling because of their low importance in the production and accumulation of biomass and the high variability of these components.

Dried samples of stem wood, stem bark, shoots, and foliage were processed separately for each tree with an IKA MF 10 laboratory microfine grinder with a 1 mm interchangeable sieve. Next, the carbon content of each sample was determined with a LECO TruMac CNS multi-element analyzer. The carbon content of branches was calculated as a weighted mean of carbon content in wood and bark, where weight was wood and bark share derived from all stem discs located within the tree crown zone. The differences in carbon content between all tree components were assessed on the basis of the nonparametric Friedman test, followed by Nemenyi post-hoc test at the significance level of $\alpha=0.05$ (Demšar 2006).

Allometric biomass equations

The models for the dry biomass of all distinguished tree components were developed using the power function (Tausch 1989, Parresol 1999):

$$Y = b_0 \cdot X_1^{b_1} \cdot \ldots \cdot X_m^{b_m} \cdot \xi \tag{1}$$

where Y is the dry biomass (in kg) of the tree component, X_1 to X_m are explanatory variables, b0 to bm are model parameters, and ξ is a multiplicative error term.

Following the standard procedure of biomass model parameter estimation, we used log-transformed form of equation 1, which justifies the use of ordinary least square linear regression and additionally ensures homoscedasticity of residuals (Parresol 1999):

$$ln(Y) = ln(b_0)+b_1X_1+\ldots+b_mX_m+\varepsilon \tag{2}$$

where ε is assumed to be normally distributed with a mean μ of 0 and standard deviation of σ. For avoiding the bias associated with back-transformation of the biomass models to the arithmetic scale, we used correction factor CF according to Sprugel (1983):

$$\hat{Y} = exp\ (\widehat{ln\ (Y)}) \cdot CF \tag{3}$$

where,

$$CF = exp\left(\frac{SEE^2}{2}\right) \tag{4}$$

$$SEE = \sqrt{\frac{\sum_{i=1}^{n}\left(ln(Y_i)-\widehat{ln(Y_i)}\right)^2}{(n-p)}} \tag{5}$$

where, n is the sample size and p is the number of estimated parameters.

We defined and tested models with different levels of variable availability, starting from the simplest model that included only DBH as an explanatory variable, which has been widely used in similar studies (Zianis et al. 2005). We also included tree height in the form of volume equivalent (DBH^2H) as recommended by Dutcă et al. (2019) and compared its performance against the model with directly measured tree VOB or VUB. Despite the fact that the model with VOB or VUB has no practical application because acquiring both is a laborious procedure, testing it against the model with DBH^2H can clarify the extent to which the use of volume equivalent is justified and useful. Moreover, using directly measured VOB or VUB is assumed to increase the biomass allocation assessment for individual trees. Recent studies have indicated the high potential of using additional variables related to crown parameters and stem dimensions in the crown zone to increase the accuracy of biomass prediction for crown components (Forrester et al. 2020). Although such variables are usually unavailable in traditional forest measurement, modern remote sensing techniques with airborne and terrestrial laser scanning makes it relatively easy to incorporate them into biomass modeling. Therefore, we tested a set of additional explanatory variables related to tree crown, i.e., crown length, CW, and volume as well as stem features related to crown zone, i.e., diameter at the crown base (DCB) and two form quotients, where crown base diameter was related to diameter at breast height (QCB1) or to diameter at the half of tree length (QCB2).

To evaluate models transformed into the logarithmic scale, we applied commonly used statistical criteria and tests for the assessment of significance of linear regression, i.e., adjusted coefficient of determination (adj. R^2), Akaike information criterion (AIC), standard error of regression (SEE), and t-test, with significance of the model parameters at $\alpha=0.05$. Additionally, visual inspection for homoscedasticity and normality assumptions of the model's residual were performed.

Biomass and carbon allocation

On the basis of assessment of developed biomass equations, the most accurate model for each tree component was selected and applied to all black pine trees (n=129). The obtained biomass was converted into carbon amount according to the mean carbon content estimated in the distinguished components. The biomass and carbon allocation, determined as a fraction of a specific component in total dry biomass or in total carbon mass, were calculated for individual trees. The differences between biomass and carbon allocation patterns were assessed by paired t-test at $\alpha=0.05$, while the differences in biomass or carbon allocation for trees of different social status were assessed by the Kruskal-Wallis test at $\alpha=0.05$.

Biomass and carbon allocation can be alternatively assessed as a ratio of mass of specific component to stem volume. This ratio is known as conversion and expansion factor, and it is widely introduced for biomass estimation from stock volume, which is a very common characteristic used in forestry (Somogyi et al. 2007, Teobaldelli et al. 2009). Hence, biomass conversion and expansion factors (BCEF) and carbon conversion and expansion factors (CCEF) of each distinguished component were calculated for all trees. The differences between BCEF and CCEF for trees of different social status were assessed by the Kruskal-Wallis test at $\alpha=0.05$.

