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**Site-effects on biomass allometric models for early growth plantations of Norway spruce (*Picea abies* (L.) Karst.)**

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**Abstract:**

Although it is commonly assumed that biomass allometric models are site specific, evaluations of site-effects are rarely undertaken. In this paper we develop biomass-allometric models to determine site influences. This study is based on data from 240 Norway spruce trees (*Picea abies* (L.) Karst.), growing in 24 early-growth plantations. A multilevel modelling approach was adopted and intraclass correlation was used to evaluate site effects. Results indicated that biomass allometric models were highly specific to sites and that, depending on the biomass component and the type of predictor adopted, some 33% and 86% of overall model variance could be attributed to forest stand effects. The remaining variance was attributable within stand variability. Stem biomass was the most site-specific biomass component whereas branch biomass was the least influenced by site effects. Diameter at collar height (D) was less site-specific than height (H) in predicting biomass. Using D and H within the same model as distinct predictors, although improving the model fit, increased the model site-specificity. However, when D and H were combined in one predictor expression (i.e.  $D^2H$ ), this reduced model site specificity, despite requiring fewer parameters than other models. This also compensated for undesirable collinearity effects amongst predictor variables. Furthermore, for the sampled diameter range, the site-specificity was mainly driven by biomass allocation pattern (to branches, needles and roots). The considerable between site variability of allometric relationships suggests that consideration of stand effects is essential for the robust prediction of biomass.

**Keywords:** site-specific biomass model; tree components; allometric equation; tree diameter; tree height; intraspecific variability

## 1. Introduction

Forests play an important role in the global carbon cycle [1,2], and it is well established that increasing forest area can immediately influence rates of carbon sequestration by increasing capacity for carbon dioxide uptake through the accumulation of new plant biomass [3].

European forests have expanded in area by 21.2 million hectares since 1990, increasing at a rate of 0.85% per year, as a result of afforestation and natural regeneration [4]. However, despite apparent increase in forest area, other research suggests that the European forest carbon-sink may be at the point of saturation [5], and this is believed to be due to decrease in stem volume increment rate. An increased rate of afforestation is therefore needed if earlier net gains in the forest carbon sink are to be maintained [5]. As one of the most extensively grown and economically important species in Europe, Norway spruce (*Picea abies* [L.] Karst.), it is widely used in afforestation schemes for production, protection and erosion control [6,7].

Biomass allometric models are commonly used to estimate carbon accumulation in forests [1,8]. Despite recent advances in remote sensing and other survey instruments, allometric models remain fundamental to biomass prediction and for calibrating emerging technologies and new approaches to estimation [9–11]. Biomass allometric models are regression models that use tree diameter and/or height to predict biomass [12,13], and due to the importance of Norway spruce throughout Europe, there is considerable interest in their application to this species [14–20].

Developing generalized biomass allometric models with high prediction accuracy and precision is widely regarded to be a challenging undertaking [21–24]. Among other refinements wood density has been used to improve biomass prediction [24,25], as it is well known that wood density is highly heritable [26]. This is consistent with a view that interspecific genetic variability is related to, and can be explained by wood density variation. Height-diameter (H–D) ratio is also used to improve prediction accuracy of allometric models [21,23,24]. As each forest site has particular environmental conditions, and because it is widely understood that H–D ratio is in part affected by environmental conditions [27–29], it follows that the inclusion of height (together with diameter) in allometric models may explain the site effect. However, wood density and height has been shown to make relatively little contribution to improving prediction of biomass at particular forest stands [30]. It is therefore unlikely that either accurate generalized allometric models will be developed or predictions will improve without first understanding the factors that drive variation in such models and how the variance is partitioned within and between stands.

Because site-specificity is an important constraint in developing accurate generalized allometric models, the development of new allometric models often involves an investment of

substantial resources to record and model biomass at individual sites. Investigating the site-specificity of allometric models is potentially useful in many ways, such as: (i) identifying the conditions under which it is fact possible to apply any one given allometric model to other forest stands; (ii) guiding the selection of statistical means and modelling algorithms appropriate to circumstances. Because range of covariates (i.e. diameter at breast height, DBH; tree height) is often limited within a forest stand, researchers commonly sample trees from more than one forest stand. Sampling more than one tree from each of multiple stands, results in clustered data. The decision to allow or adjust for a clustering effect (of forest stand on allometric model), is determined by the extent to which variance is attributable to a forest stand effect. If there is no discernible site-specificity effect, then it is acceptable to apply methods that disregard clustering. Conversely, disregarding site-specificity/forest-stand effects when they are apparent is likely to bias standard errors with downstream consequences for model uncertainty and hypothesis testing.

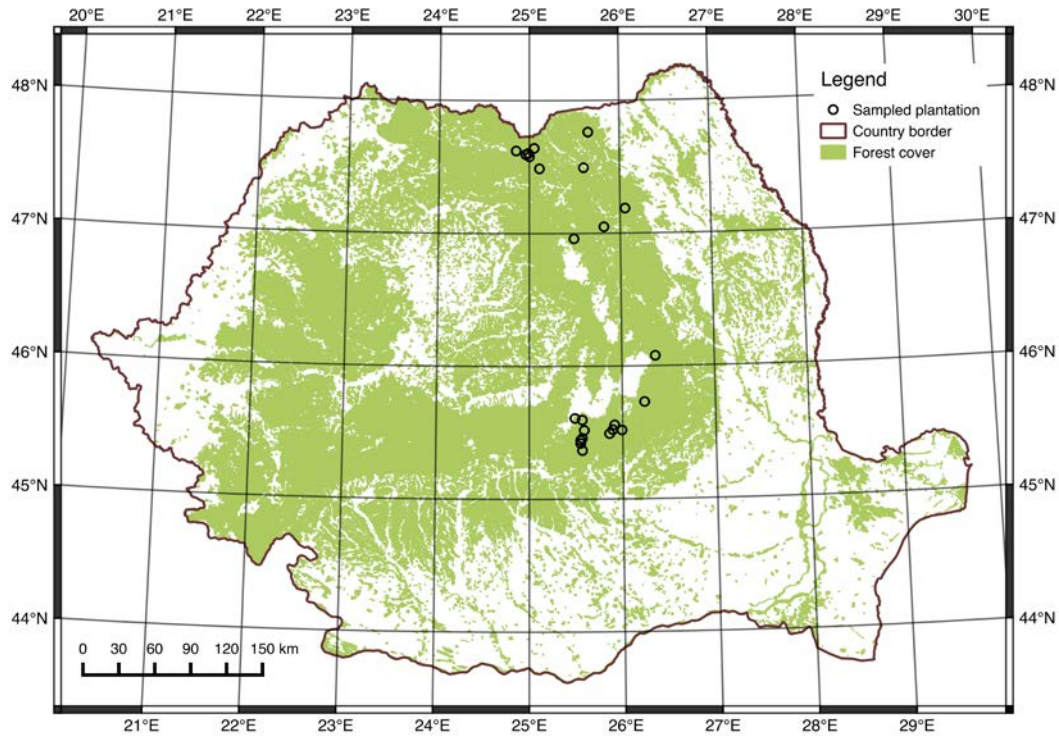
The aim of this paper was to develop biomass allometric models for Norway spruce trees based on data sampled from multiple forest stands and to evaluate site effects on allometric models, with a view to determining the following:

