



Similar foliage area but contrasting foliage biomass between young beech and spruce stands

Porovnateľná plocha avšak kontrastná biomasa asimilačných orgánov medzi mladými porastmi buka a smreka

Bohdan Konôpka^{1,2}*, Jozef Pajtík^{1,2}

¹National Forest Centre-Forest Research Institute Zvolen, T. G. Masaryka 2175/22, SK – 960 92 Zvolen, Slovakia

²Czech University of Life Sciences, Faculty of Forestry and Wood Sciences, Kamýcká 1176, CZ – 165 21 Prague, Czech Republic

Abstract

The study focuses on two young stands of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) of the same age (12-year-old) with similar sized trees grown at near identical sites. After performing a destructive sampling technique which included all tree compartments except fine roots; allometric equations were constructed for all tree components. Diameter at stem base (d_0) was utilized as an independent variable for the equations. The models expressed not only biomass of woody parts (branches, stem and coarse roots) and foliage but also foliage area and specific leaf area (SLA). Results indicate that the basic morphological properties of foliage vary in both species along the vertical crown profile. In spruce, contrasting values of needle area and SLA were recorded among needle sets (based on year of establishment). On a tree level, both spruce and beech had similar foliage areas however, beech had a larger biomass comprising of woody parts while spruce biomass was dominated by foliage. Therefore the leaf mass ratio (LMR) defined as the ratio between foliage biomass and total tree biomass, as well as leaf area ratio (LAR) defined as the ratio between leaf area and total tree biomass were much larger in spruce than in beech species. On a stand level, spruce manifested a higher value ($18.64 \text{ m}^2 \cdot \text{m}^{-2}$) of leaf area index (LAI) than beech ($12.77 \text{ m}^2 \cdot \text{m}^{-2}$). Moreover, while the biomass of foliage was 4.6 times higher in spruce than in beech, total biomass of woody parts were similar in both stands. These contrasts indicate very different growth strategies and biomass allocations between beech and spruce at the young growth stages.

Keywords: *Fagus sylvatica*; *Picea abies*; leaf area index; specific leaf area; woody and foliage biomass

Abstrakt

Výskum sa zamerl na mladé porasty buka lesného (*Fagus sylvatica*) a smreka obyčajného (*Picea abies*) rovnakého veku (12 rokov), veľmi podobných dimenzií stromov, rastúcich na totožnom stanovišti. Na základe odberu vzorníkov celých stromov (všetky časti okrem jemných koreňov) sme skonštruovali alometrické vzťahy pre stromové komponenty. Ako nezávislá premenná sa použila hrúbka na báze kmeňa (d_0). Modely vyjadřili nielen biomasu konárov, kmeňa, hrubých koreňov a asimilačných orgánov, ale aj plochu asimilačných orgánov a špecifickú listovú plochu (specific leaf area; SLA). Zistili sme, že základné morfológické vlastnosti asimilačných orgánov variovali pri obidvoch drevinách pozdĺž vertikálneho profilu koruny. V prípade smreka sa zistili odlišné hodnoty plochy ihlič a SLA medzi jednotlivými ročníkmi ihlič. Na úrovni stromu mali buky oveľa viac biomasy drevných častí ako smrek, opačná situácia bola pri asimilačných orgánoch. Preto hodnoty podielu medzi biomasou asimilačných orgánov a celkovou biomasou stromu, ako aj pomeru medzi plochou asimilačných orgánov a celkovou biomasou stromu boli výrazne vyššie pri smreku než buku. Na úrovni porastu mala smrečina vyššie hodnoty indexu listovej plochy, t. j. LAI ($18,64 \text{ m}^2 \cdot \text{m}^{-2}$) v porovnaní s bučinou ($12,77 \text{ m}^2 \cdot \text{m}^{-2}$). Kým biomasa asimilačných orgánov bola 4,6-krát väčšia v smrekovom než v bukovom poraste, biomasa drevných častí bola porovnateľná v obidvoch porastoch. Tieto kontrasty naznačujú výrazne odlišnú rastovú stratégiu, resp. alokáciu biomasy medzi bučinami a smrečinami v mladých štádiách.

Kľúčové slová: *Fagus sylvatica*; *Picea abies*; index listovej plochy; špecifická listová plocha; biomasa asimilačných orgánov a drevných častí

1. Introduction

Foliage plays a crucial role in the growth and development of woody tree parts as they are the principal photosynthesizing organs. Besides photosynthesis, leaves store carbohydrates and mineral nutrients, thus, they are an important tree compartment for carbon sequestration (Kozłowski & Pallardy 1997). Moreover, foliage is relatively short-living tree organ and in addition to photosynthetic and respiratory functions, it can contribute substantially to biochemical cycling in the forest ecosystem including carbon fluxes (Vogt 1991; Härkönen et al. 2010). At the same time, they are very

responsive to external factors as well as subjected to phenological cycles and growth rhythmus (Bussoti et al. 2000). In studies by Barna (2004) and Ciosa et al. (2012) significant modifications on beech foliage size and mass density was identified in response to contrasting light conditions.

Reich et al. (1998) explained that specific leaf area (SLA) is the most frequently used indicator of leaf structure. By definition, leaves will have a lower value of SLA if they are denser (e.g. a greater mass per volume) or thicker. Besides the morphological meaning of SLA, the indicator can serve as a conversion factor by converting foliage weight to foliage area. In general, the quantity of particular compartments of

*Corresponding author. Bohdan Konôpka, e-mail: bkonopka@nlcsk.org, phone: +421 45 5314 323

the tree body can be expressed by allometric equations, usually implementing tree height or diameter (often measured 130 cm from the ground level i.e. at breast height; DBH) as independent variables (West 2009). Pajtk et al. (2008) suggested that while allometric relations were frequently developed for older stands, young forests were usually omitted. This applies for both woody parts of trees and foliage. Estimates of foliage biomass in young European beech and Norway spruce on a local scale were created in the Czech Republic by Kantor et al. (2009). Xiao & Ceulemans (2004) developed allometric equations for both branch and tree levels in young Scots pine (*Pinus sylvestris*). The authors considered branch level and vertical position of whorl as an independent variable in the equations. In general, research that considers both foliage biomass and SLA are lacking.

