

Plasticity in above-ground biomass allocation in *Fagus sylvatica* L. saplings in response to light availability

B. Jarčuška, M. Barna

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Abstract. The paper presents the production and allocation of aboveground biomass in 7-yr-old saplings of European beech (*Fagus sylvatica* L.) growing along an environmental gradient with a total light transmittance (*Tot*) ranging from 6% to 80%. Non-overtopped individuals, not suppressed by surrounding saplings were sampled at the end of growing season. The total aboveground biomass production on the gradient varied within 1.7-261.0. Light in the log-log linear relationship accounted for 83% of this variability. The plants growing in the shade had lower mass of aboveground compartments, lower total leaf area, higher fraction of biomass allocated in foliar mass and lower in the woody mass compared to the plants growing in the high-light environment. The major changes in effects of light availability on biomass allocation occurred up to about 20% of *Tot*. Decreasing accessible light was responsible for a non-linear increase in interceptive leaf area per unit of biomass and decrease in amount of biomass allocated per a unit of branch and stem length – necessary for leaf display. There was a close correlation between mass of aboveground plant compartments, documented by Pearson's *r* values of 0.98-0.99. Accompanied with different plant size, observed differences in biomass partitioning in response to light could be viewed as plastic adjustment to environmental heterogeneity in even-aged European beech saplings.

Keywords European beech, saplings, light, biomass allocation.

Author. Benjamín Jarčuška, Milan Barna (benjamin.jarcuska@gmail.com) - Institute of Forest Ecology, Slovak Academy of Sciences, Štúrova 2, 960 53 Zvolen, Slovakia.

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Introduction

The lack of light in understory of tree com-

munities has significant impact on the performance of woody plants growing in the understory, by reducing their growth and sur-

vival rate (e.g., Pearcy 2007, Jarčuška 2009), and thus influencing the dynamics of the whole community. Plants cope with limited light supply through adapting a range of their traits at all levels of biological organization, from leaf to the whole plant, a faculty that is backed-up phylogenetically and ontogenetically (Valladares & Niinemets 2008).

The morphological, anatomical and physiological (biochemical) functional adaptive responses to decreasing light availability in shade-tolerant European beech (*Fagus sylvatica* L.) natural regeneration at the leaf level are well studied: an increase in the specific leaf area (leaf area per dry weight, cm^2g^{-1}), the shade leaves showing bigger leaf area, a lower stomatal density, a lower chlorophyll a/b ratios, higher chlorophyll amounts on dry weight basis, therefore, the shade leaves are much better adapted to the dynamical light environment (sunflecks) in the forest understorey (Lichtenthaler et al. 1981, Eschrich et al. 1989, Küppers & Schneider 1993, Aranda et al. 2001, Valladares et al. 2002). Juvenile trees growing in forest understorey respond to shading by increasing their lateral growth at the cost of height increments at the crown level (Stănciou & O'Hara 2006). Also, their leaf phenology is different from that of the adult trees (Barna et al. 2009). The adjustment of plant traits to different environmental conditions, referred as phenotypic plasticity, is a means to cope with environmental heterogeneity. These plastic responses, spanning from chloroplast to the whole plant, enhance the light capture and the photosynthetic utilization and, consequently, increasing plant performance in the shade (Valladares & Niinemets 2008).

In the case of the whole-plant response to light availability in 1-2 years old seedlings and saplings, the response to shading was a decrease of the plant biomass production (van Hees 1997). However, regarding the biomass allocation in individual plant parts, probably due to different methodical approaches and different light levels used in their studies, the

studies presents different results (van Hees 1997, van Hees & Clercx 2003, Ammer 2003, compared with Welander & Ottosson 1998, Valladares et al. 2002, and Löff et al. 2005). The researches comparing older individuals (old 4–8 yrs) confirm a shift in biomass allocation and, on the other hand, they concern individuals not growing all the time in the same/similar light conditions (Curt et al. 2005, Prévosto & Balandier 2007, Hofmann & Ammer 2008).

