

Allometric Models of Foliage Biomass in Scots Pine (*Pinus sylvestris* L.)

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Received: 17 May 2010

Accepted: 5 October 2010

Abstract

Presented analyses were connected with modelling foliage biomass of Scots pine (*Pinus sylvestris* L.) growing in northern and western Poland.

In order to realize the study, a total of 38 one-hectare experimental plots were established in commercial pine monocultures growing on sites optimal for this species at a given geographical location. A total of 114 trees aged 32-114 years were felled and their needle weight and the weight of needles and young, 1-year old twigs were measured.

Since social variation in the stand could affect the fit of the model, for each social class of tree position an individual allometric equation was proposed, based on easily measurable biometric traits of trees. Analysis of stepwise backward regression was conducted in order to determine variables in these equations.

It turned out that to estimate foliage biomass of predominant and dominant trees, it seems most appropriate to apply diameter at breast height and tree age. In turn, for co-dominant trees, apart from diameter at breast height and tree age, the model needs to include additionally tree height and crown length.

Moreover, due to the fact that the dependence between needle weight and the weight of needles and young twigs is practically linear, prediction was conducted for the biomass of foliage with young twigs. From the practical point of view, this makes it possible to precisely determine needle biomass on the basis of the weight of needles with young, 1-year-old shoots.

Keywords: foliage biomass, *Pinus sylvestris* L., allometric equations, tree crowns, social class of tree position

Introduction

Under the influence of environmental changes, the level of biomass in individual trees and its structure in the stand

may fluctuate, particularly when they are caused by global climate change or changes in forest economy [1]. Thus, estimation of biomass of trees and stands should not be based only on earlier studies, but rather requires continuous verification, which would make it possible to include quantitative changes in individual components of biomass.

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The most accurate way to determine values of wood biomass is to cut down the trees under investigation and perform appropriate measurements. However, destructive harvesting of forest biomass in sample plots is a time-consuming procedure and generates considerable uncertainty when the obtained results are extrapolated to larger areas. Undoubtedly, the most common approach to obtain biomass estimates at stand level is through regression equations that are fitted to morphometric measurements taken from destructive samplings of individual trees. Subsequently, these regressions (also known as size allometry relationships) are used to estimate biomass of sample plots, within which diameters and heights for all trees have been measured [2].

Allometric equations may thus be tools facilitating determination of selected biomass components based on easily measurable variables such as breast height diameter of trees, tree height, or simply traceable crown parameters. Models of this type may be particularly suitable for the prediction of carbon sequestration, and as a consequence may contribute to the determination of CO₂ balance [3]. The importance of reduced emission of greenhouse gases, mainly carbon dioxide, was stressed in the resolutions of the Kyoto Protocol. At the time of trade in emission rights, forestry worldwide faces new challenges in which relatively fast inventory of foliage biomass is an important element of the applied method thanks to modelling CO₂ exchange in forest ecosystems [4, 5].

Pioneering studies on the volume and structure of biomass on selected tree species of Central Europe were conducted by Burger [6-8]. His studies concerned, among other things, quantitative description of foliage biomass in main forest tree species, including Scots pine (*Pinus sylvestris* L.). Investigations on dependences between foliage biomass and wood structure and growth conditions, initiated by Burger, were continued by many researchers [9-13].

One of the theories (Pipe Model Theory) proposed by Shinozaki [14, 15] presents dependencies between foliage biomass or crown size and stem conductive area. In order to estimate foliage biomass of trees and maintain an appropriate hydraulically conductive area, this theory was further developed by other researchers [2, 16-19]. Interesting conclusions were given by Vanninen et al. [12], who in the analysis of the effect of age and site on the distribution of biomass in Scots pine showed a strong relationship between the outer area (coat) of the crown and needle weight. In turn, Mikšysa et al. [21] conducted an analysis in Lithuania, which showed a dependence of the aboveground biomass weight in Scots pine, including that of needle weight on breast height diameter and height of trees, which according to those authors made possible modelling of biomass for a single tree.

Numerous studies on models used in inventorying foliage biomass were conducted in Scandinavia [22-25], but they concerned mainly birch, spruce, and pine.

Zianis et al. [2] in their monograph presented a collection of over six hundred equations of biomass for 39 species of trees growing in Europe. This list, for 25 tree species,

was extended by Muukkonen and Mäkipää [26] to include a further 188 models. In the above-mentioned studies a total of 206 models were presented for Scots pine (*Pinus sylvestris* L.), of which 38 concerned foliage biomass. A generally used model in the description of allometric interdependencies is function:

$$Y = aX^b$$

...where a and b are parameters of an allometric function, Y – a dependent variable and X – an independent variable. They are frequently used in the description of biomass of the whole tree or its selected component [23, 27-29].