- i) the extent of site-specificity in biomass allometric models;
- ii) how site-specificity varies with each of the biomass components being predicted;
- iii) how site-specificity varies between individual predictors/indicators;
- iv) the underlying causes and possible consequences of site-specificity in allometric models.

## **2. Material and methods**

### **2.1. Study sites**

The study area, in Eastern Carpathians of Romania (Fig. 1), extends some 330 km between southerly and northerly latitudinal extremes of 45.44°N and 47.77°N respectively. Sample site elevations were between 641 and 1543 m above sea level, with mean annual temperature ranging from 2.6 to 7.3 °C and mean annual precipitation from 643 to 933 mm. Data was collected from 24 randomly selected plantations between 2009 and 2010. Ages of sampled trees ranged from 4 to 15 years (Table 1). Species composition was entirely Norway spruce, planted at an initial stand density of 5,000 saplings per hectare (on a grid of 2.0 m × 1.0 m). However, due to mortality, stand density at the time of sampling was found to be between 3100 and 4800 trees per hectare. Sampled stands had not been subject to thinning or other forest management intervention to reduce stocking levels.



**Fig. 1.** Locations of sampled plantations in the Eastern Carpathians of Romania.

**Table 1**

Summary characteristics of sampled plantations

Plantation number	Aspect	Slope (°)	Altitude (m)	Stand density <sup>1</sup>	Age of trees (years)
1	South-East	5.7	1107	4800	4
2	East	14.0	1371	4750	6
3	South-West	2.9	1024	4700	6
4	South-East	38.7	1048	4750	7
5	East	26.6	818	3750	7
6	North	8.5	706	4050	7
7	North	9.1	1350	3050	7
8	North-East	17.7	989	3300	8
9	North	1.1	1094	4600	8
10	North-East	2.3	937	4800	8
11	South	12.9	999	4700	8
12	West	1.7	941	4500	8
13	South	15.6	1004	3950	9
14	North-West	6.8	641	4800	9
15	South-West	8.5	1142	4750	9
16	West	33.0	742	4700	11
17	North-West	5.7	1114	3850	11
18	South-West	11.3	961	3400	11
19	South	42.0	1563	3100	12
20	South	11.3	1122	4300	12
21	South-West	1.7	688	4750	12
22	North-East	16.7	901	4400	13
23	East	2.9	942	3550	13
24	South-West	2.9	1085	4550	15

<sup>1</sup> number of trees per hectare.

## 2.2. Biomass measurements

In each plantation, a 200 m<sup>2</sup> sample plot was selected as being representative of the overall conditions of the immediate forest stand. Root collar diameter and height measurements were taken for all trees and used to calculate the ‘mean height’ (i.e. the height of tree of mean collar area; this is analogous to mean basal area but measured at collar instead of breast height). At each stand, ten trees with dimensions that of ‘mean height’ were selected and destructively sampled for biomass measurements that also included roots. A total of 240 trees were sampled, with root collar diameter (referred hereafter as diameter - D) ranging from 0.6 to 10.0 cm, and height (H) between 53.0 and 552.0 cm. This dataset, therefore, satisfies the minimum requirement that samples should represent a range of one order of magnitude to be useful for allometric studies [31]. Root collar diameter was used instead of diameter at breast height because approximately 50% of sampled trees were less than 1.3 m in height. For each sampled tree total biomass was divided in four categories (stem - ST, branches - BR, needles - ND and roots - RT), which was oven dried at 80°C to constant weight, and then electronically weighed to a precision of ±0.1 g.

## 2.3. Statistical analysis

All variables were expressed as natural log transformations (ln) to ensure a linear relationship between variables and to correct for heteroskedasticity and thereby meet assumptions for purposes of applying a Random Intercept Model. Dependent variables were: ln(TB), ln total biomass; ln(AB), ln aboveground biomass (calculated as the sum of stem, branch and needle biomass); ln(ST), ln stem biomass; ln(BR), ln branch biomass; ln(ND), ln needle biomass; and ln(RT), ln root biomass. Independent variables were: ln(D), ln root collar diameter; ln(H), ln height; and ln(D<sup>2</sup>H), the natural logarithm of the product diameter squared and height.

A multilevel modelling approach was used to differentiate the effects of between and within stand variance. The study was designed so that a Random Intercept Model (RIM) could be applied. Within stands, sampled trees were of similar height, maximizing therefore the likelihood of observing the entire range of height-diameter variability (within-stand variability). The RIM allowed intercepts to vary with the forest stand, whereas the slope is fixed for all stands. The distribution of intercepts is assumed to be normal with the mean value  $\alpha$  and standard deviation  $\sigma_\alpha$ . The allometric models tested for ln biomass (ln(B)), in their log-linear form, were:

$$\ln(B)_{ij} = \alpha + \beta \times \ln(D)_{ij} + \epsilon_{ij} + u_i \quad (\text{Eq. 1})$$

$$\ln(B)_{ij} = \alpha + \beta \times \ln(H)_{ij} + \epsilon_{ij} + u_i \quad (\text{Eq. 2})$$

$$\ln(B)_{ij} = \alpha + \beta \times \ln(D^2H)_{ij} + \epsilon_{ij} + u_i \quad (\text{Eq. 3})$$

$$\ln(B)_{ij} = \alpha + \beta \times \ln(D)_{ij} + \gamma \times \ln(H)_{ij} + \epsilon_{ij} + u_i \quad (\text{Eq. 4})$$

where  $\beta$  and  $\gamma$  are the fixed slopes;  $\alpha$  is the fixed part of the intercept (the overall intercept);  $u_i$  is the random error component of the intercept,  $u_i \sim N(0, \sigma_\alpha^2)$ , and represents the error component at level 2 (at forest stand level);  $\epsilon_{ij}$  is the random residual error,  $\epsilon_{ij} \sim N(0, \sigma_\epsilon^2)$ ;  $j = 1 \dots N$  (number of stands);  $i = 1 \dots n_j$  (the trees within stand).

