

Pôvodné práce – *Original papers***ABOVE-GROUND NET PRIMARY
PRODUCTIVITY IN YOUNG STANDS
OF BEECH AND SPRUCE**JOZEF PAJTÍK^{1,2}, BOHDAN KONÔPKA^{1,2}, RÓBERT MARUŠÁK²¹National Forest Centre - Forest Research Institute Zvolen, T. G. Masaryka 2175/22,

SK – 960 92 Zvolen, e-mail: pajtik@nlcsk.org

²Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129,
CZ – 165 21 Praha 6 - Suchbátka

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One of the expected consequences of climate change and its inherent phenomena to forest ecosystems is the gradual modification of their tree species composition (i.e. expansion of resistant species instead of less resistant ones). Climate change accompanied with increasing temperatures and a lack of precipitations may present a threat especially to spruce stands in the European part of the temperate zone. European beech is one of the possible forest tree species which might replace the potentially endangered spruce. In this paper, we observed, by using a combination of continual measurements and destructive whole-tree sampling, standing stocks of above-ground biomass (i.e. stem, branches, and foliage) and its annual net primary productivity (NPP) in naturally regenerated young stands of beech and spruce. We intentionally selected a site where the changing climate conditions are better suited to the ecological demands of beech rather than spruce (the species is dominant in the observed area). We recorded only small differences in the standing stock of stems of the beech, if based on tons per ha. However, this is in favor of spruce if based on cubic meters per ha. The largest difference between the species was found for the standing stock of foliage, spruce retained three times the biomass of beech. Also, beech allocated more carbohydrates to stem than spruce. On the other hand, we estimated nearly the same production of foliages and branches in both stands.

Keywords: *Fagus sylvatica*, *Picea abies*, net primary productivity, above-ground biomass, standing stock, tree compartments

1. Introduction

Since forests store approximately 80% of the total terrestrial aboveground carbon (SIX *et al.*, 2002) they would play a principal role in the mitigation of the climate change process (JANDL *et al.*, 2007). For instance, JANSSENS *et al.* (2003) estimated that in European conditions, forests absorb about 10% of emissions with agricultural land being a source and forests a sink of CO₂.

At the same time, BRUNNER & GODBOLD (2007) stated that the temperate forests in Central Europe stored about 110 t C per ha in tree biomass and 65 t C per ha in the soil (without roots). This means that nearly 2/3 of a forest ecosystems' C pool was fixed in tree biomass. At the same time, circa 3/4 of biomass is located in the aboveground compartments and 1/4 in the root system (BRUNNER & GODBOLD, 2007). In general, an essential

part of tree biomass is obviously found in the stem (WEST, 2010). However, this assumption relates mostly to middle-age and old forest stands. Rather different biomass partitioning patterns exist in small trees. Specifically, young stages of tree growth typically have a rather high portion of carbohydrates invested into branches and foliage sometimes even prevailing over the quantity in the stem (KOZŁOWSKI & PALLARDY, 1997).

Distinct changes in tree biomass allocation to the particular compartments with an increasing stand size (age) in young stages of European beech and Norway spruce were shown by KONŌPKA *et al.* (2010). The paper indicated that while the contribution of stem to total aboveground biomass increased, the contribution to branches and foliage decreased with increasing stand size. In general, aboveground tree compartments, as for carbon fixation span, can be separated into two groups: those with a fast turnover (foliage) and those with a slow turnover (stem and branches). Hence, changes in the proportion of compartments with contrasting carbon sequestration times can be assumed as well. Implicitly, the role of forest stands in carbon cycling and fixation should be analyzed and interpreted with respect (besides some other factors) to growth stage, eventual size and age.

One of the most efficient and rather simple ways to express tree biomass quantity and its structure by the compartments is using allometric equations based on easily measurable tree characteristics, often diameter and/or height (WEST, 2009). While plenty of papers show allometric equations for old European beech and Norway spruce stands (CIENCIALA *et al.*, 2005; WIRTH *et al.*, 2004; FEHRMANN & KLEINN, 2006; SEIDL *et al.*, 2010) only a few authors focus on their young growth stages (e.g. CLAESSON *et al.*, 2001; PAJTIK *et al.*, 2011a). At the same time, equations for tree compartment biomass estimated for large and older trees are not generally applicable to young trees (WIRTH *et al.*, 2004).

Our previous paper (KONŌPKA *et al.*, 2010) indicated a certain tendency of biomass allocation patterns with regard to tree size. However, changes in biomass partitioning patterns were based on estimative height increments focusing at tree level. Consequently, we decided to make a step forward in this field and demonstrate in this current paper how the structure of aboveground standing biomass changes inter-annually in young stands of European beech and Norway spruce – both grown at the same site. Here, our calculations were based on empiric material of real stand growth (height and diameter increments of trees in the stands) in the specific years of observation. At the same time, a partial aim of the work was to construct stand-specific allometric equations for the aboveground compartments, i.e. stem, branches and foliage. A further mission of this paper was to estimate aboveground net primary productivity (NPP) and its structure in the particular years of our study.

