Allometry of winter buds in beech (*Fagus sylvatica* L.) natural regeneration with respect to its volume and dry weight estimation

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Abstract

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Allometric relationships among bud's fresh volume (V), length (L), maximal diameter (MD), basal diameter (BD), and dry weight (W) in beech (*Fagus sylvatica* L.) saplings manifest strong mutual correlations. These correlations depend on the bud type determined by bud position on shoot, shoot type and shoot position in crown. However, in most cases the differences among the bud types are not distinct – individual types can be classified into several overlapping groups. The bud type significantly influences bud shape characterised by the ratios of BD to MD, and BD to L; on the other hand, it has no influence on MD/L and bud density (V/W). Influence of accessible light on bud shape and density also depends on bud type. For non-destructive estimation of V and W, we have prepared a regression model using as independent variable the volume of cylinder enclosing the bud (V_{cyl}). This model could explain 98% of the variation in V and W, with a relative accuracy of 6.4% for V, and 5.4% for W (P = 0.95). The performance of the model was verified by a test allowing us to conclude that the model outputs are comparable with directly measured values.

Key words

allometry, European beech, volume and dry weight estimation, winter bud

Introduction

The growth of plants and the other modular organisms runs through initiation of organ primordia from meristematic cells, and development of these primordia into fully grown plant organs. For permanent plants of temperate and cold zone is typical "rhythmic growth" displaying endogenous periodicity and cessation of extension. The germs of shoots developing within a given growing season had already been created in buds in the preceding vegetation period ("preformation"; BARTHÉLÉMY and CARAGLIO, 2007).

ROLOFF (1987) studying the morphogenetic bud cycle of European beech (*Fagus sylvatica* L.) observed that new leaves were mostly formed in June and July; and that the growth of the leaf primordia mainly occurred in August and September. This author stated that all primordia for the next growing season had already been fully developed in the buds by August, and that at the same time there was initiated primordia formation for the year after the next. These results have been proved experimentally also by ESCHRICH et al. (1989). The growth of beech shoots in the current year is chiefly influenced by the amounts of assimilates created in the preceding year, and, consequently, by environmental conditions throughout this year (e.g. MASAROVIČOVÁ, 1985). LÖF and WELANDER (2000), and WELANDER and and OTTOSSON (1997) have confirmed that the length and number of beech shoots in the current year was mainly dependent on environmental conditions in the preceding year (soil water content and light availability). ROLOFF (1987) also concluded that the environmental conditions (e.g. drought) in early summer influenced number of leaves in the next year, while late summer conditions (drought) affected the size of these leaves. This statement is in contradiction with the findings of

Löf and Welander (2000), and Welander and Ottosson (1997) according to whom the leaf area in 2-yr-old beech individuals was solely influenced by the current-year conditions. This contradiction could be explained by the different ontogenetic stages of the investigated plants.

Considering these facts, I hypothesise that the preformation of beech shoots should be reflected also in strength of correlation between the parameters of buds (length, diameter, volume, dry weight) and parameters of shoots sprouted from these buds (e.g. shoot length, dry mass, leaf area and dry mass) in the next year. Quantification of these relations requires inputting values of bud parameters as independent variables. In this context, the objective of my contribution was to evaluate the allometry of buds situated on different parts of shoots, on different types of shoots and in different parts of crowns of naturally regenerating beech trees, and to provide input data for regression models for non-destructive estimation of volume and dry weight of beech buds.

Material and methods

Shoots with winter buds were collected in November/December 2008 in forest stands in three localities situated in central Slovakia: (i) Staré Hory, 48°50'41" N, 19°06'44" E, Veľká Fatra Mts, (ii) Vígľašská Huta-Kalinka, 48°30'13" N, 19°15'06" E, Javorie Mts, and (iii) Jasenie, 48°51'36" N, 19°25'38" E, the Nízke Tatry Mts, all the three at 680–740 m a.s.l. The mean annual temperature at these sites is 6–7 °C (Šťastný et al., 2002), mean annual precipitation total is 700–1,100 mm (Faško and Šťastný, 2002). More details about the localities can be found in Jarčuška (2010) and Jarčuška and Barna (2010).