According to optimal allocation theory (cf. Bloom et al. 1985), it could be expected that saplings growing under low light supply should increase their leaf mass fraction and leaf area per total aerial mass ratio, compared to the ones growing under higher light levels. The aim of this study is therefore to compare the production and allocation of aboveground biomass in naturally regenerated even-aged beech saplings growing - all the time - under relatively unchanged conditions, on a wide sunlight gradient.

Material and methods

Study plots

The individuals for biomass analysis were sampled from two stands, located in the central part of the Western Carpathians, Slovakia: the Javorie Mountains (J hereafter, $48^{\circ}30'13''\text{N}$, $19^{\circ}15'06''\text{E}$), and the Nízke Tatry Mountains (NT hereafter, $48^{\circ}51'36''\text{N}$, $19^{\circ}25'38''\text{E}$). The stands are situated at 680-740 m a.s.l., on Dys-tric Cambisols (FAO, 2011). The mean annual temperature ranged between 6-7 °C, while the mean annual precipitation (2001-2008) was 876 ± 130 mm (J) and 844 ± 171 mm (NT) (mean \pm S.D., data from the Slovak Hydrometeorological Institute, Bratislava).

The canopy layer of the stands consists mostly of European beech (proportion more than 70%). In both stands, allochthonous Norway spruce (*Picea abies* (L.) Karst.) is admixed, while in NT also European silver fir (*Abies*

alba Mill.), sycamore maple (*Acer pseudoplatanus* L.) and European ash (*Fraxinus excelsior* L.). The diverse patterns of solar radiation in these localities have been formed randomly, by windthrows (gaps of various size, created in summer 2001) and forest management practices (clear-cut, applied at the same time); more details are available in Jarčuška & Barna (2011).

Plant material and biomass analysis

The study material (J - 24 individuals, NT - 20 and 44 individuals) was sampled randomly from 7 years old, naturally regenerated, undamaged individuals growing under broad light gradient and showing no symptoms of attack by pathogens. Seven years old individuals were sampled after survey of beech natural regeneration presented in the understory (in the sapling layer) of the stands, as it was the most common age cohort within the natural regeneration. The tree age was identified by counting bud-scars on the main stem and on the lowest vital branch and on the remaining stem part (Jarčuška & Barna 2011). We selected only the individuals non-overtopped, not suppressed by surrounding saplings. The sampling was carried out at the end of growing season, in September 2008.

All the trees were measured for tree height, stem length, and stem diameter at the base (average of two measurements mutually perpendicular) before harvesting. The leaf area was determined based on leaves selected randomly by ten from each sample tree (by five from each crown half), which were placed in plastic bags in an ice box and transported to the laboratory. Leaf area of ten sampled leaves was measured with a LI-3000A Portable Area Meter (LiCor, USA). The total length of tree branches and the number of leaves were determined in the lab. The dry biomass of all beech saplings was specified according to the fractions of branches, leaves and main stems, with a precision of ± 0.001 g, after drying at 70°C to

a constant mass. Foliar area in the mid-crown was calculated by multiplying the dry mass of leaves with specific leaf area (leaf area to its dry weight ratio, SLA hereafter) of the five leaves sampled in the half part of crown. Then, the leaf areas of the both crown halves were added together, to obtain the total leaf area per tree. The mean leaf area was calculated as the ratio of the total leaf area to the leaf number.

Light conditions

For all saplings, hemispherical photos were taken at level of the leading shoot. The photographs were done under uniform cloudy sky conditions, in summer 2008. Underexposed images (-2 steps of exposure values) were obtained with using a Canon EOS 400D (Canon, Ōta, Tokyo, Japan), using a lens with a view angle of 180° (so called “fish-eye”)(Sigma 4.5 mm F2.8 EX DC - Sigma, Bandai, Fukushima, Japan). The threshold level (separation of the black/white pixels) was determined for each photo separately, using the blue colour channel and the automatic algorithm of Nobis & Hunziker (2005), as implemented in SideLook 1.1 software (Nobis 2005). For the captured images, the relative amount of the total solar radiation transmitted through the crown canopy (*Tot* hereafter) was computed with Gap Light Analyser 2.0 (GLA, Frazer et al. 1999), knowing the setting rules (more details in Jarčuška 2011a).