Furthermore, the ratios of tree component categories were modelled as:

$$R_{ij} = \alpha + u_i + \epsilon_{ij} \quad (\text{Eq. 5})$$

Where R is the dependent variable and is represented by the proportions of tree components (i.e. Root-to-Shoot ratio calculated as RT/AB; and comparable treatments for ST/TB, BR/TB, ND/TB and RT/TB). The parameters may be interpreted similarly to those presented in Eqs. 1-4. To find if R was significantly influenced by age, the following model was used:

$$R_{ij} = \alpha + \beta \times \text{Age}_{ij} + \epsilon_{ij} + u_i \quad (\text{Eq. 6})$$

The use of multilevel model for assessing the effect of age (Eq. 6) is justified by the need to correct  $p$ -values for the ‘nuisance effect’ of data clustering caused by greater homogeneity of trees within stands than between trees in the overall sample.

### 2.3.1. Intraclass correlation coefficient (ICC)

ICC expresses the proportion of total model variance attributable to stand effects:

$$ICC = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\epsilon^2} \quad (\text{Eq. 7})$$

where  $\sigma_\alpha^2$  is the variance of the intercept ( $\sigma_\alpha$  is the random effect of the intercept) due to differences between forest stands and  $\sigma_\epsilon^2$  is the residual variance ( $\sigma_\epsilon$  is residual random effect), due to tree differences within stands. ICC was used to evaluate the site-specificity of models.

### 2.3.2. Variance inflation factor (VIF)

The VIF was calculated to assess the collinearity of  $\ln(D)$  and  $\ln(H)$  in predicting biomass, following Zuur et al. [32] R script.

### 2.3.3. Akaike Information Criterion (AIC)

AIC was used for model selection:

$$AIC = 2k - 2\ln(L) \quad (\text{Eq. 8})$$

where  $k$  is the number of model parameters,  $L$  is the maximum likelihood estimation.

The data was analysed using R version 3.3.0, package ‘nlme’ (Linear and Nonlinear Mixed Effects Models) [33].



#### 2.4. How to use the models for prediction of biomass?

To use model for prediction, a back transformation of linear models is required. Therefore, the biomass ( $B$ , expressed in grams) can be predicted by independent variable ( $P$ , which could be  $D$  – expressed in cm,  $H$  – in cm or  $D^2H$  – in  $\text{cm}^3$ ) using the following equation:

$$B = e^\alpha \times P^\beta \times \lambda \quad (\text{Eq. 9})$$

Where  $\alpha$  and  $\beta$  are the coefficients derived from Eqs. 1-3. However, when two independent variables are used (Eq. 4) the back transformed equation is:

$$B = e^\alpha \times D^\beta \times H^\gamma \times \lambda \quad (\text{Eq. 10})$$

Because in logarithmic scale the distribution of errors is different to that in arithmetic scale, the back transformation requires a bias correction to the intercept:  $\lambda = \exp(RSE^2/2)$ , where  $RSE$  is the residual standard error [34,35]. The standard errors computed in logarithmic scale should not be used as they are, in the arithmetic scale (back transformed). Instead, the arithmetic 95% confidence interval can be computed by back transformation of logarithmic 95% confidence interval limits (e.g.  $e^{(\alpha \pm 1.96SE)}$ , not  $e^\alpha \pm e^{1.96SE}$ ).

#### 2.5. The impact of site-effects on biomass prediction at stand level

To assess site-effects on biomass prediction, the total biomass stock ( $\text{Mg ha}^{-1}$ ) for each plantation, was calculated by measuring  $D$  and  $H$  in each of the  $200 \text{ m}^2$  sample plots, then by applying (i) the generic models that are based on a single intercept value ( $\alpha$ , in Eqs. 1-4) derived from all intercepts (one for each plantation); and (ii) the specific models based on specific values of the intercept for each plantation. In summary, the specific models are tailored for each plantation, however, the slope is common to all plantations. Furthermore, the percent difference ( $\text{Diff} (\%)$ ) between these two stocks was calculated:

$$\text{Diff} (\%) = \frac{\hat{B}_g - \hat{B}_s}{\hat{B}_s} \times 100 \quad (\text{Eq. 11})$$

Where  $\hat{B}_g$  is the predicted biomass using the generic models (i.e. (i) above) and  $\hat{B}_s$  is the predicted biomass using specific models (i.e. (ii) above).

### 3. Results

The parameters of the multi-site allometric models are presented in Table 2. The ICC (Eq. 7) values for site-specificity of allometric models ranged between 0.3273 and 0.8574 (Table 2). Forest stand effects therefore accounted for between 33% and 86% of total model variance, the remained being attributable to within stand tree effects. ICC values were greater for those models that included height as a predictor. Diameter was therefore less site-specific than height

in predicting biomass. In one model (Eq. 4) the use of both independent variables site-specificity was greater than when using D alone (Eq. 1), but less than when using H alone (Eq. 2) to predict biomass. However, combining both predictors (Eq. 3), resulted in a reduced ICC, compared to Eq. 4. For one response variable (i.e. stem biomass), the ICC value was even less than that obtained for Eq. 1. Stem biomass demonstrated the greatest site-specificity among biomass components, whereas branch biomass was the least site-specific.

**Table 2**

Biomass Allometric Models. Notes: (i) dependent variables were  $\ln(\text{TB})$ ,  $\ln(\text{AB})$ ,  $\ln(\text{ST})$ ,  $\ln(\text{BR})$ ,  $\ln(\text{ND})$  and  $\ln(\text{RT})$ , and predictors were  $\ln(\text{D})$  (Eq. 1),  $\ln(\text{H})$  (Eq. 2),  $\ln(\text{D}^2\text{H})$  (Eq. 3) and  $\ln(\text{D})+\ln(\text{H})$  (Eq. 4); (ii) regression parameters are presented with their standard errors; (iii) each model is presented with the variance of the intercept, total model variance, Intraclass Correlation Coefficient (ICC, Eq. 7), Akaike Information Criterion (AIC, Eq. 8) and residual standard error (RSE).