The shoots were collected from 0.8–1.5 m high individuals, undamaged, without symptoms of attack by pathogens. From each individual, I took the terminal shoot and a long shoot from the upper crown half; and one long and one short shoot from the lower crown part (Table 1; Fig. 1a). From the total number of 48 trees growing in sites differing in solar radiation supply (17 sites, 5–70% of total solar radiation transmitted through the crown canopy), I sampled in summary 258 shoots with more than 840 buds.

Relative amount of accessible solar irradiation was determined based on hemispheric photos captured with fish-eye lens Sigma 4.5 mm F2.8 EX DC (Sigma, Japan) mounted at Canon EOS 400D (Canon, Japan) during summer 2008 and 2009, and analysed by softwares SideLook 1.1 (Nobis, 2005; Nobis and Hunziker, 2005), and Gap Light Analyser 2.0 (Frazer et al., 1999). For more details about hemispherical image analysis, see Jarčuška (2008), and Jarčuška and Barna (2010).

I measured these three dimensions of buds: length, diameter at the base and diameter across the widest part. The measurements were taken with an electronic digital calliper with an accuracy of 0.01 mm (Fig. 1c). Then, the shoots were stored in a fridge (for maximum 7 days). The bud volume (and length repeatedly) were determined with a programme WinRhizo 2004a (Régent Instruments, Canada), performing at an accuracy level of 1.0 mm^3 . The software itself represents standard methods for determining quantitative traits of plant's root system (e.g. Jaloviar et al., 2009). The scanned buds were dried up at a temperature of 80 °C for 48 hours. Finally, the weight (mass) was determined with an accuracy of 0.001 g (Mettler AE 200; Mettler, Switzerland).

The statistical processing of the data was carried out with using only the values of those buds the length of which measured manually by a calliper did not differ from the length measured by WinRhizo by more than 5% – as the storing in the fridge could caused them to shrink ($n = 674$). For the purpose of this study, the buds were divided into seven classes ("bud types"), see Table 1. Allometric relationships between the measured traits of different bud types were determined by using a simple linear regression for fresh bud volume (V) versus bud length (L), maximum diameter (MD),

Table 1. List of 3-cipher codes for "bud type" used in the study

Cipher in the code	Meaning	Code No.	Meaning
1st	Shoot position in crown	1	Upper crown part
		2	Lower crown part
2nd	Shoot type	1	Terminal shoot
		2	1st-order lateral (long) shoot
		3	2nd-order lateral (short) shoot
3rd	Bud position on shoot	1	Terminal bud
		2	Lateral bud (axillary)

basal diameter (BD), and dry weight (W). Log-transformation of the dependent as well as the independent variables was used to obtain their normality and homoscedasticity. Differences among elevations and slopes were tested using a Tukey multiple comparison test (Zar, 1999). The ratios of BD to MD, BD to L, and MD to L reflected in characteristic bud shapes; and the ratio V to W reflected in the bud density ($cm^3 g^{-1}$), were compared by using the main effects anova with factors: "shoot position in crown", "shoot type" and "bud position on shoot". Tukey HSD post-hoc test was computed to determine significant differences between the compared bud types. Response of bud shape and density to the relative amount of total accessible irradiation was assessed by means of Kendall´s Tau correlation.

For the design of the regression model for non-destructive determining of fresh volume and dry weight of buds, I used this independent variable: "volume of cylinder enclosing the bud" (V_{cyl}) with the diameter equal to the bud's maximum diameter and the height equal to the bud's length. After having tested the differences among models for individual bud types, the linear models were parameterised based on randomly chosen portion of data (approx. 90%, uniformly for all bud types). To test whether the resulting models are reasonable, there were validated with the remaining data. Theoretical values of bud volume and weight were calculated from the regression equations (designed models) and then they were regressed against the measured data. Standard t-tests were applied to find out whether the slopes and intercepts of the regression lines differed significantly from unity and zero, respectively. Also the average ratios of the predicted-to-measured values were calculated for values where predicted exceeded measured data, and vice versa. All statistical analyses were performed using Statistica 6.0 (StatSoft, USA).

