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Specific leaf area and leaf area index in developing stands of *Fagus sylvatica* L. and *Picea abies* Karst.

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Abstract

European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* Karst.) are two of the most ecologically and economically important forest tree species in Europe. These two species co-occur in many locations in Europe, leading to direct competition for canopy space. Foliage characteristics of two naturally regenerated pure stands of beech and spruce with fully closed canopies were contrasted to assess the dynamic relationship between foliage adaptability to shading, stand LAI and tree growth. We found that individual leaf size is far more conservative in spruce than in beech. Individual leaf and needle area was larger at the top than at the bottom of the canopy in both species. Inverse relationship was found for specific leaf area (SLA), highest SLA values were found at lowest light availability under the canopy. There was no difference in leaf area index (LAI) between the two stands, however LAI increased from 10.8 to 14.6 m²m⁻² between 2009 and 2011. Dominant trees of both species were more efficient in converting foliage mass or area to produce stem biomass, although this relationship changed with age and was species-specific. Overall, we found larger foliage plasticity in beech than in spruce in relation to light conditions, indicating larger capacity to exploit niche openings.

Introduction

Competition for light and resulting mortality are the most critical processes driving development of young forest stands (King, 1990). As the canopy closes, in particular in stands originating from natural regeneration, tree height relative to neighbours, but also position within a crown dictate light availability to foliage (Niinemets *et al.*, 2001; Richardson *et al.*, 2001). Leaves and needles are the only tissues with the capacity to capture energy and thus drive forest growth. Foliage responds very sensitively to growth conditions within a stand and has been shown to adapt its morphology (Bussotti *et al.*, 2000), structure (Kull *et al.*, 1999) and metabolism (Hallik *et al.*, 2009) in response to light intensity.

Vertical distribution of foliage, but also changes in the size of individual leaves, have both been attributed to relative light conditions within the stand (Johansson, 1996). The relationship between light availability and specific leaf area (SLA, defined as leaf area per unit leaf mass) varies among tree species (Niinemets, 2010). No consensus currently exists as to whether different tree species exhibit greater leaf size plasticity in relation to light availability. Several studies report larger plasticity of leaf morphology in shade-intolerant than in shade-tolerant species (Oguchi *et al.*, 2005; Sanchez-Gomez *et al.*, 2006; Portsmouth and Niinemets, 2007), while others found the reverse (Paz, 2003; Delagrange *et al.*, 2004) or no variation (Paquette *et al.*, 2007). In addition to shade tolerance, SLA in trees is also influenced by tree age and size (Steele *et al.*, 1990; Niinemets and Kull, 1995). It is important to point out that tree age, size and irradiation gradient along the canopy are strongly correlated. Older and taller trees are likely to generate deeper canopies, which expose foliage to irradiation levels ranging from full to a fraction of full sunlight (Niinemets, 2010).

Efficient light capture is of crucial importance to trees growing in dense stands with high level of competition for light (Pearcy *et al.*, 2005). Trees maximise capture of available light by developing layered canopies with several strata of overlapping leaves. Defined as the total one-sided foliage area per unit ground area, Leaf Area Index (LAI) controls light interception, but also acts as a determinant of carbon and water exchange between forest canopy and the atmosphere (Leuschner *et al.*, 2006), primary production (Long and Smith, 1990) and rainfall interception (Herbert and Fownes, 1999). Whilst the definition and measurement of leaf area is fairly straightforward in broadleaves, three different definitions have been proposed for conifers: total needle surface area, half of the total needle surface area, and projected needle area. The latter definition was used in this paper as it is commonly accepted as the most practical, but also indicative of the needle surface involved in light interception at any one time (Chen *et al.*, 1997). Forest stand LAI is determined by leaf size, total number of leaves per tree, but also by stem density (Leuschner *et al.*, 2006).