Total stock and annual biomass and carbon accumulation

The total stand dry biomass and carbon stock were calculated as the sum of predicted biomass for all trees and for groups of trees of different social status. Because stem wood is a crucial tissue in terms of carbon sequestration, the mean annual wood biomass accumulation (MAWBA) and mean annual wood carbon accumulation (MAWCA) were calculated for individual trees as a ratio of the mass of wood or carbon to tree age. Simultaneously, to assess actual stand productivity, the corresponding current annual wood biomass accumulation (CAWBA) and current annual wood carbon accumulation (CAWCA) were introduced. The CAWBA was determined for 14 biomass sample trees by multiplying the mean annual volume increment from the last five years, derived from the stem analysis procedure, described by Newton (2004), and the specific wood gravity (SWG), which was calculated as follows:

$$SWG = \left(\frac{SWB}{VUB} \right) \tag{6}$$

where, SWB is dry stem wood biomass and VUB is stem volume under bark. CAWCA was calculated as product of CAWBA and carbon content accumulated in stem wood.

Among all tree variables, the VUB showed the strongest linear relationship with CAWBA and CAWCA; therefore, models of the following form were fitted:

$$CAWBA = b_0 + b_1 \cdot VUB \tag{7}$$

$$CAWCA = b_0 + b_1 \cdot VUB \tag{8}$$

According to these models, the CAWBA and CAWCA for all black pine trees were estimated. Finally, the differences in wood biomass and carbon annual accumulation for trees of different social status were assessed by the Kruskal-Wallis test at the significance level of $\alpha=0.05$. Additionally, the differentiation of the total stand wood biomass and carbon accumulation in tree groups of different social status was determined.

Results

Biomass allometric models

All developed biomass models presented in Table 3 were statistically significant (F-test,

$p<0.05$), and all the estimated parameters were also statistically significant (t-test, $p<0.05$). Even the simplest biomass models that included only DBH as an explanatory variable generally performed well, explaining 80.13% (foliage) to 99.16% (bark) of the variance of tree component biomass.

The addition of tree height in the form of volume equivalent DBH^2H resulted in only slight improvement of the explained variance by 0.06%, 0.39%, 0.52%, and 0.79% for shoots, foliage, total biomass, and wood, respectively, but simultaneously lowered the model performance for bark and branches by −0.44% and −0.45%, respectively. Replacement of the DBH^2H with VOB led to an apparent improvement in the model only for branches (by 2.73%) and resulted in only a small increase in explained variance (not exceeding 0.65%) for wood, foliage, and total biomass, while a decrease in coefficient of determination, −0.19% and −1.33%, was observed for shoots and bark, respectively.

Despite the expected significant improvement of the biomass models after inclusion of crown size variables, models with crown length, CW, or crown volume as a single predictor explained less biomass variance than DBH alone. Attempts to use crown variables in multiple regression models with DBH or H resulted in a lack of significance for model parameters due to high correlation between covariates. DCB, on the other hand, proved to be a very important variable for modeling biomass, especially for crown components. The use of DCB alone as a predictor resulted in the highest explained variance among all the tested models for branches, shoots, and foliage (Table 3). Additionally, the introduction of DCB or its derivatives (QCB1 or QCB2) in multiple regression models with DBH or H, except for bark component, resulted in much higher explained variance of biomass than those for models with widely used variables such as DBH or DBH^2H.

Carbon content

The average carbon content significantly (t-test, $p<0.05$) exceeded 50% of the dry mass of all the analyzed tree components and with corresponding standard error was 50.94% ± 0.34%, 52.96% ± 0.11%, 51.38% ± 0.26%, 54.02% ± 0.25%, and 52.32% ± 0.14% for wood, bark, branches, shoots, and foliage, respectively (Figure 2).

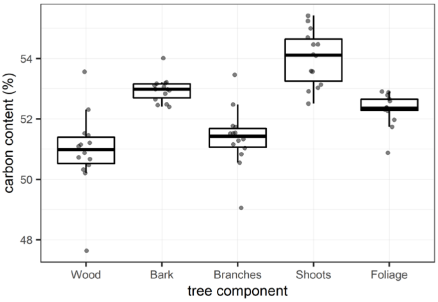

Figure 2 Carbon content in the distinguished tree components; median (thick horizontal line), interquartile range (box), and 1.5 interquartile range (whiskers).

According to Friedman test followed by Nemenyi post-hoc test ($p<0.05$), the content of carbon in stem wood was the lowest among the analyzed components and significantly different from that of bark, shoots, and foliage. The highest carbon content was found in shoots and bark, which were not significantly different.

Biomass and carbon allocation

The black pine trees in the analyzed stand allocated 74.49% ± 0.28% of the dry biomass in stem wood, 12.37% ± 0.12% in bark, 8.00% ± 0.24% in branches, 1.15% ± 0.02% in shoots, and 3.99% ± 0.08% in foliage (Figure 3). Among all the analyzed tree components, biomass allocation was significantly different for trees of different social status (Kruskal-Wallis test, $p<0.05$). For trees of higher social status, a lower share of wood and bark was observed, i.e., the share of wood was 5.35% lower for predominant trees than for dominated trees, while the corresponding share of bark was 2.87% lower. In contrast, the share of all crown components was significantly higher for trees of high social status. Biomass allocation to branches, foliage, and shoots was higher for predominant vs dominated trees by 6.21%, 1.59%, and 0.40% respectively.

