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Foliage and fine roots in terms of growth efficiency – a comparison between European beech and Norway spruce at early growth stages

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ABSTRACT: The quantification of stems (under- and overbark), foliage and fine roots in 14-year-old stands of European beech and Norway spruce grown on the same site were evaluated. Therefore, 60 trees of each species were sampled, dry masses of stems and foliage were established and expressed by allometric equations with stem diameter as an independent variable. The spruce allocated a much larger portion of biomass into the foliage than beech. The equations on a tree level were constructed also for specific leaf area and one-sided projected leaf area. Moreover, the quantity and morphological characteristics of fine roots in both stands were surveyed through soil coring. While standing stocks of fine roots were similar in the stands of both tree species, significant interspecies differences occurred in morphological properties of roots. Growth efficiency, expressing annual stem production on a variety of foliage and fine root parameters was calculated. The largest differences, specifically fivefold in favour of spruce, were found in growth efficiency based on a number of root tips.

Keywords: allometric equations; fine root morphology; leaf area; stem diameter; stem mass production; interspecies differences

Plants including forest trees are composed of a structural complex of organs which are characterized not only by their forms but also by their specific functions. Compartments of forest trees in elementary structuring are: foliage, branches, stem and root system. Kozlowski and Pallardy (1997) explained that the physiologically most active parts of trees are foliage and fine roots (the latter are usually characterized by the upper diameter of 1 or 2 mm; see for instance Smit et al. 2000).

It is well known that while foliage is involved in photosynthesis, roots – especially their tiny fragments and tips – serve for the absorption of nutrients and water from the soil medium. These two cardinal processes make up conditions for development and production of woody compartments, specifically branches, stem and coarse roots.

In many scientific works, the structuring of produced biomass into separate plant organs is called as "biomass allocation" (e.g. Poorter et al. 2012). The proportion of the specific parts in total plant biomass is determined by species, genetic properties, and is controlled by external conditions to a large extent (Kozlowski, Pallardy 1997). Recently, issues related to tree biomass allocation have prevailingly been studied with regard to carbon cycling and sequestration in forest ecosystems (Litton et al. 2007). At the same time, since foliage and fine roots are compartments with the shortest lifespan of all tree parts, they are the most dynamic elements of carbon rotation in forests (Helmisaari et al. 2002).

Internal and external factors modify not only quantitative but also qualitative properties of the

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particular tree compartments. It is evident especially in the case of foliage and fine roots which react to growth conditions sensitively through morphological adaptations. Foliage for instance changes size, weight and consequently also specific leaf area (SLA; i.e. foliage area expressed per weight unit) according to light intensity (e.g. Barna 2004; Closa et al. 2012). In scientific literature SLA is the most frequent indicator of foliage structure (Reich et al. 1998). Besides the indication of morphological features it may serve also as a conversion factor for expressing the area of assimilatory organs from their mass either on a tree or stand level. In fact, measurements of foliage properties are much more complex for some species of evergreen trees (prevailingly coniferous) than for deciduous ones (usually broadleaved). In the case of some evergreen tree species, differences between needles of specific age must be considered (see e.g. Zha et al. 2002).

As for morphological properties of fine roots a variety of indicators have been used, they are often composed of two root parameters – in the form of a ratio. The ratio between length and mass of fine roots (specific root length; SRL) or between the number of root tips and root mass (specific density of root tips; SDT) is used most frequently. These indicators were implemented for instance as characteristics of soil properties (Ostonen et al. 2007), changes in soil conditions (Konôpka, Takáčová 2010), or specific stand conditions (Kucbel et al. 2011).

As it was mentioned above, tree development and growth may be in process thanks to the input of external energy and matters absorbed by foliage and root system (especially fine roots and tips). From ecological, physiological and productive points of view a plenty of authors (e.g. Gersonde, O'Hara 2005; Konôpka et al. 2010) focused on a relationship between the quantity of assimilatory organs and production of tree biomass. Commonly ratios of stem mass production to unit area or mass of foliage were used, which is called growth efficiency (GE). We suggest that GE will be studied not only in the context of foliage but also in terms of fine roots. In general, research activities focused on tree fine roots were much less frequent in comparison with all other compartments (Brunner, Godbold 2007). At the same time, information on the relationship between quantitative and/or qualitative properties of foliage and fine roots is still missing for forest trees. This kind of knowledge would help to explain development and growth strategies in the individual tree species with regard to environmental conditions, potentially it would serve also for process modelling of these phenomena.

The principal aim of this paper is to quantify the biomass of foliage and fine roots, and to estimate some qualitative parameters of these compartments in young European beech and Norway spruce stands. Another goal is to estimate the production of stem mass and GE, i.e. stem production expressed per unit area and weight of foliage and fine roots. Based on these findings we will make interspecies comparisons between beech and spruce at young growth stages.

MATERIAL AND METHODS

Site description

The studies were performed in the Vrchslatina research site (48°38'50''N and 19°36'12''E) located at an altitude of 960 m a.s.l. belonging to the southernmost part of the Veporské vrchy massif, Central Slovakia. The site is located ca 10 km northeast of the town of Hriňová, the area belongs to the Kriváň Forest Enterprise, the Poľana Forest Unit. Long-term average of the annual amount of precipitation is about 900 mm, average temperature 6°C.

