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Allometric relationships for surface area and dry mass of young Norway spruce aboveground organs

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ABSTRACT: Tree-level allometric functions for a precise predicting of stem, branch and leaf mass and surface area of three needle-shoot age classes were estimated from measurements of crown and stem dimensions in 34 harvested Norway spruce (*Picea abies* [L.] Karst.) trees. Trees were grown within a 16-years-old stand in the Beskids Mountains. The results showed stem parameters (stem diameter at breast height – dbh, stem volume – Vs and stem sapwood area – SA) to be highly correlated (r > 0.98) with stem mass/area and total aboveground mass of tree. Crown parameters – volume (Cv) and surface area (Ca) were the best predictors for individual branch and needle age-classes mass (r > 0.92) or area (r > 0.85), specifically for mass and surface areas of young branches and needles. dbh most correctly predicted the branch and leaf mass/surface area of older (> 2 years) shoots. The measured parameters: dbh, SA, tree height, crown length, Ca and Cv showed a high dependence on the tree position within the stand (r > –0.81). Thus, these parameters could be modified by silviculture.

Keywords: allometry; biomass; *Picea abies*; sapwood; surface area

Many studies have been focused on allometry, wood-mass inventory, carbon (C) sequestration, and biomass expansion factors as the first step for the evaluation of C sinks of different plant ecosystems. To identify and quantify these terrestrial C sinks, evaluation of CO_2 human-induced emissions and information for C balance accounting are highly needed nowadays. Temperate forest ecosystems have recently been identified as important C sinks (Jenssens et al. 2003). Carbon sinks might be associated with an environmental changes (elevated [CO_2], air temperature, N deposition etc.) and large areas of managed fast-growing young forests. Vetter et al. (2005) reported that sink strength changes were more significant at higher elevations (600–900 m a.s.l.). Norway spruce (*Picea abies* [L.] Karst.) is a dominant tree species (35%) in Central European forests (e.g. Wirth et al. 2004). It covers 55% of the total forested area of the Czech Republic mostly just at high elevations (see www.uhul.cz).

Measurements of different plant-organ mass (fresh or dry) and surface area are very important for studies of energy and material exchange between forest canopy and atmosphere, and ecosystem dynamics modelling as well (Vose et al. 1994). The knowledge of the individual tree-component mass and their allocation is essential to build mechanistic and growth models (Jarvis, Leverenz 1983). Allometry describes relations or mutual proportions between different plant organs, especially relations between simply measured stem or crown dimensions and other plant-organ mass or surface area. Behind the total ecosystem or timber production, leaf area and mass have the greatest importance because they contribute to evaluation of forest stand health status (Czech forest law supplement No. 78/1996) or production potential (Waring 1979).

Stem diameter (measured usually at the breast height, i.e. at 1.3 m above the ground surface – dbh) and tree height (H) are basal (easy measurable) dendrometric parameters. Increment of stem di-

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ameter strongly depends on the effectiveness of C assimilation (Waring 1979) and on the total C balance of the tree since C is reallocated preferentially to branches and roots (Gordon, Larson 1968; Waring 1987).

Less attention has been paid to an interrelationship between plant organ masses or surface areas and crown dimensions. Nevertheless, crown dimensions are major determinants of the radiation regime (Kellomaki et al. 1986), canopy closure, size of bare core and stand self-pruning (Mäkela 1997). Crown dimensions are dependent on the species, locality (i.e. soil and climatic conditions) and especially on the growth space (i.e. stand structure and competition). Tree production tightly correlates with the whole crown surface area or with the sunny exposed surface area, i.e. its effective part (Assmann 1968; Maguire, Hann 1988). Thus, crown dimensions enable good approximation for evaluation of leaf or needle amounts under favourable irradiances. Crown length is the parameter easiest to measure.

This study is focused on the determination of allometric relationships in Norway spruce aboveground organs. These allometric relationships will form the input into eco-physiological studies and growth or C uptake models, e.g. MAESTRO (Wang, Jarvis 1990). Furthermore, this study partially helps to cover a lack of information for the calculation of C sink in young forests or small wood mass in Central Europe.