Dependent variable	Predictor	Eq.	$\alpha$ (SE)	$\beta$ (SE)	$\gamma$ (SE)	Intercept variance	Total variance	ICC	AIC	RSE
$\ln(\text{TB})$	$\ln(\text{D})$	1	4.0980 (0.0491)	2.2778 (0.0376)	N.A.	0.0182	0.0412	0.4405	-155.2	0.1519
	$\ln(\text{H})$	2	-5.8505 (0.5590)	2.4558 (0.1101)	N.A.	0.1421	0.1658	0.8574	-106.8	0.1538
	$\ln(\text{D}^2\text{H})$	3	0.7644 (0.1003)	0.8035 (0.0134)	N.A.	0.0196	0.0374	0.5229	-207.3	0.1337
	$\ln(\text{D})+\ln(\text{H})$	4	-0.1377 (0.5343)	1.4115 (0.1082)	1.0239 (0.1265)	0.0263	0.0436	0.6038	-207.5	0.1314
$\ln(\text{AB})$	$\ln(\text{D})$	1	3.8371 (0.0445)	2.3264 (0.0342)	N.A.	0.0142	0.0388	0.3647	-145.3	0.1570
	$\ln(\text{H})$	2	-6.3653 (0.5597)	2.5165 (0.1103)	N.A.	0.1424	0.1663	0.8566	-105.2	0.1544
	$\ln(\text{D}^2\text{H})$	3	0.4671 (0.0969)	0.8158 (0.0129)	N.A.	0.0179	0.0366	0.4893	-199.0	0.1368
	$\ln(\text{D})+\ln(\text{H})$	4	-0.5992 (0.5405)	1.3999 (0.1097)	1.0764 (0.1280)	0.0264	0.0443	0.5964	-199.9	0.1337
$\ln(\text{ST})$	$\ln(\text{D})$	1	2.7209 (0.0487)	2.2564 (0.0371)	N.A.	0.0119	0.0233	0.5102	-213.4	0.1068
	$\ln(\text{H})$	2	-7.7002 (0.4239)	2.5454 (0.0835)	N.A.	0.0803	0.0965	0.8320	-200.9	0.1274
	$\ln(\text{D}^2\text{H})$	3	-0.6700 (0.0711)	0.8084 (0.0095)	N.A.	0.0095	0.0208	0.4543	-320.3	0.1067
	$\ln(\text{D})+\ln(\text{H})$	4	-2.4168 (0.3940)	1.2511 (0.0808)	1.2325 (0.0937)	0.0125	0.0227	0.5514	-336.7	0.1010
$\ln(\text{BR})$	$\ln(\text{D})$	1	2.3250 (0.0547)	2.5084 (0.0421)	N.A.	0.0208	0.0634	0.3273	-17.9	0.2066
	$\ln(\text{H})$	2	-8.6705 (0.6571)	2.7123 (0.1295)	N.A.	0.1904	0.2355	0.8086	38.8	0.2123
	$\ln(\text{D}^2\text{H})$	3	-1.2879 (0.1323)	0.8767 (0.0177)	N.A.	0.0332	0.0699	0.4746	-39.7	0.1916
	$\ln(\text{D})+\ln(\text{H})$	4	-1.3230 (0.7077)	1.7455 (0.1473)	0.8854 (0.1691)	0.0342	0.0710	0.4813	-38.0	0.1918
$\ln(\text{ND})$	$\ln(\text{D})$	1	3.0724 (0.0652)	2.2201 (0.0499)	N.A.	0.0321	0.0719	0.4461	-24.8	0.1996
	$\ln(\text{H})$	2	-6.6488 (0.6568)	2.3985 (0.1294)	N.A.	0.1935	0.2310	0.8376	-0.5	0.1937
	$\ln(\text{D}^2\text{H})$	3	-0.1402 (0.1544)	0.7780 (0.0206)	N.A.	0.0478	0.0817	0.5844	-49.3	0.1843
	$\ln(\text{D})+\ln(\text{H})$	4	-1.2124 (0.7657)	1.3277 (0.1530)	1.0391 (0.1805)	0.0605	0.0936	0.6462	-49.4	0.1820
$\ln(\text{RT})$	$\ln(\text{D})$	1	2.5280 (0.0723)	2.1599 (0.0553)	N.A.	0.0395	0.0878	0.4502	21.4	0.2197
	$\ln(\text{H})$	2	-6.9264 (0.5826)	2.3328 (0.1148)	N.A.	0.1443	0.1999	0.7217	78.5	0.2358
	$\ln(\text{D}^2\text{H})$	3	-0.6427 (0.1438)	0.7633 (0.0192)	N.A.	0.0389	0.0846	0.4592	11.4	0.2140
	$\ln(\text{D})+\ln(\text{H})$	4	-0.1957 (0.7718)	1.6202 (0.1615)	0.6548 (0.1847)	0.0379	0.0839	0.4513	12.6	0.2145