Allometric equations facilitating estimation of needle biomass of pines based on biometric traits were applied in studies by Marklund [30] in Sweden and Cienciala et al. [31] in the Czech Republic. The latter authors attempted to provide a parametrization of functions of individual elements of biomass for Scots pine (*Pinus sylvestris* L.) in Central Europe. Aboveground biomass as well as its individual components were analyzed for different types of non-linear regression models assuming breast height diameter, tree height, tree age, and length and diameter of the crown as independent variables. The best biomass models were obtained using three variables, i.e. diameter at breast height (DBH), tree height, and crown length, with the latter being characterized by the best results in the estimation of aboveground biomass.

Analysis of crown biomass of Scots pine in the Ural Mountains and in Kazakhstan was performed by Hoffmann and Usoltsev [32] and in Russia by Monserud et al. [33] in Poland studies on foliage biomass in Scots pine were initiated by Lemke [34, 35]. In 2007 investigations were conducted by Socha and Weżyk [29], while in 2008 - by Turski et al. [36]. The latter authors presented an allometric equation for the estimation of fresh needle biomass as well as those of needles covering twigs for individual trees. In their equations they used diameter at breast height, height, and age of trees as independent variables.

It seems that literature presenting attempts to develop allometric equations for the estimation of needle biomass in Scots pines growing in Poland is relatively scarce. The advisability of studies on the subject is also justified by high variability and adaptability of this species.

The aim of this study was to develop and compare regression models for the estimation of fresh needle biomass and biomass of fresh shoots covered with needles for production pine stands, taking into consideration their social class.

Methods

Investigations were conducted in northern and western Poland in production pine stands (Fig. 1). Mean sample plots were located in 38 pine positions situated within the limits of the natural range of this species in Europe. Sixteen mean sample plots were established in the Miastko forest district:

Table 1. Characteristics of stands and sample trees.

Site ID	Site name	Site location	Sampled trees (n)	Tree age (years)	DBH (cm)	Tree height (m)	Crown length (m)	Needle mass (kg)	Needle and branch mass (kg)
1	Miastko	54°01'N 16°59'E	48	32-114	8.5-37.2	11.8-28.3	2.6-11.9	3.13-39.74	4.68-60.13
2	Bytnica	52°09'N 15° 10'E	42	34-36	12.1-35.2	12.0-28.0	1.9-10.2	3.89-45.26	5.40-68.50
3	Złotow	53°21' N 17° 02' E	24	63-103	18.0-41.6	13.9-29.6	4.8-13.3	9.97-47.75	14.87-73.98

- (1) (54°01'N 16°59'E, altitude 80±25m a.s.l., mean annual temperature 7.2°C, annual precipitation 566-644 mm, length of vegetative period 197 days), 14 in the Bytnica forest district
- (2) (52°09'N 15°10'E, altitude 60±15m a.s.l., mean annual temperature 8.0°C, annual precipitation 555-640 mm, length of vegetative period 222 days) and eight in the Złotów forest district
- (3) (53°21' N 17°02' E, altitude 70±25m a.s.l., mean annual temperature 8.0°C, annual precipitation 570-644 mm, length of vegetative period 220 days) (Table 1).

Investigations were conducted in cycles, in September 2004 and 2008. In the investigations a total of 114 *Pinus sylvestris* L. trees were used, aged from 32 to 114 years, growing under diverse growth and development conditions.

Then analyses of distribution were prepared for the basic biometric (taxation) characters of trees, i.e. diameter at breast height and tree height (Fig. 2).

In our study mensuration methods were applied simultaneously for the selection of mean sample trees according to Kraft (1884) and Ulrich II, in accordance with which in each analyzed stand a 1ha experimental plot was established. In the first stage each stand was classified according to Kraft [37], and the next the main stand (Kraft's classes I, II, and III) were divided into three diameter subclasses using the Ulrich II method [38].

For this purpose breast height diameters and heights were measured for all trees. Next the main stand was divid-

ed into three diameter classes with equal numbers of trees in each class. On the basis of mean height and mean cross section area at breast height the size of the mean sample tree was determined for each class. Mean sample trees were selected in such a way that they simultaneously corresponded to the commonly applied, subjective classification developed by Kraft [1884], in which the division of the stand into classes was performed due to the subjective size of tree crown and height.

In the conducted analyses only the main stand (the first three Kraft's classes) was taken into consideration, since the proportion of Kraft's classes in single species pine stand was approx. 12% for class I, 40% for class II, and 35% for class III, respectively [39]. In turn, in a mature, properly tended production stand the proportion of the first three Kraft's classes was as high as 96% [40].

This type of a combination of mensuration and natural classification methods ensures the maintenance of the same scheme of tree selection for all experimental plots and eliminates subjectivity of Kraft's classification.

Selected sample trees were felled and next their length was measured to 10 cm and length of live crown was measured, which was assumed to be the distance between the first live branch and crown top. The size of the assimilating organ was characterized using the weight of fresh 1-year-old, needle-covered twigs and the weight of fresh needles. All needle-covered 1-year-old twigs were collected individually from crowns of felled sample trees and next they were



Fig. 1. Location of the study.

