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Biomass allocation influenced by canopy closure in a young spruce stand

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ABSTRACT: Growth intensity of particular tree components is controlled by a variety of factors and as a consequence, biomass allocation also changes over time. Since the allocation of biomass controls the carbon regime in a forest stand, tree standing stock and biomass structure, with regard to tree components: fine and coarse roots, stem, branches and needles, were estimated in a young Norway spruce stand based on repeated tree sampling, soil coring and allometric equations (modelled for 2009 and 2013, i.e. for 12- and 16-years-old trees). Large differences were found between the two models in the contribution of the tree components to aboveground biomass. Between the first and fifth year of the experiment, belowground to aboveground biomass ratio as well as short-lived to long-lived tree part ratio manifested decreasing tendencies. At the same time, the stand possibly reached the maximum standing stock of both needles and fine roots. It is concluded that for biomass allocation estimates in young stands, not only stand-specific but also time-specific allometric relations should be constructed and implemented. Further, there appears to be a canopy closure threshold beyond which biomass allocation is different from the situation in sparse young spruce stands.

Keywords: tree allometry; repeated sampling; tree components; *Picea abies;* carbon sequestration and cycling

Biomass measurements of all tree components are important, not only from the aspect of wood production, when whole trees are used for the production of energy and paper, but also for a variety of non-production forest functions. Recent scientific interests in estimating biomass quantity and structure have focused on two principal research topics: tree physiology and forest ecology (West 2009) and are often related to concerns in climate change and potential carbon sequestration (King et al. 2007). Since trees produce biomass through photosynthesis, it is essential to understand how the tree growth occurs in all components and also how growth strategies are reflected in optimizing biomass allocation under certain ecological conditions (e.g. Enqusit, Niklas 2002).

Growth intensity of particular tree components (i.e. biomass partitioning or allocation) is controlled by a variety of internal (e.g. Wullschleger et al. 2005; Dowell et al. 2009) and external factors (Poorter, Nagel 2000; Luo et al. 2012). Therefore related research activities cover a broad field, including climate change, i.e. the gradual increase of CO_2 concentrations (Poorter, Nagel 2000) and the occurrence of drought episodes (Schall et al. 2012). As for carbon sequestration in trees, biomass allocation into the specific components is critical, since some components are ephemeral and others long-lived (Litton et al. 2007). For example, while stem, coarse roots, and also most branches exit during the lifespan of the tree, the lifespan of foliage and fine roots is usually a couple of months to a maximum of a few years. Logically, the tree components with a short lifespan are the most dynamic elements for carbon rotation in forest trees and after their decomposition,

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a fundamental amount of carbon is released via heterotrophic respiration to the atmosphere. For instance in Norway spruce the lifespan of needles is around 5 yr (Schmidt-Vogt 1977) and that of fine roots (defined as those with maximum diameter of 2 mm) is slightly over 1 year (Brunner et al. 2013). On the other hand, the turnover of woody parts in spruce stands is between approximately 90 years for commercial forests and over 200 years for old-growth forests (Schmidt-Vogt 1977).

Studies conducted on tree biomass quantity often use allometric relations or biomass expansion factors (e.g. Marklund 1987; Cienciala et al. 2006; Seidl et al. 2010; Skovsgaard et al. 2011). However, most of these studies omitted young growth stages of trees; trees that are usually defined as individuals with diameter at breast height below 7 cm (Wirth et al. 2004). Previously, allometric relations for whole-tree biomass in young Norway spruce trees have been constructed for naturally regenerated stands in Slovakia (Pajtík et al. 2008) and for plantations in Romania (Dutca et al. 2010). Biomass allocation differs between young (small) and old (large) trees (e.g. Lehtonen et al. 2004; Wirth et al. 2004). Konôpka et al. (2010) showed that while the contribution of stem to total biomass increased for Norway spruce, contribution of branches, needles and especially roots decreased with increasing tree size. Since our previous work focused on a tree level, further work expressing tree biomass standing stock and structure on a stand level is required. At the same time, the previous sampling on trees did not include all belowground biomass as the tiny root fragments are often broken during the sampling procedure and are prevailingly lost. Therefore, additional sampling, providing data on fine root standing stock on a stand level, is implemented in this study.

Recent research, aimed at the total biomass standing stock (e.g. Helmisaari et al. 2002; Yuste et al. 2005), used a combination of tree sampling for the estimation of foliage, branches, stem, coarse roots and soil coring for fine root biomass. While old forest stands are relatively stable and the contribution of particular tree components to the biomass standing stock can be assumed, the biomass structure in young trees (stands) changes with tree growth, i.e. inter-annually. Thus, it is anticipated that allometric models for particular tree components change with tree growth.