Carbon allocation in wood of the analyzed black pines was 73.95% ± 0.28%, while it was 12.77% ± 0.13%, 8.00% ± 0.25%, 1.21% ± 0.03%, and 4.07% ± 0.09% in bark, branches, shoots, and foliage (Figure 3). Although the above values seem to be very similar to those describing biomass allocation pattern, the carbon allocation pattern was significantly different for all tree groups of different social status (t-test, $p<0.05$). Hence, carbon allocation was significantly higher than biomass allocation for bark, branches, shoots, and foliage but consequently lower for wood.

The calculated values of BCEFs and CCEFs shown in Figure 4 correspond well with the previously presented results of biomass allocation and were significantly different for trees of different social status (Kruskal-Wallis test, $p<0.05$). A detailed analysis revealed that BCEFs and CCEFs values for wood and bark were higher for trees of lower social status, while for all crown components, higher values of conversion and expansion factors were observed for trees of higher social status.

Table 3 Summary of log-normal regression $\ln(y) = b_0 + b_i \ln(X_i)$ for specific components of the destructively sampled black pine trees (n=14).

Tree comp	Ind var	b_0 (SE)	b_1 (SE)	b_2 (SE)	adj. R^2	AIC	SEE	CF
Wood	DBH	-1.8493 (0.3708)	2.2238 (0.1076)	-	0.9704	-22.44	0.0947	1.004489
	DBH^2H	-4.0733 (0.4082)	0.9911 (0.0409)	-	0.9783	-26.77	0.0811	1.003294
	VOB*	5.9852 (0.0195)	0.9712 (0.0339)	-	0.9844	-34.68	0.0687	1.002364
	H, DCB	-5.5779 (1.5192)	2.7839 (0.5706)	0.9992 (0.102)	0.9838	-30.11	0.0700	1.002452
Bark	DBH*	-2.6751 (0.1702)	1.9317 (0.0494)	-	0.9916	-44.25	0.0434	1.000944
	DBH^2H	-4.5576 (0.2699)	0.856 (0.0271)	-	0.9872	-38.35	0.0536	1.001438
	VOB	4.1279 (0.0217)	0.8312 (0.0377)	-	0.9739	-28.41	0.0765	1.002928
Branches	DBH	-10.8487 (1.2322)	4.1998 (0.3575)	-	0.9133	11.19	0.3145	1.050712
	DBH^2H	-14.9373 (1.6241)	1.8606 (0.1629)	-	0.9088	11.9	0.3227	1.053435
	VOB	3.9486 (0.0766)	1.8429 (0.1331)	-	0.9361	6.91	0.2700	1.037110
	DCB	-4.2145 (0.4126)	2.7907 (0.1463)	-	0.9654	-1.68	0.1987	1.019932
	DBH, QCB1*	-4.5812 (1.7353)	2.8717 (0.4013)	2.6530 (0.6494)	0.9624	0.26	0.2071	1.021668
Foliage	DBH	-7.9777 (1.4883)	3.1562 (0.4319)	-	0.8013	16.47	0.3799	1.074838
	DBH^2H	-11.1135 (1.893)	1.4046 (0.1898)	-	0.8052	16.19	0.3761	1.073286
	VOB	3.141 (0.1057)	1.3754 (0.1836)	-	0.8091	15.24	0.3724	1.071787
	DCB*	-3.0709 (0.6313)	2.1256 (0.2238)	-	0.8728	10.23	0.304	1.047288
	H, QCB2	-15.2386 (5.1762)	6.2012 (1.6302)	3.5374 (0.8233)	0.8717	11.13	0.3053	1.0477
Shoots	DBH	-9.0271 (1.2169)	3.1028 (0.3531)	-	0.8543	10.84	0.3107	1.049436
	DBH^2H	-12.0836 (1.5603)	1.3782 (0.1565)	-	0.8549	10.78	0.31	1.04922
	VOB	1.9021 (0.0886)	1.3453 (0.1539)	-	0.853	10.96	0.312	1.049869
	DCB*	-4.0731 (0.5721)	2.0430 (0.2029)	-	0.8854	7.48	0.2755	1.038681
	H, QCB2	-17.1288 (5.1573)	6.3758 (1.6243)	3.1163 (0.8203)	0.8603	11.03	0.3042	1.047343
Total AB	DBH	-2.1051 (0.3988)	2.3872 (0.1157)	-	0.9703	-20.4	0.1018	1.005195
	DBH^2H	-4.4795 (0.4649)	1.0626 (0.0466)	-	0.9755	-23.13	0.0924	1.004274
	VOB*	6.3049 (0.0226)	1.0414 (0.0392)	-	0.9819	-27.99	0.0796	1.003169
	H, DCB	-4.8956 (1.6600)	2.5243 (0.6234)	1.1507 (0.1114)	0.9832	-27.63	0.0765	1.002928

Note: *The allometric models chosen as best for the prediction of tree component biomass; b_0, b_1, b_2 – regression parameters with standard error (SE), adj.R^2 – adjusted coefficient of determination, AIC – Akaike information criterion, SEE – standard error of the regression, CF – correction factor; Tree comp: Tree component; Ind. var.: Independent variables