2. Materials and methods

2.1. Site description

The site “Vrchslatina” is located in the southern part of the Veporske vrchy massif at cca 960 m above sea level (48° 38' 55'' N, 19° 36' 07'' E). A more detailed description of the research site is given in KONŌPKA *et al.* (2013b). Since NPP and biomass allocation may be affected by climatic conditions, we measured temperature and precipitation at the site. Monthly means for 2009 – 2012 as well as monthly means for a reference periods from 1961 to 1990 are shown in the paper of KONŌPKA *et al.* (2013b). On this site, we selected two neighbouring stands of pure European beech and pure Norway spruce, both naturally regenerated after a stand clearance with ages between circa 12 – 14 years. Both stands were approximately 0.7 ha in size making up compact clumps (groups of trees) of varying density with a few scattered gaps dominated by *Calamagrostis epigejos* (L.). The specific clumps were mostly composed exclusively by either beech or spruce trees.

In April 2009, we established 5 plots in beech and also 5 plots in the spruce stand. The plots were circular and placed to avoid atypical spots (e.g. gaps, stand ages and so on). The plots had a radius of between 0.7 and 1.0 m, their size depended on stand density and was adjusted to include cca 30 – 50 individuals of beech or spruce. Every year since 2009, we measured basic characteristics of the trees, specifically: diameter at stem base (d_0), diameter at breast height ($d_{1.3}$) and tree height. The measurements were done outside the growing season (either very early spring or late autumn). The diameters were measured by means of digital callipers with a precision of 0.1 mm – on a stem base for all trees, and 130 cm from the ground level for those which exceeded this height. Tree heights were measured by a wooden meter – for trees up to a height of 2 m with a precision of 1 cm, for higher ones with a precision of 5 cm. Then, mean diameters, mean heights and mean stem volume were calculated as weighted arithmetic mean from plot average numbers weighted by plot sizes. To calculate the mean height we used the Lorey procedure. To the express stem volume of trees the approach as in our previous paper was used (PAJTIK *et al.*, 2011a). Then, mean stem volume was calculated as an average from stem volumes for all trees on the plots.

Quantities of biomass (expressed as dry weight) for foliage, branches and stem of the specific aboveground tree compartments were expressed by these allometric equations:

$$W_i = e^{(b_0 + b_1 \cdot \ln d_0)} \cdot \lambda \quad [1]$$

$$W_i = e^{(b_0 + b_1 \cdot \ln h)} \cdot \lambda \quad [2]$$

$$W_i = e^{(b_0 + b_1 \cdot \ln d_0 + b_2 \cdot \ln h)} \cdot \lambda \quad [3]$$

where W_i is biomass for compartment i (foliage, branches, stem, woody parts together, entire aboveground part),

d_0 is diameter at the stem base, h is tree height, b_0 , b_1 , a , b_2 are coefficient, λ is logarithmic transformation bias.

To construct the allometric equations which express the biomass of aboveground tree compartments using diameter and/or height as independent variables, 80 spruces (20 individuals for each specific bio-sociological position, i.e. dominant, co-dominant, sub-dominant and suppressed) and 60 beeches (15 individuals for each specific bio-sociological position) were cut at the site in September 2009. Thus, we were able to make site- and stand-specific equations.

By a combination of data on tree diameters and heights with allometric equations, standing stock of the specific tree compartments on a hectare base was calculated. In this way, standing biomass stock of live trees in April of the current year as well as the quantity of trees which died in the period between Aprils of the consecutive years were estimated. Detailed descriptions of tree sampling, laboratory procedures, construction of allometric equations and estimations of tree standing biomass on a stand level are shown in the papers of PAJTIK *et al.* (2008) and KONÓPKA *et al.* (2010).

In this paper, biomass for the above-ground tree compartments is calculated through the equation [3], it means that both tree diameter and height are used as independent variables. Hence, biomass of stem, branches and foliages were estimated. However, for needle biomass in spruces, a different approach has to be used. In fact, the biomass of needles was composed prevailingly of four sets (separated by year of birth) and a very small amount of five-year-old needles. First, we estimated needle mass of the spruces expressed as a status in April 2010. This amount was determined from an allometric model, i.e. by using sample trees taken in September 2009, minus the mass of needles accumulated in litter collectors (see also KONÓPKA *et al.*, 2013b) in the period between September 2009 and April 2010. If this “starting” needle amount is marked as B_{2010} , then, biomass of spruce needles in the specific years is calculated by means of the algorithms:

$$B_{2009} = B_{2010} - b_{2009} + L_{2009} \quad [4]$$

$$B_{2011} = B_{2010} - b_{2010} + L_{2010} \quad [5]$$

$$B_{2012} = B_{2011} - b_{2011} + L_{2011} \quad [6]$$

where B_i is total needle stock in April of year (i), b_i is stock of needles born in the current year (i), L_i is quantity of needle litter collected between April of previous year (i) and April of consecutive year (i+1).