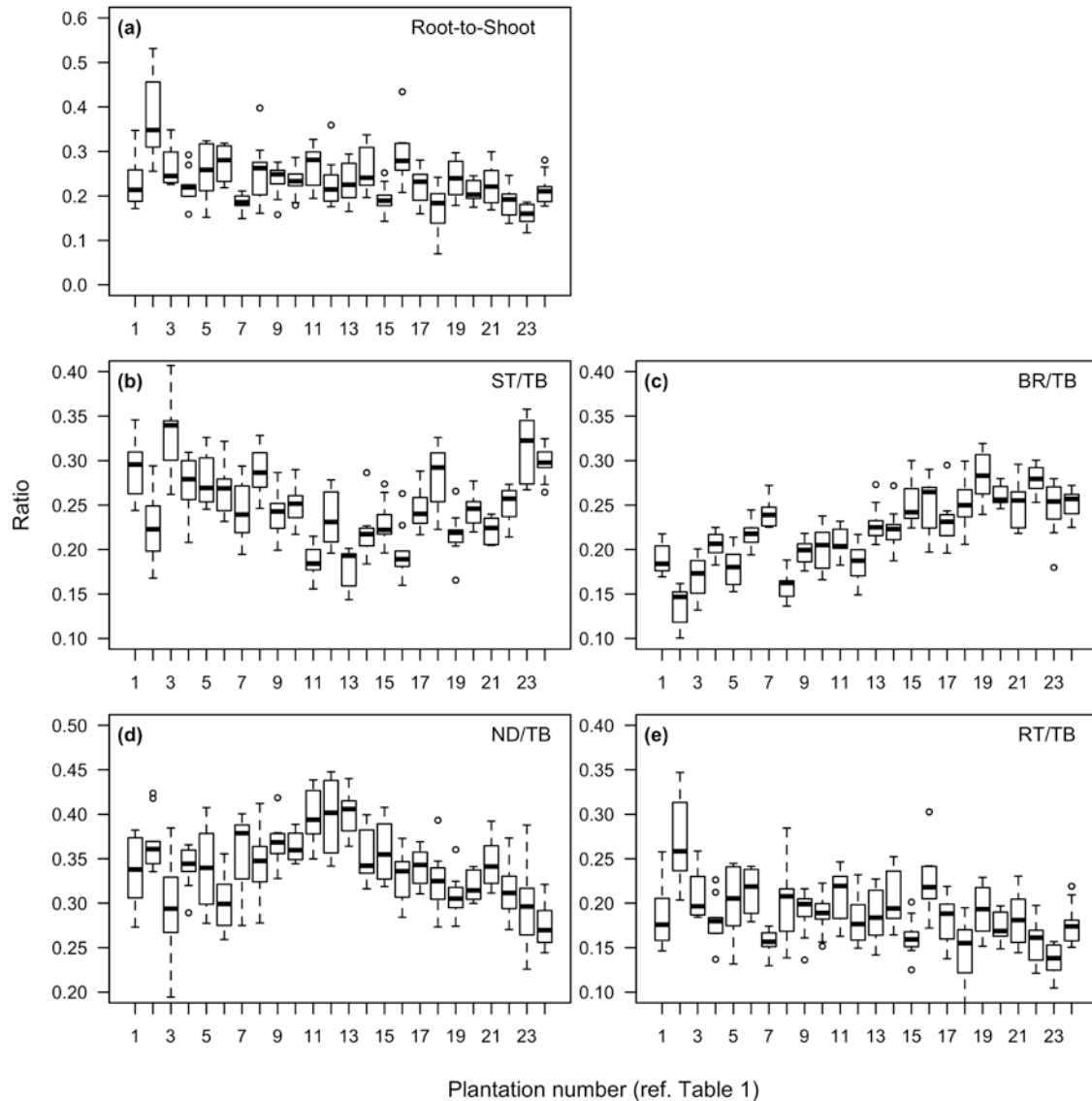
Diameter-based models produced lower AICs, and diameter was a more reliable predictor for biomass than height. Including height as an additional independent variable (Eq. 4) to predict biomass, improved prediction for all models (with reduced AIC values compared to D or H alone, see Table 2). The improvement in prediction was associated with an increase in site-specificity (indicated by greater ICC) compared to Eq. 1. However, combining D and H within a single independent variable (Eq. 3) although not reducing the AIC, resulted in a lower ICC than for Eq. 4.

The relationship between height and diameter was also highly site-specific. As much as 77% of total variance in H–D relationship was attributable to differences between forest stands and only 23% was due to individual tree within-stand variation.

Because  $\ln(H)$  and  $\ln(D)$  were highly correlated (Pearson  $r = 0.972$ ) these variables were tested for collinearity effects in Eq. 4 using variance inflation factor (VIF). VIF values obtained were 6.38 when predicting TB, 7.21 when predicting ST, 8.37 when predicting BR, 5.73 when predicting ND and 8.89 when predicting RT. These values indicate that  $\ln(H)$  and  $\ln(D)$  are highly collinear and, therefore, exhibit redundancy with respect to explaining the distribution of the dependent variable. This collinearity has resulted in increased standard errors for Eq. 4 compared to Eq. 3.

Furthermore, when testing whether the relationship between  $\ln(B)$  and  $\ln(D)$  was affected by  $\ln(H)$ , it was found that with respect to predicting TB, the interaction was found to be significant ( $p = 0.031$ ). The interaction effect was also significant for predicting AB ( $p = 0.015$ ), BR ( $p < 0.001$ ) and ND ( $p = 0.027$ ). However, the effect was not significant when predicting ST ( $p = 0.941$ ) and RT ( $p = 0.181$ ).

The proportions of tree components revealed large site effects. Root-to-shoot ratio (Fig. 2, a) greatly varied between-sites (ICC = 0.450), and significantly declined with age ( $p = 0.027$ ). Furthermore, all individual tree components, when expressed as ratios of total tree biomass (Fig. 2, b-e) were found to be highly site specific. ICC varied from 0.456 for RT/TB up to 0.755 for BR/TB. The values obtained for ST/TB and ND/TB were 0.634 and 0.494 respectively. ST/TB revealed a declining trend up to 8-9 years old trees (Fig. 2, b; plantation 12-13). This appeared to be followed by an upward recovery. Opposite trends to ST/TB were observed for ND/TB (Fig. 2, d). The proportion of branch biomass (i.e. BR/TB) increased with age ( $p < 0.001$ ). Conversely, the proportions of needle biomass and root biomass (out of total tree biomass) significantly decreased with tree age ( $p = 0.026$  and respectively  $p = 0.027$ ). As the number code for each plantation also corresponds to an age gradient (Table 1), age trends in the data are also apparent from Fig. 2.



**Fig. 2.** Boxplot comparisons of distributions for (a) Root-to-Shoot, (b) ST/TB, (c) BR/TB, (d) ND/TB and (e) RT/TB ratios within and between plantations (numbered 1–24). Notes: (i) tree ages by plantation number were: #1, 4 years; #2–3, 6 years; #4–7, 7 years; #8–12, 8 years; #13–15, 9 years; #16–18, 11 years; #19–21, 12 years; #22–23, 13 years; and #24, 15 years; (ii) Boxplot central lines represent median values, boxes represent the mid-quartile ranges; lines extend to values within upper and lower quartile limits; outliers beyond the interquartile range are represented as individual points.

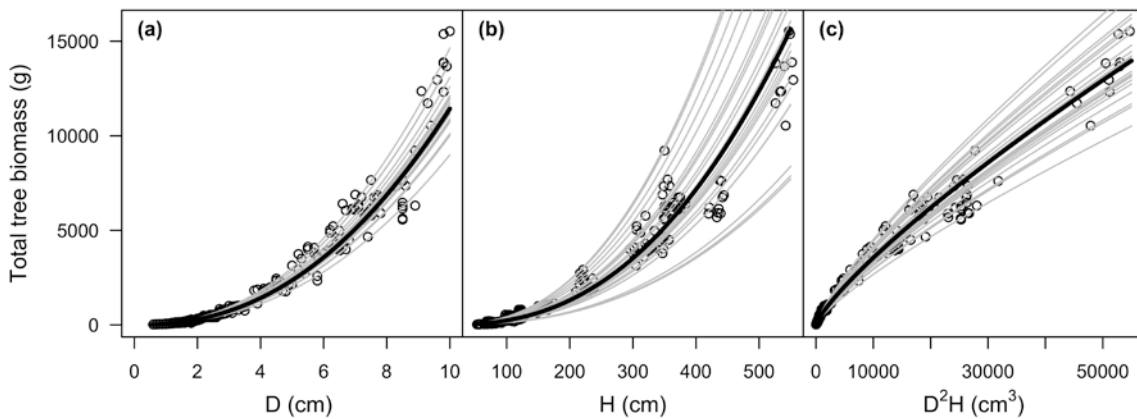
The consequences of site-effects on allometric models resides in the underestimation or overestimation of biomass at stand level. Data analyses revealed that when using D as a predictor (Fig. 3, a), the generic allometric model overestimated stand-level biomass by a margin of up to 27.2% (Table 3). The consequences of using H as predictor of biomass (Fig. 3, b), were more severe, yielding overestimations of up to 103.0% and underestimations by as

much as 75.9%. When both D and H were used to predict biomass, levels of over- and underestimations were somewhere between those produced by D and H alone.