The bedrock is built of granodiorite covered with the soil classified as Cambisol (Humic, Eutric). The textural class of the fine earth fraction is qualified as sandy loam. Though the rock fragment content is relatively high (about 30–35 volume percent in the entire assessed soil profile), almost all rock fragments are in the fraction of fine gravel (0.2–0.6 cm) and so it does not influence the soil properties negatively. Values of pH measured in hydro suspension were between 5.1 and 5.4 and values measured in $CaCl_2$ extract were between 4.3 and 4.6 (gently decreasing towards the soil surface). The C/N ratio values (about 17 in the upper 10 cm of soil) indicate good quality of soil organic matter.

The site was covered prevailingly by groups of young forest stands which were exclusively composed of either beeches or spruces. The area of the young stand complex comprised about 0.7 hectare. Treeless patches among the groups of beeches or spruces were occupied by the grass community with bushgrass (*Calamagrostis epigejos*) as a dominant species. The young forest stands originated from natural regeneration and their age was around 14 years. More detailed descriptions of the site and forest stands are given in Konôpka et al. (2013a).

Tree measurements

At the beginning of the experiment, five circular plots were established in beech stands and another five plots in spruce stands. The radius of the plots varied between 70 and 100 cm, its size depended on stand density intending to include 30–50 trees. The trees on the plots were measured twice in 2011 – in March and November. Specifically, stem diameters on the ground level (diameter d_0 hereinafter) and tree heights were recorded. These measurements served to calculate some basic stand characteristics, i.e. number of trees per hectare, mean diameter and mean height, basal area (based on d_0).

During September 2011 we harvested 60 individuals of beech and 60 of spruce for determination of aboveground tree compartments. The sample trees were selected outside of circular plots and in such a way that they would represent the full range of tree sizes recorded in the stands. The sampled trees were cut according to specific compartments, i.e. stem and branches with foliage. The samples were transported to a laboratory. Here we measured stem diameter d_0, bark was separated from stems as well as foliage from branches. Then, stem, stem bark and foliage were oven dried (below 95°C for 48 h) and weighed to the nearest 0.1 g. These values were used for the construction of stand-specific allometric equations expressing stem mass (under- and overbark) and foliage mass using diameter d_0 as independent variable. The allometric equation (after logarithmic transformation) was as follows:

$$y = e^{(b_0 + b_1 \times \ln d_0)} \times \lambda \qquad (1)$$

where:

b_0, b_1 – regression coefficients,
d_0 – diameter,
λ – logarithmic bias.

A more detailed description of the procedure for the construction of this type of allometric relations was given for instance in Pajtík et al. (2008). Further, allometric relations expressing stem mass and data on diameter d_0 measured on the plots in March and November (i.e. diameter increments in the stands were considered) were combined to calculate stem mass production at the level of stands.

Foliage sampling

To conduct more detailed analyses of foliage, 40 trees of beech and spruce were selected so that 10 individuals always represented a specific biosociological position (i.e. dominant, subdominant, codominant, and suppressed). On each selected beech, 9 samples of foliage were taken, always 3 samples from the upper, middle and lower part of the tree crown. Sampling in spruce differed from that in beech. Since the spruces had five needle age classes, starting from 2007, each of them had to be included in the sampling. Thus, 3 samples (comprised of 10 needles) were taken not only with regard to the vertical profile but also by the age class. Therefore, 15 samples were taken from each selected spruce. Besides that, the selected spruces were used to determine a contribution of each age class to the total needle mass. Thus, we cut separately specific needle classes, dried and weighed them to establish dry masses.

Individual samples of foliage were scanned and consequently their one-sided projected areas (leaf areas hereinafter) were measured by the Leaf Area Measurement software to the nearest 0.1 mm^2. Then, the foliage was oven dried (85°C for 24 h) and weighed to the nearest 0.0001 g. Data on the area and weight of assimilatory organs were used to calculate SLA on a foliage level. Then, the values from 9 foliage samples were used to calculate average foliage area, mass and SLA. By means of a logarithmically transformed allometric equation SLA on a tree level was determined based on diameter d_0. Using the allometric relations for foliage mass and SLA, the total leaf area of the crown was expressed as follows:

$$\mathrm{LA} = m \times \mathrm{SLA} \qquad (2)$$

where:

LA – leaf area in beech,
m – mass of leaves,
SLA – specific leaf area.

While only one model was necessary for beech, five models (specific for each needle age class) had to be constructed for spruce needles. The final model of total leaf area in the crown was calculated by means of an allometric relation for SLA of each needle age class and mass proportion of each needle set in the total needle biomass using the equation:

$$\mathrm{LA} = \sum_{1}^{p} \mathrm{LA}_k = \sum_{1}^{p} (m \times P_k \times \mathrm{SLA}_k) \qquad (3)$$

where:

LA – leaf area in beech,
k – 1st, 2nd, ..., 5th – needle age class,
m – mass of leaves,
P_k – contribution of specific needle age class to the total needle biomass,
SLA – specific leaf area.

Fine root sampling

Besides studies on aboveground tree parts in beech and spruce, we focused on the quantity and morphological properties of fine roots (up to 1 mm in diameter). Therefore in April 2011 we collected 15 soil cores of both beech and spruce stands.

The soil cores were collected randomly all over the stands avoiding the areas of circular plots. We used a metal auger with the inner diameter of 7 cm, penetrating the soil environment to the depth of 50 cm. In fact, we did not include any deeper soil layers because our previous studies showed that there were only few fine roots at the depth of 40–50 cm (Konôpka et al. 2013b).