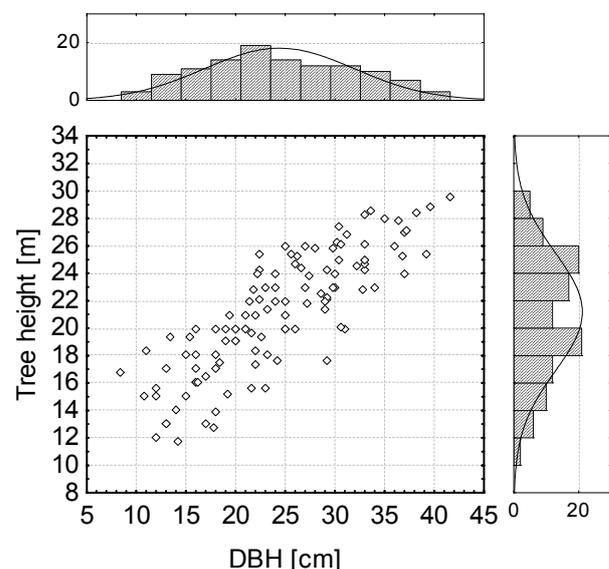


Fig. 2. Distribution of sample trees by diameter and height.

Table 2. Correlation coefficients.

	Tree height	Crown diameter	Crown length	Tree age	Needle weight	Weight of needles and branches
Breast height diameters	0.834	0.882	0.769	0.766	0.968	0.961
Tree height		0.790	0.689	0.765	0.772	0.758
Crown diameter			0.770	0.720	0.837	0.836
Crown length				0.615	0.754	0.745
Tree age					0.630	0.612
Needle weight						0.994

Coefficients are statistically significant at $p < 0.05$.

weighed to 0.001 kg. Then all needles were removed from cut twigs and their weight was determined to 0.001 kg.

Ranges of variation of all traits analyzed in the study and biomass components are presented in Table 1.

All investigated traits were significantly correlated with one another. The highest coefficient of correlation, $r = 0.994$, was found for the traits of *needle weight* and *weight of needles and branches*, which together with a graphic presentation of the dependence between these traits (Fig. 3) suggests that this dependence is linear, i.e. takes the form

$$Z = aY + b \tag{1}$$

...where Z and Y denote *weight of needles and branches* and *needle weight*, while a and b are unknown parameters.

More attention was thus focused on modelling values of *needle weight*. The exploratory analysis showed that not all dependencies between *needle weight* and the other traits of trees were linear. For example, the dependence between *needle weight* and *tree height* was markedly non-linear (Fig. 4). For this reason and due to the fact that the investigated traits were traits of the same tree, allometric equations were applied to model *needle weight* [40, 41] in the form:

$$Y = b_0 X_1^{b_1} X_2^{b_2} \dots X_5^{b_5} \tag{2}$$

...where Y denotes *needle weight*, X_1, \dots, X_5 , then DBH, *tree height*, *crown diameter*, *crown length*, and *tree age*, b_0, b_1, \dots, b_5 , respectively, are unknown parameters. This equation, after a logarithm was found, took the form:

$$\ln Y = \ln b_0 + b_1 \ln X_1 + b_2 \ln X_2 + \dots + b_5 \ln X_5 \tag{3}$$

...and is the equation of multivariate linear regression. The corresponding linear model takes the form

$$\ln Y = \ln b_0 + b_1 \ln X_1 + b_2 \ln X_2 + \dots + b_5 \ln X_5 + e \tag{4}$$

...where e is the vector of random errors with a multivariate normal distribution, whose components are uncorrelated (4).

A significant dependence between the analyzed traits presented in Table 2 suggests that the number of variables in equation (2) is too high. Knowledge brought to the

regression equation by two significantly correlated variables is usually only slightly bigger than the knowledge contributed by one of them. In order to eliminate from equation (3) the least significant variables, stepwise backward regression was applied to determine coefficients of this equation [42]. In this method formula (3), containing all independent variables, was assumed as the initial model and values of two significance levels were established for the F-Fischer's statistics: p_1 to introduce variables into the model and p_2 to eliminate variables from model ($p_1 \leq p_2$).

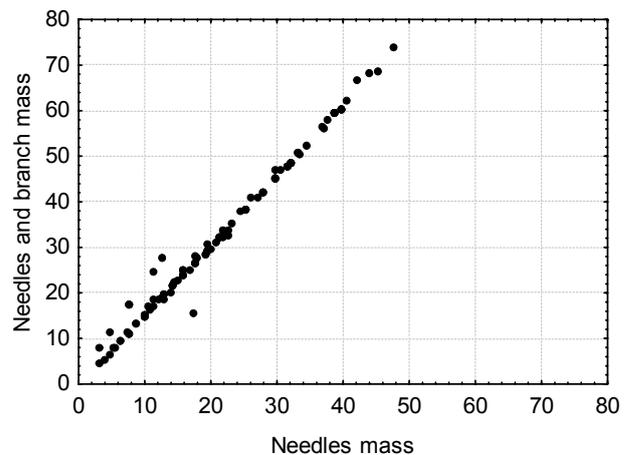


Fig. 3. Weight of needles and branches versus needle weight.