The aim of the paper is to estimate the biomass standing stock originating from natural regeneration in a young Norway spruce stand and to analyse changes in biomass structure according to tree components: needles, branches, stems, coarse roots and fine roots over five consecutive years (2009–2013) at both the tree and stand level, with regard to physiological and ecological properties.

MATERIAL AND METHODS

Site and stand description. The study site Vrchslatina (48°38'N; 19°36'E) is located in central Slovakia on the border of the districts Detva and Brezno and belongs to the town of Hriňová. The altitudinal range is between 950 and 970 m a.s.l. and the area, 8.43 ha, is owned by the Forests of the Slovak Republic, Forest Enterprise in Kriváň, Poľana Forest District.

The site belongs to the fir-beech altitudinal forest zone and the area represents optimum ecological conditions for beech and is the southernmost limit of naturally occurring spruce in Slovakia. The site is situated in the geomorphological unit Veporské vrchy Mts., in the subunit Sihlianska Plateau. The subunit is composed mainly of porphyric granodiorites, biotite tonalites and granites with prevailing Cambisols derived from the parent material. The soil on the site is classified as both Humic and Eutric Cambisols and the textural class of the fine earth fraction is sandy loam. The pH values measured in hydro-suspension fluctuate between 5.1 and 5.4 while the pH values measured in $CaCl_2$ extract were between 4.3 and 4.6 (gradually decreasing towards the soil surface). The content of soil organic carbon is higher than the average for Slovakia with soil organic carbon content almost 7% in the A horizon and approximately 1% at the depth of 50 to 100 cm. The total carbon storage of soil to a depth of 100 cm was estimated at nearly 1,970 kg per 100 m^2 and the C:N ratio indicates good quality soil organic matter (Konôpka et al. 2013).

In 2006, the complex of young spruce clusters increased under a sparse canopy of mature trees that were subsequently harvested in the next 2–3 yr. Aerial photographs (see Konôpka et al. 2013) show that only a few individual mature trees existed on the site in 2002 and those trees were located outside of the study plots. By 2006, no mature trees remained on the site. In 2009, the target spruce stands did not cover the entire area with some areas among the forest complexes colonized by grass communities dominated by bush grass (*Calamagrostis epigejos).* The trees were between 12 and 16 years old when the field work was conducted between 2009 and 2013.

Tree measurements and sampling. In 2009, five circular plots (randomly selected) were established in spruce stands. The radius of each plot was 1 m and included approximately 40–60 trees. All trees inside the plots were labelled and basic tree characteristics were measured. Specifically, tree height and diameter at stem base (d_0 hereinafter) were recorded. The measurements were repeated in early spring over five consecutive years (2009, 2010, 2011, 2012 and 2013). Then, average values of tree heights as arithmetic means and tree diameters d_0 as quadratic means were calculated on a plot level for the individual years.

Two tree samplings were performed in the middle of the growing season in the first (2009) and in the last (2013) year of experiments. The first sampling in 2009 included 80 individuals of spruce trees that were randomly selected outside of the circular plots. The trees were excavated and fine roots (diameter up to 2 mm) were extracted from the root systems and disposed. Diameter d_0 was measured on sample trees and they were packed into paper bags and transported to the laboratory. Branches with needles and coarse roots were separated from the stem. The stems were debarked and wood was packed separately from bark. The sample branches, still bearing needles, were stored in a well-ventilated and dry room and after a few weeks the needles were shed. All needles were separated from the branches. Particular tree components, e.g. needles, branches, stem, bark peeled off the stem, and coarse roots were oven-dried at a temperature of 95°C for 2–3 days until a constant weight was reached and weighed. The second tree sampling in 2013 represented 60 spruce trees selected in a similar way like in 2009. However, belowground biomass was not included. The reason for omitting the coarse root sampling was a finding from our previous experiments which showed that the contribution of coarse roots to whole-tree biomass changed sharply with the tree size up to diameter d_0 of ca 30–40 mm. Then, spruces with diameter d_0 over 40 mm manifested the contribution of coarse roots to tree biomass nearly changeless with further growth, i.e. with the increasing tree size (Pajtík et al. 2008). The processing of the samples including the separation of components and quantification of their dry mass was conducted in the same way as for the samplings harvested in 2009.