Information on foliage mass or more specifically foliage area, relative to the mass of woody components in trees can identify the efficiency of tree individuals (or tree species) to apply assimilatory organs for total tree growth. The leaf mass ratio (LMR); the ratio of the leaf dry mass to the total dry plant mass as well as the leaf area ratio (LAR); the ratio of the leaf area to the total dry plant mass have been used to describe the interaction between ecological structure and tree production (e.g. Pickup et al. 2005; Shipley 2006; Milla et al. 2008). Further studies use tree leaf mass or leaf area relative to production of woody compartments to estimate growth efficiency on a tree or stand level (e.g. Jack et al. 2002; Konôpka et al. 2010; Konôpka & Pajtk 2013).

Leaf area index (LAI) is a stand characteristic which very closely correlates to net primary production, stand transpiration and rainfall interception of forests (e.g. Herbert & Fownes 1997; Gower et al. 1992; Van Dijk & Bruijnzeel 2001). LAI is defined as one-sided green leaf area per unit ground surface in broadleaf canopies. For coniferous species, three different definitions have been alternatively used: (i) total needle surface area per unit ground level, (ii) half of the total needle surface area per unit ground area and (iii) projected needle area per unit ground area. While definitions (i) and (ii) are reality more exact, (iii) is the most practical concept for measurements, therefore, is most frequent used.

In a review by Bréda (2003) ground-based measurements of LAI were considered controversial and a basic approach for establishing LAI was suggested by measuring leaf area on a sub-sample of foliage and related to dry mass (e.g. SLA). Finally, the total dry mass of foliage collected within a known ground-surface area is converted into LAI by multiplying by SLA. However, the protocol of foliage sampling must respect the variability of leaf size and density, especially in terms of light availability (e.g. Closa et al. 2012). Most probably, light diffusion on the foliage depends mainly on the crown position in the canopy and the location of foliage along the tree crown. In fact, different foliage growth and retention strategies between species (especially evergreens versus deciduous) in relation to light availability might be important for carbon stock and cycling in forest ecosystems and should be considered in forest management. Thus, such knowledge might be implemented, for instance in creating the ideal tree species composition in forests with the aim to sequester carbon and mitigate climate change.

The paper shows allometric equations using tree size (stem diameter) as an independent variable for both foliage and woody biomass as well as foliage area in young European beech and Norway spruce trees. The model for foliage area considers intra-stand and intra-crown variability with complexity mainly in spruce trees. The principal goal of the work is to make inter-specific comparisons in foliage mass and foliage area (i.e. LAI) between young stands of beech and spruce with regard to standing stock of woody parts. The final goal is to discuss inter-specific differences in foliage biomass (foliage area) and woody parts biomass as well as the ratio between quantities of foliage and woody components in terms of physiological and ecological aspects.

2. Materials and methods

2.1. Site and stand description

The site (see also Konôpka et al. 2013) is situated in the southern part of the Veporske Hills (48° 38' 55"N and 19° 36' 07" E) and belongs to the geographical unit of the Slovak Ore Mountains. The prevailing bedrock is granodiorit, soil Humic Cambisol, with low portion of skeleton, pH (in H₂O) was 5.13, 5.23, and 5.38 at soil depths 0–10, 10–35, and 35–65 cm respectively. The altitude is 960 m a.s.l. and the annual sum of precipitation is close to 900 mm, the mean annual temperature is 5.5 °C.

Two neighboring stands of nearly pure European beech (*Fagus sylvatica*) and pure Norway spruce (*Picea abies*), both naturally regenerated, with the same ages (about 12 years) were studied. The young beech forest is ca. 0.5 ha large and consists predominantly of dense stands of beech with few scattered gaps that are colonized by *Calamagrostis epigejos* dominating grass. The young spruce forest is ca. 0.7 ha large and has a similar spatial structure to that of the beech stand.

2.2. Measurement and sampling

To measure tree heights and stem diameters d_0 (on the ground level), five circle-like plots were established in both the beech and spruce stands during the early growing season in 2011. The plots, with a radius of 100 cm, were fixed in the stands and incorporated around 40 trees each. The central tree of the plot was labeled with a plastic strip. Then, all of the trees within the circle were marked with iron tags with consecutive numbers. Tree heights and diameters d_0 were measured on labeled individuals.

Beech (60 pieces) and spruce (80 pieces) trees were sampled outside of the circle plots in September 2011. All tree components excepting roots with diameter under 1 mm (very fine roots) were evaluated. Height and diameter d_0 of the sampled trees were measured. The trees were divided into foliage and other (woody) components, i.e. branches, stem and coarse roots. Of the woody compartments, stems were exposed to the most detailed measurements. Specifically, the stems were divided into 4 or 5 length sections. Then, the volume of each section was calculated according to Newton's formula:

$$V = L * (A_b + 4 * A_m + A_s) / 6$$

where V is the section volume, L the section length, A_b the cross-sectional area at the larger end, A_m the cross-sectional area at the midpoint, A_s the cross-sectional area at the smaller end.

Then, all tree components were oven-dried (temperature of 95 °C) for a few days and finally the dry masses of woody parts (branches, stem, coarse roots) and foliage were weighed.

For additional foliage sampling extra 40 beech and 40 spruce trees were selected from the stands, outside of the circle plots. The trees were chosen to cover the entire diameter range recorded in the plots. Height and diameter d_0 of the trees were measured and samples of foliage were taken from the upper, middle and lower third of the crowns. Three beech foliage and 30 spruce needles were sampled from each crown part (upper, middle and lower). As for spruce needles we sampled all needle sets, i.e. established in 2011, 2010, 2009, 2008, 2007, rarely in 2006.

The individual beech leaves and groups of 10 spruce needles were scanned on the scanner EPSON Expression 10000, then, oven-dried at a temperature of 95 °C for 48 hours and weight. The areas of the foliage were measured by the “Leaf Area Measurement” software.

Moreover, 16 spruce samples were selected and their needle biomass divided according to year of establishment. They were subsequently oven-dried and weighed. This measurement was required for the estimation of needle set (divided by year of establishment) as a contribution to total needle biomass.

2.3. Mathematical and statistical procedures

To construct allometric relations for biomass of woody parts (branches, stem and coarse roots) and foliage against diameter d_0 , data originating from 80 spruce samples and 60 beech samples were implemented. Biomass of the tree components was expressed as:

$$W_i = e^{(b_0 + b_1 \ln DAB)} * \lambda$$

where W_i is the biomass of a particular component (woody parts or foliage), d_0 is the diameter at stem base, b_0 , b_1 and b_2 are coefficients, λ is transformation bias. Detailed procedures for the construction of this type of relationship is given for instance in Pajtkî et al. (2008).