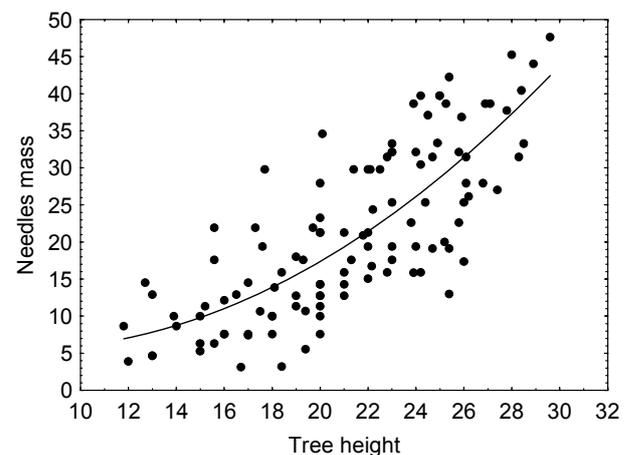


Fig. 4. Needle weight versus tree height.

Table 3. Results of analysis of covariance with Kraft's classes as a factor and *tree height* as a concomitant variable.

	Sums Squares	Degrees of freedom	Mean Squares	F	p
General mean	50,570.11	1	50,570.11	694.8278	0.000000
Kraft's classes	5,956.29	2	2,978.15	40.9194	0.000000
	8,078.67	111	72.78		

In the first step values of F statistic were calculated as well as the corresponding significance levels p for each independent variable, and then this variable was eliminated from the model, for which the calculated significance level exceeded the value p_2 . In successive steps the procedure of eliminating a variable from the model was repeated. Next, each of the variables removed in previous steps was added to the model and the one for which the calculated significance level was lower than p_1 was left out. The procedure was completed when no more variables could be eliminated or added to the model. In order to verify the adequacy of such a created model the analysis of residuals was performed.

All analyses were conducted using the STATISTICA 8.0 package.

Results

In the first stage of analysis of data for the estimation of parameters in model (3) for all trees, irrespective of their Kraft's class, stepwise backward regression was applied. The following model was produced:

$$\ln(Y) = -2.41885 + 2.22303 \ln(X_1) - 0.12809 \ln(X_3) + 0.09613 \ln(X_4) - 0.40768 \ln(X_5) \quad (5)$$

Multiple coefficient of determination in this model was very high, amounting to $R^2=0.973$, and the standard error of estimation was 0.1053. Analysis of residuals for this model showed that it is unjustified to refute the assumption on the consistency of their probability distribution with the normal distribution (the Kolmogorow Smirnow test). Basic statistics of residuals are as follows: minimum = -0.27, mean = 0.0, maximum = 0.26, and standard deviation $\sigma=0.1034$. However, the list of residues, i.e. deviations from model (5) in relation to $\ln(\text{needle weight})$ (Fig. 5), shows that this model is well-fitted to observations for trees with a high needle weight, while it is not so well-fitted for trees with a low needle weight. Fig. 6 shows that a low needle weight was recorded primarily for codominant trees (Kraft's class III), while a higher weight was found for predominant and dominant trees (Kraft's classes I and II). This suggests that social classes of tree position may have an effect on the course of the investigated variation.

In order to verify the hypothesis, it was first checked whether after the elimination of the effect of the most important trait determining the affiliation of a given tree to a Kraft's class, (i.e. *tree height* and *needle weight*), individ-

ual classes would differ significantly. A lack of significant differences would indicate that the same model of estimating foliage biomass (*needle weight*) might be applied for all trees. For this purpose the analysis of covariance was performed for the uni-factorial experiment with a concomitant variable [44]. The factor comprised Kraft's classes and *tree height* was the concomitant variable. Results of the analysis of covariance are given in Table 3, while means and standard deviations for *needle weight* in individual classes are given in Fig. 6.

Needle weight in individual Kraft's classes differed significantly, with the highest mean needle weight recorded for trees in class I, and the lowest in class III. Thus, in order to provide a higher precision, for each Kraft's class a sepa-

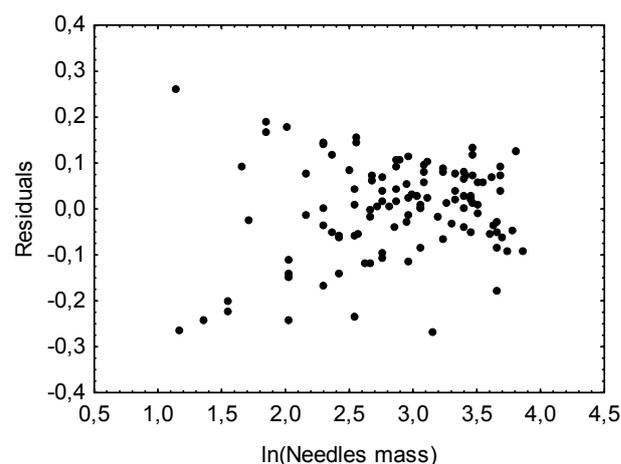


Fig. 5. Residuals of the model (4).