Results and discussion

Bud allometry

Allometric relationships among bud´s fresh volume (V), its morphological traits (L, MD, BD), and dry weight are strong correlated (adjusted R^2 ranges from 0.45 to 0.99; Table 2). These allometric relationships are mostly dependent on the bud type (bud´s position on shoot, shoot type, shoot position in crown, see Table 1), and they mainly differ in slopes (intercept of V and BD is an exception). In most cases, however, the differences among the buds are not distinct – individual types can be classified into several overlapping homogeneous groups. With increasing bud volume, the highest length growth rate was observed in buds on short shoots in the lower crown halves (code 231), the lowest was the growth rate of terminal buds (codes 111, 112). The bud type had no influence on relation between the bud volume and its maximal diameter (Table 2). MD (among morphological traits) provided the best estimation of bud volume. Relationship between V and basal diameter was less strong in comparison with the other evaluated traits. Cochard et al. (2005) found that the area of

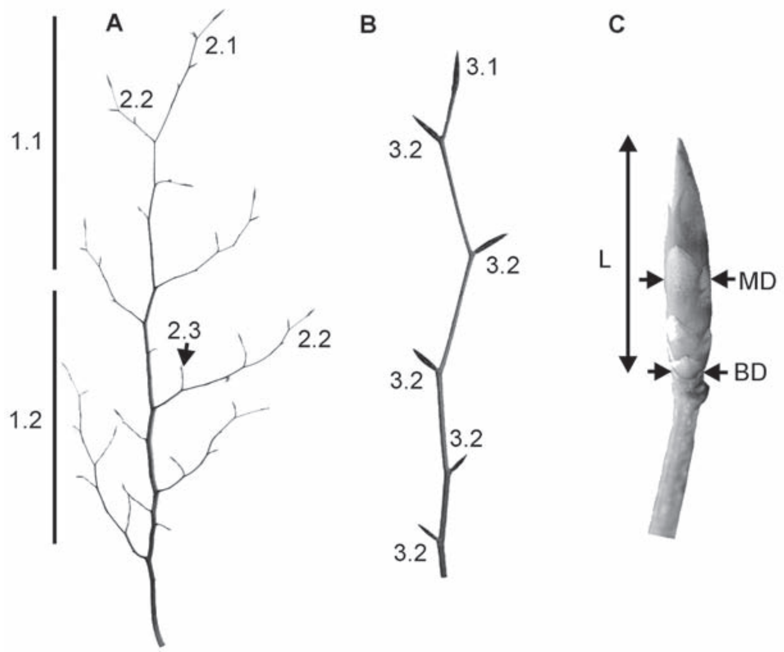

Fig. 1. Schematic representation of a seedling (A) and shoot (B), position of shoot samplingspots in the crown (1.1 , 1.2), shoot type (2.1 , 2.2 , 2.3) and types of buds on shoots (3.1, 3.2). The first cipher means the order in the code ‚bud type'; the second denotes the value itself of the number in the code (Code No.; see Table 1). (C) Measured variables of bud: (L) length, (MD) maximum maximal diameter, and (BD) basal diameter

a shoot annual ring was correlated with hydraulic conductance of xylem, and that high xylem conductance was associated with the occurrence of a large number of leaf primordia in buds. Consequently, we may expect a significant correlation between BD and characteristics of biomass sprouted from these buds. Dry weight of buds from the upper crown part correlated with their volume stronger than in case of buds from the lower crown (R^2_{adj} = 0.99 and 0.94–0.97, respectively; Table 2). A possible explanation is in lower accessibility and bigger variability of light in lower crown parts (cf. Petritan et al., 2009). Cochard et al. (2005) reports an example of buds on lower branches of mature beech trees manifesting a high correlation between the fresh mass of buds and dry mass of leaf primordia (R^2 = 0.94), and also with the number of leaf primordia in the bud (R^2 = 0.91).