Then, total foliage area (LA) on a tree level against stem diameter d_0 was expressed by using data on foliage biomass (W_f) and specific leaf area (SLA):

$$LA = W_f * SLA$$

where W_f is based on allometric equation:

$$y = e^{(b_0 + b_1 \ln d_0)} \lambda_1$$

and similarly SLA as:

$$y = e^{(b_2 + b_3 \ln d_0)} \lambda_2$$

After implementing both relationships the following formula was devised:

$$LA = (e^{(b_0 + b_1 \ln d_0)} \lambda_1) (e^{(b_2 + b_3 \ln d_0)} \lambda_2) = e^{(a_0 + a_1 \ln d_0)} \lambda$$

where $a_0 = b_0 + b_2$, $a_1 = b_1 + b_3$ and $\lambda = \lambda_1 \lambda_2$.

In fact, LA was expressed on a tree level by using SLA data typical for the middle part of the crown. This simplified procedure was used after finding that the foliage in the middle crown was representative as the average SLA with foliage from upper and lower portion of the crown showing extreme values.

As for LAI in beech, the following approach was implemented: LA was calculated for each tree recorded on the circle plots using individual value of d_0 . Consequently, sum of LA for all trees on a plot represents total LA on the plot with a known area. Then, total LA on a plot divided by the plot area represents LAI on a plot base. Final (average) LAI for the beech stand was expressed as:

$$LAI_j = \frac{\sum LA_{ij}}{S_j}$$

where LA_{ij} is leaf area for i -tree on the j -plot and S_j is area on the j -plot.

In case of LAI for spruce, the procedure was more difficult because of the different needle sets (divided by the year of birth) manifest contrasting values of SLA. Therefore, each needle set on a tree level was considered and expressed separately. Biomass of k -needle set for all trees on j -plot (W_{jk}) was as follows:

$$W_{jk} = \sum_{i=1}^n W_{ij} * P_k$$

where n is the number of tree on the plot, P_k is the contribution of k -needle set on the total needle biomass.

To evaluate the contribution of k -needle set to the total needle biomass, data from 16 spruce samples (dry masses of needle sets were measured separately with regard to year of establishment) were utilized. Since no statistical differences were found for the contributions of the needles sets to total needle biomass among trees with different sizes (i.e. diameters d_0), mean values of P_k for specific needle sets were used for further calculations regardless of tree size. Calculation of SLA in spruce was done by using the same concept as in the beech stand, meaning that data was considered on needle properties from the middle part of crowns. LA for k -needle set and for j -plot was expressed as:

$$LA_{jk} = \sum_{i=1}^n (W_{ij} * P_k * SLA_{ijk})$$

Consequently LAI was calculated for j -plot as follows:

$$LAI_j = \frac{\sum_{k=1}^p LA_{jk}}{S_j} = \frac{\sum_{i=1}^n \sum_{k=1}^p (W_{ijk} * P_k * SLA_{ijk})}{S_j}$$

Then, LMR is defined as the ratio between biomass of foliages to whole-tree biomass:

$$LMR = \frac{W_l}{W_w}$$

Similarly, LAR is characterized as ratio between leaf area to whole-tree biomass:

$$LAR = \frac{TPLA}{W_w} = \frac{W_l * SLA_p}{W_w}$$

where $TPLA$ is the total projected leaf area, W_l is the biomass of foliage, W_w is the whole-tree biomass and SLA_p is one-sided specific leaf area.

All statistical analyses were performed by the Statistica 10 (Statsoft, Tulsa, USA) program package.

3. Results

Two forest stand complexes; one comprising of beech and the other spruce trees had not only similar ages but also other similar characteristics on a stand level (Table 1). Similarities existed especially in volume of mean stem (501 cm³ and 647 cm³ in beech and spruce, respectively), and in basal area measured on the ground level (69.5 m².ha⁻¹ and 80.2 m².ha⁻¹ in beech and spruce, respectively). Certain contrasts were recorded for height to diameter ratio (125.9 cm.cm⁻¹ and 76.3 cm.cm⁻¹ in beech and spruce, respectively). The contrasting ratio in the stands is related to inter-specific differences between height and diameter on a tree level, which was observed for individual trees of all sizes (Fig. 1).

Table 1. Stand characteristics (average ± standard error) for European beech and Norway spruce.

Stand characteristics	European beech	Norway spruce
Number of trees [ths.ha ⁻¹]	125 ± 12	98 ± 7
Mean tree height [cm]	287 ± 22	211 ± 5
Mean diameter d_0 * [cm]	2.66 ± 0.12	3.23 ± 0.11
Height to diameter d_0 ratio [cm.cm ⁻¹]	125.9 ± 8.5	76.3 ± 2.5
Volume of mean stem [cm ³]	501.1 ± 56.7	646.6 ± 34.5
Basal area* [m ² .ha ⁻¹]	69.5 ± 7.0	80.2 ± 4.6

* Both diameter d_0 and basal area were measured at ground level.

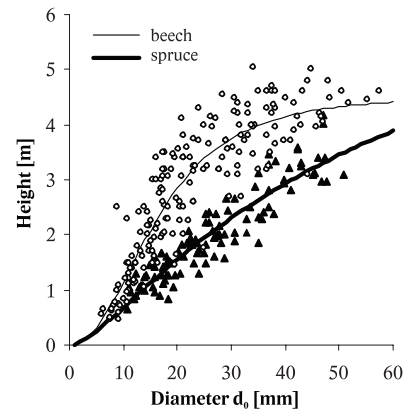


Fig. 1. Relationship between stem diameter d_0 and tree height in beech and spruce. Equations for the relationship were as follows: $h_b = \frac{d_0^2}{80.52 + 1.65d_0 + 0.23d_0^2}$ in beech, and $h_s = \frac{d_0^2}{57.58 + 7.69d_0 + 0.11d_0^2}$ in spruce.