The stock of needles born in specific years (b_i), 2010 and 2011, was determined from felled sample trees. In both years, we felled 40 spruces (10 pieces of each bio-sociological status), the needle sets born in the said years were separated, oven-dried and weighed. An allometric model for the needles was constructed according to equation [3].

To estimate the litter of needles, three open collectors sized 27 × 27 cm were placed on each plot in April 2009. Then, litter was harvested from the collectors in circa 6-weeks intervals. The mass of needles found after certain periods in the collectors reflected a loss of needles between two occasions. In beech foliages, the sum of litters harvested during one growing season was used as a reference value of figures obtained via allometric equations on a stand level.

Finally, total above-ground biomass and production was calculated as a sum of all compartments (stem, branches and foliages) on a tree level. Then, values of above-ground biomass and production were expressed on the plot levels (by summarizing all trees recorded on the plots) and up-scaled on a hectare base.

All mathematical and statistical operations were performed using the Statistica 10.0 program.

3. Results and discussion

The measurements proved large inter-annual differences in the basic stand characteristics of both beech and spruce (Table 1). While a number of trees diminished, tree size increased considerably.

Histograms of tree distribution by diameter and height classes are shown in Figure 1. Spruce has shown

Table 1. Basic stand characteristics of the beech and spruce in the springs of 2009 – 2012

Stand characteristics	European beech			
	April 2009	April 2010	April 2011	April 2012
Number of trees [ths. ha ⁻¹]	157	150	136	125
Mean tree height [cm]	225	272	323	373
Mean diameter d_0 [cm]	1.89	2.13	2.43	2.67
Average stem volume [cm ³]	233.1	313.2	452.2	594.9
Stand characteristics	Norway spruce			
	April 2009	April 2010	April 2011	April 2012
Number of trees [ths. ha ⁻¹]	176	154	134	98
Mean tree height [cm]	172	212	242	301
Mean diameter d_0 [cm]	1.88	2.29	2.71	3.23
Average stem volume [cm ³]	224.6	336.0	495.8	860.4