Bud type (Table 1) had an important influence on bud shape characterised by the ratios of BD to MD, and BD to L, with factor "bud position on shoot" manifesting a stronger effect (Table 3). The highest values of BD/MD were observed in lateral buds on long (terminal

Table 2. Linear models for regression lines describing dependence of bud volume (x) on bud length, maximum diameter, base diameter and weight (y). The regression equation is $(\log)y = a + b(\log)x$. All regressions were found statistically significant ($p < 0.001$). The values of intercepts and slopes were divided into homogeneous groups based on the results of the Tukey multiple comparison test (Zar, 1999) at a 0.05 significance level. Bud type abbreviations are in Table 1 (L) denotes bud length, (MD) maximum diameter, (BD) basal diameter, (W) dry weight of bud, (V) bud fresh volume, (R^2_{adj}) adjusted R^2.

y	Bud type	n	Intercept (a)		Slope (b)		R^2_{adj}
L	111	40	0.6841	*a*	0.3176	*ab*	0.89
	112	166	0.7060	*a*	0.3053	*a*	0.91
	121	72	0.6706	*a*	0.3262	*ab*	0.89
	122	204	0.6431	*a*	0.3464	*bc*	0.90
	221	55	0.6092	*a*	0.3776	*bc*	0.80
	222	81	0.6295	*a*	0.3617	*abc*	0.82
	231	56	0.5652	*a*	0.4138	*c*	0.84
MD	111	40	–0.2094	*a*	0.3551	*a*	0.95
	112	166	–0.1543	*a*	0.3240	*a*	0.95
	121	72	–0.1912	*a*	0.3451	*a*	0.95
	122	204	–0.1651	*a*	0.3298	*a*	0.93
	221	55	–0.1567	*a*	0.3244	*a*	0.81
	222	81	–0.1543	*a*	0.3180	*a*	0.72
	231	56	–0.1380	*a*	0.3024	*a*	0.81
BD	111	40	–0.3562	*abc*	0.3570	*a*	0.79
	112	166	–0.1737	*a*	0.2691	*b*	0.84
	121	72	–0.2827	*bc*	0.3179	*ab*	0.82
	122	204	–0.2106	*c*	0.2823	*ab*	0.81
	221	55	–0.2121	*b*	0.2494	*ab*	0.45
	222	81	–0.2056	*b*	0.2538	*ab*	0.55
	231	56	–0.2287	*b*	0.2633	*ab*	0.67
W	111	40	–3.1330	*a*	0.9686	*ab*	0.99
	112	166	–3.1657	*a*	0.9810	*b*	0.99
	121	72	–3.1921	*a*	0.9985	*ab*	0.99
	122	204	–3.1896	*a*	0.9975	*ab*	0.97
	221	55	–3.2617	*a*	1.0535	*a*	0.97
	222	81	–3.1880	*a*	0.9889	*ab*	0.94
	231	56	–3.2262	*a*	1.0199	*ab*	0.95

and lateral) shoots in the upper crown halves (Table 4). Neither MD/L nor bud density (V/W; $cm^3 g^{-1}$) depended on the bud type.

Accessible light had negative influence on BD/L and MD/L in lateral buds on long shoots in upper crown halves (code 122); on the other hand, in case of buds on long shoots in lower crown part (222), this influence was positive. With increasing light supply decreased bud density on short shoots (231), that means that their volume increased faster than their dry weight (Kendall $\tau = 0.26$, $p < 0.01$; Table 5).

Strong correlation between morphometric parameters of buds and their dry weight with bud volume provides a sound background for designing models for non-destructive determination of volume and dry weight of all the buds involved in interest.

Design and testing of a model for estimation of bud fresh volume and dry weight

Because there were no significant differences between bud types defined by comparing regression equations expressing dependence of volume and of bud's dry weight on the volume of the bud-enclosing cylinder (V_{cyl}; Table 6), I have created models for estimation of V and W that did not depend on the bud type. In these models, V_{cyl} (independent variable) accounted for 98% of variation in bud volume and also in bud dry weight (Table 7). Relative accuracy of prediction at a 95% significance level was 6.4% for bud fresh volume, and 5.4% for bud dry weight. For example, the determination coefficient value for relationship between leaf area and rectangle length × width obtained by Masarovičová and Požgaj

Table 3. Influence of shoot position in crown, shoot type and bud position on shoot on bud morphology (ratios of BD/MD, BD/L, MD/L) and bud density (V/W). Outputs from anova. (L) denote: bud length, (MD) maximum diameter, (BD) basal diameter, (W) dry weight of bud, and (V) bud fresh volume