The soil cores were put into plastic bags and transported to a laboratory. The samples were deep-freezer stored until further processing. Later defrosted samples were spread on a plastic pad and live fine roots of beech and spruce were separated from the soil. The fine roots were carefully washed and ca 1/5 of them was scanned.

The images were analysed by the WinRHIZO program (Regent Instruments, Quebec, Canada). The output of the analysis showed these fine root parameters: average root diameter, total length, number of branchings, surface area, number of root tips. Then, these morphological parameters were expressed as fine root mass or unit length.

Thus, we obtained: SRL, SDT, specific root weight (SRW; root mass per unit root volume), specific root surface (SRS; root surface per unit root mass), and specific branching density (SBD; number of branchings per unit root mass).

All fine roots were oven dried (85°C for 24 h) and weighed to the nearest 0.0001 g. The quantity and morphological features determined for the known space (i.e. the volume of sampled soil column – that was ca 550 cm^3) were also calculated per unit stand area.

Growth efficiency estimates and statistical analysis

Data on stem production and properties of foliage and/or fine roots (all results were expressed on the same area unit basis, specifically 1 m^2) were used for the calculation of GE in beech and spruce. Thus, GE was expressed as stem production per units of area or mass in foliage, further, per units of fine root mass, fine root surface, and per million root tips.

Since all allometric relations expressing tree compartments were linearized by means of logarithmic transformation, parameters of regression equations were calculated by the least-squares method. Logarithmic bias (λ) was estimated according to the method suggested by Marklund (1987). The Kruskal-Wallis test was used (on a 95% probability level) to test interspecies differences in tree and stand parameters, and the GEs. Statistical analyses were performed by the Statistica 10 (Statsoft, Tulsa, USA) program package.

RESULTS AND DISCUSSION

Stand development indices

The per-hectare number of trees in the beech stand in March 2011 was about 135,000 then in November 2011 it dropped to 125,000 (Table 1). An evident decrease in the number of trees was in spruce, from 134 to 98 thousand trees per hectare. This phenomenon relates most probably to a harsh competitive pressure for light in the spruce stand because the crowns caused more intensive shading than in the beech stand. After further comparisons of the stands we realized that the spruce stand had larger mean stem diameter d_0 but a reverse situation was for mean tree height. Similar values in both stands were in mean stem volume and stem base.

Table 1. The characteristics of beech and spruce stands as measured in March and November 2011 (means and standard deviations)

Stand characteristic	Beech		Spruce	
	March	November	March	November
Number of trees (10^3·ha^{-1})	135 ± 10	125 ± 12	134 ± 10	98 ± 7
Mean tree height (cm)	253 ± 16	287 ± 22	164 ± 7	211 ± 5
Mean diameter d_0 (cm)	2.43 ± 0.09	2.66 ± 0.12	2.71 ± 0.12	3.23 ± 0.11
Mean stem volume (cm^3)	391 ± 36	501 ± 57	355 ± 34	647 ± 35
Basal area* (m^2·ha^{-1})	62.9 ± 6.4	69.5 ± 7.0	75.7 ± 2.5	80.2 ± 4.6