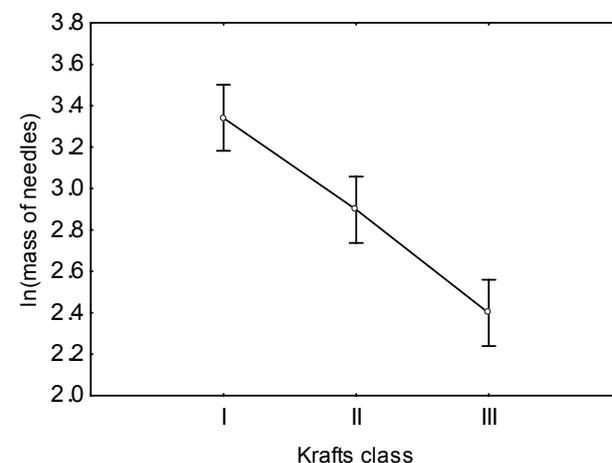


Fig. 6. Means and standard deviations of Needle weight in particular Kraft's classes.

Table 4. Parameters and multiple determination coefficients of model (3) in individual Kraft's classes.

Kraft's class	$\ln b_0$	X_1	X_2	X_3	X_4	X_5	R^2	Standard error of estimation	Residuals		
									min	max	σ
I	-1.84186	1.88891	0	0	0	-0.27843	0.940	0.1001	-0.27	0.14	0.0973
II	-2.44707	2.46885	0	0	0	-0.58429	0.965	0.0996	-0.28	0.19	0.0969
III	-2.22473	2.16348	0.38818	0	0.27048	-0.78965	0.973	0.0949	-0.22	0.18	0.0897

rate regression model was created for *needle weight*, depending on the other traits of trees. Assumptions on the independence (non-correlation) of observations are satisfied due to the manner of data collection. In individual Kraft's classes each tree came from a different position.

Values of parameters in model (3), values of multiple coefficients of determination in individual classes and results of residual analysis are presented in Table 4. Plots of residues depending on the observed values are shown in Fig. 7. It may be observed that models for *needle weight* derived separately for each Kraft's class are characterized by a much better fit to observations than model (5) for all classes jointly. The standard error of estimation and standard errors of residuals are in each of them smaller than in model (5). Plots of residuals depending on observed values (Fig. 7) indicate that in contrast to model (5), the variance of residuals does not depend on needle weight. Graphs for observed values in relation to predicted values also show a higher accuracy of models derived for individual Kraft's classes.

It was observed that in Kraft's classes I and II only two independent variables $\ln(\text{DBH})$ and $\ln(\text{tree age})$ remained in the model, but still this model is very well-fitted to the observations. In turn, for trees of Kraft's class III in model (3), apart from $\ln(\text{DBH})$ and $\ln(\text{tree age})$, similarly as in model (5) we need to include also $\ln(\text{tree height})$ and $\ln(\text{crown length})$.

The estimation of parameters of the model (3) for each Kraft's class was performed by nonlinear least squares Levenberg – Marquardt method, having regard to the model only those variables, which in Table 4 correspond to nonzero coefficients. Then we obtain:

for Kraft's class I

$$Y = 0.207414 X_1^{1.813457} X_5^{-0.279572} \quad R^2 = 0.97 \quad (6)$$

for Kraft's class II

$$Y = 0.096651 X_1^{2.43049} X_5^{-0.580382} \quad R^2 = 0.98 \quad (7)$$

for Kraft's class III

$$Y = 0.101226 X_1^{2.397642} X_2^{0.053893} X_4^{0.164082} X_5^{-0.66241} \quad R^2 = 0.98 \quad (8)$$

...where: X_1 – DBH, X_2 – tree height, X_3 – crown diameter, X_4 – crown length, X_5 – tree age.