MATERIAL AND METHODS

Experimental site: Experimental plot (EP) is situated at the Experimental Ecological Study Site Bílý Kříž (Czech Republic, 49°30´N, 18°32´E, 908 m a.s.l.) in the Beskids Mountains. The EP is located in a moderately cold and wet region. The climate there (over the last 10 years) has been characterized as cold (annual mean temperature 5°C), humid (annual mean air humidity 80%) with a high amount of precipitation (from 1,100 to 1,400 mm annually). The time duration of the growing season is on average 190 days (over the last 10 years). The soil type is classified as Ferric Podzol, which lies on the parent material/bedrock – sandstone (flysch type). The soil texture is loamy/sand-loamy, created from 30 to 40% by gravel. Soil depth is 60–80 cm. Fertilization was applied three times at a dose of 3 t/ha by dolomite limestone (in 1983, 1985 and 1987).

All measurements were done on 20-years-old (stand age is 16 years) Norway spruce (*Picea abies* [L.] Karst.) trees grown within the plot 12 × 10 m. EP represented the entire surrounding spruce monoculture, located on a gently descending slope of SSW orientation. Stand density was approximately 3,100 trees per hectare. Mean values (± standard error, SE) of H and dbh were 7.0 ± 0.2 m and 8.4 ± 0.4 cm, respectively. Mean index of competition was 2.6 ± 0.3. Mean (± SE) dimensions of the tree crown were: 6.5 ± 0.5 m in length and 2.5 ± 0.2 m in maximal diameter. The mean crown projection area was 4.9 ± 0.6 m^2. In total, 37 trees were sampled.

Experimental design: stem diameter at the living crown base (DCB, at a constant height of 0.5 m above the ground), stem diameter (dbh) and sapwood area (SA) at breast height, and crown diameter at the crown base (Dc) were measured before tree cut. Tree height (H) and living crown length (Hc) were measured after tree cut. The sapwood proportion was estimated by a translucent method upon inspection of cores removed from 23 trees. In order to simplify the crown shape evaluation in practice, mean Dc was estimated from distance measurements between the opposite points of the crown boundary. Then, the crown projected area (Cp) was taken as a surface area of the circle. Crown shape was assumed to be conical, and then the surface area of the crown envelope (Ca) as well as crown volume (Cv) were derived from Dc and Hc. Other characteristics describing e.g. the crown shape as the crown ratio (Cr; i.e. living crown length to crown radius at crown base ratio) or the ratio of crown width to stem diameter at breast height (Dcs = Dc/dbh) characterizing the growth space (Assmann 1968) were also derived.

To evaluate the tree position within the plot, tree competition index (Ic) was calculated using the formula presented by Avery and Burkhart (1983). Four neighbouring trees were included in this formula.

Branch cutting was done per one meter high sections (upward from the bottom of the canopy) in all trees. Sampled branches of each section were collected together and dried (100°C, 48 h). A representative branch of average length was chosen from each section. The shoots of sampled branches were split into three age classes: c – current, c-1 – one year old and r – rest, i.e. older parts of the branch. Then, the following structural parameters were assessed: specific leaf area (SLA, i.e. dry weight to fresh projected needle area ratio), specific branch area (SBA), dry needle (LB) and branch (BB) mass, projected needle area (LAp), and total surface branch area (BAt).

The LI-3000A Portable Area Meter (LI-COR, Lincoln, NE) was used for the estimation of fresh projected needle area. The needles were dried at a temperature 100° for two days and weighed to the nearest 0.001 g (Sartorius, Japan). The total needle surface area (LAt) was established as LAp multiplied by the conversion coefficient 2.57 (Waring 1983).