In order to estimate the standing stock of fine root biomass (i.e. live roots with diameter up to 2 mm) a soil coring method was implemented. A metal auger, with the inner diameter of 7 cm, was used to the soil depth of 50 cm. The soil coring was completed in spring of each consecutive year 2009, 2010, 2011, 2012 and 2013. On each occasion, 15 soil cores were extracted representing 3 replicates from the individual circular plot. The soil columns were split by soil depths: 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, and 40–50 cm. The soil sub-columns were placed into plastic bags, transported to the laboratory and stored in a deep-freezer below –5°C until further processing. The soil samples including live fine roots of spruce were sorted and washed, then oven-dried at 85°C for 24 h and weighed to the nearest 10^{-4} g.

Tree and stand biomass calculation. Data on biomass of tree components obtained from the sampling in 2009 and actual tree diameter d_0 were used for the construction of allometric models on a tree level. The allometric equation was used in Eq. (1):

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

where:

W_i – biomass of component i (needles, branches, stem over or under bark, bark, coarse roots and whole tree biomass),

d_0 – diameter at the stem base,

b_0, b_1 – coefficients,

λ – logarithmic transformation bias.

For a more detailed description of the procedure for the construction of biomass allometric relations see Pajtík et al. (2008) and for an explanation of the use of logarithmic transformation, reverse transformation and λ see Baskerville (1972) and Marklund (1987). A similar procedure was used for processing data from the tree sampling in 2013. However, only components of aboveground tree biomass could be expressed directly from the empiric material.

Combining data on the frequency of diameter d_0 in circular plots and allometric models, actual standing stock of tree biomass and structure (separately needles, branches, stem, bark and coarse roots) were expressed for spring 2009. The standing stock of aboveground biomass in a spruce stand for spring 2013 was expressed by allometric models constructed from samplings in 2013. The coarse root standing stock was calculated by using a ratio between coarse root biomass and aboveground biomass estimated from the sample trees harvested in 2009. Finally, the fine root standing stock in the particular years was estimated via upscaling from fine root biomass on the known area (38.5 cm^2; as quantified by soil coring) to a hectare unit base. The total tree biomass standing stock including all components (i.e. needles, branches, stem, bark, coarse and fine roots) was estimated per 100 m^2 (i.e. 1.0 are) in 2009 and 2013. All mathematical and statistical operations were performed in the STATISTICA 10.0. (StatSoft, Prague, Czech Republic)

Table 1. Basic stand characteristics by research plots in spring 2009 and spring 2013

Stand characteristics in year		Plot number					Mean ± SD
		1	2	3	4	5	
Number of trees (individuals per 100 m^2)	2009	1,213	2,041	2,860	1,557	1,819	1,898 ± 620
Mean tree height (m)		1.37	1.05	1.08	1.39	1.51	1.27 ± 0.20
Mean diameter d_0 (mm)		22.2	17.5	15.1	20.7	19.7	19.0 ± 2.8
Basal area* (m^2 per 100 m^2)		0.46	0.45	0.43	0.47	0.48	0.46 ± 0.02
Number of trees (individuals per 100 m^2)	2013	508	898	653	759	710	706 ± 141
Mean tree height (m)		2.87	2.45	2.51	2.54	3.09	2.66 ± 0.28
Mean diameter d_0 (mm)		46.6	36.8	36.0	35.8	37.8	38.6 ± 4.5
Basal area* (m^2 per 100 m^2)		0.87	0.96	0.66	0.77	0.80	0.81 ± 0.11

*basal area is expressed by measurements of d_0 at the ground level

RESULTS AND DISCUSSION

Development of stand characteristics

Between spring 2009 and spring 2013, stand size and number of trees in the spruce stand changed significantly (Table 1; Fig. 1). On a stand level, mean stand height increased from 1.27 m to 2.66 m, stand diameter d_0 enlarged from 19.0 mm to 38.6 mm. Basal area, based on diameter d_0, increased from 0.46 m^2 to 0.81 m^2 per 100 m^2 and the number of trees per 100 m^2 dropped from 1898 to 706 individuals. As for the tendency of all stand characteristics, inter-annual changes differed between 2009–2011 and 2011–2013. It is supposed that the differences in the rates of the stand development relate to canopy closure and as a consequence, changes in the light regime in the stand. While in spring 2009 individual tree crowns were mostly not or just slightly overlapping, in spring 2010 it was observed that the crown canopy had closed. In that time, light access to the stand was limited and this is reflected in tree growth and biomass allocation in consecutive years. Therefore, the "behaviour" of stand development changed, specifically with a one-year delay (i.e. since 2011). For instance, the number of trees per 100 m^2 between 2011 and 2012 decreased from 1392 to 989 (i.e. by ca 1/3), which caused the stagnation of basal area. High mortality of trees (mostly of the smallest saplings) since 2011 resulted in an increased rate of mean stand height. In general, survival and growth of trees in young stands is predominantly controlled by light conditions (e.g. Claveau et al. 2002; Metslaid et al. 2005; Lutz, Halpern 2006). This indicates that high tree mortality in young stands was reflected not only in the number of live trees, but also in other stand characteristics, especially basal area and mean height.