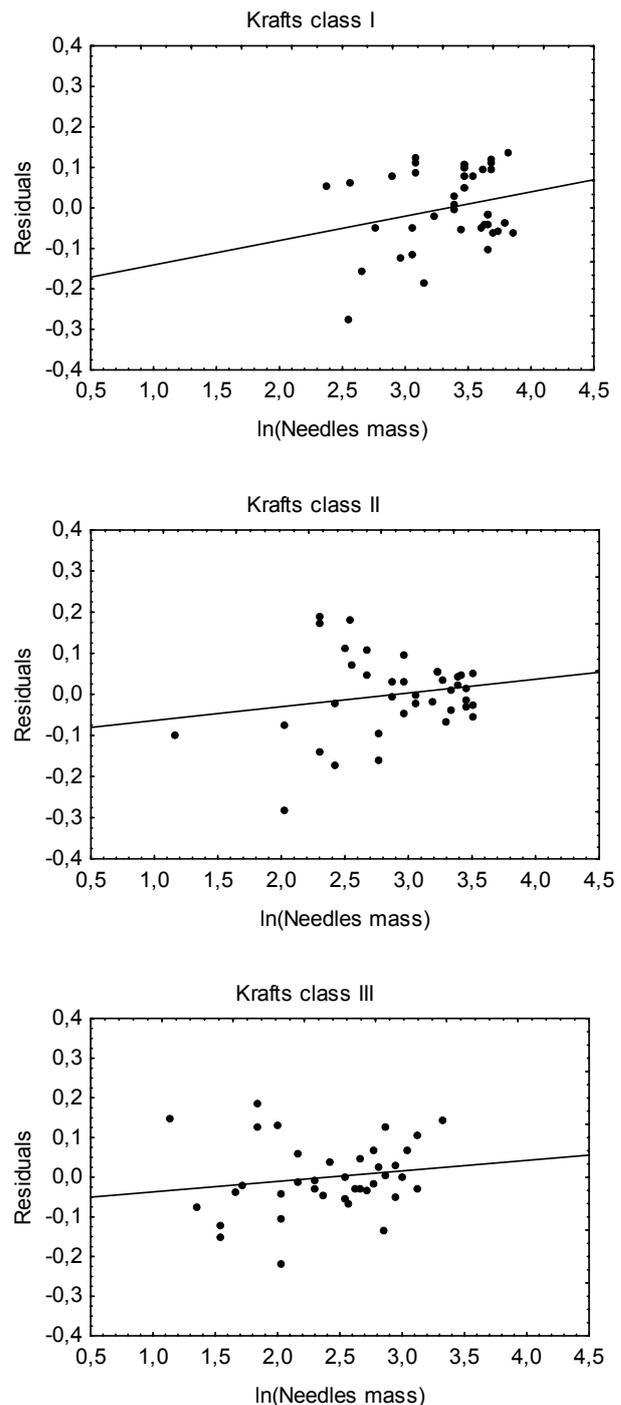


Fig. 7. Residues in individual Kraft's classes.

It may be observed that for all trees an increase in DBH (X_1) results in increased *needle weight*, whereas an older *tree age* (X_2) causes a reduction of *needle weight*.

In order to predict values of the *weight of needles and branches*, parameters of model (1) were estimated for each Kraft's class. The following equations were generated:

for Kraft's class I

$$Z = 0.887407 + 1.505528 Y \quad (9)$$

for Kraft's class II

$$Z = 1.838742 + 0.993 Y \quad (10)$$

for Kraft's class III

$$Z = 1.512152 + 0.967 Y \quad (11)$$

...where Z denotes the *weight of needles and branches*, while Y denotes *needle weight*.

Discussion

Attempts to estimate carbon sequestration undertaken worldwide may to a considerable degree be facilitated by the application, on the inventoried sample plots, equations of biomass using independent variables being biometric characters of trees [3].

Most studies concerning equations used to predict foliage biomass for whole stands are based on two or one biometric variables, i.e. breast height diameter and height of trees. Taking into consideration the occurrence of pine in Europe and the related high variation the use of only one independent variable in equations at the maintenance of relatively high accuracy seems justified only at the local scale, which is partly confirmed by investigations conducted by Muukkonen and Mäkipää [26].

Direct measurement of foliage biomass is possible only on felled trees and requires very high outlays of labour and resources. In contrast, indirect methods, as a result of high variation in Scots pine, are typically burdened with error and thus they do not ensure high accuracy. The volume (weight) of assimilatory organs of standing trees may be estimated only as approximates [35].

A majority of allometric equations found in literature concern dry biomass of the crown. The authors managed to find very few models predicting fresh needle mass of twigs with needles in pine trees.

Such an attempt was undertaken by Lemke [34, 35, 45], and on the basis of analyses he developed simple models for the estimation of fresh needle weight in Scots pine growing in central western Poland. That author proposed different equations depending on age class of the stand, while to predict fresh biomass of needles and twigs covered with needles he used breast height diameter of trees as an independent variable:

$$y = a + bx_{1,3} + cx_{1,3}^2$$

$$y = a + bx_{1,3}$$

Similar equations were proposed by Socha and Wężyk [29]:

$$y = ax_{1,3}^b$$

In contrast, Turski et al. [36] as a basic model for the estimation of biomass of fresh twigs with needles used an equation of the following form:

$$y = 0.67705w^{0.537}d_{1,3}^{3.192}h^{-1.384}$$

...where w – age of trees, $d_{1,3}$ – breast height diameter, h – tree height.