The surface branch area was calculated from the known lengths and diameters (in a middle part) of all individual shoots detached from the sampled branches. Dry mass was estimated with different accuracy for the representative branches (i.e. shoot age class, Sartorius, Japan) and for the total section mass (laboratory scale, Poland, precision 1 g). The projected area of branch (BAp) equals to the BAt divided by π. Percentage representations of individual age classes were calculated and subsequently used for the determination of the dry weight and surface area of appropriate needle-shoot age classes within the whole section branches. These accurate proportion data were used for the mass and area assessment of all sample trees except the forked ones.

The stem volume (Vs) as well as the total stem surface area (StA) was obtained as a sum of surface areas or volumes of individual stem sections, when the stems were divided into 1 m long sections in our case. Thus, the total stem volume and/or surface area were estimated from the known length and diameter measured in the middle part of each stem section. Cylindrical shape of the section was assumed. The stem mass (SB) was estimated on the basis of stem volume and stem-wood density. For that, seven small trunk blocks of roller shape were taken along five chosen tree stems and then dried and weighed.

Statistical processing of data: Shapiro-Wilk's test was used to test the normality of data distribution. Correlation coefficient according to Pearson (r) and adjusted regression coefficient (adj. r^2) were obtained using STATISTICA software. We were seeking for the simplest allometric equations in the order 1. linear, 2. linear – logarithmically transformed, 3. exponential of the second degree (i.e. quadratic), 4. common exponential, and 5. polynomial. The equation of the lowest degree with high regression coefficient was chosen as the best and presented in this publication.

RESULTS AND DISCUSSION

Before analysis, three forked trees were rejected from the data set (37 trees) to keep normal distribution of data. Tree height linearly correlated with stem diameter at breast height as well as at the crown base (adj. r^2 = 0.73 and r^2 = 0.70, respectively). After natural logarithmic transformation these correlation coefficients increased negligibly. Proportional relationships between stem and crown dimensions as well as between stem and crown own dimensions separately must exist due to mechanical and physiological demands.

Tree height correlated less with the crown parameters than with stem diameter at breast height (dbh), except the crown length and crown ratios (Cr, Dcs). Crown ratio (Cr) has the worst correlation with other characteristics in defiance of Assmann (1968). Moreover, when the stem volume, a combined characteristic of both tree height and dbh, was used instead of each parameter separately, correlation coefficients were the same as for dbh only. In the log-log scale, correlation coefficients did not show any changes, except the relationship between tree height and crown surface area (r increased from 0.89 to 0.94).

In spite of the crown shape simplification, crown volume and surface area well correlated with the stem proportions and appeared to be strongly dependent on the tree position within the stand (described by index of competition – Ic; r = –0.88, and r = –0.90, respectively). Tree competition index correlated significantly also with the stem volume, stem, branch and leaf masses, and surface area (r varied from –0.87 to –0.92). The disproportion between stem and crown dimensions could arise due to: (1) growth space changes, e.g. natural damage, thinning etc., (2) competition and priority in assimilate redistribution, (3) mineral supply changes, e.g. fertilization, and (4) variation of microclimatological factors, e.g. radiation, wind, frost etc. (e.g. Assmann 1968; Waring 1987).

The allometric formulas were presented to derive stem, branch or leaf mass and surface area for three different shoot age classes (Fig. 1, Table 1). The values of crown surface area (or crown volume) appeared to be a better predictor than dbh for branch, leaf biomasses and surface areas of all presented shoot age classes, especially the current ones. dbh had correctly predicted branch and leaf mass and surface area values of shoot age classes older than two years. The measured parameters correlated exponentially with dbh and linearly with crown surface area as well as with crown volume. We concluded that the aboveground plant organ mass/area was more sensitive to changes in dbh than the crown surface area or crown volume. Yet, in eco-physiological studies, crown parameters are important for precise prediction of different plant organs mass/area in relation to its age. Tree height appears to be an improper predictor comparing to dbh, however its (or crown length) incorporation into the allometric relationship enhanced the coefficient of determination (Dean, Long 1992; Mäkela 1997).