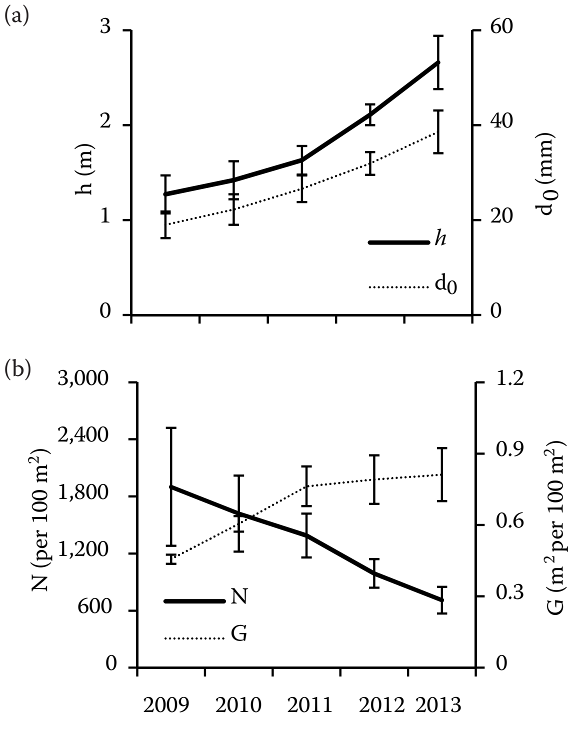

Fig. 1. Development of basic spruce stand characteristics, i.e. (a) mean tree height (h) and stem diameter (d_0), (b) stand density (N) and basal area (G) (based on diameter d_0 – measured at the ground level) between the years 2009–2013; error bars show standard deviations

Biomass allocation on a tree level

The tree sampling in 2009 and 2013 allowed for the construction of allometric models (hereinafter model 2009 and 2013, respectively) for basic tree components, i.e. coarse roots, stem (under bark), bark (on the stem), branches and needles. The results (Table 2) showed that diameter d_0 was a suitable independent variable, i.e. the models expressed all tree components with high precision. The sampling in 2009 showed that the ratio between coarse roots and aboveground biomass changed with diam-

Table 2. Statistical characteristics for allometric equations expressing the relationship between tree components, biomass and diameter d$_0$ in spruce based on sampling conducted in 2009 and 2013

Component	b$_0$ (SE) *P*	b$_1$ (SE) *P*	R^2	MSE	λ	SD
2009						
Needles	−3.079 (0.171) < 0.001	2.432 (0.054) < 0.001	0.964	0.106	1.053	0.366
Branches	−3.812 (0.182) < 0.001	2.534 (0.057) < 0.001	0.961	0.125	1.059	0.356
Stem under bark	−2.775 (0.152) < 0.001	2.310 (0.048) < 0.001	0.967	0.089	1.048	0.369
Stem over bark	−2.369 (0.142) < 0.001	2.273 (0.045) < 0.001	0.970	0.077	1.042	0.348
Bark	−3.441 (0.136) < 0.001	2.169 (0.043) < 0.001	0.970	0.071	1.039	0.334
Aboveground	−1.825 (0.144) < 0.001	2.374 (0.045) < 0.001	0.973	0.075	1.039	0.320
Coarse roots	−2.551 (0.130) < 0.001	2.054 (0.041) < 0.001	0.971	0.062	1.031	0.269
Whole tree	−1.489 (0.134) < 0.001	2.321 (0.042) < 0.001	0.976	0.065	1.034	0.295
2013						
Needles	−0.780 (0.416) 0.068	1.652 (0.101) < 0.001	0.861	0.160	1.069	0.365
Branches	0.717 (0.302) 0.022	1.371 (0.074) < 0.001	0.890	0.084	1.039	0.286
Stem under bark	−1.797 (0.232) < 0.001	2.203 (0.057) < 0.001	0.972	0.050	1.023	0.211
Stem over bark	−1.450 (0.220) < 0.001	2.160 (0.054) < 0.001	0.974	0.045	1.021	0.200
Bark	−2.397 (0.189) < 0.001	1.934 (0.046) < 0.001	0.976	0.033	1.016	0.181
Aboveground	0.130 (0.171) 0.452	1.896 (0.042) < 0.001	0.980	0.027	1.012	0.154