**Table 3**

Total biomass ( $\text{Mg ha}^{-1}$ ) for each plantation, as predicted by Equations 1-4, and comparisons of values obtained using generic vs. specific models (Diff, Eq. 11).

Plantation	TB = f(D)			TB = f(H)			TB = f(D <sup>2</sup> H)			TB = f(D, H)		
	Generic $\text{Mg ha}^{-1}$	Specific $\text{Mg ha}^{-1}$	Diff. %	Generic $\text{Mg ha}^{-1}$	Specific $\text{Mg ha}^{-1}$	Diff. %	Generic $\text{Mg ha}^{-1}$	Specific $\text{Mg ha}^{-1}$	Diff. %	Generic $\text{Mg ha}^{-1}$	Specific $\text{Mg ha}^{-1}$	Diff. %
1	0.187	0.151	+23.8	0.321	0.162	+98.1	0.200	0.150	+33.3	0.207	0.150	+38.0
2	0.131	0.144	-9.0	0.201	0.099	+103.0	0.133	0.126	+5.6	0.136	0.122	+11.5
3	0.254	0.231	+10.0	0.501	0.483	+3.7	0.290	0.239	+21.3	0.305	0.241	+26.6
4	0.452	0.400	+13.0	0.409	0.371	+10.2	0.404	0.380	+6.3	0.397	0.376	+5.6
5	0.346	0.345	+0.3	0.542	0.404	+34.2	0.370	0.355	+4.2	0.381	0.359	+6.1
6	0.783	0.766	+2.2	1.003	0.804	+24.8	0.807	0.766	+5.4	0.820	0.768	+6.8
7	0.632	0.559	+13.1	0.509	0.505	+0.8	0.559	0.529	+5.7	0.544	0.522	+4.2
8	0.407	0.320	+27.2	0.416	1.723	-75.9	0.379	0.317	+19.6	0.377	0.318	+18.6
9	0.872	0.818	+6.6	0.478	0.795	-39.9	0.683	0.793	-13.9	0.644	0.792	-18.7
10	1.166	1.192	-2.2	1.449	1.342	+8.0	1.193	1.206	-1.1	1.210	1.216	-0.5
11	2.379	2.524	-5.7	1.463	2.677	-45.3	2.009	2.549	-21.2	1.921	2.571	-25.3
12	1.965	1.855	+5.9	1.233	1.900	-35.1	1.652	1.827	-9.6	1.582	1.831	-13.6
13	1.422	1.499	-5.1	0.851	1.528	-44.3	1.177	1.460	-19.4	1.121	1.463	-23.4
14	4.508	4.430	+1.8	3.664	4.440	-17.5	4.208	4.356	-3.4	4.131	4.351	-5.1
15	7.230	8.788	-17.7	8.057	8.278	-2.7	7.632	8.591	-11.2	7.725	8.554	-9.7
16	2.855	3.146	-9.2	2.630	3.254	-19.2	2.740	3.116	-12.1	2.716	3.124	-13.1
17	10.630	13.617	-21.9	11.934	13.454	-11.3	11.473	13.491	-15.0	11.645	13.491	-13.7
18	18.836	16.500	+14.2	11.680	14.892	-21.6	17.203	15.691	+9.6	16.606	15.486	+7.2
19	7.666	7.300	+5.0	5.002	7.115	-29.7	6.912	7.154	-3.4	6.680	7.132	-6.3
20	16.100	15.686	+2.6	15.259	15.173	+0.6	16.603	15.385	+7.9	16.616	15.295	+8.6
21	20.637	23.633	-12.7	20.750	22.617	-8.3	21.842	23.130	-5.6	21.992	23.016	-4.4
22	16.872	17.307	-2.5	17.791	16.916	+5.2	18.029	17.055	+5.7	18.219	16.977	+7.3
23	29.547	35.985	-17.9	38.889	34.598	+12.4	34.723	35.360	-1.8	35.879	35.162	+2.0
24	24.978	26.047	-4.1	35.853	26.709	+34.2	29.891	26.310	+13.6	31.098	26.290	+18.3



**Fig. 3.** Total tree biomass as a function of (a) D, (b) H, and (c) D<sup>2</sup>H, as predicted by Equation (7). Note: The bolded, black line represents the overall regression (generic allometric model), grey lines represent the models that are specific to each plantation.

#### 4. Discussion

This study is concerned with the development and evaluation of biomass allometric models for young Norway spruce trees that include a site-effect. The site-specificity of models is also assessed. Results demonstrate that parameter estimates are comparable to those published by Pajtk et al. [18] in their study of naturally regenerated Norway spruce trees (of similar height and diameter dimensions) in Slovakia. However, despite the larger sample of this study, the standard errors for our models were greater than those reported by Pajtk et al. [18]. This is due to the fact that in our study the effect of the forest stand was included, and standard errors were therefore adjusted accordingly. However, if no such adjustment of standard errors were included, the values reported here would remain comparable to those published by Pajtk et al. [18].

Although the level of site-specificity in biomass allometric models is commonly unknown, it is often assumed that models are site-specific [30,36]. However, developing individual allometric models for every forest stand is unrealistic. As a result, some researchers suggest that models may be safely applied at regional level [37,38], although in forestry practice, the same allometric models are often applied at country level. Such general application is often argued on the basis that much of the site effect is due to environment and, therefore, regional use of these models may be justifiable due to relatively low spatial variation in climate and soil conditions. We demonstrate, depending on the biomass category and type of predictor used, that for young Norway spruce trees, more than 33% of the total model variance may be attributable to between stand effects. The remaining variance was attributed to within stand (individual tree) effects.