*basal area calculated for diameter d_0, i.e. on the ground level

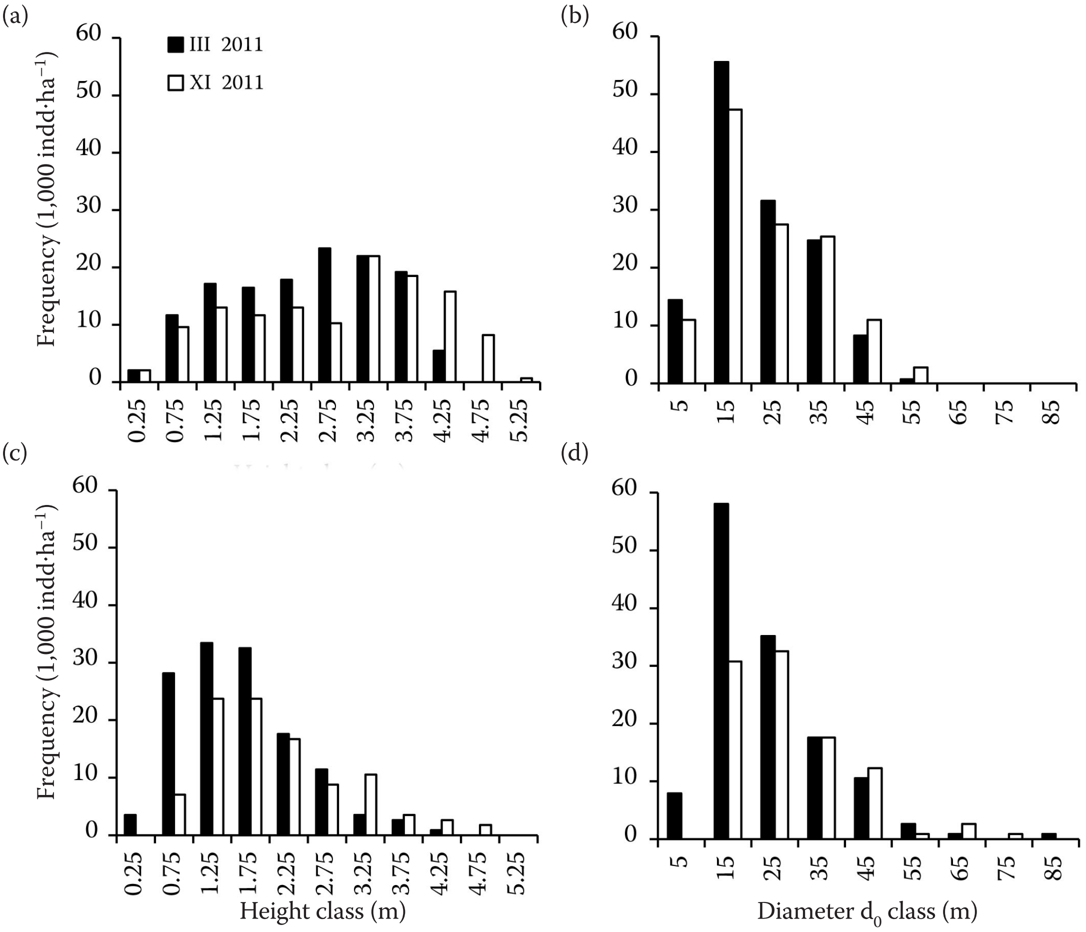

Fig. 1. Frequency diagram for tree heights (left plates) and stem diameter d_0 (right plates) in beech (upper plates) and spruce (lower plates)

As for the frequency distribution of tree heights, beech showed symmetric but spruce showed left-skewed distribution (Fig. 1a, b). In the case of diameter d_0, frequency distribution was left-skewed in both stands (Fig. 1c, d). In fact, the high density of trees (over 100 thousand per hectare) is common for this growth stage not only in spruce and beech but also it was previously recorded in full-canopy stands of sessile oak (see for instance Pajtík et al. 2008, 2011).

Allometry and growth efficiency on a tree level

Allometric relations for masses of stem (both over- and underbark) using diameter d_0 as an independent variable indicated large differences between the species (Fig. 2 and Table 2). The stems of beeches with specific diameter d_0 represented much larger mass in beech than in spruce. This difference relates to contrasting specific weights (see Pajtík et al. 2011), and also to a different ratio between height and diameter in these species; actually, this ratio was by 72% higher in beech than in spruce. Allometric equations expressing the mass of foliage brought opposite findings than in stem mass. It means that spruces with specific diameter d_0 had much larger foliage mass than beeches of the same diameter (Fig. 3 and Table 2). These allometric relations showed that the ratio of foliage mass to stem mass is dramatically higher in spruce than in beech. In general, allometric relations are missing for young growth stages of tree stands

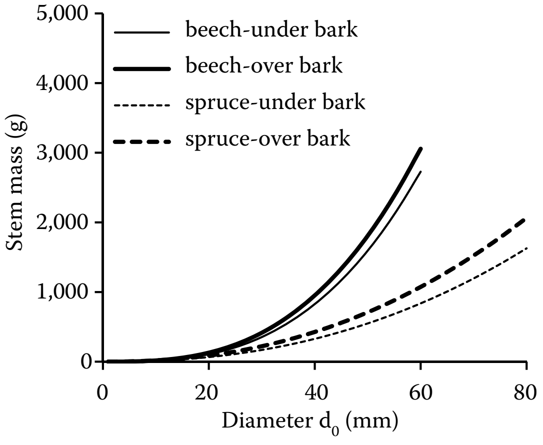

Fig. 2. Stem mass (under- and over-bark) in beech and spruce against stem diameter d_0

Table 2. Basic statistical characteristics for regression models expressing stem mass (under- and overbark) and foliage mass in beech and spruce with regard to stem diameter d_0

Species	Compartment	b_0 (S.E.) P	b_1 (S.E.) P	R^2	MSE	λ	S.D.
Beech	stem overbark	−3.800 (0.222) < 0.001	2.879 (0.070) < 0.001	0.965	0.076	1.038	0.297
	stem underbark	−4.184 (0.222) < 0.001	2.945 (0.070) < 0.001	0.967	0.076	1.038	0.296
	foliage	−6.576 (0.256) < 0.001	3.085 (0.081) < 0.001	0.960	0.102	1.047	0.308
Spruce	stem overbark	−2.369 (0.142) < 0.001	2.273 (0.045) < 0.001	0.970	0.077	1.042	0.348
	stem underbark	−2.775 (0.152) < 0.001	2.310 (0.048) < 0.001	0.967	0.089	1.048	0.369
	needles	−3.079 (0.171) < 0.001	2.432 (0.054) < 0.001	0.964	0.106	1.053	0.366

b_0, b_1 – regression coefficients with their standard errors (S.E.), R^2 – coefficient of determination, MSE – mean squared error, λ – logarithmic bias with its standard deviation (S.D.)

(Wirth et al. 2004). At the same time Pajtík et al. (2011) found that biomass allocation in European beech, sessile oak, Scots pine and Norway spruce changed most dramatically with stand development at the initial growth stages.