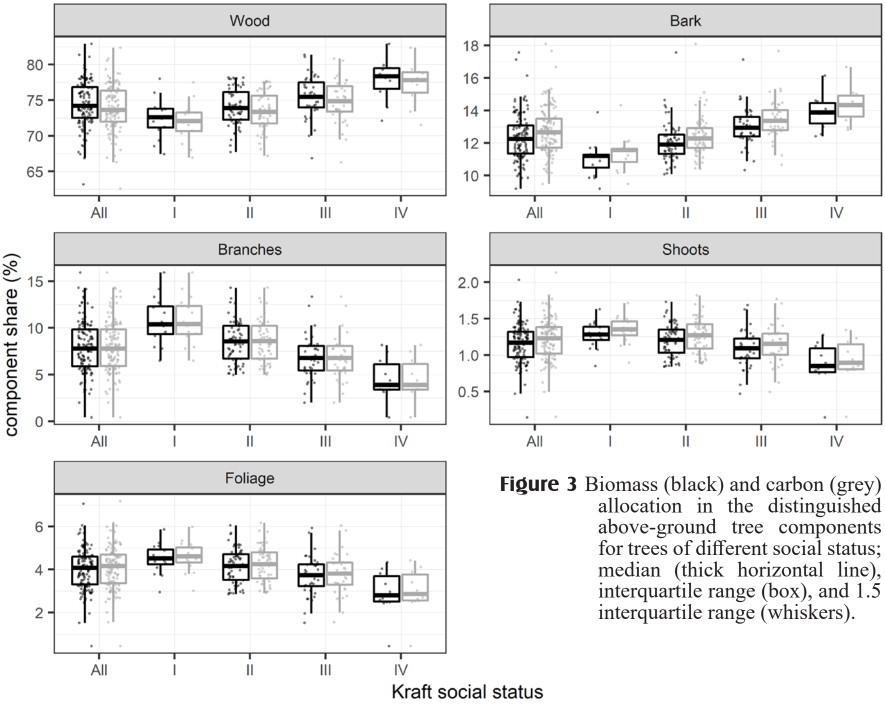

Figure 3 Biomass (black) and carbon (grey) allocation in the distinguished above-ground tree components for trees of different social status; median (thick horizontal line), interquartile range (box), and 1.5 interquartile range (whiskers).

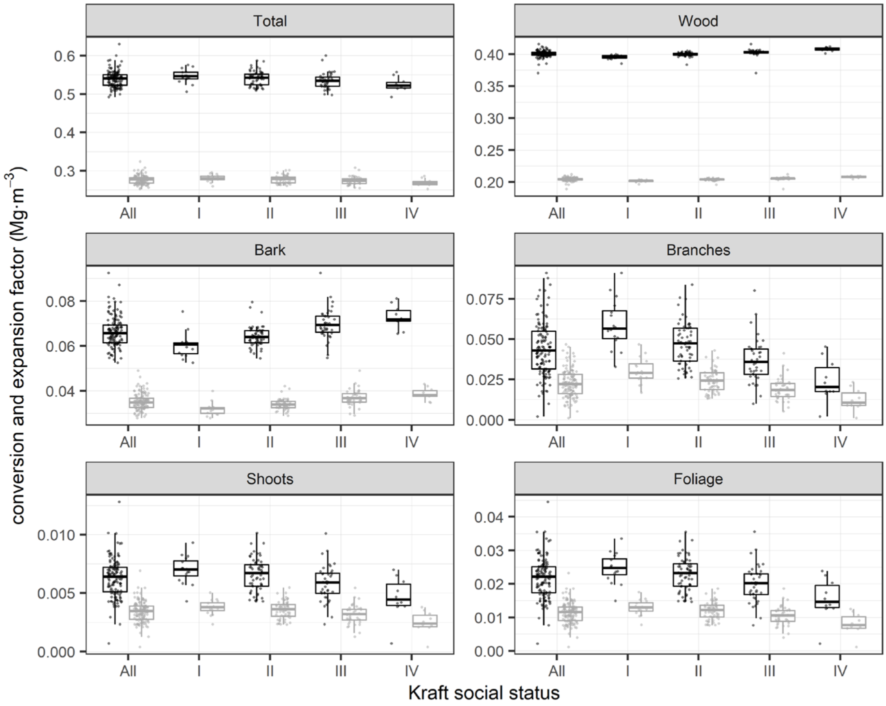

Figure 4 Conversion and expansion factors of stand biomass (black) and stand carbon (grey) for the distinguished above-ground tree components and trees of different social status.

For practical use of BCEFs and CCEFs in the process of stand biomass and carbon estimation, the weighted mean values of conversion and expansion factors must be obtained and applied. Hence, the stand total above-ground BCEF was 0.5365 ± 0.00148 Mg·m^{-3}, while it was 0.3967 ± 0.00968 Mg·m^{-3}, 0.0648 ± 0.000137 Mg·m^{-3}, 0.0464 ± 0.000258 Mg·m^{-3}, 0.0064 ± 0.0000241 Mg·m^{-3}, and 0.0222 ± 0.0000878 Mg·m^{-3} for wood, bark, branches, shoots, and foliage, respectively. The stand total above-ground CCEF was 0.2753 ± 0.000758 Mg·m^{-3}, and it was 0.2021 ± 0.000516 Mg·m^{-3}, 0.0343 ± 0.0000726 Mg·m^{-3}, 0.0238 ± 0.000133 Mg·m^{-3}, 0.0034 ± 0.0000130 Mg·m^{-3}, and 0.0116 ± 0.0000459 Mg·m^{-3} for wood, bark, branches, shoots, and foliage, respectively.