Understanding how variance is partitioned in allometric models is essential. If site-specificity is found to affect the accuracy of biomass prediction by generic biomass allometric models, such specificity may lead to the inaccurate prediction of biomass in other forests stands due to the level 2 (forest stand) errors. Although the regression line demonstrates how the mean biomass changes with a predictor, this mean response represents the overall ‘multi-group’ mean for all forest stands (Fig. 3, bold, black line). However, because of site-specificity, the intercept of each group was different, thus the mean biomass response for each group/stand was also different (Fig. 3, grey lines). This difference represents the forest stand error at level 2 ( $u_i$ , Eqs. 1-4). However, level 2 errors are assumed to be normally distributed with mean zero and standard deviation ( $\sigma_\alpha^2$ ). Therefore, testing the accuracy of a generic allometric model in a specific forest stand [30,39,40] would yield a result that strictly depends on the magnitude of this error (which is random). Thus, whether or not a generic biomass allometric model (that has  $ICC > 0$ ) is reliable or inaccurate estimator of biomass for a particular stand is largely a matter

of chance. Results demonstrate that, because of site specificity, biomass prediction errors at level 2 could be considerable, and that the use of generic model instead of one specific to the site in question resulted in prediction bias of up to 103%. On the other hand, if site-specificity were zero, then the intercepts of all forest stands would coincide (errors at level 2 would be zero), resulting in accurate predictions of biomass for all stands. Our findings strongly indicate that the application of allometric models to other forest stands within the same region (without testing for within region effects) may be unsafe.

From a site-specificity perspective, the most suitable predictor candidate for developing generic biomass allometric models would be the one that has very low site-specificity (ICC = 0 or close to zero), thereby minimizing level 2/forest-stand error. In our study, diameter exhibited less site-specificity than height, and would therefore appear to be a more suitable predictor of biomass in generic allometric models.

The main drivers of site specificity in allometric models are H–D ratio, biomass allocation pattern (to vegetative organs) wood density, and these three are moderated by genotype [41], competition [42–44] and environmental conditions [27,45–47]. Therefore, it can be expected that unique stand-level interactions between genotype, competition and environmental factors will influence H–D ratios, biomass allocation patterns and wood densities, and such stand level effects will be further reflected by the site-specificity of biomass allometric models.

#### **4.1. Why did site-specificity vary between the different biomass components?**

Stem biomass is highly dependent on H–D ratio [48]. Assuming a constant taper form and a constant wood density, stem biomass would be exclusively dependent on  $D^2H$  (when D is measured at the base of the stem). For those species where taper form and wood density is relatively constant, stem biomass remains strongly correlated with diameter and height. In our sample, for any constant diameter, the H–D ratio was found to vary between sites (ICC = 0.77), thus strongly indicating that tree height was responsible for the high site-specificity of stem biomass component. In contrast, branch and needle biomass are less dependent on H–D ratio and may be more sensitive to competition with the neighbouring trees [42,49], which is why they exhibit greater within stand variability and, consequently, are less prone site-specific effects when modelled.

#### **4.2. Why was height more site-specific than diameter in predicting biomass?**

The greater site-specificity of height as predictor is in part captured by between stand variation in H–D ratio. Assuming that stem biomass is proportional to  $D^2H$  [12], it follows that the

proportional effect of diameter on biomass is twice as great as that of height. For models where biomass is a function of height,  $B = f(H)$ , between stand effects (for a given tree height) are due to diameter variation. Thus, for any constant tree height across stands, corresponding diameter would vary between stands (due to site specificity of H–D). As diameter exerts a more powerful influence on tree biomass, diameter explains a greater proportion of biomass variance than height. It therefore follows that a biomass-diameter relationship will be less influenced by site effects than that for biomass-height. Because height is a more site-specific predictor of biomass than diameter it would be ill-advised to develop generic biomass allometric models based on height alone. Nevertheless, regarding the use of other possible biomass predictions, the combination of crown diameter (not considered in this study) with height is also attractive because of potential for data collection by remote sensing means [11].

#### **4.3. The underlying drivers of site-specificity in allometric models**

Many workers suggest that including height in models will offset site effect [21,23,24,37,50,51]. The rationale is clear; given that H–D relationship is site-specific, it is likely that for any constant diameter, height will vary between stands. It therefore follows that trees of similar diameter (and taper) but greater height will possess greater stem biomass. It is also assumed that there is a strong relationship between stem biomass and total tree biomass. Therefore, the inclusion of height in models would be expected to reduce their site-specificity. Findings reported here do demonstrate that height inclusion reduces model site-specificity, but only for stem biomass and only when the combined expression for D and H was applied (i.e.  $D^2H$ ). However, for total tree and total aboveground biomass, our results indicate an entirely opposite pattern that including height increased the site-specificity of models. To explain this seemingly anomalous finding requires a deeper analysis of the relationship between dependent variables. Firstly, site-specificity of the relationship  $\ln(TB) - \ln(ST)$  was found to be high ( $ICC = 0.68$ ), suggesting that factors other than H–D ratio may also be responsible. Additionally, on examining the site-specificity of  $\ln(TB) - \ln(BR)$ ,  $\ln(TB) - \ln(ND)$  and  $\ln(TB) - \ln(RT)$ , it became apparent that these relationships were extremely site-specific ( $ICC = 0.98, 0.97$  and  $0.98$  respectively). This indicates that there is little within stand variation of the relationships TB–BR, TB–ND, TB–RT (all of which demonstrate the pattern of biomass allocation), in contrast to considerable between stand variation. In comparison with large trees, where stem biomass forms the dominant component of total biomass, it is the tree components (i.e. branches, needles and roots) of smaller trees (the subject of this study) that account for a greater proportion of overall tree biomass. Therefore, for small trees, the main driver of site-specificity seems to be the allocation pattern to branch, needle and root biomass, and not height-diameter ratio as it was



previously suggested for large trees [24,27,37,51,52]. Summarising, the inclusion of height in allometric models did not compensate for or reduce the site-specificity of models because between site variation was largely driven by biomass allocation to branches, needles and roots. However, in mature trees, where stem proportion of total biomass is greater, one might expect H–D ratio be a more significant influence of between site variation than biomass allocation to other vegetative components, although this is not tested here.