As it was mentioned in the Introduction section, while SLA is quite easily measurable in beech (just one – current year foliage set), a more complex situation is in spruce where each needle age class represents different properties. Thus, each needle age class had to be analysed individually, in fact, our spruce stand retained five needle sets. We found that proportions of the separate needle sets in total needle biomass did not change significantly with the tree size, i.e. in relation to diameter d_0. Hence, we could use for further calculations just average values of the needle set proportions for all trees. The proportions of needle sets were as follows: born in 2007 – 1.5%, 2008 – 10.3%, 2009 – 22.0%, 2010 – 31.6%, and 2011 (current year) – 34.6%. Statistical characteristics for regression relations expressing SLA in beech and spruce in relation to diameter d_0 are shown in Table 3. Here, SLA for spruce on a tree level was calculated as weighted average (weight was proportions of the individual needle sets in the total needle mass) of SLA in the specific needle sets. The results showed that SLA on a tree level decreased with the increasing tree size in both species, but more clearly in beech (Fig. 4). These findings indicated that morphological features of foliage depended on the tree size (and/or on the bio-sociological position in the stand) that in general would relate to light conditions. Our knowledge is in accordance with results of Closa et al. (2012), who studied a young beech stand whose shaded foliage had much higher values of SLA (between ca 250 to 470 cm² per gram of mass) than the foliage exposed to sunlight (150–180 $cm^2 \cdot g^{-1}$). For instance Milla et al. (2008) stated that large leaves tend to require higher biomass investment per unit leaf area than the small ones. Therefore SLA which is a cardinal trait for a plenty of physiological and ecological issues is dependent on the leaf size variation.

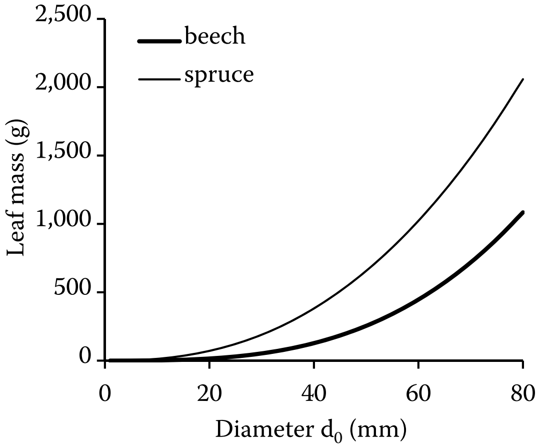

Fig. 3. Leaf mass in beech and spruce against stem diameter d_0

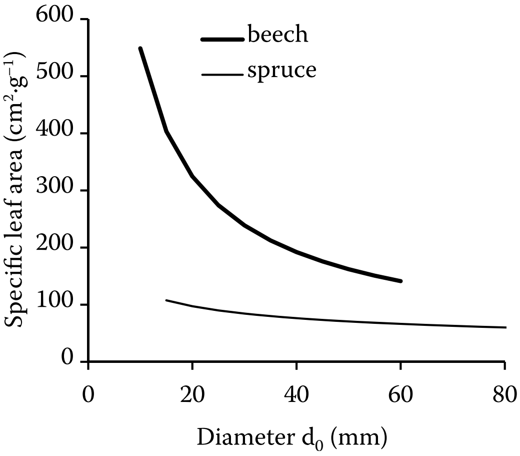

Fig 4. Specific leaf area in beech and spruce against stem diameter d_0

Table 3. Basic statistical characteristics for regression models expressing SLA in beech and spruce with regard to diameter d_0

Species and age class of foliage	b_0 (S.E.) P	b_1 (S.E.) P	R^2	MSE	λ	S.D.
Beech 2011	8.026 (0.110) < 0.001	−0.757 (0.033) < 0.001	0.816	0.051	1.026	0.239
Spruce 2007	4.890 (0.129) < 0.001	−0.242 (0.034) < 0.001	0.657	0.011	1.005	0.102
Spruce 2008	4.955 (0.119) < 0.001	−0.234 (0.031) < 0.001	0.672	0.009	1.004	0.097
Spruce 2009	5.179 (0.135) < 0.001	−0.263 (0.035) < 0.001	0.667	0.012	1.006	0.109
Spruce 2010	5.542 (0.187) < 0.001	−0.329 (0.049) < 0.001	0.629	0.022	1.011	0.150
Spruce 2011	6.036 (0.091) < 0.001	−0.427 (0.025) < 0.001	0.713	0.024	1.012	0.160

b_0, b_1 – regression coefficients with their standard errors (S.E.), R^2 – coefficient of determination, MSE – mean squared error, λ – logarithmic bias with its standard deviation (S.D.)

By combination of allometric models for foliage mass (Fig. 3) and for SLA (Fig. 4) a relationship between diameter d_0 and leaf area on a tree level was determined (Fig. 5). Interspecies comparisons showed that while the mass of foliage was much larger in spruce than in beech, the leaf area was nearly the same in both species. In the Czech Republic, allometric models for leaf mass and area of young beech and spruce trees were constructed by Kantor et al. (2009). However, the results are not compatible with ours, because they used diameter at breast height as an independent variable.

Further on a tree level, allometric relations for leaf area (Fig. 5) and for annual stem production (Fig. 6) were used to calculate GE according to diameter d_0 (Fig. 7). We found that GE was much higher in beech than in spruce. Thus, for instance GE in trees with diameter d_0 of 40 mm was 110 g of stem mass per 1 m^2 of foliage area in beech, but only 40 $g \cdot m^{-2}$ in spruce. At the same time, GE grew with the increasing tree size in both species. This situation is very probably related to contrasting levels of light availability in trees of different sizes (large trees receive more solar energy than the small ones). Therefore the unit area of foliage in suppressed (small) trees is able to produce less assimilates, consequently less woody mass, than that of dominant (large) trees. Similar findings were reported by Gspaltl et al. (2013) in a spruce pole-stage stand where GE increased with the stem volume. The authors showed the same phenomenon as our works that the sharpest change in GE rate with the tree size occurred among the smallest individuals (probably suppressed and co-dominant tree classes).