b$_0$, b$_1$ – coefficients, SE – standard errors, R^2 – coefficient of determination, MSE – mean square error, λ – logarithmic transformation bias, SD – standard deviation

eter d$_0$ only for very small trees (Fig. 2). Spruces with diameter d$_0$ over ca. 30 mm manifested rather a constant value (0.13–0.14) of the ratio. The same phenomenon was recorded in previous experiments, not only in young spruce (Pajtík et al. 2008) but also in *Fagus slyvatica, Pinus sylvestris*, and *Quercus petraea* (Konôpka et al. 2010). Bernier et al. (1995) showed in their review paper that the root/shoot ratio in Norway spruce starts from about 0.33, implying a larger contribution of roots to total tree biomass at young stages. Harris (1992) found that in most adult forest trees under normal conditions the root/shoot ratio is quite stable against the tree size having values between 0.16 and 0.20.

Our comparison of biomass quantities estimated by models constructed on tree samples harvested in 2009 differed from those based on the sampling conducted in 2013 (Fig. 3). Even though the data from the sampling in 2009 includes trees with diameter d$_0$ up to 80 mm, the sampling in 2013 recorded a diameter d$_0$ up to 150 mm. This indicates that the first sampling in 2009 recorded less stem biomass but more branch and needle biomass than the sampling in 2013. On the other hand, differences between the two models were less evident for aboveground biomass as a whole. Suggesting that if trees with identical diameters d$_0$ are considered, trees sampled in 2009 (or generally trees in the stand) allocated more biomass in needles and branches, but less in the stem than the 2013 samples. At the same time, trees from both samplings manifested similar aboveground biomasses. Fig. 4 compares model 2009 and model 2013 with regard to the component contribution to the aboveground biomass against diameter d$_0$. Model 2009 and model 2013 overlap trees with diameter d$_0$ in the interval of 20–60 mm. If the situation is simplified, model 2009 suggests a much higher contribution of needles than model 2013. The opposite situation is evident for stems. Differences between the models exist, not only in the contribution of the components to aboveground biomass but also in their tendencies (changes with diameter d$_0$). Such differences are evident especially for stem (decreasing in model 2009 but increasing in model 2013) and branches (increasing in model 2009 but decreasing in model 2013). The

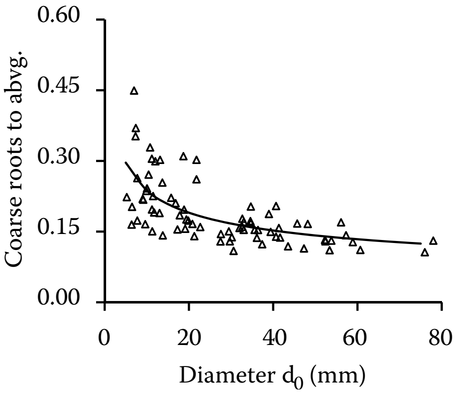

Fig. 2. The ratio between coarse root and aboveground biomass in spruce trees based on sampling conducted in 2009