Total stock, annual biomass, and carbon accumulation

The total dry above-ground biomass of the analyzed black pine stand was 191.67 Mg·ha-1, while the total carbon stock was 98.36 Mg·C·ha^{-1} (Table 4). In the stem, which is the most important part of the tree in terms of carbon sink, 164.90 Mg·ha^{-1} of dry biomass and 84.47 Mg·ha^{-1} of carbon were stored. All crown components, which have much higher turnover rate, contained only 26.77 Mg·ha^{-1} of dry biomass and 13.89 Mg·ha^{-1} of carbon.

The majority (95.3%) of biomass and carbon was stored in trees constituting the main canopy layer (Table 4). Among them, the most numerous (density: 210 tree·ha^{-1}) were the dominant trees that stored 51.5% of the total stand biomass and carbon. The second largest group was codominant trees with a density of 130 tree·ha^{-1}, which held 24.3% of biomass and carbon, while the predominant trees of the highest social status and relatively low density of 53 tree·ha^{-1} stored 19.5% of biomass and carbon. The dominated and entirely overtopped trees of the lowest social status had relatively low density of 36 tree·ha^{-1}, and both held only 4.7% of the stand total biomass and carbon.

Table 4 Biomass and carbon stock in Mg·ha^{-1} stored in the black pine stand with respect to different tree social status and distinguished tree components.

V	Tree comp	Kraft social status classes					
		All	I	II	III	IV	V
B	Wood	141.73	26.96	72.92	34.96	6.29	0.60
	Bark	23.17	4.07	11.84	6.00	1.13	0.13
	Branches	16.57	4.14	8.60	3.28	0.41	0.13
	Shoots	2.28	0.48	1.19	0.51	0.07	0.02
	Foliage	7.92	1.70	4.14	1.76	0.25	0.07
	Total AB	191.67	37.35	98.69	46.52	8.16	0.95
C	Wood	72.2	13.74	37.15	17.81	3.2	0.31
	Bark	12.27	2.15	6.27	3.18	0.6	0.07
	Branches	8.51	2.13	4.42	1.69	0.21	0.07
	Shoots	1.23	0.26	0.64	0.28	0.04	0.01
	Foliage	4.15	0.89	2.17	0.92	0.13	0.04
	Total C	98.36	19.17	50.65	23.87	4.19	0.49

Note: V: Variable; B: biomass; C: carbon; Tree comp: Tree component

The CAWBA per tree in the analyzed stand was on average 5.39 kg·year^{-1}, while the CAWCA, MAWBA, and MAWCA were 2.74 kg·year^{-1} (Figure 5), 3.88 kg·year^{-1}, and 1.98 kg·year^{-1}, respectively. Both current and mean annual accumulation of biomass and carbon were significantly different (Kruskal-Wallis test, $p<0.05$) between trees of different social status, i.e., the CAWBA and CAWCA for predominant trees were on average 2.94 times higher than those for dominated trees, while this ratio was as high as 2.68 for MAWBA and MAWCA. The relationship of the current to mean annual increment is well recognized as an indicator of the tree growth phase and its efficiency in the process of biomass and carbon accumulation in wood tissues. For trees of all social status, the current annual accumulation was higher than the mean annual accumulation; therefore, it can be assumed that none of the trees achieved the culmination of mean annual accumulation. Although all trees still showed potential for effective biomass and carbon accumulation, it should be noted that trees of high social status show much higher potential than the dominated trees.

The stand CAWBA and MAWBA were 2.316 Mg·ha^{-1}·year^{1} and 1.667 Mg·ha^{-1}·year^{1}, respectively, while the CAWCA and MAWCA were 1.180 Mg·ha^{-1}·year^{1} and 0.849 Mg·ha^{-1}·year^{1},

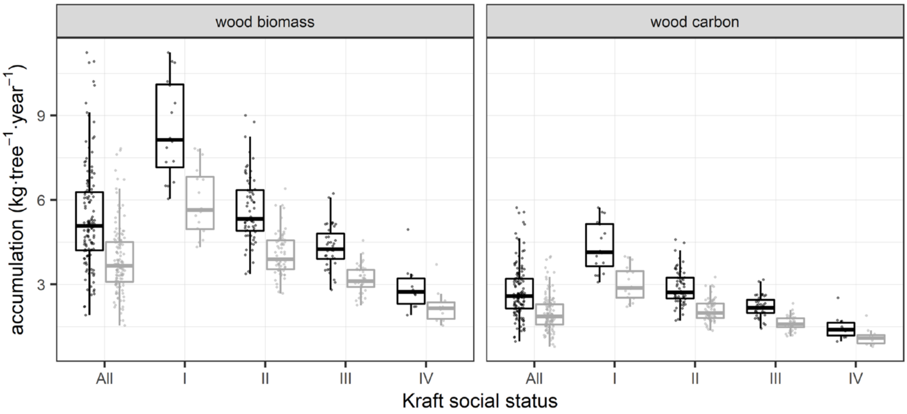

Figure 5 Tree current (CAWBA–black) and mean (MAWBA–grey) annual biomass accumulation (left chart) with current (CAWCA–black) and mean (MAWCA–grey) annual carbon accumulation (right chart) in stem wood for trees of different social status in kg·tree^{-1}·year^{-1}; median (thick horizontal line), interquartile range (box), and 1.5 interquartile range (whiskers).