Large differences in SLA of foliage were observed in both tree species in terms of foliage position in crowns as well as tree size (Fig. 2a and 2b, Tables 2 and 3). While the highest values of SLA were recorded for leaves and needles in the lower portion of the crowns, the smallest values were observed in the upper part of the crowns. At the same time, value of SLA decreased with increasing tree size. The sharpest decrease of SLA with tree size was found for trees with diameter under ca. 30 mm (i.e. suppressed individuals). At the same time, while SLA of foliage in the middle crown of beech varied between ca. 150 and 500 cm².g⁻¹, the range for spruce needles was from ca. 70 to 120 cm².g⁻¹. Differences in SLA along the crown profile are related to both foliage size

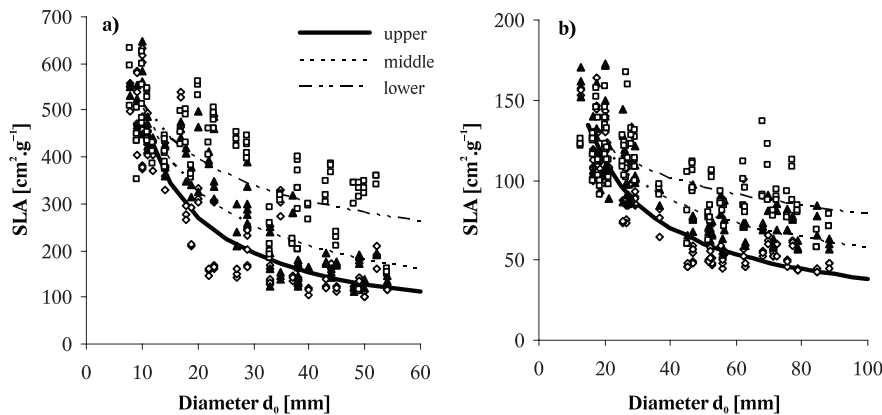


Fig. 2. Relationship between diameter d_0 and SLA in (a) beech and (b) spruce for upper, middle and lower part of the crowns.

Table 2. Statistical characteristics for equations expressing the relationship between SLA in the upper, middle and lower part of the crown in beech, eventually spruce and diameter d_0 .

Species	Part of crown	b_0	(S.E.)	P	b_1	(S.E.)	P	R ²	MSE	λ	S.D.
Beech	Upper	8.020	(0.116)	<0.001	-0.818	(0.035)	<0.001	0.823	0.057	1.030	0.266
	Middle	8.026	(0.110)	<0.001	-0.757	(0.033)	<0.001	0.816	0.051	1.026	0.239
	Lower	7.215	(0.118)	<0.001	-0.416	(0.036)	<0.001	0.544	0.058	1.027	0.230
Spruce	Upper	6.577	(0.087)	<0.001	-0.632	(0.024)	<0.001	0.859	0.022	1.011	0.148
	Middle	6.036	(0.091)	<0.001	-0.42	(0.025)	<0.001	0.713	0.024	1.012	0.160
	Lower	5.637	(0.094)	<0.001	-0.281	(0.026)	<0.001	0.505	0.025	1.013	0.164

Note: abbreviations in the table captions means; b_0 , b_1 – coefficients, S.E. – their standard errors, P – p-value, R² – coefficient of determination, MSE – mean square error, λ – logarithmic transformation bias and S.D. – standard deviation.

Table 3. Statistical characteristics for equations expressing relationship between SLA in the middle part of crown in spruce by needle sets (different years of establishment) and diameter d_0 .

Birth year (age) of needle set	b_0	(S.E.)	P	b_1	(S.E.)	P	R^2	MSE	λ	S.D.
2007+ (5 + rarely 6)	4.890	(0.129)	<0.001	-0.242	(0.034)	<0.001	0.657	0.011	1.005	0.102
2008 (4)	4.955	(0.119)	<0.001	-0.234	(0.031)	<0.001	0.672	0.009	1.004	0.097
2009 (3)	5.179	(0.135)	<0.001	-0.263	(0.035)	<0.001	0.667	0.012	1.006	0.109
2010 (2)	5.542	(0.187)	<0.001	-0.329	(0.049)	<0.001	0.629	0.022	1.011	0.150
2011 (1)	6.036	(0.091)	<0.001	-0.427	(0.025)	<0.001	0.713	0.024	1.012	0.160

Note: abbreviations in the table captions means; b_0, b_1 – coefficients, S.E. – their standard errors, P – p-value, R^2 – coefficient of determination, MSE – mean square error, λ – logarithmic transformation bias and S.D. – standard deviation.

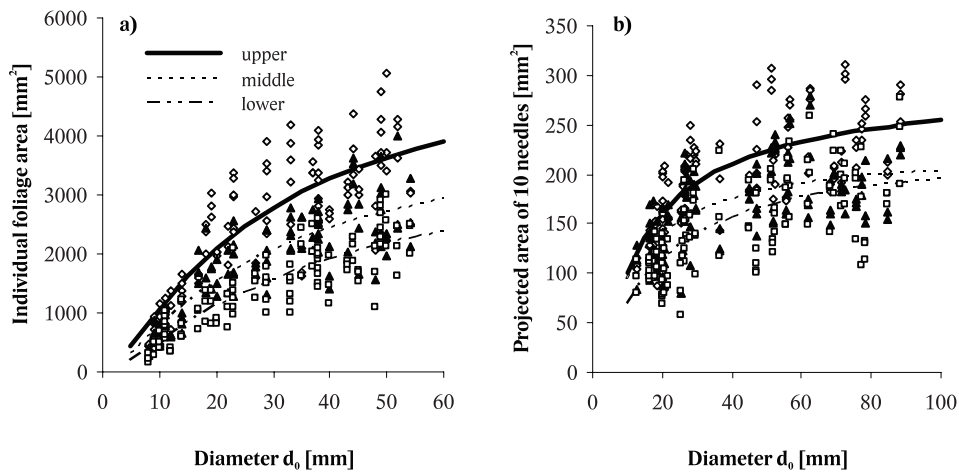


Fig. 3. Relationship between diameter d_0 and individual foliage area in (a) beech and eventually projected area of 10 needles in (b) spruce for upper, middle and lower part of the crowns.

Table 4. Statistical characteristics for allometric relations expressing leaf area in beech, eventually spruce and diameter d_0 .

Species	Part of crown	b_0	(S.E.)	P	b_1	(S.E.)	P	R^2	MSE
Beech	Upper	-0.175	(0.016)	<0.001	-0.013	(0.0005)	<0.001	0.729	377400
	Middle	-0.209	(0.018)	<0.001	-0.015	(0.0005)	<0.001	0.751	187209
	Lower	0.285	(0.024)	<0.001	0.016	(0.0007)	<0.001	0.770	113901
Spruce	Upper	0.408	(0.040)	<0.001	0.059	(0.001)	<0.001	0.546	1223
	Middle	0.359	(0.047)	<0.001	0.066	(0.001)	<0.001	0.384	1082
	Lower	0.547	(0.061)	<0.001	0.066	(0.002)	<0.001	0.471	1106

Note: abbreviations in the table captions means; b_0, b_1 – coefficients, S.E. – their standard errors, P – p-value, R^2 – coefficient of determination, MSE – mean square error, λ – logarithmic transformation bias and S.D. – standard deviation.