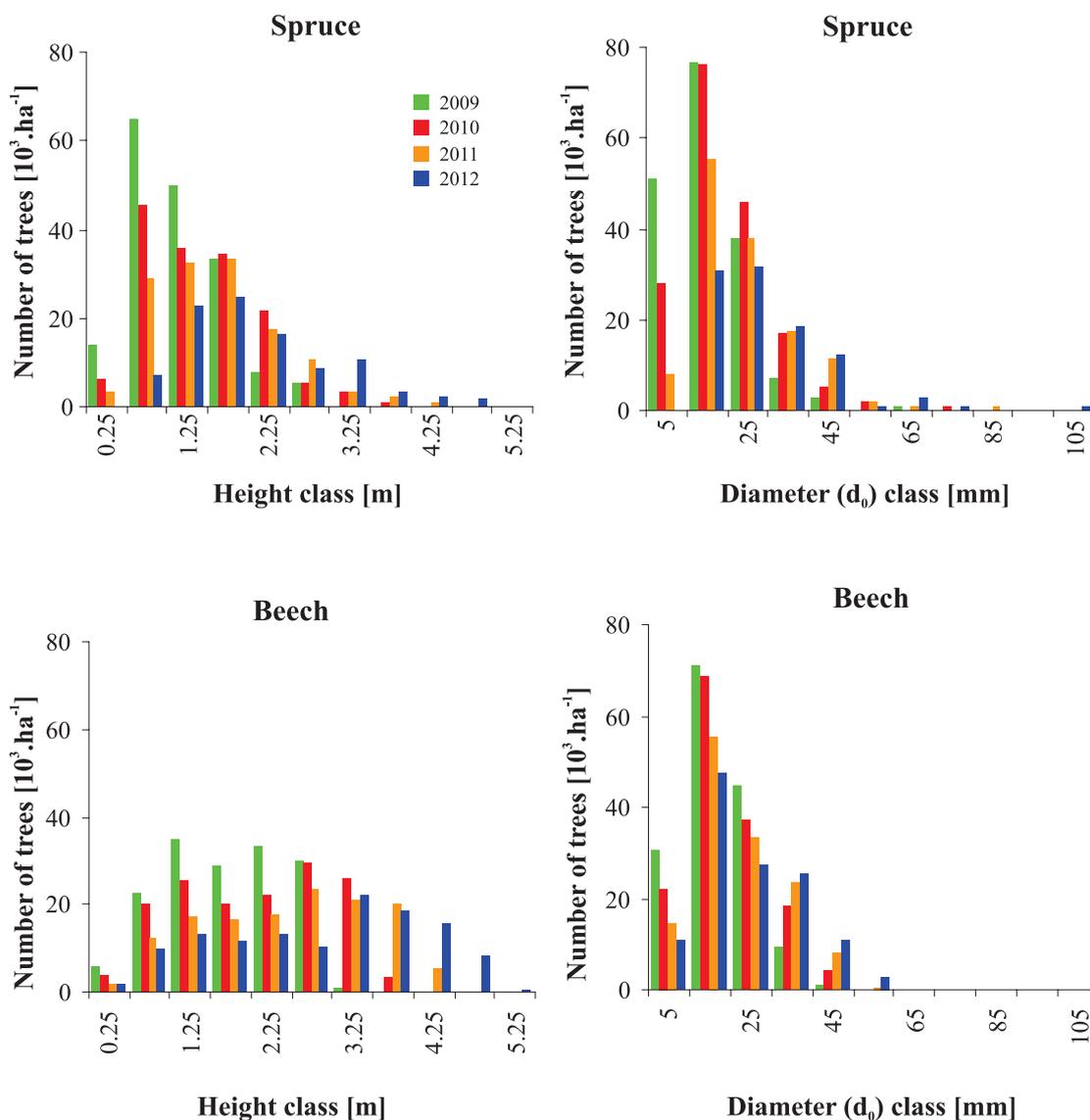


Fig. 1. Diameter and height histograms of Norway spruce and European beech found in experimental plots in April in 2009, 2010, 2011 and 2012

a slightly left-sided distribution of heights in 2009 and 2011 and a normal distribution in 2010 and 2012 (Kolmogorov-Smirnov test). Heights of spruces in the stands manifested a normal distribution in all years. As for the beech stand, heights showed up normal distribution in 2009 and 2011, but a slightly left-sided distribution in 2010 and 2012. Heights of beech manifested normal distribution in all years except for 2012 which showed a slightly right-sided distribution. Coefficients of skewness showed positive values, only the beech height distribution had negative values, indicating that most values are situated more to the right than average figures.

The number of trees per hectare in the beech stand declined in the years 2009 – 2012 by 20.4%, the mean tree height, diameter and stem volume increased by 65.7%, 41.3% and 155.2%, respectively. The inter-annual increments of the mean tree height were between 47 – 51 cm,

and the mean tree diameters were 0.24 – 0.30 cm. These increments of the mean tree parameters did not depend exclusively on growth intensity but also on the number and size of trees that died in the specific years.

As for the spruce stands, a number of the trees per hectare decreased in the entire period of observation by 44.3%, mean tree height, diameter and stem volume increased by 75.0%, 71.8% and 283.1%, respectively. The inter-annual increase of the mean tree heights were from 30 to 59 cm and mean tree diameters from 0.42 to 0.52 cm. Differences in mean tree diameters between the beeches and spruces in the first three years were low (up to 10%). On the other hand in 2012, the differences were as much as 44.6% in favor of the beeches due to the high mortality of suppressed and co-dominant spruces. This mortality influenced the height and diameter frequency distribution considerably.

Table 2. Basic statistical characteristics for allometric equations expressing biomass of aboveground tree compartments

Tree species	Tree compartment	b_0 (S. E.) P	b_1 (S. E.) P	b_2 (S. E.) P	R ²	MSE	λ	S. D.
Norway spruce	Stem	0.695 (0.269) 0.012	1.100 (0.101) < 0.001	1.380 (0.115) < 0.001	0.990	0.027	1.014	0.192
	Branches	-1.963 (0.541) < 0.001	1.824 (0.204) < 0.001	0.831 (0.230) < 0.001	0.967	0.108	1.051	0.327
	Needles	-1.888 (0.521) < 0.001	1.977 (0.196) < 0.001	0.533 (0.221) 0.018	0.967	0.100	1.049	0.337
	Needles 2009	-3.629 (0.943) < 0.001	2.025 (0.355) < 0.001	0.610 (0.400) 0.132	0.906	0.328	1.150	0.592
	Needles 2010	-3.543 (1.388) 0.015	1.799 (0.533) 0.002	1.420 (0.574) 0.018	0.919	0.249	1.116	0.583
	Needles 2011	-4.084 (0.578) < 0.001	2.065 (0.259) < 0.001	0.826 (0.361) 0.028	0.972	0.090	1.041	0.296
European beech	Stem	-1.763 (0.216) < 0.001	1.905 (0.093) < 0.001	1.069 (0.093) < 0.001	0.989	0.024	1.011	0.152
	Branches	-6.581 (0.577) < 0.001	3.265 (0.249) < 0.001	0.174 (0.248) 0.485	0.947	0.170	1.076	0.413
	Foliages	-5.943 (0.439) < 0.001	2.783 (0.190) < 0.001	0.332 (0.189) 0.083	0.962	0.098	1.045	0.305