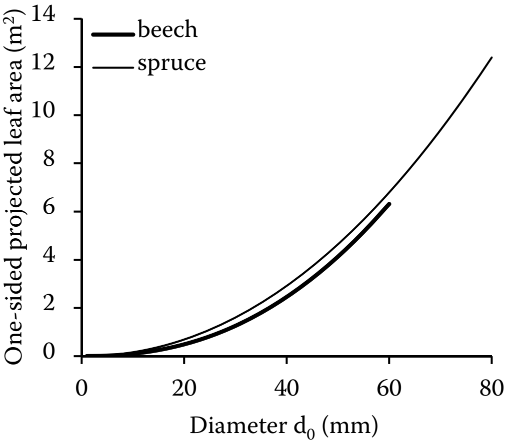

Fig. 5. One-sided projected leaf area in beech and spruce against stem diameter d_0

Growth efficiency on a stand level

Interspecies comparisons of morphological properties in fine roots indicated that beech roots are composed of a higher proportion of very thin fragments (average diameter was twice smaller in beech than in spruce; Table 4). Besides that, fine roots of beech were more frequently branched with denser occupancy of

Table 4. Morphological features in beech and spruce fine roots (means and standard deviations)

Species	Mean diameter (mm)	SRW (10^3 $g \cdot m^{-3}$)	SRL ($m \cdot g^{-1}$)	SRS (10^3 $m^2 \cdot g^{-1}$)	SDT (10^3 $tips \cdot g^{-1}$)	SBD (10^3 $branches \cdot g^{-1}$)
Beech	0.21 ± 0.01	388 ± 19	75.25 ± 2.38	47.32 ± 0.87	47.22 ±1.83	66.58 ± 2.08
Spruce	0.46 ± 0.02*	335 ± 15	19.60 ± 1.59*	30.71 ± 3.73*	8.69 ± 0.49*	9.77 ± 0.61*

*significant interspecies differences (Kruskal-Wallis test; α = 0.95), SRW – specific root weight, SRL – specific root length, SRS – specific root surface, SDT – specific density of root tips, SBD – specific branching density

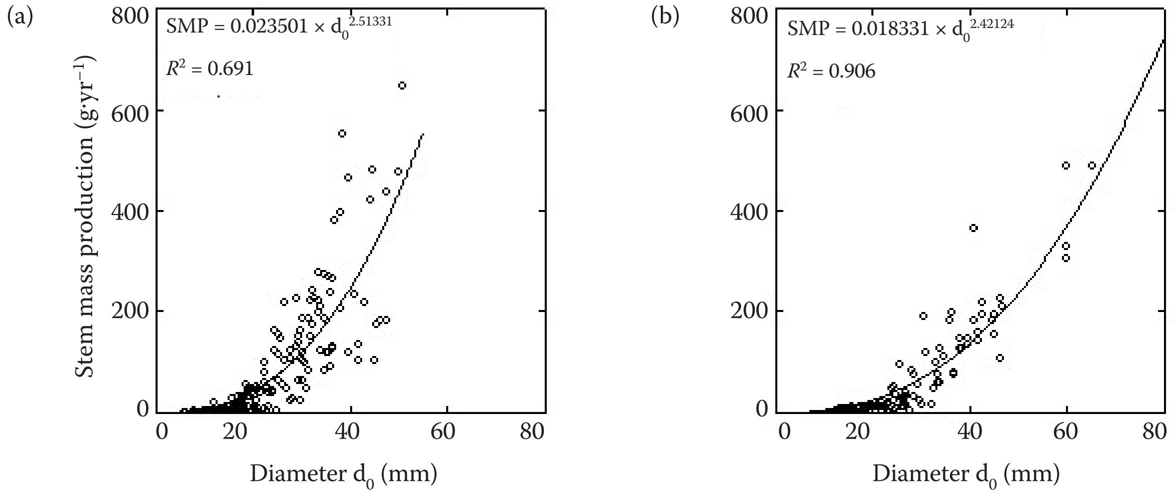

Fig. 6. Annual production of stem mass underbark in beech (a) and spruce (b) against stem diameter d_0

tips. Hence, fine roots of beech represented a four times larger surface area (that relates to the absorption potential) on a mass base in comparison with spruce. Similar results were presented by Ostonen et al. (2012), who compared SRL of fine roots in beech and spruce originating from a variety of countries using the latitude as an independent variable. They found that SRL was between two- and threefold larger in beech than in spruce. These results might suggest that beech needs a less quantity of fine roots for the production of a certain amount of stem mass than spruce. This would be applicable in case that we omit the role of hyphae of ectomycorrhizal fungi for the absorption of water and nutrients from the soil. Our results from the same stands proved that the standing stock of hyphae was much larger in spruce than in beech. It means that the "handicap" of morphological properties of fine roots in spruce might be compensated by the hyphae.

Further, we expressed standing stocks of stem biomass, foliage and fine roots as well as leaf area, surface area of fine roots and number of root tips per unit area (m^2) of stand. Moreover, the production of stem mass per 1 m^2 of stand was calculated (Table 5). While the standing stock of stem biomass was higher in beech, an opposite situation was in foliage. Standing stocks of fine roots were very similar in both stands. On the other hand, while beech stands had a larger surface area of fine roots than spruce stands, an opposite situation was in foliage area. Higher stem mass production was estimated in beech than in spruce stand.