(Fig. 3a and 3b, Table 4) and also foliage weight (data not shown). As for foliage size (area), beech leaves in the upper part of crown were approximately twofold large than those in the lower part of crown. Contrasts between spruce needles from the upper and lower part of crown were slightly smaller than those in beech.

To establish further calculations for foliage area on a tree and stand level, SLA originating from the middle part of the crown was utilized as an average value representative of the upper and lower crown. In fact, for estimating foliage area on crown level, the values from all crown parts could not be combined because contribution of foliage from upper, middle and lower portions of the crown to the total foliage biomass was not known. Moreover, it is supposed, that the main portion of foliage existed in the middle of the crown. In spruce trees, large differences in SLA were estimated between the needle sets established in the particular years (from 2007 to 2011). Values of SLA decreased with needle age (Fig. 4 and Table 3). On the other hand, all needle sets show very similar relationships in relation to tree size.

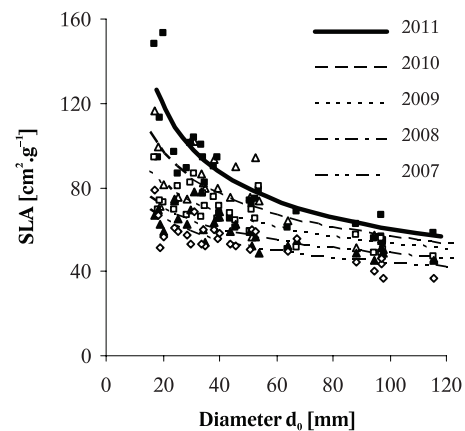


Fig. 4. Relationship between diameter d_0 and SLA in spruce (middle part of crown) by needle sets based on year of establishment (from 2007 to 2011).

Rather surprisingly, contribution of particular needles sets (i.e. 2007, 2008, 2009, 2010, and 2011) to the total needle biomass on the crown level did not show clear con-

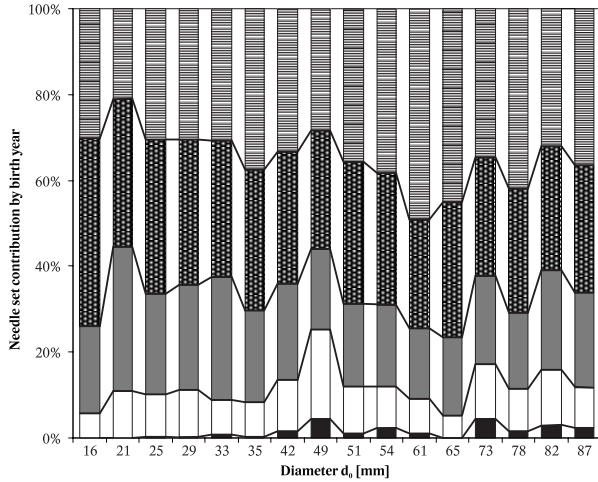


Fig. 5. Contribution of needle sets (established in 2011, 2010, 2009, 2008, and 2007 placed in the bars from up to down) to total needle biomass with regard to tree diameter d_0 (in ascending order).

trasts between trees of different sizes (Fig. 5). Thus, mean proportions of the particular needle sets were used regardless of tree size. Specifically, needle set of 2011 was 34.6%, 2010 was 31.6%, 2009 was 22.0%, 2008 was 10.3%, and 2007 was 1.5% from the total needle biomass.

By combining the equations for SLA and foliage biomass, LA on a tree level (expressed on diameter d_0) was calculated for beech:

$$LA = 1.074 e^{(1.450+2.328 \ln d_0)}$$

At the same time, equations for LA of spruce by needle sets, specifically current-year needles, 2-year-old needles, 3-year-old needles, 4-year-old-needles, 5-year-old (rarely 6-year-old) were:

$$LA_1 = 0.369 e^{(2.957+2.005 \ln d_0)}$$

$$LA_2 = 0.336 e^{(2.463+2.103 \ln d_0)}$$

$$LA_3 = 0.247 e^{(2.1+2.169 \ln d_0)}$$

$$LA_4 = 0.109 e^{(1.876+2.198 \ln d_0)}$$

$$LA_{5+} = 0.016 e^{(1.811+2.19 \ln d_0)}$$

Results of the evaluation on quantity of woody parts and foliage were modeled as well as foliage area with regard to diameter d_0 (Fig. 6a, b and c). Here, the allometric relations for dry masses of foliage and woody parts using diameter d_0 as an independent variable were implemented (Table 5). Contrasting values occurred between the species for woody parts biomass as well as for foliage biomass. On the other hand, beeches and spruces had very similar values of total foliage areas. Thus, for instance while beech trees with a diameter d_0 of 60 mm recorded a dry mass of woody parts of nearly 5000 g, spruce trees of the same diameter had a dry mass of about 2100 g. At the same time, while beech trees with a diameter of 60 mm retained foliage with dry mass around 450 g, spruce trees with the same diameter recorded as much as 1050 g dry mass. Further, foliage areas on trees with diameter d_0 of 60 mm appeared around 7.0 m² and 6.5 m² in spruce and beech, respectively.