For the purpose of practical estimation of fresh needle biomass and biomass of twigs with needles for selected groups of trees and whole stands, it was attempted in this study to develop more complex allometric models, at the same being more accurate, which takes into consideration growth dynamics of trees in the stand. This growth is reflected in the position and structure of the crown, which manifests competition between specimens and variation in the stand in terms of social classes of tree position [37].

When selecting an optimal equation for the estimation of biomass it is necessary first to take into consideration many independent variables that may affect its accuracy. Based on measurable characteristics such as diameter at breast height, tree height, and age it is possible to determine the model of biomass with relatively high accuracy only for a single tree [31, 36]. In practice, foliage biomass is rarely estimated for individual trees, since the potential for biomass inventory for whole stands with relatively high accuracy seems much more important [46, 29].

Models of foliage biomass proposed in this study refer to specific social classes of tree position in the stand and thanks to this fact considerably improve the accuracy of biomass prediction in relation to models taking into consideration the stand as a whole (i.e. a set of individual specimens with varied traits). Accuracy of prediction referring to the entire stand (Fig. 8a) is much lower than in models taking into consideration its social variation (Figs. 8b, 8c, 8d). Thus it may be assumed that the division of the stand into Kraft's classes considerably increased the prediction potential of equations and affected their accuracy.

Models were developed in such a way that they facilitated the estimation of foliage biomass on the basis of easily measurable biometric traits of trees (6, 7, 8) and the estimation of biomass of needles alone, when the weight of needles together with twigs was the independent variable (9, 10, 11).

Since Cienciala et al. [31] in the determination of biomass of live branches together with needles recommended the use of as many as four variables (i.e. diameter at breast height, tree height, crown length and age of trees) at the first stage of work on the construction of models all measured variables were taken into consideration (i.e. tree height, length and diameter of the crown as well as tree age). However, it turned out that in case of predominant trees (Kraft's class I) and dominant trees (Kraft's class II) only two variables – breast height and tree age – are sufficient for foliage biomass prediction. The use of diameter at breast