Data analysis

The effect of light on aboveground biomass production and allocation in beech saplings in their seventh growth season was assessed by simple linear and nonlinear Model I. In regression analyses, the per cent of the total transmitted light (*Tot*) was used as an independent variable, while other variables - the total biomass, biomass of leaves, branches, stem, the fractions of leaves, branches, stem, and wood (branches + stem) mass in % of total aboveg-

round biomass as dependent ones. Differences between the slopes of regression lines, expressing relationship between weight of all plant compartments and light amounts, were tested by the interaction term in the General Linear Model. If there were not found significant differences among the aboveground plant compartments, we tested for further differences among the plant compartments – using the analysis of covariance (with compartments as the main factor and light availability as the covariate). If necessary, log10-transformation was used in order to meet conditions of normality (Shapiro-Wilk test), homoscedasticity and linearity (Sokal & Rohlf 1995) and Pearson product-moment correlation was used to evaluate the association between the *Tot* and other measured/calculated variables. The probability values less than 0.05 being were considered as significant. For all the analysis

it was used Statistica 6.0 (Statsoft Inc., Tulsa, Oklahoma, USA).

Results

The studied trees were supplied with about 5 to 80% of the total sunlight (Figs 1–4). There were identified more than 150-fold differences in the total aboveground biomass between the individuals (ranging from 1.72 g to 260.96 g) in the concerned light conditions. While biomass of stem and branches across the light gradient varied more than 200 and 330-fold, respectively, the leaf biomass only about 70 times (Table 1). The light explained 76 to 84% of this variation (Figure 1). The total interceptive leaf area ranged between 280 and 9610 cm², the total branch length from 18 cm to 11.22 m, and number of leaves from 23 to 725

Table 1 Descriptive statistics for the variables of interest measured in 7-yr-old *Fagus sylvatica* saplings (n = 44). Abbreviations: (S.D.) standard deviation, (max/min) maximum/ minimum ratio, and (coef. var.) coefficient of variance

Variables*	Mean	S.D.	Minimum	Maximum	Max/min	Coef. var.
Tot %	21.64	19.61	5.92	82.35	13.91	90.66
TM g	37.56	56.89	1.72	260.960	151.37	151.49
SM g	22.82	35.87	0.77	159.70	207.13	157.23
BM g	7.40	11.34	0.16	54.15	334.28	153.25
LM g	7.34	9.87	0.66	47.11	71.94	134.45
SF %	58.05	5.47	44.72	67.75	1.52	9.43
BF %	17.69	4.38	7.96	26.71	3.35	24.77
LF %	24.25	5.94	15.55	43.85	2.82	24.49
D mm	9.9	4.8	3.8	24.5	6.45	48.14
L cm	92.5	41.1	28.5	203.2	7.13	44.35
BL cm	270.5	249.2	18.0	1122.5	62.36	92.13
TLA cm ²	2092.74	2148.20	279.75	9607.29	34.34	102.65
LN pcs.	185.68	176.90	23.00	725.00	31.52	95.27
MLA cm ²	11.14	2.02	7.64	15.48	2.03	18.10
SLA cm ² g ⁻¹	363.61	78.70	181.20	510.47	2.82	21.64

*Abbreviations: Tot – relative total irradiation, TM – total aboveground biomass, SM – stem biomass, BM – branch biomass, LM – leaf biomass, SF – stem fraction, BF – branch fraction, LF – leaf fraction, D – stem diameter, L – stem length, BL – total branch length, TLA – total leaf area, LN - leaf number, MLA – mean leaf area, SLA – specific leaf area