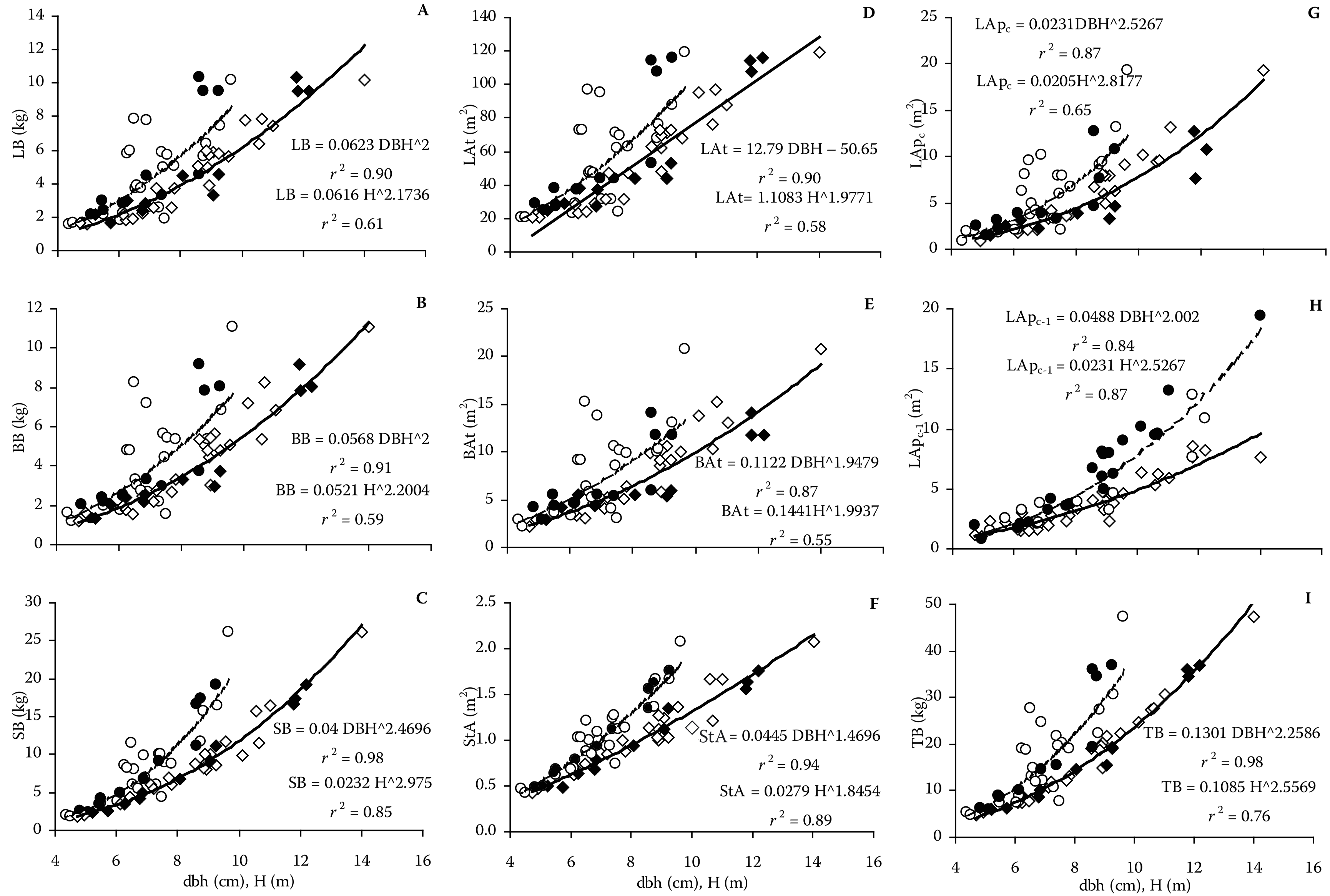

Fig. 1. Allometric relationships between stem diameter at breast height (dbh, diamonds, solid line) or tree height (H, circles, dashed line) and leaf dry mass of tree (LB; A), branch mass (BB; B), stem mass (SB; C), total leaf surface area (LAt; D), total branch surface area (BAt; E), total stem surface area (StA; F), projected needle area of all current needles (LAp_c; G), projected needle area of one-year old needles (LAp_{c-1}; H), and total aboveground mass (TB; I). Full circles or diamonds represent inner trees, empty marks represent other surrounding sampled trees; total $n = 34$