	Shoot position in crown		Shoot type		Bud position on shoot	
	F	*P*	*F*	*P*	*F*	*P*
BD/MD	8.38	**0.0039**	5.55	**0.0041**	66.15	**0.0000**
BD/L	3.01	0.0832	4.08	**0.0174**	22.74	**0.0000**
MD/L	0.02	0.9021	0.63	0.5311	0.13	0.7175
V/W	0.69	0.4067	1.02	0.3616	0.73	0.3921

Table 4. Trait ratios mean and SE (in brackets) comparison tests between bud types of beech natural regeneration individuals. Means from a given line followed by the same letter are not significantly different at the 5% threshold based on Tukey HSD post-hoc test. Bud type abbreviations are given in Table 1. For trait ratios abbreviations see Table 3.

	Bud type						
	111 (*n* = 40)	112 (*n* = 166)	121 (*n* = 72)	122 (*n* = 204)	221 (*n* = 55)	222 (*n* = 81)	231 (*n* = 56)
BG/MG	0.726 (0.001) *ab*	0.792 (0.005) *d*	0.732 (0.008) *ab*	0.777 (0.005) *cd*	0.707 (0.009) *a*	0.757 (0.008) *bc*	0.739 (0.009) *abc*
BG/L	0.110 (0.003) *abc*	0.117 (0.001) *c*	0.108 (0.002) *ab*	0.115 (0.001) *bc*	0.105 (0.002) *a*	0.113 (0.002) *abc*	0.112 (0.002) *abc*
MG/L	0.151 (0.003) *a*	0.148 (0.001) *a*	0.149 (0.002) *a*	0.148 (0.001) *a*	0.148 (0.003) *a*	0.149 (0.002) *a*	0.152 (0.002) *a*
V/W [$cm^3 g^{-1}$]	1.560 (0.025) *a*	1.571 (0.012) *a*	1.570 (0.019) *a*	1.570 (0.011) *a*	1.563 (0.021) *a*	1.596 (0.018) *a*	1.613 (0.021) *a*

Table 5. Relationship between relative amount of accessible total irradiation versus bud shape (BD/MD, BD/L, MD/L) and bud density (V/W). Kendall´s rank correlation coefficients (τ) are shown with the significance levels (not significant are not in bold, * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$). Bud type abbreviations are given in Table 1. For trait ratios abbreviations see Table 3.

Bud type	BD/MD	BD/L	MD/L	V/W
111	–0.02	0.12	0.16	–0.05
112	0.09	–0.01	–0.09	–0.00
121	0.09	0.02	–0.08	0.02
122	–0.02	**–0.12***	**–0.16*****	0.02
221	0.11	**0.31*****	**0.38*****	–0.13
222	0.01	**0.18***	**0.19***	–0.06
231	0.05	–0.06	–0.08	**0.26****

(1988) in their comparative analysis of leaf area in three oak species ranged 0.79–0.98. Cicák (2003, 2008), applying his method of calculation coefficients for estimation of morphological parameters and dry weight on European beech leaves on spring shoots, obtained for response of calculation coefficient values to the leaf number on a shoot a value R^2 ranging 0.88–0.97.

I tested these models with an independent set of buds (n = 62). They could explain 98% and 99% of variation in the measured bud volume and dry weight, respectively (Fig. 2). Intercepts and slopes of these relationships were not significantly different from zero and one, respectively P for V: $P_{intercept}$ = 0.67, P_{slope} = 0.67, and for W: $P_{intercept}$ = 0.99, P_{slope} = 0.48). The average ratios of predicted-to-measured values were both close to unity (1.05, 1.02 for V and W, respectively). For the two variables, more than 60% of the predicted values were higher than the measured values (Table 8). The average ratio for the group with predicted > measured values as well as the group with measured > predicted values was lower for dry weight of buds than for bud's volume. The values scattering along the $y = x$ line respond the differences between the predicted and measured values of the evaluated variables associated with different bud response in fresh volume and dry mass to the volume of bud-enclosing cylinder V_{cyl} (Table 6) and also associated with the variability within the individual bud types.