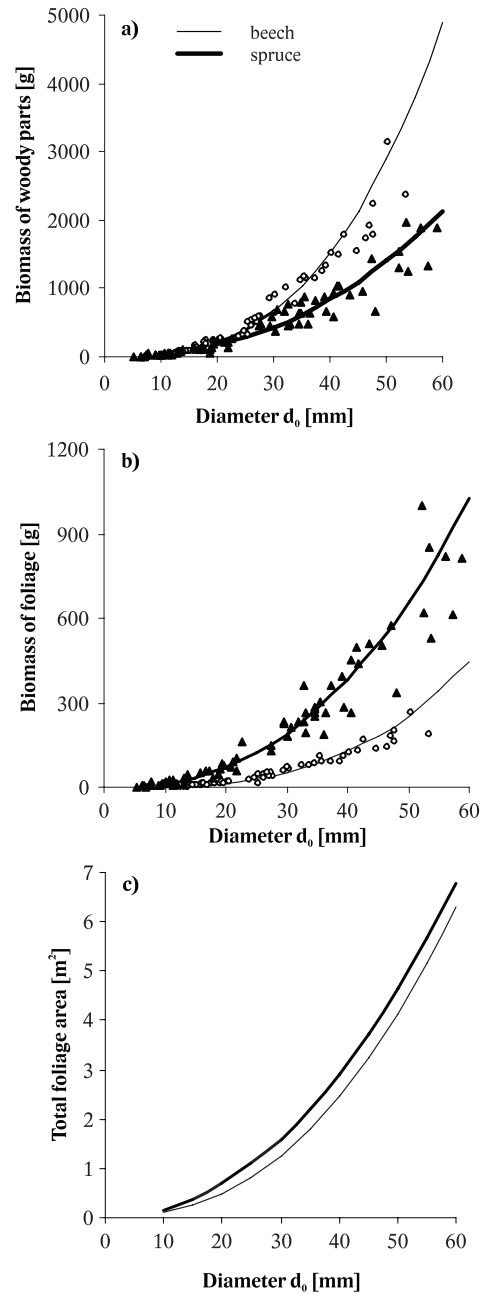


Fig. 6. Relationship between diameter d_0 and biomass of (a) woody parts (branches, stem, coarse roots), (b) foliage and (c) total foliage area in beech and spruce.

Interspecific difference in the proportion of foliage biomass on total tree quantity between beech and spruce are clear by using LMR (Fig. 7a). While value of LMR in beech was around 0.08 (g.g⁻¹), in spruce value was close to 0.30 (g.g⁻¹). In both species, the value slightly increased with increasing diameter d_0 . As for LAR of very small trees (i.e. diameter d_0 of 10 mm), the same value (34 cm².g⁻¹) was recorded in both species (Figure 7b). Then, the values decreased with increasing diameter in both species, but more significantly in beech. Therefore, while beech trees with diameter of 60 mm manifest value of LAR 12 cm².g⁻¹, spruce trees with the same diameter had a LAR slightly over 20 cm².g⁻¹.

Table 5. Statistical characteristics for allometric relations expressing mass of foliage and woody compartments (branches, stem and coarse roots) in European beech and Norway spruce using diameter d_0 as an independent variable.

Species	Compartment	b_0	(S.E.)	P	b_1	(S.E.)	P	R^2	MSE	λ	S.D.
Beech	Leaves	-6.576	(0.256)	<0.001	3.085	(0.081)	<0.001	0.960	0.102	1.047	0.308
	Woody parts	-3.357	(0.191)	<0.001	2.889	(0.060)	<0.001	0.974	0.056	1.027	0.238
	Tree together	-3.318	(0.188)	<0.001	2.900	(0.060)	<0.001	0.975	0.055	1.026	0.234
	Needles	-3.079	(0.171)	<0.001	2.432	(0.054)	<0.001	0.964	0.106	1.053	0.366
Spruce	Woody parts	-1.719	(0.138)	<0.001	2.283	(0.043)	<0.001	0.974	0.069	1.035	0.296
	Tree together	-1.489	(0.134)	<0.001	2.321	(0.042)	<0.001	0.976	0.065	1.034	0.295

Note: abbreviations in the table captions means; b_0 , b_1 – coefficients, S.E. – their standard errors, P – p-value, R^2 – coefficient of determination, MSE – mean square error, λ – logarithmic transformation bias and S.D. – standard deviation.

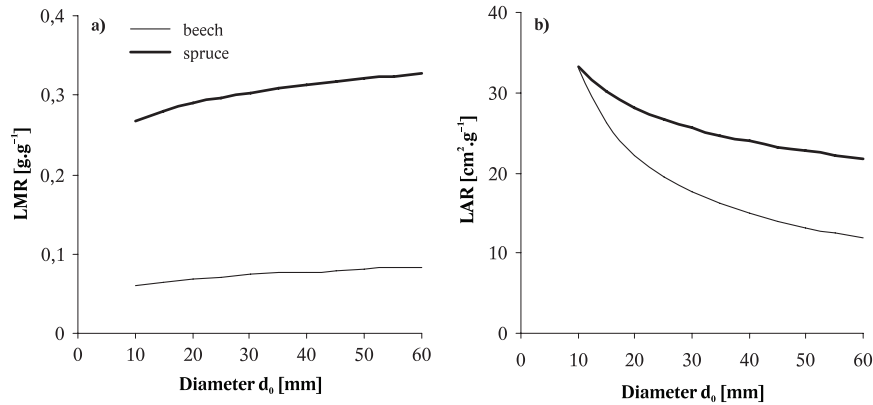


Fig. 7. Relationship between diameter d_0 and (a) LMR and (b) eventually LAR in beech and spruce.

Table 6. Characteristics of foliage and woody parts on a stand level (average \pm standard error) for European beech and Norway spruce stand.

Stand characteristics	European beech	Norway spruce
Weight of foliage [$g.m^{-2}$]	603 \pm 77	2773 \pm 151
Weight of woody components [$g.m^{-2}$]	7195 \pm 824	5980 \pm 322
LAI [$m^2.m^{-2}$]	12.77 \pm 1.7	18.64 \pm 1.08
LMR [$g.g^{-1}$]	0.069 \pm 0.009	0.290 \pm 0.003
LAR [$cm^2.g^{-1}$]	22.2 \pm 2.0	24.7 \pm 0.7

Interspecific differences in biomass were clear also on a stand level (Table 6). Specifically, the beech stand maintained 4.6 times less foliage biomass than the spruce stand (603 $g.m^{-2}$ versus 2773 $g.m^{-2}$). On the other hand, the beech stand shows slightly more biomass stock of woody parts than the spruce stand (7195 $g.m^{-2}$ against 5980 $g.m^{-2}$). At the same time LAI was nearly 50% higher in the spruce stand than in the beech stand (18.64 $m^2.m^{-2}$ and 12.77 $m^2.m^{-2}$, respectively). While only little interspecific differences were recorded for LAR (22.2 $cm^2.g^{-1}$ for beech and 24.7 $cm^2.g^{-1}$ for spruce) more than four times higher values of LMR occurred in the spruce stand (0.290 $g.g^{-1}$) than in the beech stand (0.069 $g.g^{-1}$).