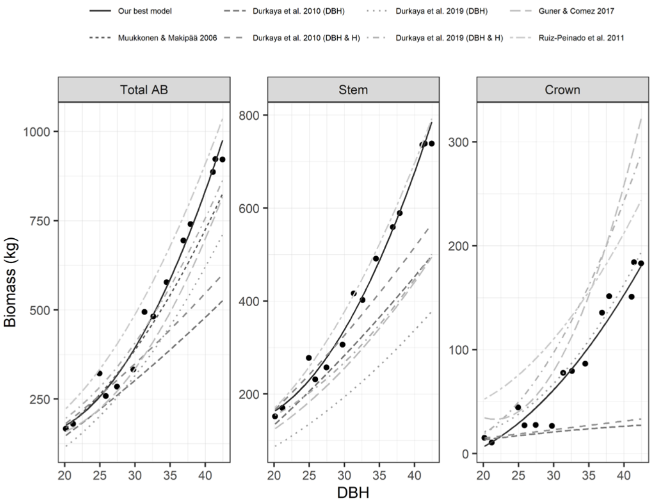

Figure 6 Comparison of real total above-ground, stem, and crown biomass for the analyzed black pines (black dots) with predictions using available models: our best models, models of Durkaya et al. (2010, 2019), Guner & Comez (2017), and Ruiz-Peinado et al. (2011), and Gasparini provided by Muukkonen & Mäkipää (2006).

Table 5 Stand current (CAWBA) and mean (MAWBA) annual biomass accumulation with current (CAWCA) and mean (MAWCA) annual carbon accumulation in stem wood with respect to trees of different social status in Mg·ha^{-1}·year^{-1}.

Accum	Kraft social status classes					
	All	I	II	III	IV	V
CAWBA	2.316	0.455	1.193	0.563	0.097	0.009
MAWBA	1.667	0.317	0.858	0.411	0.074	0.007
CAWCA	1.180	0.232	0.608	0.287	0.049	0.005
MAWCA	0.849	0.162	0.437	0.210	0.038	0.004

Note: Accum: Accumulation

respectively (Table 5). The relationship of current to mean accumulation was greater than 1 for both biomass and carbon, which indicates that from the point of natural cycle of stand development, the culmination of the stand mean annual accumulation was not yet achieved. Hence, the analyzed stand still had potential to maximize the annual biomass and carbon accumulation level. The most important group of trees from this aspect are dominant trees, which accumulate over 51% of biomass and carbon, while over 24% and over 19% are accumulated by codominant and predominant trees, respectively. Dominated and entirely overtopped trees of the lowest social status play only a minor role in the process of biomass and carbon accumulation, which did not exceed 5%.

Discussion

Biomass of individual tree components is the basis for determining forest carbon stock.

Some studies assumed the carbon content at 45% for leaves and 50% for wood (Whittaker & Likens 1973, Houghton 1996, Gower et al. 2007). However, other studies have shown that such simplification could be a potential source of significant errors in the estimation of total carbon stock, because carbon content depends on the tree component and ranges from less than 40% to over 55% (Jagodziński et al. 2012). Moreover, the compilation provided by Thomas & Martin (2012) shows that the content of carbon in plant organs depends on the geographic zone, i.e., carbon content in wood ranges between 41.9% and 51.6% in the tropical zone, between 45.7% and 60.7% in the subtropical/Mediterranean zone, and between 43.4% and 55.6% in the temperate/boreal zone. It also varies for different groups of plants, i.e., carbon content in wood is on average 50.8% ± 0.8% for gymnosperms, which is approximately 3% higher than that for angiosperms (47.7% ± 0.3%) (Thomas & Martin 2012).

The carbon content in wood of black pine reported in the present study (51.0% ± 0.34%) was lower than that reported by Guner & Comez (2017) in Turkey (53.6% ± 0.1%), but higher than that observed in the study of Herrero de Aza et al. (2011) in northern Spain (46.5% ± 0.4%). These differences in the wood carbon content could be related not only to different geographic locations and specific site characteristics but also to processing of the collected biomass samples; this is because the drying process causes some carbon loss, resulting from evaporation of volatile organic compounds. Carbon loss related to this phenomenon can be as high as 2.5% ± 0.3% for tropical angiosperm species and little lower for gymnosperm species of the temperate zone (2.1% ± 1.4%), followed by broadleaves species (1.3% ± 0.6%) (Thomas & Martin 2012).

In the present study, drying was performed at 105 °C, while it was performed at substantially lower temperature in the studies of Herrero de Aza et al. (2011) (75 °C) as well as in the study of Guner & Comez (2017) (65 °C). In our study, bark had on average 2.0% higher carbon content than wood, which confirms the findings of Herrero de Aza et al. (2011) and Guner & Comez (2017) where bark carbon content was 3.4% and 1.1% higher than that of wood, respectively.

The practical results of the study are allometric models that allow to assess the biomass of individual tree components, while the calculated expansion factors (BCEFs and CCEFs) can be easily incorporated into stand level biomass and carbon estimations. The study was oriented to provide models of different levels of complexity and to show whether the addition of more complex variables that are more difficult and laborious to acquire is justified. The obtained results showed that the most popular tree biometric feature DBH can generally alone explain a large part of variation of the biomass of different black pine components, which is in accordance with previous studies (Zianis et al. 2005, Dutcă et al. 2019).