The proposed methods for non-destructive estimation of fresh volume and dry weight of winter buds in beech natural regeneration are based on easily measurable morphological parameters, and perform with a high accuracy and out of dependence on the type of bud and amount of light supply.

Table 6. Linear models for regression lines explaining the dependence of volume of cylinder enclosing the bud V_{cyl} (diameter of cylinder equal to the maximum bud's diameter, height equal to the bud's length) (x) on the bud's volume and dry weight (y) for individual bud types. The regression equation is (log)$y = a + b$(log)x. All regressions were statistically significant (P < 0.001). The values of intercepts and slopes have been divided into homogeneous groups based of the results of the Tukey multiple comparison test (Zar, 1999) at 0.05 significance level Abbreviations for bud type are given in Table 1. (W) denotes dry weight of bud, (V) bud's volume, (R^2_{adj}) adjusted R^2.

y	Bud type	n	Intercept (a)		Slope (b)		R^2_{adj}
V	111	40	–0.1306	*a*	0.9611	*abc*	0.98
	112	166	–0.2623	*a*	1.0227	*c*	0.98
	121	72	–0.1311	*a*	0.9581	*abc*	0.97
	122	204	–0.1776	*a*	0.9771	*abc*	0.98
	221	55	–0.0930	*a*	0.9134	*a*	0.94
	222	81	–0.0727	*a*	0.8933	*ab*	0.89
	231	56	–0.1051	*a*	0.9221	*abc*	0.94
W	111	40	–3.2762	*a*	0.9389	*a*	0.99
	112	166	–3.4378	*a*	1.0116	*c*	0.99
	121	72	–3.3423	*a*	0.9668	*abc*	0.98
	122	204	–3.3839	*a*	0.9853	*abc*	0.97
	221	55	–3.3931	*a*	0.9841	*abc*	0.95
	222	81	–3.3190	*a*	0.9282	*ab*	0.93
	231	56	–3.3640	*a*	0.9645	*abc*	0.94

Table 7. Results of linear regression analysis on bud fresh volume, and dry weight of European beech (*Fagus sylvatica* L.) natural regeneration (saplings) with the volume of cylinder enclosing the bud (V_{cyl}) as an independent variable (n = 610). Regression coefficients (standard error in brackets) and adjusted percentage of variation explained (R^2_{adj}) are presented. The regression equation is (log)$y = a$ + (log)bx. All regressions were found statistically significant (P < 0.0001).

Model	Intercept	Slope	Syx	R^2_{adj}
Volume	–0.239749 (0.008072)	0.981349 (0.005700)	0.05033	0.980
Weight	–0.422385 (0.007705)	0.991274 (0.005440)	0.04804	0.982

Table 8. Average ratio of the predicted-to-measured values (of bud's volume and dry weight) where the predicted value exceeded measured (P > M), and vice versa (M > P; standard error in brackets)

	P > M		M > P	
	Ratio	%	Ratio	%
Volume	1.11 (0.02)	61	1.07 (0.01)	39
Weight	1.07 (0.01)	65	1.07 (0.01)	35