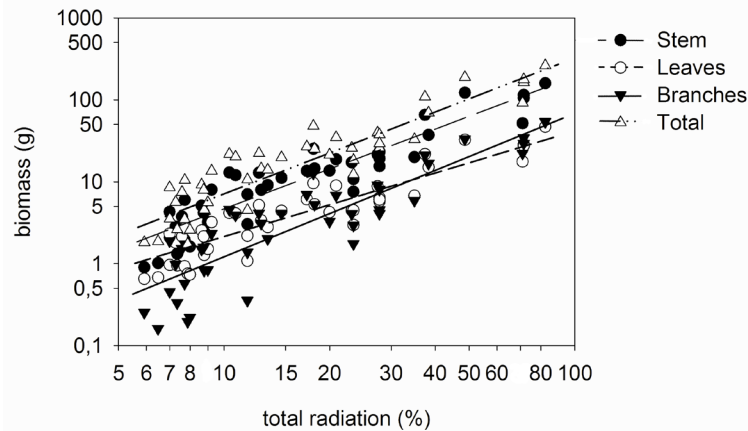


Figure 1 Relationship between the relative total solar radiation and stem ($\log y = -1.005 + 1.650 \log x$, adjusted $R^2 = 0.84$, $P < 0.001$), leaves ($\log y = -1.040 + 1.355 \log x$, adjusted $R^2 = 0.83$, $P < 0.001$), branches ($\log y = -1.643 + 1.739 \log x$, adjusted $R^2 = 0.76$, $P < 0.001$), and total above-ground biomass ($\log y = -0.695 + 1.590 \log x$, adjusted $R^2 = 0.83$, $P < 0.001$) of 7-yr-old saplings. The slope coefficients of regression lines are not significantly different ($P = 0.13$), the intercepts are ($P < 0.05$, Tukey HSD test)

pcs (Table 1).

The amount of aboveground biomass allocated in leaves (i.e. leaf fraction) shows a quadratic nonlinear decrease in response to light – explaining 67% of leaf mass variability. In the case of stem and branch fraction, light does not explain more than 23% for each (Figure 2), after pooling of wood biomass, however, solar radiation accounted for 62% of its variability (data not shown). The relationship between the light availability and aboveground biomass fractions loses its statistical significance at 20% of the total sunlight (Figure 2). The values of leaf area ratio, i.e. the ratio of leaf area to total aboveground biomass (LAR, Figure 3), ranged from 31.45 to 186.29 cm² per g of aboveground biomass (Table 1). LAR decreased with increasing light which accounted for 79% of variable's variance.

The amount of biomass necessary for creation a unit length in branches bearing interceptive leaf area decreased with decreasing light accessibility (Figure 4A). Therefore, shaded individuals could bear more leaf mass per

shoot mass unit compared to sunny ones. Stem mass to stem length ratio showed the same, negative nonlinear relationship with accessible light (Figure 4B).

Light had a strong impact on most of the measured variables, its influence was less pronounced only at the mean leaf area (MLA, Table 2). MLA correlated significantly only with the total leaf area. All aboveground plant mass compartments correlated very strongly – their Pearson's r reached 0.98-0.99. Total leaf area had the strongest degree of correlation with leaf mass. Stem diameter correlated most with the total and leaf biomass, and with branch length. In overall, stem diameter correlated stronger than stem length with other variables (Table 2).

Discussion

Light is one of principal resources for plant survival and growth, therefore the existence of plant species in an environment with varying light supply depends either on their speciali-