Data on stem production in combination with characteristics of foliage and fine roots (Table 5) were used for determination of GE. At the same time, stem production was expressed per both unit mass and area of foliage and fine roots. Further, stem production was linked to the number of root tips. GE calculated on a variety of bases is given in Table 6. GE based on the mass and also area of foliage was higher in the beech stand than in the spruce stand. This phenomenon might relate to

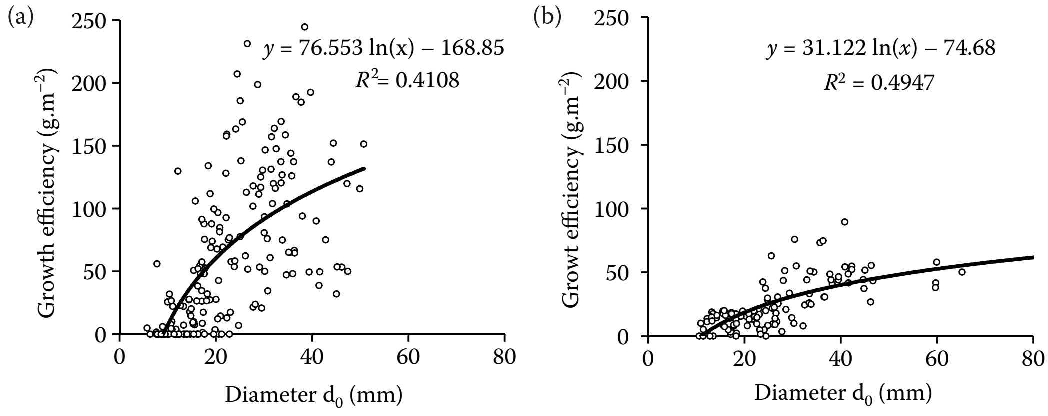

Fig. 7. Growth efficiency expressed as annual production of stems underbark per foliage unit area in beech (a) and spruce (b) against stem diameter d_0

Table 5. Quantitative characteristics of stems and foliage in beech and spruce expressed per square meter of stand area (means ± standard deviations)

Characteristics	Beech	Spruce
Standing stock of stems overbark ($g \cdot m^{-2}$)	4 476 ± 496	3142 ± 178*
Standing stock of stems underbark ($g \cdot m^{-2}$)	3 856 ± 437	2431 ± 139*
Standing stock of foliage ($g \cdot m^{-2}$)	603 ± 77	2626 ± 151*
Standing stock of fine roots ($g \cdot m^{-2}$)	494 ± 95	402 ± 82
Area of foliage ($m \cdot m^{-2}$)	12.77 ± 1.40	18.64 ± 1.08*
Surface area of fine roots ($m^2 \cdot m^{-2}$)	23.42 ± 5.31	12.30 ± 3.29*
Number of root tips (10^6 indd$\cdot m^{-2}$)	33.12 ± 10.02	4.18 ± 1.19*
Production of stems overbark ($g \cdot m^{-2} \cdot yr^{-1}$)	1 011 ± 131	714 ± 53*
Production of stems underbark ($g \cdot m^{-2} \cdot yr^{-1}$)	887 ± 116	572 ± 42*

*significant interspecies differences (Kruskal-Wallis test; α = 0.95)

Table 6. Growth efficiency in beech and spruce stands as production of stems underbark expressed as a variety of foliage and fine root parameters (means ± standard deviations)

Growth efficiency based on	Beech	Spruce
Foliage mass ($g \cdot g^{-1}$)	1.47 ± 0.10	0.22 ± 0.01*
Foliage area ($g \cdot m^{-2}$)	69.46 ± 4.20	30.69 ± 1.11*
Fine root mass ($g \cdot g^{-1}$)	1.80 ± 0.73	1.42 ± 0.40
Surface of fine roots ($g \cdot m^{-2}$)	37.90 ± 8.94	46.51 ± 12.70
Number of root tips ($g \cdot 10^{-6}$ tips)	26.88 ± 3.85	143.00 ± 15.42*

*significant interspecies differences (Kruskal-Wallis test; α = 0.95)

contrasting ages in leaves and needles. While beech bears only current-year leaves, needles retained in spruce crowns were between 1- and 5-years old. According to results of Kayama et al. (2007) photosynthetic rates decreased continuously with needle senescence. Moreover, the assimilatory system of spruce in comparison with that of beech might endure more intensive shading (both among the whorls and among tree individuals), it means less light energy reaching the foliage surface in spruce than in beech if expressed per unit area.

As for GE expressed as the fine root mass, a higher value was found out in beech than in spruce, however, a reverse situation occurred for GE calculated as the fine root surface. The largest interspecies differences in GE, namely in favour of spruce, were revealed if the number of root tips was used as a base. However, as it was mentioned above, we found the much larger mass of hyphae in the spruce stand than in the beech stand. We assume that the hyphae of ectomycorrhizal fungi would enhance GE as calculated per fine root unit surface and/or per number of root tips (it is related to the enlarged surface area of the root system by means of hyphae; e.g. Bolan 1991). Hence, we can anticipate that while beech is characterized by better morphological properties of fine roots for the acquisition of resources, spruce fine roots might enhance their absorptive capability thanks to the intensive association with ectomycorrhizal fungi.