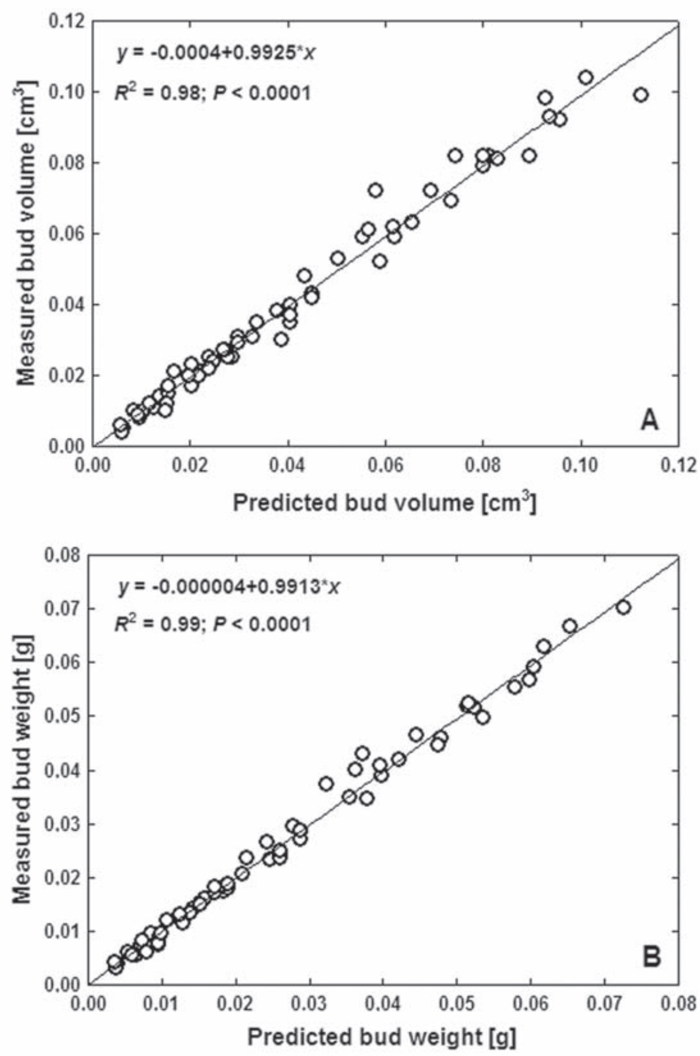

Fig. 2. Relationship between predicted and measured bud fresh volume (A), and dry weight (B) of beech natural regeneration saplings (n = 62). Predicted values were calculated based on regression equations listed in Table 7. The regression equation is of the form y = a + bx. Intercepts were not significantly different from zero and slopes were not significantly different from unity.

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Alometria na úrovni zimných púčikov prirodzeného zmladenia buka *Fagus sylvatica* L.) s ohľadom na stanovenie ich objemu a suchej hmotnosti

Súhrn

Primordiá jarných výhonkov buka lesného (*Fagus sylvatica* L.) sú vytvorené v púčiku už v predchádzajúcom vegetačnom období. Preto možno predpokladať, že sa tento proces odrazí v sile korelácie medzi charakteristikami púčikov – dĺžka (L), maximálny priemer (MD), priemer na báze (BD), čerstvým objem púčika (V) a hmotnosťou sušiny (W) a charakteristikami z nich vypučaných výhonkov (napr. dĺžka výhonku, jeho hmotnosť, listová plocha, váha sušiny). Kvantifikovanie týchto vzťahov si vyžaduje nedeštruktívne stanovenie hodnôt nezávislých premenných. Cieľom tohto príspevku je preto na základe zhodnotenia alometrie púčikov nárastu buka vytvoriť regresné modely umožňujúce stanovenie V a W púčikov buka.

Alometrické vzťahy medzi V púčika nárastu buka a jeho L, MD, BD a W sú vzájomne silno korelované. Tieto vzťahy zväčša závisia od typu púčika charakterizovaného jeho polohou na výhonku, typu daného výhonku a umiestnenia výhonku v korune. Vo väčšine prípadov však rozdiely medzi jednotlivými typmi púčikov nie sú jasne odlíšiteľné – jednotlivé typy sú zaradené do viacerých vzájomne sa prekrývajúcich homogénnych skupín. Typ púčika vplýva významne na tvar púčika charakterizovaný pomermi BD ku MD a BD ku L, nevplýva na pomer MD/L a špecifickú hmotnosť púčika (V/W). Vplyv dostupného svetla na tvar a špecifickú hmotnosť púčika závisí taktiež od jeho typu.

Na nedeštrukčné stanovenie V a W boli vytvorené lineárne regresné modely s charakteristikou ‚objem valca opísaného púčiku' (V_{cyl}) použitou ako nezávislou premennou. Tento model s relatívnou presnosťou 6,4 % pre V a 5,4 % pre W (P = 0,95) vysvetľoval 98 % variability V a W púčikov zmladenia buka. Test vytvoreného modelu na nezávislom súbore dát potvrdil, že jeho použitie prináša výsledky porovnateľné s priamym meraním zisťovaných charakteristík.

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