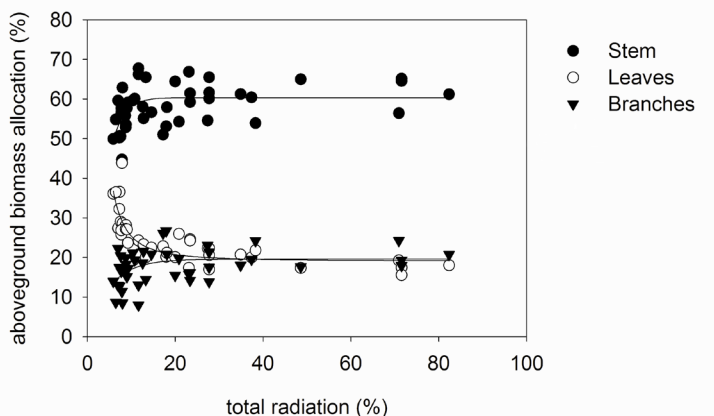


Figure 2 Relationship between the relative total solar radiation and stem fraction ($\log y = 60.3146 - 93.6576/(1 - 0.0121x)^{1/0.0346}$, adjusted $R^2 = 0.23$, $P < 0.003$), leaf fraction ($\log y = 1.2647 + 0.7378/x + 6.1892/x^2$, adjusted $R^2 = 0.67$, $P < 0.001$), and branch fraction ($\log y = 1.2765(1 - \exp^{0.3259x})$, adjusted $R^2 = 0.16$, $P < 0.004$) of aboveground biomass of 7-yr-old saplings. The figure presents untransformed variable to illustrate better the observed pattern.

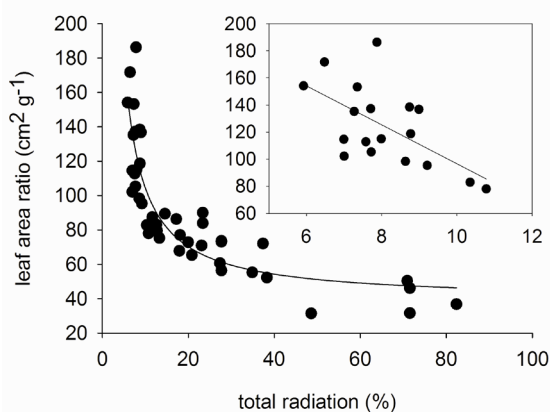


Figure 3 Relationship between the relative total solar radiation and leaf area to the total aboveground dry mass ratio ($\log y = 1.5785 + 5.9411/x - 14.8309/x^2$, adjusted $R^2 = 0.79$, $P < 0.0001$) in 7-yr-old saplings. The inset demonstrates the relationship between the total solar radiation and leaf area ratio for saplings growing at the lowest light level ($\log y = 2.5210 - 0.0543x$, $n = 18$, adjusted $R^2 = 0.40$, $P < 0.003$). The figure presents untransformed variable to illustrate better the observed pattern.

zation to different light conditions or on their ability to adapt their phenotypes to the current situation (Valladares 2000, Valladares & Niinemets 2008).

The negative effect of reduced light availability on growth/size of young beech individu-

als observed in the present study is well known (van Hees 1997, Löff et al. 2005, Balandier et al. 2007). Besides the length growth of the main axis and/or total biomass size, reduced light influenced allocation of biomass into plant's compartments – branches, leaves and stem (Ta-