#### **4.4. Ecological implications**

Variance in species-specific allometric models is indicative of the plasticity of biomass allocation, and is therefore indicative of a genotype capacity to respond with phenotypes that are adjusted to prevailing environmental conditions [47]. It is therefore only to be expected that the relationship between biomass and tree dimensions (morphological traits) will vary between forest stands (the source of between-stand allometric variance), in response to differences in: climate and soil conditions; levels of tree competition (which may depend on development stages within rotation cycles); and genotype (between-stand genetic variation). Site-specificity is expressed as the proportion of total model variance (the sum of within- and between-stands variance) that is attributable to between-stand variance. If within- is equal to between-stands variance, site-specificity is 50%. Our data revealed that forest stand variance could be considerably greater than that within stand effects. The most site-specific model encountered in this study (aboveground biomass predicted by height, see Table 2), demonstrated that forest stand effects were nearly six times greater than within-stand allometric variance.

Both within- and between-stands allometric variances are produced by the spatial diversity of genotype, competition and environmental conditions. It is to be expected that because stands generally occupy relatively small and homogenous areas, within-stand environmental conditions will range less widely than between stands. In contrast, studies of genetic variation report greater within-stand effects for Norway spruce growing in autochthonous stands, than that between-stands [53,54]. Therefore, in natural forests, we may conjecture that the main vector driving within-stand allometric variability may be genotype, and that for between-stands variability is environment. However, this may not hold for planted forests, as many progenies may be seeded from the fewer trees, and therefore share a similar genotype. Our study was only of plantation stands, which have been demonstrated to be less genetically diverse than natural forests [55]. Since lower genetic variability within the forest stand also reduces morphological variation in tree dimension and in the allocation of biomass to tree parts, this may increase the relative proportion of overall variation explained by between stand effects. Therefore, as a consequence of their lesser genetic variation, plantations may

exhibit a greater proportion of site-specific variation when compared to natural forests. This is consistent with the findings of Chave et al. [24] who in studies of pantropical natural forests reports that only 21.4% of the variance in biomass allometry (for which aboveground biomass was predicted from D, H and wood density) was explained by between sites effects and that the remaining 78.6% was attributable to tree variation within sites.

Intraspecific genetic variation accounts for the fact that individual trees may respond uniquely to similar environmental stimuli, resulting in variations in tree architecture and wood density (these two traits define tree biomass allometry). Trees with similar genotypes, may adopt different biomass according to prevailing environmental conditions. As a general rule, trees will allocate greater biomass to that component that will allow them to capture more of the resource that most strongly limit their growth [56]. Poorter et al. [46] demonstrated that, among the environmental factors they considered, irradiance had the strongest effect on allocation. As a result, competition for light stimulates trees to invest in height growth, which in turn, may confound expected H–D relationships. This is consistent with our findings of a highly site-specific H–D ratio, and, as consequence, stem biomass was the most site-specific biomass component.

The site-specificity of allometric models may be also be a function of genetic diversity whereby relatively high between site allometric (and tree growth-form) variation and low within site variation would also be indicative of low within stand genetic variation. Such allometric variation could therefore perhaps be useful as a subsidiary indicator of population genetic diversity.

#### **4.5. Collinearity in allometric models**

Equations 3 and 4 contain both independent variables (D and H). In equation 3 the two variables are combined in a single expression but are independently expressed equation 4. Collinearity is the phenomenon by which strong linear relationships exist between two or more explanatory (predictor or independent) variables in multiple regression [57,58]. This is clearly relevant to biomass allometric models, as D and H are always correlated. When highly correlated, D and H will inevitably be redundant or repetitious some proportion of biomass variation. In such cases, although models may express the combined predictive power of all the explanatory variables used, they may not provide reliable results as to the predictive value of a particular explanatory variable (here D or H) or of the degree to which it is redundant in relation to the other predictors. Thus, regression coefficients are not precise (less identifiable), as is reflected by their standard errors. However, a further concern of collinearity is that regression coefficients become sensitive to small changes in the dataset which destabilise models so that (in this case) such

changes alter coefficients and profoundly affect biomass prediction. Dormann et al. [57] demonstrated that the collinearity affects seriously model prediction when predictors are highly correlated (Pearson  $r > 0.7$ ). In our study  $\ln(D)$  and  $\ln(H)$  were also found to be very highly correlated (Pearson  $r = 0.972$ ), and the variance inflation factor (VIF) of 6.38 for total biomass confirmed that predictors were highly collinear.

As with data clustering, collinearity increases standard error [57] extending the range of confidence intervals and increasing model uncertainty. Such increases in standard error lead to underestimates in the calculated statistics (and confidence) in regression coefficients so that the probability of falsely accepting a null hypothesis in a  $t$ -test ( $t$  scores) is increased, leading to type II errors (false negatives). Therefore, collinearity increases the  $p$ -values (in ANCOVA or multiple regression) and conceals the main effect.

Merging (or combining) two independent variables (e.g.  $D$  and  $H$ ) in one (i.e.  $D^2H$ ) overcomes limitations of collinearity, and also results in a less complex 'simple' regression model. Our findings demonstrated that the combined expression for  $D$  and  $H$  also reduced the site-dependency of the model (i.e. improved its generic application) when compared to the equivalent multiple regression model. However, some further investigation is required to more fully understand the statistical consequences of combining such expressions, and whether this approach can reliably predict biomass.

Therefore, we do not recommend using  $D$  and  $H$  as distinct independent variables to predict biomass (Eq. 4), because of high site-specificity and the collinearity that exists between  $D$  and  $H$ . However, our results suggest that diameter and height may be used together when combined as a single independent variable ( $D^2H$ ), providing interpretation proceeds with appropriate checks and due caution.

#### **4.6. Further directions**

The development of a reliable species-specific and generic biomass allometric model able to predict biomass across a diverse range of forest stand types will depend on discovering a predictor that fully accommodates forest stand effects (i.e. has zero or very low site-specificity). This will require an understanding of how allometry responds to genetic, competition and environmental variation as well as the effects of their interaction.

### **5. Conclusions**

Having developed allometric models for Norway spruce trees and evaluated their site-specificity, our findings indicate that site-specificity for models ranged between 33 and 86%, depending upon the predictor used and target biomass component to be predicted. Diameter was

demonstrated to be less site-specific than height. Branch biomass was the least site-specific biomass component whereas stem biomass was the highest (i.e. exhibited greatest between site variation). For the tree size classes represented by this study, site-specificity appeared to be mainly driven by differences in biomass allocation pattern to branches, needles and roots. The consequences of site-specificity are the potential for systematic errors in biomass prediction at stand level. In the sample evaluated by this study, the use of generic allometric models produced overestimations of total biomass at stand level of up to 103% and underestimations of up to 76%. The level of bias depended on the type of predictor applied. The highly site-specific nature of allometric models indicates that site effects cannot be ignored by further studies if these are to result in reliable models for biomass prediction and inference.

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