Jack et al. (2002) pointed out that so far interspecies comparisons of GE of forest trees were missing; that kind of information would help to elucidate ecological demands and growth strategies of trees. Therefore, we assume that our results will help to understand these phenomena in terms of stem, foliage and fine root development in young full-canopy stands of beech and spruce.

CONCLUSIONS

Comparative studies in young stands proved that beech in comparison with spruce allocated much more biomass to the stem than to foliage. On the other hand, both tree species had similar values of foliage area that was related to higher SLA in beech than in spruce. Standing stocks of fine roots were similar in both stands, however, we found significant interspecies differences in fine root morphology. Beech fine roots were thinner and more intensively branched with higher density of root tips than spruce fine roots. GE expressed as annual stem production per unit area of foliage was much higher in beech than in spruce. GE in both species increased with the tree size. The phenomenon probably relates to light availability to the crown of trees which is determined by a biosociological position in the stand. If GE was expressed as fine root mass, the values were higher in beech; an opposite situation occurred if GE was calculated as the fine root surface area. The largest interspecies differences (more than fivefold in favour of spruce) were revealed for GE expressed as the number of roots tips. We assume that in the case of GE based on fine root parameters (especially on surface area and number of root tips) interspecies differences might relate, besides other factors, also to the status of mycorrhizal fungi associated with the tree species. The results of this work might contribute to the knowledge useful for instance in process modelling in beech and spruce of young growth stages.

References

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.

Bolan N.S. (1991): A critical review of the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant and Soil, ***134***: 189–207.

Brunner I., Godbold D.L. (2007): Tree roots in a changing world. Journal of Forest Research, ***12***: 78–82.

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.

Gersonde R.F., O'Hara K.L. (2005): Comparative tree growth efficiency in Sierra Nevada mixed-conifer forests. Forest Ecology and Management, ***219***: 95–108

Gspalt M., Bauerle W., Binckley D., Sterba H. (2013): Leaf area and light use efficiency patterns of Norway spruce under different thinning regimes and age classes. Forest Ecology and Management, ***288***: 49–59.

Helmisaari H.S., Makkonen K., Kellomäki S., Valtonen E., Mälkönen E. (2002): Below- and aboveground biomass, production and nitrogen use in Scots pine in eastern Finland. Forest Ecology and Management, ***165***: 317–326.

Jack B.S., Sheffield M.C.P., McConville D.J. (2002): Comparison of growth efficiency of mature longleaf and slash pine trees. General Technical Reports, ***48:*** 81–85.

Kantor P., Šach F., Černohous 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.

Kayama M., Kitaoka S., Wang W., Choi D., Koike T. (2007): Needle longevity, photosynthetic rate and nitrogen concentration of eight spruce taxa planted in northern Japan. Tree Physiology, ***27***: 1585–1593.

Konôpka B., Takáčová E. (2010): Effects of liming and NPK-fertilization on the soil and fine roots in a Norway spruce stand, Nízke Tatry Mts. Ekológia (Bratislava), ***29***: 28–39.

Konôpka B., Pajtík 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., Pajtík J., Šebeň V., Bošeľa M., Máliš F., Priwitzer T., Pavlenda P. (2013a): The Research Site Vrchslatina – an experimental design and the main aims. Lesnícky časopis – Forestry Journal, ***59***: 203–213.

Konôpka B., Pajtík J., Maľová M. (2013b): Fine root standing stock and production in young beech and spruce stands. Lesnícky časopis – Forestry Journal, ***59***: 163–171.

Kozlowski T.T, Pallardy S.G. (1997): Physiology of Woody Plants. San Diego, Academic Press: 411.

Kucbel S., Jaloviar P., Špišák J. (2011): Quantity, vertical distribution and morphology of fine roots in Norway spruce stands with different stem density. Plant Root, ***5***: 46–55.

Litton C.M., Raich J.W., Ryan M.G. (2007): Carbon allocation in forest ecosystems. Global Change Biology, ***13***: 2089–2109.

Marklund L.G. (1987): Biomass Functions for Norway Spruce (*Picea abies* L. Karts.) in Sweden. Umeå, Swedish University of Agricultural Sciences: 27.

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.

Ostonen I., Püttsepp Ü., Biel C., Alberton O., Bakker M.R., Löhmus K., Majdi H., Metcalfe J.D., Olsthoorn A.F.M., Pronk A.A., Vanguelova E., Weih M., Brunner I. (2007): Specific root length as an indicator of environmental change. Plant Biosystems, ***141***: 426–442.

Pajtík 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.

Pajtík 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.

Poorter H., Niklas K.J., Reich P.B., Oleksyn J., Poot P., Mommer L. (2012): Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist, ***193***: 30–50.

Reich P.B., Walters M.B., Ellsworth D.S., Vose J.M., Volin J.C., Gresham Ch., Bowman W.D. (1998): Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. Oecologia, ***114:*** 471–482.

Smit A.L., Bengough A.G., Engels C., van Noordwijk M., Pellerin S., van de Geijn S.C. (2000): Root Methods. A Handbook. Berlin, Springer-Verlag: 587.

Wirth C., Schumacher J., Schulze E.D. (2004): Generic biomass functions for Norway spruce in Central Europe – a meta-analysis approach toward prediction and uncertainty estimation. Tree Physiology, ***24***: 121–139.

Zha T., Wang K.Y., Ryppö A., Kellomäki S. (2002): Impact of needle age on the responses of respiration in Scots pine to long-term elevation of carbon dioxide concentration and temperature. Tree Physiology, ***22***: 1241–1248.

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