The introduction of tree height or tree volume as an explanatory variable only slightly increased the accuracy of biomass prediction and only for stem components. For crown components, significant model improvement was observed using variables related to stem features in the crown zone, such as diameter at crown base and quotients based on this diameter.

The use of diameter crown base features for improving biomass estimation of crown components confirms the pipe model theory (Shinozaki et al. 1964), while the use of quotients can be treated as equivalent to the surrogates, which were found to be essential for foliar dry matter estimation, as demonstrated by (Valentine et al. 1994). According to some studies (Grote & Reiter 2004, Forrester et al. 2020), the crown allometry is determined mainly by inter-tree competition, while in allometric models for crown components, direct crown measurements, i.e., its length, width, and relative length to the greatest extent, reflect tree competitive status. However, our study showed that using these variables solely in the models led to lower explained variance of crown biomass components than that for models with only DBH, while attempts to incorporate them as additional explanatory variables in multiple regression introduced too high variance inflation factor (O'Brien 2007), resulting from the high collinearity of variables.

Our finding that the introduction of tree diameter at crown base, alone or in combination with other stem diameters as form quotients is very useful for crown biomass estimation may seem to be little important in traditional forest inventory, but seems to be a very promising solution for biomass estimation combined with the current increasingly popular remote sensing techniques such as terrestrial laser scanning (Hackenberg et al. 2015) or vehicle-based laser scanning (Lin et al. 2010). Moreover, it can be easily incorporated into 3D imagery applications for popular handheld devices, thus providing a relatively quick and widely accessible source of environment monitoring, especially from the perspectives of involving global citizens in the data collection process in the future (Molinier et al. 2016).

A practical example of incorporating the CW into the total above-ground biomass models of black pine from Croatia was useful in the remote sensing approach which can be found in Balenović et al. (2015). The provided equations have, however, relatively low level of variance explained (R^2 from 0.598 to 0.821), and their application to our dataset (not presented here) resulted in unreliable high variability of predictions.

Despite the tested potential of different explanatory variables for biomass estimation, the majority of existing biomass equations include DBH alone and rarely incorporate tree height. In a compilation by Zianis et al. (2005), supplemented by Muukkonen & Mäkipää (2006), there were 795 biomass models, including only four models developed for total above-ground woody biomass, crown, dead branches, and stump biomass of black pine in Italy (Muukkonen & Mäkipää 2006). Similar models were developed later for black pine from Turkey (Durkaya et al. 2010, Guner & Comez 2017, Durkaya et al. 2019) and Spain (Ruiz-Peinado et al. 2011).

The application of the abovementioned models to our dataset suggests that black pines from different geographical locations have not only different total above-ground biomass but also share different biomass allocation patterns (Figure 4).

Total above-ground biomass of the tested black pines, regardless of tree diameter, was slightly smaller only from trees in Spain (Ruiz-Peinado et al. 2011), but was substantially larger than those reported in other studies (Durkaya et al. 2010, Guner & Comez 2017, Durkaya et al. 2019), especially for the largest trees with DBH over 32 cm. These differences also suggest that equations developed for the native range of the species cannot be easily applied for other tree populations and that constructing one general model for black pine in Europe should consider a wide range of site properties. This finding is in accordance with the results achieved for other tree species such as Norway spruce (Wirth et al. 2004) and black alder (Ochał et al. 2014). The observed differences between the different models became even more evident when the allocation pattern between stem and crown was considered (Figure 4).

Apart from two models for predicting unrealistic small values of crown biomass (Durkaya et al. 2010), it seems that the analyzed pines and those from Spain (Ruiz-Peinado et al. 2011) share similar stem biomass, but at the same time, the crown biomass of the analyzed trees was much smaller.

A particularly interesting finding is that black pines from Turkey (Durkaya et al. 2010, Guner & Comez 2017, Durkaya et al. 2019) and Italy (Muukkonen & Mäkipää 2006) have smaller stem biomass but simultaneously have substantially higher biomass of crown. This phenomenon suggests that the analyzed black pines had much better crown efficiency than those in native range, resulting in bigger biomass produced per crown unit. It can possibly influence the potential of the species in the process of carbon sequestration, especially as the stem is the most important tree part in terms of carbon sink.

Regardless of the tree's social status, it was observed that the carbon allocation pattern was significantly different from biomass allocation pattern, i.e., relatively lower carbon share was found in stem wood than in other tree components. On the other hand, the obtained results clearly showed that tree social status significantly influences both biomass and carbon allocation patterns. Trees of lower social status tend to allocate relatively more biomass and carbon into stem components than trees of high social status, which is characterized by higher share of crown components. These observations are in line with the results of studies on Scots pine allocation conducted in southern Poland (Ochał et al. 2013) and also confirmed in northern premature and mature Scots pine populations (Wertz et al. 2020). Moreover, some studies indicated that competition pressure from neighboring trees is a crucial factor that drives and regulates the distribution of biomass (Grote & Reiter 2004, Zhou et al. 2018, Wertz et al. 2020). The impact of tree social status on biomass allocation can also be seen in different BCEFs and CCEFs for trees sharing similar social status in the stand. These findings prove that both biomass and carbon allocations are site-specific, as local factors that determine a tree's social status structure are key factors here. Consequently, one can expect that stands of different silviculture treatments, e.g., semi-natural stands of moderate thinning and intensively managed plantations, will have their own biomass and carbon allocation patterns, which should be assessed individually and lead to different allometric models, BCEFs, and CCEFs.