4. Discussion and conclusion

4.1. Tree level biomass estimates

Biomass estimates of woody compartments were higher in beech than in spruce; however the opposite situation occurred for foliage biomass. Similar results in Pajtkî et al. (2011) demonstrate that foliage of coniferous species (Nor-

way spruce and Scots pine) contribute significantly more to the total tree biomass than broadleaf species (European beech and Sessile oak). This knowledge is also in accordance with Konôpka et al. (2010) who found that spruce foliage (considering it as organ of photosynthesis) of young trees produced between two and four times more biomass of woody components than that of beech.

These results suggest large variability of foliage morphological properties (expressed by SLA) along tree crowns and between trees of different dimensions in both beech and spruce. This indicates that light intensity is likely to stimulate both size and tissue density. Closa et al. (2012) recorded a higher SLA for shade foliage in young European beech stands. SLA values similar to this study are recorded for beech leaves by Barna (2004). Specifically, lower values of SLA were estimated in dominant and co-dominant beech trees than in subdominant trees. In addition, value of SLA increased from the upper to lower part of the crown with values ranging from ca. 120 to 460 $cm^2.g^{-1}$ (Barna 2004), 180 – 480 $cm^2.g^{-1}$ (Closa et al. 2012) and 190 – 240 $cm^2.g^{-1}$ (Leuschner et al. 2006). Concerning SLA in spruce, our values are slightly higher than those of Hager & Sterba (1985) who recorded a range of 30 – 70 $cm^2.g^{-1}$ from 17-year-old stand. However, the needles in the upper and middle part of the largest trees were inside the range recorded by Hager & Sterba (1985). In spruce, SLA of needles decreased with age. Gilmore et al. (1995) suggested that current needles of *Abies balsamea* had an SLA approx. by 30% larger than 5-year-old needles.

These results proved very different values of the SLA (ca. 3 times) between beech and spruce and suggesting that the unit of foliage beech biomass is much more efficient as for

size of surface area than spruce. This is further reflected in the ratio between mass of foliage and total tree mass (LMR), i.e. about four times larger in spruce than beech. Besides SLA, lower efficiency of foliage biomass unit in the photosynthesis (or wood production) is most probably related to presence of older needle sets in spruce, which would be less efficient than younger spruce needles (e.g. Freeland 1952). Moreover, it is supposed that older needle sets, as well as needles in the lower part of crown could suffer from lack of light availability and contribute negligible values to tree photosynthesis.

4.2. Stand level biomass estimates

The number of trees in both stands was extremely high and is related to successful natural regeneration in both European beech and Norway spruce stands. It is assumed that the extremely high number of trees alters the light conditions in the stand, especially in the spruce stand where light availability at the ground level was very low. On the other hand, both the beech and spruce stands had some tree-free patches. Even though the patches were avoided during the establishing the plots as diffused side light from the gap edges is possible. It is suggested that the side lighting could contribute to the high number of trees (especially for survival of suppressed trees). In general, light intensity is very important for needle growth and development of structure in foliage (Kozłowski & Pallardy 1997). Gebauer et al. (2012) showed evidence of modifications of xylem structure and even function (especially hydraulic efficiency) in Norway spruce needles as response to light intensity. Moreover, these anatomical adaptations of Norway spruce needles occur for instance due to thinning of the forest stands as higher values of leaf mass per area (parameter opposite to SLA) were found for spruce needles in thinned stands compared to unthinned stands (Gebauer et al. 2011).

On the stand level, an interesting result is that while standing stock of woody parts was comparable in both stands (ca. 20% higher in beech than spruce), huge differences (4.6 fold) were noted in the case of foliage biomass. Moreover, LAI was almost 50% higher in the spruce stand than in the beech stand. LAI in a variety of forest tree species is usually up to $10 \text{ m}^2 \cdot \text{m}^{-2}$ (e.g. Bréda 2003; Eriksson et al. 2006; Leuschner et al. 2006) but exceptionally also slightly over this value (e.g. Albrektson 1980; Ford 1982). These results are usually from older stands and often from man-made forests. On the other hand, Waring & Schlesinger (1985) explain that LAI values in some coniferous forests can be as high as $20 \text{ m}^2 \cdot \text{m}^{-2}$. Nock et al. (2008) found that LAI decreased with increasing tree size in *Acer saccharum* and *Betula alleghaniensis*. Thus, while trees with DBH of 30 cm had LAI of 7.5 and $8.5 \text{ m}^2 \cdot \text{m}^{-2}$; trees with DBH of 70 cm have a LAI of 4.0 and $6.0 \text{ m}^2 \cdot \text{m}^{-2}$ in *Acer* and *Betula*, respectively.

It is supposed that large difference in LAI between the beech and spruce stands is related mainly to their contrasting physiological capacity (for instance low photosynthetic activity of older needle sets in spruce) and also to specific ecological demands (e.g. higher shade tolerance of beech). Moreover, it is expected that the current values of LAI estimated in both stands are close to the maximum thresholds which

could be reached during the whole-life stand development on the site. Further stagnations or declines of leaf areas in the stands are very probable as a result of tree reduction (mortality due to high competition intensity) and also a gradually decreasing LMR as a natural tendency in relations to tree/stand age (see also Konôpka et al. 2010). The conclusion that LAI in older stands are lower is in accordance with findings from comparisons between these results and other studies (e.g. Albrektson 1980; Ford 1982; Bréda 2003; Eriksson et al. 2006; Leuschner et al. 2006).

This study indicates that beech and spruce, at the young growth stages, have contrasting growth strategies that results in specific biomass allocation. Much more assimilates were allocated into the woody parts in beech than in spruce while the opposite allocation pattern was evident for foliage biomass. It seems that beech foliage biomass is more efficient at producing woody tissues (components as branches, stem and coarse roots) than spruce needles. This might relate, besides other factors, to higher values of SLA recorded in beech in comparison to spruce. Moreover, this could be connected to different age structures of assimilatory organs between the tree species. While during growing season, all beech foliage are always from the current year, in our spruce stand as much as two thirds of needle biomass originated from the previous years.

Acknowledgement

The research activities were supported by the Slovak Research and Development Agency (projects APVV-0268-10, APVV-0273-11, APVV-0584-12) and the Ministry of Agriculture of the Czech Republic (contract No. QI102A079). Dr. Jennifer Clear is acknowledged for valuable comments and also language revision on the manuscript.