Table 3. Biomass standing stock by tree compartments in tons per hectare (in April of current year)

Tree compartment	Beech				Spruce			
	2009	2010	2011	2012	2009	2010	2011	2012
Stem	17.439	25.219	35.058	44.716	13.838	19.766	25.420	31.418
Stem*	36.597	46.980	61.499	74.363	39.530	51.744	66.437	84.319
Branches	5.526	8.151	11.867	15.125	7.689	11.483	15.558	19.028
Foliages	0.000	0.000	0.000	0.000	13.611	15.306	17.873	19.418

* expressed on volumetric base ($m^3 \cdot ha^{-1}$).

Table 4. Annual biomass production by tree compartments in tons per hectare a year

Tree compartment	Beech			Spruce		
	2009	2010	2011	2009	2010	2011
Stem (A)	7.785	10.175	10.107	6.165	6.408	7.039
Stem*	10.390	14.971	13.468	12.683	16.422	20.526
Branches (B)	2.626	3.802	3.378	3.901	4.487	3.992
Foliages (C)	3.803+	4.847+	6.025+	4.031	5.421	5.650
Aboveground biomass (A+B+C)	14.214	18.870	19.569	14.097	16.316	16.681

* expressed on volumetric base ($m^3 \cdot ha^{-1}$), + calculated through allometric equation.

By using allometric equations (see Table 2 for their parameters) we were able to calculate the standing stock of the specific tree compartments at the beginning of the growing seasons in 2009 – 2012 (Table 3). The stem standing stock grew in the beech stand between 2009 and 2012 from 17.4 to 44.7 $t \cdot ha^{-1}$ (i.e. 2.6 fold) and in the spruce stand from 13.8 to 31.4 $t \cdot ha^{-1}$ (2.3 fold). There was a sharper increase of stem standing stock in the beech than in the spruce stand, even though in the case of stem volume it was the reverse. This happened for two reasons; the first reason was large tree mortality in the spruce stand and the second there was a higher value of wood density in the beech. A similar situation is assumed also for the standing stock of branches as well as total aboveground woody biomass. In all the years of observation, the standing stock of branch biomass was higher in the spruce than the beech stands. Particularly in 2012, the branch biomass standing stocks were 19.4 $t \cdot ha^{-1}$ and 15.1 $t \cdot ha^{-1}$

in the spruce and beech, respectively. The standing stock of foliages could not be compared between the beech and spruce stands because the beech leaves were not developed yet, thus, we used an inter-species comparison in the productions (Table 4). We assume that the values in the spruces might be over-estimated in terms of litter amount occurrence during the development of the current year's needles. Between the years 2009 – 2011, the standing stock of leaf biomass increased from 3.8 $t \cdot ha^{-1}$, however, standing stock of the spruce needle biomass was much larger (between 13.6 $t \cdot ha^{-1}$ and 17.9 $t \cdot ha^{-1}$).

Biomass allocation in the specific tree compartments can be expressed in a variety of ways. Most frequently these two approaches are used: 1) by contribution of the tree compartments to the total standing biomass (YUSTE *et al.*, 2005; SŁOT *et al.*, 2012; KONŌPKA *et al.*, 2013), or ii) through an allometric method in which the amount of a certain tree compartment is expressed to the biomass of

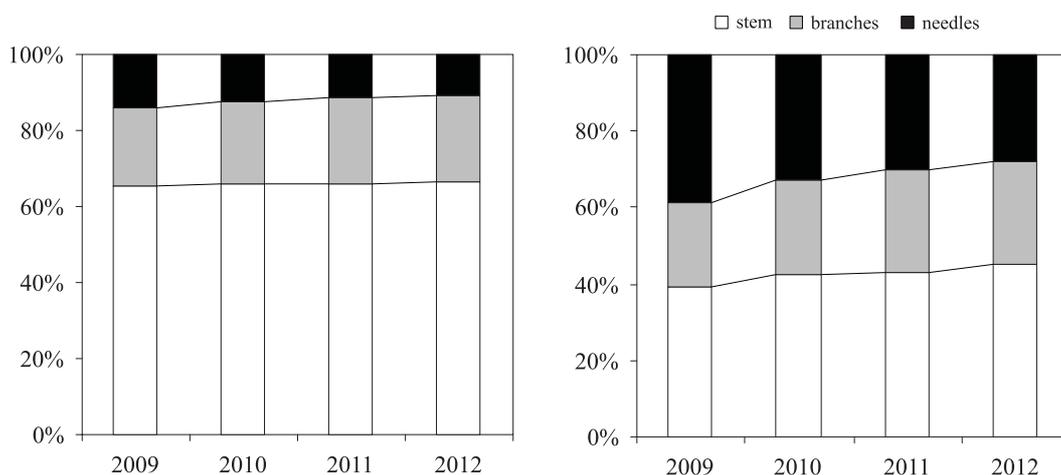


Fig. 2. Contribution of the specific tree compartments to total aboveground biomass in beech (left plate) and spruce (right plate)