Although the role of forest ecosystems in mitigating the observed climate change can be discussed, their importance in terms of carbon sink and a source of renewable energy is certain. Hence, the growth potential of key forest-forming species is a very important topic, especially considering marginal populations outside of the species native range, which are most susceptible to the observed climate changes.

The volume of the analyzed black pine stand in our study (357.3 $m^3 \cdot ha^{-1}$) was higher than that reported for similar pure, even-aged stands in Croatia (Balenović et al. 2015), where the average volume of the stands was 237.9 $m^3 \cdot ha^{-1}$ and ranged from 182.8 $m^3 \cdot ha^{-1}$ to 308.3 $m^3 \cdot ha^{-1}$. It was also higher than the average volume of black pine stands of Serbia, where it reached 300 $m^3 \cdot ha^{-1}$ in a 55-year-old stand growing in favorable conditions (Sikanja 2015). In contrast, it was much lower than the volume of black pine stands of similar dominant height class located in the mountainous region of southern-west Bulgaria, where it was on average as high as 527.51 $m^3 \cdot ha^{-1}$, ranging between 406.50 and 793.40 $m^3 \cdot ha^{-1}$ (Stankova & Shibuya 2007). Comparison of the carbon stock per hectare locates the analyzed stand (98.36 MgC·ha-1) between stands reported by Guner & Comez (2017), where stand of similar age and density stored 71.12 $MgC \cdot ha^{-1}$ while stand of higher density stored 103.45 $MgC \cdot ha^{-1}$. The current accumulation of biomass recorded in the study was as high as 2.316 $Mg \cdot ha^{-1} \cdot year^{-1}$, whereas it was 1.180 $MgC \cdot ha^{-1} \cdot year^{-1}$ for carbon, which corresponds to 4.62 $m^3 \cdot ha^{-1} \cdot year^{-1}$ of volume increment. The observed volume increment was higher than 3.83 $m^3 \cdot ha^{-1} \cdot year^{-1}$ for black pine recorded in Serbia (Sikanja 2015) and close to the upper margin of range (2.8-5.0$m^3 \cdot ha^{-1} \cdot year^{-1}$) reported for Croatian black pine stands (Balenović et al. 2015), which indicates very high potential for biomass and carbon accumulation in black pine.

The role of black pine, which is now one of the most important productive species in the Mediterranean region, like in Turkey (Tolunay 2011), can potentially increase, even outside of its native range, and that this species can be considered as a replacement for Scots pine, especially in central Europe. This opinion may be supported by the fact that both these species share similar volume growth efficiency (Aguirre et al. 2019); moreover, black pine is reported to be resistant to drought and wind and shows higher shade tolerance than Scots pine (Isajev et al. 2004). Additionally, our results suggest that black pine is even more efficient than Scots pine in terms of carbon sequestration, because although both species have very similar BCEF values (Wojtan et al. 2011), the analyzed black pines had higher carbon content by 3.94% for stem wood, 5.86% for bark, and 2.02% for foliage than those reported for Scots pine (Węgiel & Polowy 2020).

Although the study from the Cuenca Mountains of Spain indicate that black pine is sensitive to extreme droughts (Lucas-Borja & Vacchiano 2018) and the results from the mountainous island of Corsica located in the Western Mediterranean basin indicate that declining water availability may reduce Corsican pine's potential distribution range (Szymczak et al. 2020), black pine can be considered as a potential beneficent of the observed climate changes as this species seems to be tolerant to drought in terms of its resilience (Proutsos & Tigkas 2020), especially considering that trees of high social status play the most important role in the stand's biomass and carbon accumulation (Martín-Benito et al. 2008).

Conclusions

The results obtained in this study revealed that black pine has overall higher carbon content than the average value of 50% and is widely accepted and used for the estimation of carbon content in forests; hence, the total carbon stock of black pine stands may be underestimated. Because the carbon content in specific tree components of black pine is different, averaging it for the entire tree should consider the biomass allocation pattern. Additionally, our results clearly show that the allocation of biomass and carbon depends on tree social status, i.e., with the increase in tree social status, the stem share decreases in favor of the share of branches and foliage. Therefore, for stand level biomass and carbon modeling, the factors influencing the stand social structure, e.g., site fertility and silviculture treatment intensity, should be considered.

The assessment of allometric biomass models at the tree level, especially for crown components, indicates that the inclusion of stem features in the crown zone, i.e., diameter at crown base or its derivatives, can significantly improve the estimation accuracy; moreover, the use of these predictors can be quite important from a wider perspective of incorporating the remote sensing techniques into forest inventory.

The importance of the conducted site-specific analyses lies in the fact that they revealed significant differences in biomass and carbon allocation between different tree populations.

Combining the results of studies from different locations, i.e., within and outside of the native range of species, leads to comprehensive understanding of biomass and carbon allocation patterns and provides ground for developing general allometric models and performing meta-analysis.

Our results also showed that the studied black pine can be as productive and even outperform populations growing in native range.

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