References

- Albrektson, A., 1980: Relations between tree biomass fractions and conventional silvicultural measurements. *Ecological Bulletins*, 32:315–327.
- Barna, M., 2004: Adaptation of European beech (*Fagus sylvatica* L.) to different ecological conditions: leaf area size variation. *Polish Journal of Ecology*, 52:35–45.
- Bréda, N., 2003: Ground-based measurements of leaf area index: A review of methods, instruments and current controversies. *Journal of Experimental Botany*, 54:2403–2417.
- Bussoti, F., Borghini, F., Celesti, C., Leonzio, C., Bruschi, P., 2000: Leaf morphology and macronutrients in broadleaved trees in central Italy. *Trees*, 14:361–368.
- Closa I., Irigoyen, J. J., Goicoechea, N., 2012: Microclimatic conditions determined by stem density influence leaf anatomy and leaf physiology of beech (*Fagus sylvatica* L.) growing within stands that naturally regenerate from clear-cutting. *Trees*, 24:1029–1043.
- Eriksson, H. M., Eklundh, L., Kuusk, A., Nilson, T., 2006: Impact of understory vegetation on forest canopy reflectance and remotely sensed LAI estimates. *Remote Sensing of Environment*, 103:408–418.
- Ford, E. D., 1982: High productivity in a polestage Sitka spruce stand and its relation to canopy structure. *Forestry*, 55:1–17.
- Freeland, R. O., 1952: Effect of age of leaves on rate of photosynthesis in some conifers. *Plant Physiology*, 27:685–690.

- Gebauer, R. R., Volařík, D., Urban, J., Borja, I., Nagy, N. E., Eldhuset, T. D. et al., 2011: Effect of thinning on anatomical adaptations of Norway spruce needles. *Tree Physiology*, 31:1103–1113.
- Gebauer, R., Volařík, D., Urban, J., Borja, I., Nagy, N. E., Eldhuset, T. D. et al., 2012: Effects of different light conditions on xylem structure of Norway spruce needles. *Trees*, 26:1079–1089.
- Gilmore, D. W., Seymour, R. S., Halteman, W. A., Greenwood, M. S., 1995: Canopy dynamics and the morphological development of *Abies balsamea*: effect of foliage age on specific leaf area and secondary vascular development. *Tree Physiology*, 15:47–55.
- Gower, S. T., Vogt, K. A., Grier, C. C., 1992: Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. *Ecological Monographs*, 62:43–65.
- Härkönen, S., Pulkkinen, M., Duursma, R., Mäkelä, A., 2010: Estimating annual GPP, NPP and stem growth in Finland using summary models. *Forest Ecology and Management*, 259:524–533.
- Hager, H., Sterba, H., 1985: Specific leaf area and needle weight of Norway spruce (*Picea abies*) in stands of different densities. *Canadian Journal of Forest Research*, 15:389–392.
- Herbert, D. A., Fownes, J. H., 1997: Effects of leaf aggregation in a broad-leaf canopy on estimates of leaf area index by the gap-fraction method. *Forest Ecology and Management*, 97:277–282.
- Jack, B. S., Sheffield, M. C. P., McConville, D. J., 2002: Comparison of growth efficiency for mature longleaf and slash pine trees. General Technical Reports.
- Kantor, P., Šach, F., Černošou, V., 2009: Development of foliage biomass of young spruce and beech stands in the mountain water balance research area. *Journal of Forest Science*, 55:51–62.
- Konôpka, B., Pajťík, J., Moravčík, M., Lukac, M., 2010: Biomass partitioning and growth efficiency in four naturally regenerated forest tree species. *Basic and Applied Ecology*, 11:234–243.
- Konôpka, B., Pajťík, J., 2013: Foliage and fine roots in terms of growth efficiency – a comparison between European beech and Norway spruce at early growth stages. *Journal of Forest Science*, 11:436–446.
- Konôpka, B., Pajťík, J., Šebeň, V., Bošela, M., Máliš, F., Priwitzer, T. et al., 2013: The Research Site Vrchslatina – an experimental design and the main aims. *Lesnícky časopis - Forestry Journal*, 59:203–213.
- Kozłowski, T. T., Pallardy, G., 1997: *Physiology of Woody Plants*. San Diego, Academic Press, 411 p.
- Leuschner, Ch., Voss, S., Foetzki, A., Clases, Y., 2006: Variation in leaf area index and stand leaf mass of European beech across gradients of soil acidity and precipitation. *Plant Ecology*, 182:247–258.
- Milla, R., Reich, P. B., Niinemets, U., Castro-Díez, P., 2008: Environmental and developmental controls on specific leaf area are little modified by leaf allometry. *Functional Ecology*, 22:565–576.
- Nock, C. A., Caspersen, J. P., Thomas, S. C., 2008: Large ontogenetic declines in intra-crown leaf area index in two temperate deciduous tree species. *Ecology*, 89:744–753.
- Pajťík, J., Konôpka, B., Lukac, M., 2008: Biomass functions and expansion factors in young Norway spruce (*Picea abies* [L.] Karst) trees. *Forest Ecology and Management*, 256:1096–1103.
- Pajťík, J., Konôpka, B., Lukac, M., 2011: Individual biomass factors for beech, oak and pine in Slovakia: a comparative study in young naturally regenerated stands. *Trees*, 25:277–288.
- Pickup, M., Westoby, M., Basden, A., 2005: Dry mass costs of deploying leaf area in relation to leaf size. *Functional Ecology*, 19:88–97.
- Reich, P. B., Walters, M. B., Ellsworth, D. S., Vose, J. M., Volin, J. C., Gresham, Ch. et al., 1998: Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and life span: a test across biomes and functional groups. *Oecologia*, 114:471–482.
- Shiple, B., 2006: Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. *Functional Ecology*, 20:565–574.
- Van Dijk, A. I. J. M., Bruijnzeel, L. A., 2001: Modelling rainfall interception by vegetation of variable density using an adapted analytical model. Part 1. Model description. *Journal of Hydrology*, 247:230–238.
- Vogt, K., 1991: Carbon budget of temperate forest ecosystems. *Tree Physiology*, 9: 69–86.
- Waring, R., Schlesinger, W. H., 1985: *Forest ecosystems: concepts and management*. Orlando, Academic Press, 340 p.
- West, P. W., 2009: *Tree and forest measurement*. Dordrecht, Springer, 191 p.
- Xiao, C. W., Ceulemans, R., 2004: Allometric relationships for below- and aboveground biomass of young Scots pines. *Forest Ecology and Management*, 203:177–186.