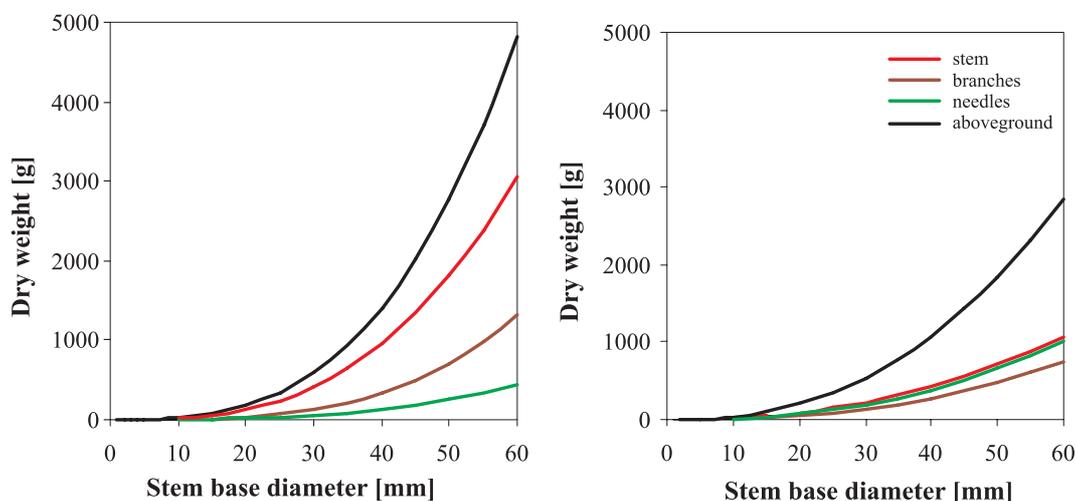


Fig. 3. Dependence of biomass by compartments on tree diameter d_0 in beech (left plate) and spruce (right plate)

another compartment (ENQUIST&NIKLAS, 2002; POORTER *et al.*, 2011), ultimately this is based on basic tree characteristics – diameter and/or height (PAJTIK *et al.*, 2008; ENQUIST&NIKLAS, 2002). To derive this relationship, a logarithmic transformation of traditional allometric equation is used (HUXLEY, 1932; GOULD, 1966). Our paper shows results obtained via both approaches. If we compare the contribution of the specific tree compartments to the total above-ground standing stock (Figure 2), large inter-annual differences are evident for stem and foliage. While in the year 2009 the needle biomass of the spruce made up 38.7% of aboveground standing stock, the beech leaves contributed only to 14.2%. The contribution of the foliage gradually decreased over time, and in 2012 the spruce needles made up 27.8% and the beech leaves 10.8% of aboveground biomass standing stock. In 2009, the share of the stems contributed to the aboveground biomass by 65.1% in the beech and 39.4%

in the spruce stands. This share gradually increased during the years of observation. In fact, a gradual increase of stem contribution, and decrease of foliage contribution to total tree biomass in young stands of beech and spruce and also oak and pine with tree (stand) size are shown in our previous works (PAJTIK *et al.*, 2008; PRIWITZER *et al.*, 2009; PAJTIK *et al.*, 2011a, b).

The proportions of branches to the aboveground biomass were similar in both species. In 2009, the proportions were 20.6% in the beech stand and 21.9% in the spruce stand, these gradually increased in the period of observation. Biomass allocation among the tree compartments with respect to tree diameter d_0 is given in the Figure 3. The biomass was calculated by means of classic allometric equations, which were logarithmically transformed and then retransformed to the form [1] (MARKLUND, 1987). Coefficients of the equations are in Table 2.