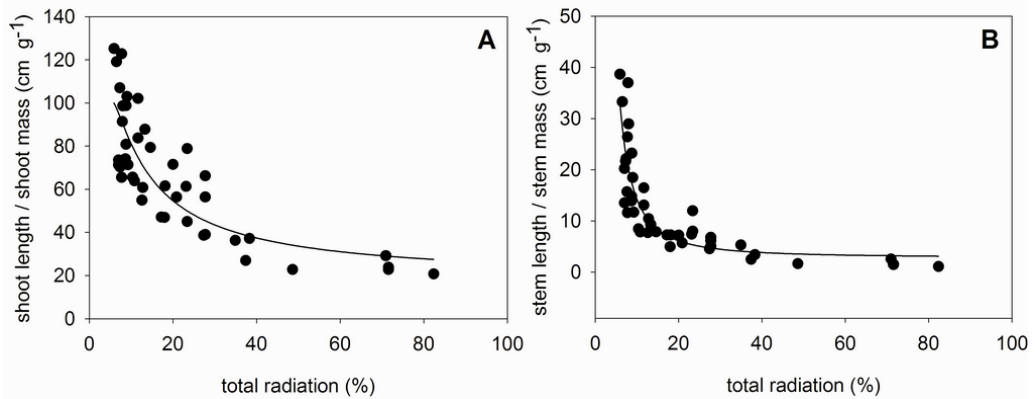


Figure 4 Relationship between the relative total solar radiation and (A) total branch length to branch dry mass ratio ($\log y = 2.0793 - 0.0184x + 0.0001x^2$, adjusted $R^2 = 0.80$, $P < 0.0001$), and (B) stem length to stem dry mass ratio ($\log y = 0.1552 + 14.4238/x - 42.0815/x^2$, adjusted $R^2 = 0.82$, $P < 0.0001$) in 7-yr old saplings. The figures present untransformed variables to illustrate better the observed pattern

Table 2 Pearson correlation matrix for 7-yr-old *Fagus* sapling biomass and other measured variables

Variables	TM	SM	BM	LM	D	L	BL	TLA	LN	MLA	SLA
Tot	0.91	0.90	0.92	0.91	0.92	0.81	0.89	0.89	0.83	<i>0.35</i>	-0.79
TM		0.99	0.99	0.99	0.94	0.83	0.93	0.95	0.92	0.27	-0.75
SM	-		0.98	0.99	0.93	0.83	0.91	0.94	0.91	0.28	-0.74
BM	-	-		0.99	0.93	0.82	0.95	0.95	0.92	0.26	-0.75
LM	-	-	-		0.94	0.84	0.94	0.96	0.94	0.25	-0.76
D	-	-	-	-		0.91	0.94	0.93	0.91	0.25	-0.80
L	-	-	-	-	-		0.90	0.87	0.89	0.22	-0.76
BL	-	-	-	-	-	-		0.94	0.95	0.18	-0.78
TLA	-	-	-	-	-	-	-		0.94	<i>0.33</i>	-0.70
LN	-	-	-	-	-	-	-	-		0.07	-0.76
MLA	-	-	-	-	-	-	-	-	-		-0.04

Abbreviations: Tot – relative total irradiation, TM – total aboveground biomass, SM – stem biomass, BM – branch biomass, LM – leaf biomass, D – stem diameter, L – stem length, BL – total branch length, TLA – total leaf area, LN – leaf number, MLA – mean leaf area, SLA – specific leaf area. Correlations significant at $P < 0.001$ are shown in bold, and $P < 0.05$ in bold-italic. The other values are not statistically significant ($P > 0.05$).

ble 1). The observed effect of light on biomass partitioning within plants is in accordance with observations of other authors. Poorter & Nagel (2000) in their review 130 mentioned observations from 40 publications, Dezzotti (2008) for three *Nothofagus* species, Gleason et al. (2011) for seedlings of five Australian rain-forest spe-

cies, or Löf et al. (2005) in beech seedlings and Prévosto & Balandier (2007) in 5-years old beech saplings. On the other hand, Curt et al. (2005) found significant effect of light in four years old beech saplings after two years of treatment only for leaf fraction, while Prévosto & Balandier (2007) observed lower vari-

ability in leaf area ratio (LAR) in response to light in 5 years old saplings and lower amount of explained variability in LAR compared to our findings. These discrepancies could be explained by transplanting shock (Ammer 2007), previous growth conditions (Eschrich et al. 1989), as they used it were seedlings grown in a nursery, and also by the short-term duration of experiment (Curt et al. 2005; Prévosto & Balandier 2007).

Light explained between 84% of total aboveground biomass variance (Figure 1) and from 16 to 67% of aboveground biomass fractions' variability (Figure 2). Hofmann & Ammer (2008) observed 80% of total woody mass (above- and belowground) variation explained by light availability (PAR). They also reported 60% of branch fraction variability explained by total dry woody mass of beech individuals and non-significant relation between stem fraction and total woody mass. The relationship between the light availability and aboveground biomass fractions loses its statistical significance at about 20% of the total sunlight (Figure 2). Light availability well below 40% of accessible light is presented as an upper threshold for height growth (Jarčuška 2009).