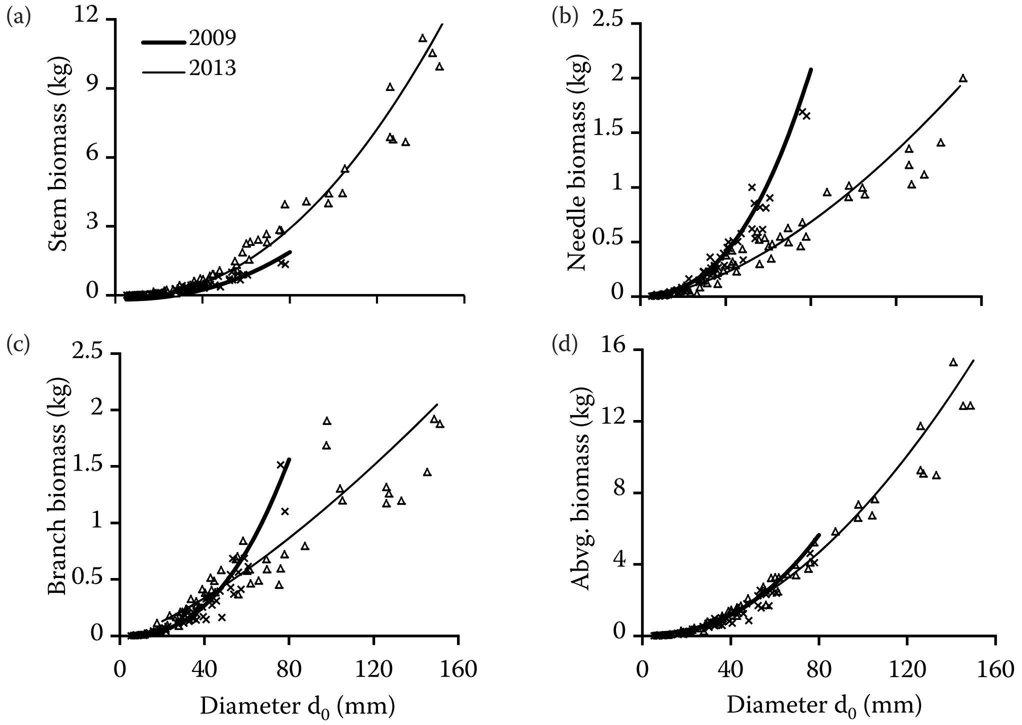

Fig. 3. Allometric relations on a tree level for (a) stem, (b) needles, (c) branches, and (d) aboveground biomass against diameter d_0; comparison between model 2009 and model 2013

changes in biomass allocation in young spruce between 2009 and 2013 were so large that allometric equations based on sampling in the first year were unsuitable for the last year of our experiment. These findings concerning changes on biomass allocation are in accordance with Kantola and Mäkelä (2006), where the proportion of branch biomass increases and that of needles decreases with increasing tree height inside the developing crown in a young Norway spruce stand. The crown ratio in very young trees is nearly 100% and branches therefore account for a large biomass pool. After canopy closure the proportion of branch biomass decreases together with the crown ratio.

Biomass allocation on a stand level

Contrary to other components, biomass of fine roots was estimated exclusively on a stand level for all years of observation (Fig. 5a). Maximum standing stock of fine root biomass (64.8 kg per 100 m^2) was recorded in 2013 and minimum (51.0 kg per 100 m^2) in 2012. Quantities of fine root biomass were similar in the years 2009, 2010, 2011, and 2013, less fine root biomass (but not statistically significantly; HSD test with $\alpha = 0.05$) occurred in 2012. It is supposed that the lower standing stock of biomass in 2012 might be caused by extensive tree mortality in the previous years and/or unfavourable conditions in the growing season of 2011. Meteorological measurements on the

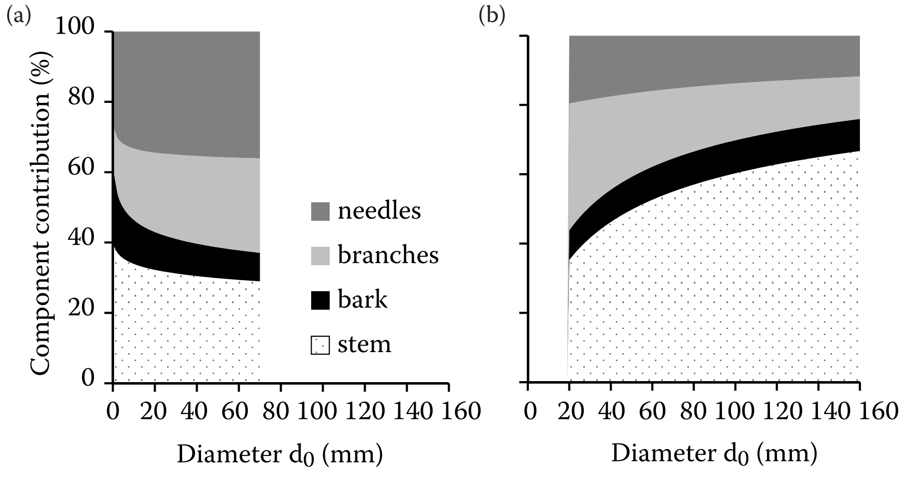

Fig. 4. Contribution of components (stem, bark, branches, needles) to aboveground biomass on a tree level against diameter d_0; according to (a) model 2009 and (b) model 2013