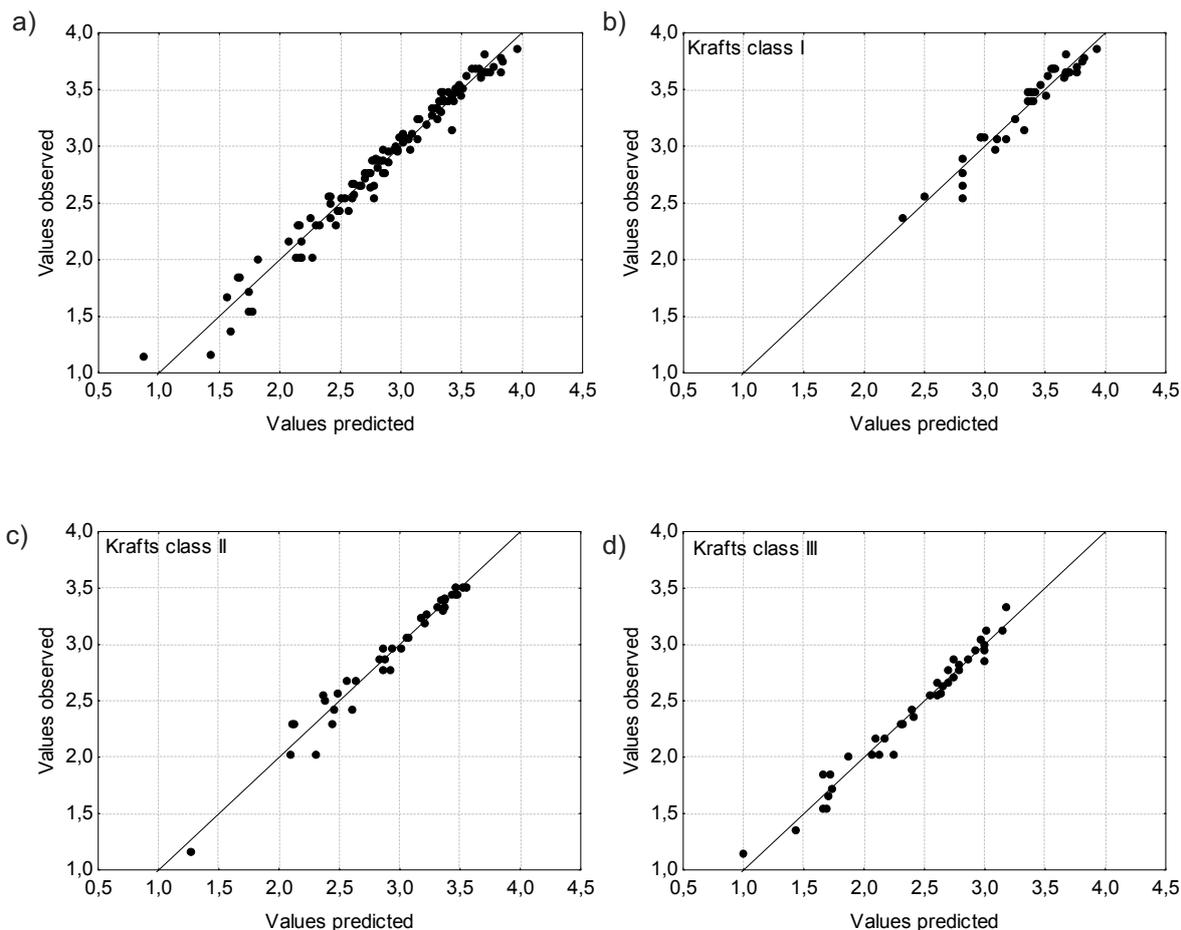


Fig. 8. a) Accuracy of foliage biomass prediction for all observations. b) Accuracy of foliage biomass prediction for observations in Kraft's class I. c) Accuracy of foliage biomass prediction for observations in Kraft's class II. d) Accuracy of foliage biomass prediction for observations in Kraft's class III.

height and tree age in the developed models is consistent with studies conducted by Curiel Yuste et al. [46] and Zianis et al. [28].

In turn, for the determination of foliage biomass in codominant trees (Kraft's class III), in order to ensure similar accuracy as that for the other social classes of tree position in the stand it is necessary to have data on tree height (X_2) and crown length (X_4). This may result from the fact that trees included in the codominant layer (Kraft's class III) comprise typically the most numerous group in the stand [47], thus the layer exhibiting the highest variability.

Taking advantage of the fact that the dependence between needle weight and weight of twigs covered with fresh needles is practically rectilinear, prediction of biomass was conducted for foliage together with young twigs. The obtained equations (9, 10, 11), after transformation, facilitate an accurate estimation of foliage biomass on the basis of the weight of needles with young twigs, which may considerably reduce labour consumption of field work, at the same time ensuring high accuracy.

In the course of the analysis of recorded results it was observed that age of trees is strongly associated with foliage biomass. Similar conclusions were drawn by Socha and Wężyk [29]. They stated that in comparison to diameter at

breast height and height of trees, age seems a better predictor of foliage biomass. This most probably results from the fact that all biometric traits of trees (including crown biomass) are functions of age. Moreover, architecture of trees and related crown weight will be dependent on the hydraulic system of plants and biomechanical limitations. These limitations most probably consist in an appropriate distribution of weight at a proper scale of anatomical elements. Thus for the estimation of biomass it seems justified to use, apart from age, also diameter at breast height, changing in the course of life of a tree, which directly results for the functions served by the stem.

Such a strong relationship of the assimilatory apparatus with diameter at breast height and age of trees may also be justified by the Pipe Model Theory [14, 15] which searches for a close relationship between the hydraulically conductive part of the stem and the volume of the assimilatory apparatus [18].

Maintenance of this equilibrium requires considerable adaptability from woody plants. It results from investigations conducted by Jelonek et al. [48, 49] that estimation of foliage biomass on the basis of the conductive area of xylem (sapwood) should be performed at the division of the main stand into social classes of tree position. In certain cases requiring high accuracy, this may weigh in favour of

the necessity to determine biomass separately for characteristic groups of trees, exhibiting a specific system of dependencies between the set of physiological functions, biomechanical limitations, and plant architecture.

In view of the recorded results, authors also confirmed an opinion expressed by Zianis et al. [28], who stated that when the number of mean sample trees seems insufficient for the construction of accurate equations or when stands are characterized by high variability, it is justified to apply several equations in order to provide a possibly more accurate prediction of traits.

The potential for estimation of foliage biomass taking into consideration social classes of tree position in the community seems important due to the uneven proportions of individual classes at different development phases of the stand, and the anthropogenic factor referring to silvicultural measures. Development of separate models may thus significantly affect:

- 1) the accuracy of equations (models), and
- 2) provide foresters with a tool for a more thorough analysis of matter cycle in production forest ecosystems.

However, it needs to be remembered that a wider application of equations developed in this study requires their confirmation by similar investigations conducted on pine from different regions of Europe, grown under diverse growth and development conditions.

Conclusions

1. Results indicate that it is not possible to apply one model to all trees in the stand. If in case of predominant and dominant trees for a satisfactorily accurate estimation of needle weight it is enough to use observations of two traits (X_1 , X_5), then for codominant trees it is necessary to know also the values of two other traits, i.e. tree height (X_2) and crown length (X_4).
2. The application of easily measurable biometric tree traits, as well as known tree age and social class of tree position in the stand, are good foundations for the development of empirical equations useful in the estimation of foliage biomass in Scots pine. However, such equations are burdened with an error of $(100 - R^2)\%$, resulting from high variation in this species and its varied individual adaptability.
3. Allometric equations developed on the basis of conducted studies may be used to model foliage biomass of entire stands as well as individual social classes of tree position. Thus they may be used in ecological studies and may prove helpful in studies on carbon sequestration. However, it should be remembered that the proposed equations need to be verified for other positions of this species.

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