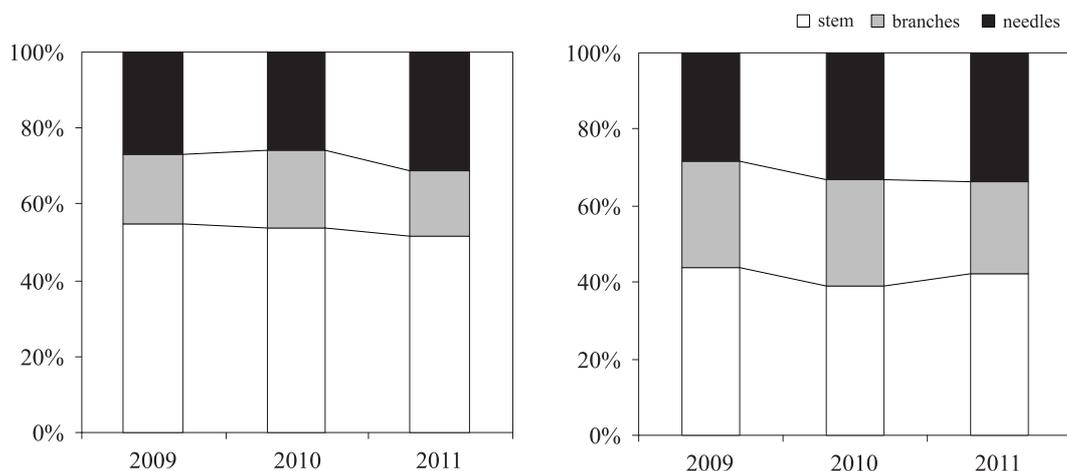


Fig. 4. Contribution of the specific tree compartments to aboveground net primary productivity in beech (left plate) and spruce (right plate)

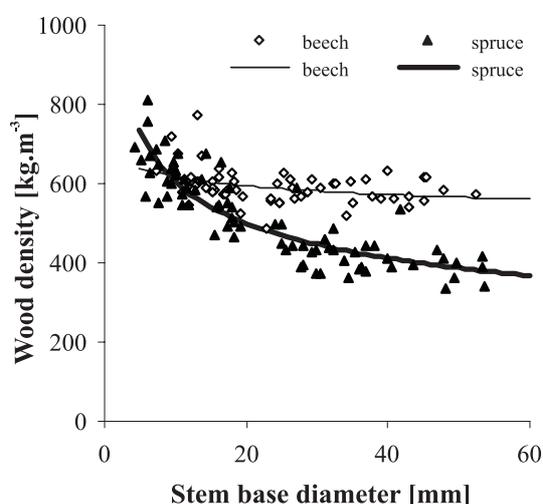


Fig. 5. Specific weight of beech and spruce stems with regard to tree diameter d_0

The largest contribution to the above-ground NPP in both tree species was found to be stems, followed by foliage and branches. Production of the compartments in the specific years was similar in both tree species (Table 4, Figure 4). Annual aboveground NPP increased from 14.2 t.ha⁻¹ to 19.6 t.ha⁻¹ in the beech, and from

14.1 t.ha⁻¹ to 16.7 t.ha⁻¹ in the spruce stand. However, in the case of volumetric expression of stem production, larger figures are shown for the beech than spruce stand. This is a consequence of the different wood densities of the species (Figure 5) and also contrasting developments in the number of trees. In general, it is usual for young spruce stands from natural regeneration to experience sharp decreases in the number of trees; this is caused by low light intensity under the canopy (PAJTIK *et al.*, 2008; DUTCA *et al.*, 2010). Thus, the above-ground NPP in the spruce only slightly increased during 2011 in spite of large diameter increments (see also BOŠEĽA *et al.*, 2013). On the other hand, a small increase of the NPP in the beech during 2011 was related to small diameter and height increments (also BOŠEĽA *et al.*, 2013). Inter-specific differences in foliage quantities are much larger for standing stock than in NPP, because the production only covers the current year spruce needles. Besides certain inter-annual differences in NPP, rather large differences were recorded for losses on tree compartments (Table 5).

Figure 6 demonstrates a comparison of aboveground NPP by compartments between the species and the years. The largest inter-species differences are for the stem biomass this was significantly larger in the beech than spruce stands especially in 2010 and 2011. Branch

Table 5. Inter-annual losses on tree compartments in tons per hectare a year

Tree compartment	Beech			Spruce		
	2009	2010	2011	2009	2010	2011
Stem	0.005	0.336	0.449	0.237	0.754	1.041
Stem*	0.007	0.452	0.604	0.469	1.729	2.644
Branches	0.001	0.086	0.120	0.107	0.412	0.522
Foliages	3.216 ⁺	4.120 ⁺	4.787 ⁺	2.336	2.854	4.105

* expressed on volumetric base (m³.ha⁻¹), ⁺ data originating from litter collectors.