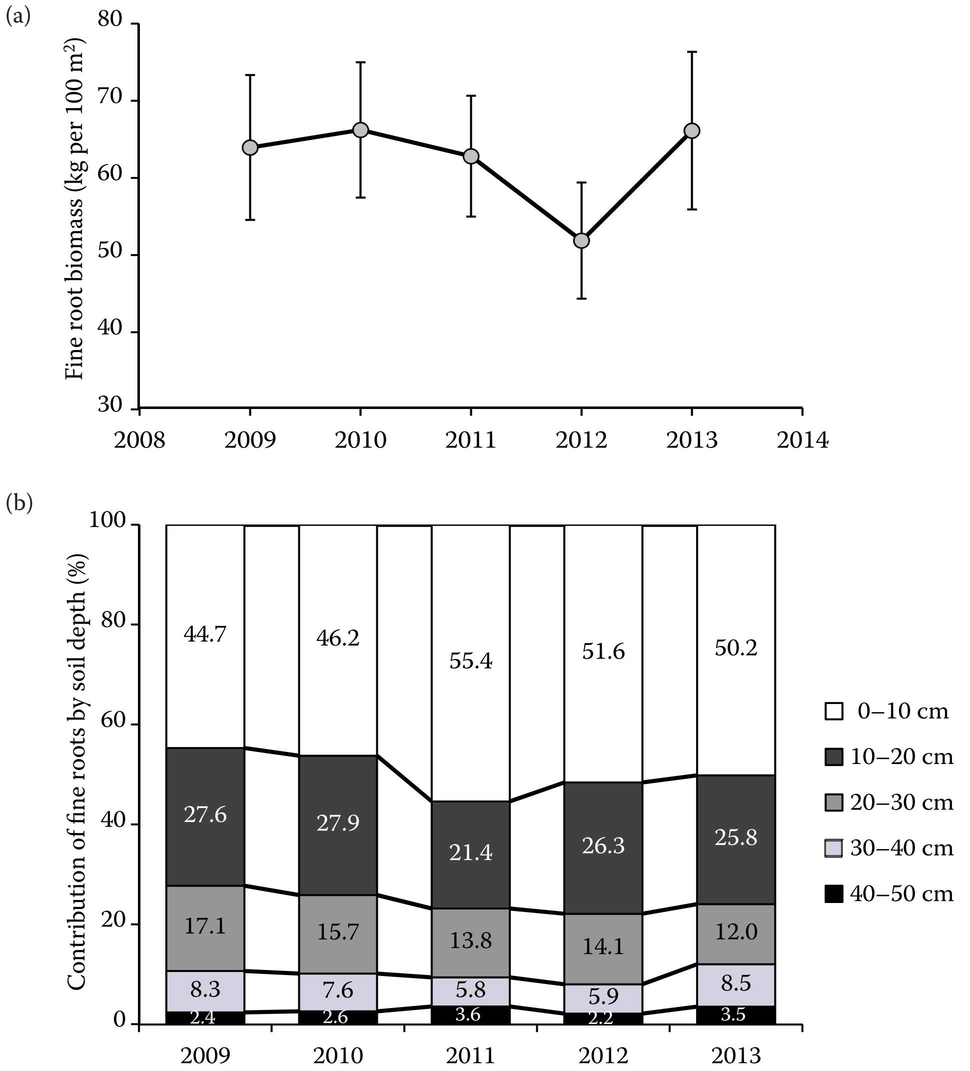

Fig. 5. Standing stock of fine roots (means and standard deviations) (a) and vertical distribution (b), expressed as percentage share, in the spruce stand for the years 2009, 2010, 2011, 2012, and 2013; no significant inter-annual differences were found (HSD test with α = 0.05)

site show for instance that autumn 2011 was extraordinarily dry (Konôpka et al. 2013) and might be an indication of stressful conditions for fine roots. Moreover, a decreased number of trees by ca 400 individuals per 100 m^2 between spring 2011 and spring 2012 might also influence the standing stock of living fine roots. Soil coring provides not only the total standing stock of fine roots, but also information on their vertical distribution (Fig. 5b). Although some inter-annual differences occurred in the vertical distribution between the years, biomass of fine roots always decreased with soil depth. Thus, the contribution of fine roots to their biomass at the specific soil depths was 44.7–50.2% (0–10 cm), 21.4–27.9% (10–20 cm), 12.0–17.1% (20–30 cm), 5.8–8.5% (30–40 cm) and 2.2–3.6% (40 to 50 cm). Decreasing fine root biomass with soil depth was shown in a variety of forest ecosystems (e.g. Xiao et al. 2003; Ostonen et al. 2004; Makita et al. 2011; Olesinski et al. 2011). The phenomenon is subjected to heterogeneities (decreasing concentrations) of nutrients, water and oxygen resources along the vertical profile of soil, sometimes also to physical properties of soil (Kroon, Viseer 2003).