Table 1. Allometric relationships between crown surface area (Y = a Ca + b) and branch or leaf mass and surface area of different needle-shoot age classes. BB – total branch mass, Ca – crown envelope surface area, LB – total leaf mass, BAt – total branch surface area, LAt – total needle surface area (LAt = 2.57 LAp) , LAp – projected needle area, TB – total aboveground mass; low indexes describe needle-shoot age class: c – current, c-1 – one year old, *r* – older age class, adj. r^2 – adjusted regression coefficient

Y	a	b	adj. r^2	Y	a	b	adj. r^2
BB	2.488/10	–2.336	0.96	BAt	3.398/10	–1.264	0.92
BB_c	$1.764/10^{-2}$	–0.190	0.85	BAt_c	$5.500/10^{-2}$	–0.382	0.85
BB_{c-1}	$2.082/10^{-2}$	–0.188	0.87	BAt_{c-1}	$4.396/10^{-2}$	–0.034	0.68
BB_r	2.103/10	–1.958	0.96	BAt_r	2.333/10	–0.382	0.95
LB	2.906/10	–2.692	0.93	LAt	3.451	–16.851	0.96
LB_c	$6.748/10^{-2}$	–0.777	0.91	LAp_c	3.246/10	–3.338	0.92
LB_{c-1}	$5.476/10^{-2}$	–0.530	0.89	LAp_{c-1}	2.291/10	–1.830	0.88
LB_r	1.684/10	–1.385	0.90	LAp_r	6.918/10	–4.827	0.91
TB	1.0913	–10.5433	0.95				

The bare inner core (i.e. non-foliated area in the central region of crown) was not taken into consideration for the crown volume calculation. It is presumed that the size of the bare core is proportionally increasing with the crown volume enlargement and with the irradiance reduction inside of the crown (Jack, Long 1992). The relatively high priority of carbohydrate allocation to branches thereby reduces their availability for the stem mass production. Hence, the bare inner core played an important role in the proportion of both leaf and branch mass, and the crown and stem parameters. Long and Smith (1990) showed similarly that the leaf to the whole crown mass ratio dropped stepwise with the increase in crown dimensions.

Ludlow et al. (1990) and Mäkela and Sievanen (1992) presented crown length and crown surface area to be the best parameters for leaf biomass evaluation by allometric functions. Zeide and Pfeifer (1991) found the linear relationship (in log-log scale) between leaf biomass and crown surface area for ten coniferous species. Some relationships between mean crown size and stem wood production were by analogy found independent of conifer species and stand density (Smith et al. 1991; Jack, Long 1992).

On the basis of correlation coefficient estimation, the set of "linear-like" and exponential allometric equations was used for the aboveground organ mass evaluation and comparison with measured data. Exponential equations showed higher averaged values of errors for the calculation of stem (2.7%), branch (10%) and leaf (3.9%) mass of stand. These errors varied positively less comparing to the variation of linear-like equation errors for individual trees. The averaged errors for the total aboveground mass estimation were similar 1.9% and 1.4% for exponential and linear-like equations. For the presented data, the average errors in total aboveground mass retrieval as a sum of estimates of individual component mass were: (*i*) 3.3% (exponential equations used), and (*ii*) 1.2% (linear-like equations used).

The paper of Wirth et al. (2004) dealing with five Central European countries (including the CR) is a source of allometric equation for *Picea abies*. Unfortunately, this paper presents allometric equations for individual components, but the equation for total aboveground mass derivation is missing. Summarization of individual components leads to uncertainty and error propagation as shown above, especially if exponential equations are used.