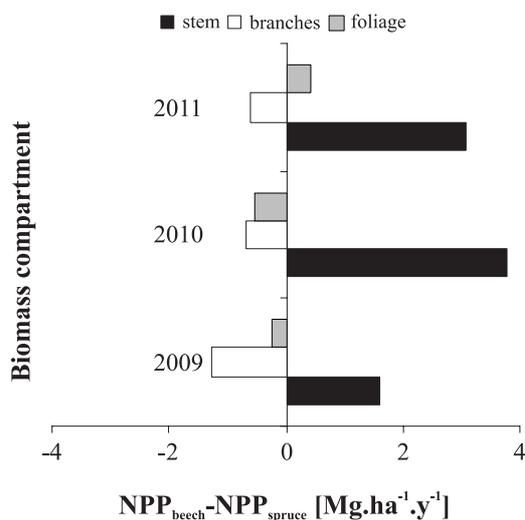


Fig. 6. Differences in NPP of the aboveground tree compartments between European beech and Norway spruce (years 2009 – 2011). Positive values are in favor of beech, negative ones in favor of spruce

productions were larger in the spruce than beech stands; on the other hand, foliage productions were rather similar in both tree species. Here, we would like to point out contrasting strategies of foliage turnover between the species. These features govern a higher role for beech foliages in carbon cycling than in the case of the spruce needle.

4. Conclusion

We studied the above-ground biomass standing stock and production by tree compartments in young beech and spruce stands grown under the same site conditions. The beech stand manifested relatively low tree mortality and maintained high tree density. Here, subdominant trees tried to reach the main crown layer and many suppressed trees survived in the under-layer. Most beech trees were high and slim with a high height to diameter ratio. On the other hand, the spruce stand was standard with a high share of tree mortality which suppressed; subdominant trees lacked light. The live trees invested carbohydrates to stem thickening, thus, they were lower but thicker than those in the beech stand.

Contrasting figures between the stands were found for the standing stock of stems with regard to different bases (volumetric versus biomass). A larger aboveground NPP was recorded in the beech than in the spruce stand; this is partly related to the higher wood density of beech. Large inter-species differences existed in the standing stocks of foliages, spruce manifested an amount three-fold larger than beech. However, the reverse situation is expected for interspecies differences if we focus on the role of foliages in carbon cycling (evergreen against deciduous species).

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Resumé

V tejto práci sme pomocou kombinácií kontinuálnych meraní a deštruktívnych odberov vzorníkov sledovali a porovnali zásobu nadzemnej biomasy a ročnú primárnu produkciu (NPP) v prirodzene obnovených mladých porastoch buka a smreka. Na vybranej lokalite predpokladáme, že zmenené klimatické podmienky budú lepšie vyhovovať buku pred v súčasnosti prevládajúcim smrekom. Lokalita Vrchslatina sa nachádza v južnej časti Veporských vrchov v nadmorskej výške 977 m nad morom (48° 38' 50'' N, 19° 36' 07'' E). Priemerné ročné zrážky sa pohybujú okolo 900 mm, priemerná ročná teplota je 5,2 °C.

Na sledovanej lokalite sme pozorovali odlišný priebeh rastu buka a smreka. Pri buku bola pozorovaná menšia medziročná mortalita, udržiaval sa až prehustený zápoj, v ktorom sa aj podúrovňové stromy snažili dostať do úrovne. Toto sa prejavilo na tvare kmeňov, ktoré sú tenké a vysoké. Štíhlostný koeficient sa pri stromoch so strednou hrúbkou a strednou výškou postupne zvyšoval od 1,19 do 1,40. Pri smreku dochádza k vyššej mortalite, vrastavé a podúrovňové stromy odumierajú z dôvodu nedostatku svetla. Stromy rastú viac do hrúbky, čo sa odráža aj na štíhlostnom koeficiente, ktorý bol po celé obdobie viac-menej konštantný a pohyboval sa v rozpätí 0,89 až 0,93 (tab. 1). Zásoby kmeňa sú pri smreku v jednotlivých rokoch o 3 – 10 m³.ha⁻¹ väčšie ako pri buku (tab. 3). Po prepočítaní na sušinu je vplyvom rozdielnej objemovej hmotnosti (obr. 5) celková zásoba sušiny drevných častí (kmeň a konáre) väčšia pri buku (tab. 3). Najväčší rozdiel medzi drevinami je v zásobe asimilačných orgánov, ktorá je pri smreku viac než trojnásobná (tab. 3 a 4). Počas rastu dochádza pri obidvoch drevinách k zvyšovaniu podielu kmeňa a znižovaniu podielu asimilačných orgánov (obr. 2). Hlavný medzi-druhový rozdiel pri pomerne vyrovnaných hektárových zásobách je v rozdelení nadzemnej biomasy medzi komponenty, kde buk alokuje do kmeňa viac asimilátov ako smrek (obr. 2 – 4).

Pri porovnaní ročnej NPP asimilačných orgánov a konárov neboli zistené žiadne významné rozdiely medzi sledovanými drevinami (obr. 6). Ukázali sme, že zásoby nadzemnej biomasy ako aj NPP buka a smreka boli v mladých plnozakmenených porastoch z prirodzeného zmladenia na danom stanovišti podobné (tab. 3 a 4).