The estimates on a stand level showed that during the period 2009–2013, tree biomass in a spruce stand increased 2.2-fold, specifically from 449 kg to 986 kg per 100 m^2 (Table 3). While biomass of needles and fine roots changed only negligible, branch biomass increased 2.7 times, stem biomass (over bark) 3.4 times and coarse roots 2.1 times. It means that also biomass structure (allocation) changed considerably (Table 4). If the contribution of the particular components to total stand biomass is considered, only small changes were recorded for branches (17.1% and 20.8% in 2009 and 2013, respectively) and coarse roots (12.5% and 11.8% in 2009 and 2013, respectively). However, the contribution of needles decreased by 1.9 times (from 25.6% to 13.7%), and also fine roots by 2.1 times (from

Table 3. Standing stock of biomass in kg per 100 m^2 in the spruce stand by tree components in 2009 and 2013 (± SD)

Year	Needles	Branches	Stem over bark	Coarse roots	Fine roots	Tree biomass
2009	114.8 ± 14.6	76.9 ± 11.7	138.4 ± 24.8	56.0 ± 4.2	62.7 ± 9.1	448.8 ± 52.8
2013	135.4 ± 20.6	204.9 ± 33.4	464.5 ± 67.8	116.0 ± 17.7	64.8 ± 9.9	985.6 ± 141.9
Increase	20.6 ± 27.4	128.0 ± 38.7	326.1 ± 81.1	60.0 ± 18.7	2.1 ± 4.1	536.8 ± 156.0

Table 4. Contribution of tree components (%) to the whole-tree biomass in the spruce stand in 2009 and 2013

Year	Needles	Branches	Stem over bark	Coarse roots	Fine roots	Tree biomass
2009	25.6	17.1	30.8	12.5	14.0	100.0
2013	13.7	20.8	47.1	11.8	6.6	100.0
Difference	–11.9	3.7	16.3	–0.7	–7.4	0.0

14.0% to 6.6%). The opposite trend occurred for stem over bark that increased by 1.5 times (from 30.8% to 47.1%). In fact, since the calculation of the standing stock of coarse roots was based on the *in situ* sampling conducted in 2009 but not in 2013 (here we used the knowledge from the country model, see Pajtík et al. 2009, in combination with *in situ* allometric model 2009), this estimation should be considered with caution. However, we can surely state that both the ratio between belowground and aboveground biomass and the ratio of short-lived parts (needles and fine roots) to long-lived parts (woody components such as coarse roots, stem over bark and branches) manifested decreasing tendencies during the period of observation.

It is supposed that the young, very dense spruce stand reached the maximum standing stock of both needles and fine roots. Fine root standing stock increased in young stands, only at very young growth stages, with fine root biomass of coniferous forests reaching a maximum at the approximate time of canopy closure (Vogt et al. 1987). Later, the fine root quantity remained stable (poor sites) or slightly decreased (fertile sites). In addition, the highest values of leaf area index were found in young coniferous forests (Waring, Schlesinger 1985). Vogt et al. (1987) stated that biomass (or surface area) of foliage and fine roots is equilibrated, therefore peaks of biomass in both tree components would occur synchronically. Hence, it can be predicted for the spruce stand that while biomass of woody parts (coarse roots, stem and branches) will keep increasing, biomass of fine roots and needles would remain at the same level.

CONCLUSIONS

The results show very dynamic development and growth processes in a young (from 12- to 16-years-old) spruce stand originating from natural regeneration. During five years of observations, the number of trees decreased 3.7-fold, the most dramatic decrease was found between the third and fourth year. It is supposed that the enhanced tree mortality was related to the canopy closure which significantly reduced light in the stand. These changes in the light regime perhaps influenced biomass allocation on both the tree and stand level. The ratio between belowground and aboveground biomass as well as the ratio of short-lived parts to long-lived parts manifested decreasing tendencies. These modifications in biomass allocation very probably influenced the carbon regime of forest stand.

It can be concluded that changes in the allocation of biomass in a young spruce stand between the first and fifth year of observation were so large that allometric equations based on samplings in different years (model 2009 and model 2013) were not comparable. The smallest differences between the models were for total aboveground tree biomass. These results suggest that allometric models based on tree sampling in young stands might be less sensitive to time for estimating the whole-tree standing stock than for their allocation (considering the components). Therefore, it appears that for biomass allocation estimates in young stands, not only stand-specific but also time-specific allometric relations should be implemented. Finally, it is concluded that there is a canopy closure threshold beyond which biomass allocation is different from the situation in sparse young spruce stands.

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