While fluctuations in leaf fraction for the given light gradient were almost 3-fold, there were 6-fold in LAR. Higher LAR found in tree seedlings and saplings under low light conditions are interpreted as mechanisms improving their light capture (Poorter & Nagel 2000, King 2003), primarily thanks to a bigger specific leaf area (SLA, Table 2) and larger leaf fraction (Figure 2). In such a way, the leaf area displayed per unit of leaf biomass reaches its maximum.

Plastic allocation of metabolic products to different plant compartments, expressing the response of regenerating trees to uneven light availability, is considered as an important factor allowing plants to survive in shade, while increasing their extension rates and competitive ability in sun (King 2003). Similar role like the plasticity in biomass allocation within

plant's compartments serve also to the changes in plant physiology, phenology, and morphology, at different levels of organization (e.g., Arranda et al. 2001, Valladares et al. 2002, Curt et al. 2005, Barna et al. 2009). Phenotypic plasticity of ecologically important traits, in response to different environments, is the fundamental property of the organisms, enabling them to cope with adverse environmental conditions (Sultan 2000).

In general, the findings of the present study are in accordance with previous observations (e. g., Valladares et al. 2002, Löf et al. 2005): decreased light availability increases biomass allocation into leaves, as light capturing structures, at the cost of woody biomass. Hofmann & Ammer (2008) considered a shift in biomass distribution in even-aged plants as a result, mainly, of the plant size, i.e., total woody mass (see above). Conclusions of Prévosto & Balandier (2007) are similar in the case of ratio of leaf area to total aboveground mass (LAR). Also, Konôpka et al. (2010) explained the large intra-specific variability in biomass allocation within beech trees under 10-yr old as a function of their diameter size, however, they did not take a possible differences in growth history of sampled trees' light environment among stands into account (cf. Jarčuška & Barna 2011). However, it is not possible to separate the size-effect from the effect of light in even-aged individuals, because their size is dependent on and therefore correlated with light availability (see Table 2). In other words, to speak about changes in plant biomass allocation, in response to light, as the plastic outcome requires sorting the effect of plant size from the effect of light. If the differences in biomass allocation disappear after application of the allometric analysis, it could be concluded that the difference in allocation was due to size difference (Poorter & Nagel 2000). This phenomenon has been called 'apparent plasticity' (Weiner 2004). As Poorter & Nagel (2000) pointed out, it is not correct to consider that differences in biomass allocation are only

of interest if they exist at a common plant size – to understand the functioning of a plant in its environment, then it is actual allocation of biomass along with the actual physiology and morphology that determines a performance of the plant at that moment (Poorter & Nagel 2000). Besides, they reported for 130 observations (from 40 publications) that light and size affect aboveground biomass distribution interactively. Similarly, Claveau et al. (2005) demonstrated allocational effect of interaction between light and size based on example of saplings of evergreen boreal and sub-boreal species.

Conclusion

Seven year-old beech saplings growing in shade (< 20% of light) had lower mass of aboveground compartments, lower total leaf area, higher fraction of biomass allocated in foliar mass and lower in the woody mass, compared to plants growing in the high-light environment. With decreasing light supply, interceptive leaf area per unit of biomass showed a non-linear increase, and the amount of biomass of branches and stems necessary for leaf display decreased. With increasing growth of an individual, increases the ratio of non-photosynthetic to photosynthetic tissues ratio, entailing increase in respiration costs, responded by more light requirements of plants. Accompanied with different plant size, observed differences in biomass partitioning in response to light could be viewed as a plastic adjustment to the environmental heterogeneity in even-aged European beech saplings. Additional research is needed to answer the questions concerning the concurrent influence of growth and ontogenesis on the biomass allocation in beech natural regeneration affected by light availability.

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