The coefficient of correlation between sapwood area and leaf surface area was very high (r = 0.96). The relationship between sapwood and leaf areas supported the pipe model theory (Shinozaki et al. 1964). Each tree upheld 0.45 ± 0.08 (m^2/cm^2) of the projected leaf area (LAp) per unit of sapwood area (SA). This ratio ranged for the individual trees from 0.38 to 0.63. O'Hara et al. (1999) published the mean value of LAp/SA (SA estimated at the crown base) to be 0.422 for *Picea abies* (Germany). Significant correlations between tree competition index and LAp (r = –0.90) and between tree competition index and SA (r = –0.90) were found. Thus, the relationship between leaf area and SA was site-specific. A decrease was expected with a decrease in the tree age and height (McDowell et al. 2002). Factors influencing this relation were similar like in the case of crown – stem relation, but they differed in principles and functions (e.g. Robichaud, Methven 1992; Shelburne, Hedden 1996). SA highly correlated with all aboveground organ mass and surface area and its individual age classes ($r > 0.87$; except current branch mass, $r = 0.76$, and one year old branch surface area, $r = 0.85$). The high correlation was observed especially between SA and stem mass/surface area/total aboveground mass ($r = 0.99$). Unfortunately, SA is obtained destructively.

CONCLUSIONS

The set of allometric equations to predict aboveground plant organ mass and surface area of young Norway spruce trees (with dbh in the range from ca 5 to 15 cm) was presented. They partially fill a lack of functions for trees below the merchantable wood threshold. dbh appeared to be a better and more easily measurable parameter for the evaluation of different spruce organ mass or surface area than the tree height (H) was. On the basis of our results, in forest practice it should be sufficient to measure dbh only for the calculation of total aboveground mass.

Crown surface area (Ca) and crown volume (Cv) correlated well with stem dimensions. dbh, H, Ca and Cv were strongly dependent on the tree position within the stand (evaluated by index of competition, Ic). Other stem and crown parameters (including the sapwood area) and mass and surface area of aboveground organs (per needle/shoot age classes) also decreased significantly with increasing Ic. In forest practice and management, Ic should be affected by thinning impacts.

Even in the case of high crown shape simplification (i.e. cone), Ca and Cv were shown to be very important characteristics for estimation of the mass and/or surface area of aboveground organs according to their age. Thus, measurement of crown dimensions was found to be crucial for precise evaluation of mass and/or area of aboveground plant organs. dbh most correctly predicted the total aboveground, branch and leaf mass/surface area, particularly of older (> 2 years) needle-shoot age classes. The incorporation of any other stem or crown parameters into these allometric equations showed only a negligible influence on the resulting mass/surface value accuracy.

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Alometrické vztahy pro plochu povrchu a biomasu nadzemních orgánů mladého smrku ztepilého

ABSTRAKT: Alometrické vztahy pro přesné stanovení plochy povrchu a biomasy kmene stromu a tří ročníků jehlic a větví smrku ztepilého (*Picea abies* [L.] Karst.) z parametrů kmene a koruny byly získány při destrukční analýze 34 mladých smrků rostoucích v 16leté smrkové monokultuře v Moravskoslezských Beskydech. Výsledky ukazují vysokou korelaci (r > 0,98) parametrů kmene – výčetní tloušťky (dbh), objemu (Vs) a plochy vodivé části běle (SA) s povrchem a biomasou kmene a celkovou nadzemní biomasou stromu. Parametry koruny (tvar~ kužel) – objem (Cv) a plocha povrchu (Ca) nejlépe korelovaly s biomasou (r > 0,92) a plochou povrchu (r > 0,85) mladých ročníků větví a jehlic. Podle dbh lze přesněji stanovit plochu povrchu a biomasu starších (> 2 r.) ročníků jehlic a větví. Stanovené parametry kmene a koruny: dbh, SA, H, délka koruny, Ca a Cv vykazují vysokou negativní závislost na indexu kompetice (r > –0,81), proto je lze modifikovat pěstebními zásahy.

Klíčová slova: alometrie; biomasa; *Picea abies*; běl; plocha povrchu

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