Despite a considerable amount of literature describing foliage characteristics and the development of LAI in growing forests, studies investigating the relationship between LAI and foliage and stem biomass allocation are rare. Although LAI plays a key role in the conversion of radiative energy to biomass, little is known about the mechanisms linking light interception and biomass allocation in trees. Description of foliage mass and foliage area, together with data on mass of wood compartments may allow for an investigation of growth efficiency of foliage. Several authors (e.g. (Pickup *et al.*, 2005; Shipley, 2006; Milla *et al.*, 2008) used the ratio between leaf and total plant dry plant mass (leaf mass ratio – LMR) or between leaf area and of total plant dry mass (leaf area ratio - LAR) to describe ecological and production interactions. However, none of these studies allow for the description of the dynamic relationship between foliage plasticity, stand LAI and tree growth. Konôpka *et al.* (2010) and Jack *et al.*, (2002)

described growth efficiency in temperate trees, albeit only on the basis of biomass partitioning and did not describe foliage dynamics.

Allometric relations are frequently used to assess biomass partitioning to various pools in forests (Claesson *et al.*, 2001; Wirth *et al.*, 2004; Fehrmann and Kleinn, 2006; Cienciala *et al.*, 2008; Pajtić *et al.*, 2011). In general, biomass contained in a particular tree compartment can be predicted by an allometric equation usually using tree height or diameter (at breast height, *i.e.* DBH) as predictor variables (West *et al.*, 2009). Estimates of foliage biomass in young beech and spruce stands were put forward by Kantor *et al.* (2009), whilst Xiao and Ceulemans (2004) established allometric equations for foliage at both branch and tree levels in young Scots pine. The latter study attempted to consider the vertical position of a whorl as one of the independent variables predicting foliage biomass. Having said that, biomass allometric equations by definition predict only foliage mass and do not offer any information about foliage area. Since leaf area and its stratification is key determinant of forest stand productivity, this paper aims to link allometric relations to foliage area and stand LAI. Developing stands of pure *Fagus sylvatica* L. (beech) and pure *Picea abies* Karst. (spruce) with fully closed canopy are contrasted and their growth performance compared.

In particular, this paper links up information on foliage mass and foliage area for two of the most important European forest tree species growing on the same site. There are several levels at which these two species can be contrasted. As a deciduous tree, beech produced all of its foliage in current year, spruce on the other hand retains its needles for up to 5 years, possibly leading to higher LAI in spruce. Beech is shade-tolerant, while spruce is classified as intermediate in relation to its shade tolerance (Ellenberg and Leuschner, 1996). Lastly, since the selected site is located at the lower elevation limit of spruce in this area of Europe, climate

change is expected to favour beech leading to eventual replacement of spruce by beech at this elevation. Thus this study offers insights into effects of climatic warming on growth performance of forests currently occupying the climatic boundary between the two species. In this study, we hypothesised that (i) spruce has higher LAI than beech, (ii) dominant trees of both species have higher leaf mass ratio.

Materials and methods

Site description

The experimental site was located in the southern part of Slovak Ore Mountains, 977 m above sea level (48°38'50" N and 19°36'12" E). Annual sum of precipitation is close to 900 mm, while mean temperature is 5.2 °C. The soil type has been classified as Humic Cambisol on granodiorit bedrock, with a high stone content and pH (H₂O) of 5.1, 5.2, and 5.3 in the soil depths 0-10, 10-35 and 35-65 cm, respectively. Two neighbouring stands of pure beech and spruce were examined. Both stands originate from natural regeneration following a clearcut of preceding high forest. At the start of measurements presented in this study, both stands featured trees about 12-14 years of age. The beech stand was composed of dense groups of beech trees with a few scattered gaps colonised by *Calamagrostis epigejos* L. The structure of the spruce stand was similar to that of beech, however no grass cover was present due to shading by spruce trees. Detailed description of the site characteristics can be found in Konôpka *et al.*(2013).

Size distribution, biomass and foliage sampling

Five circular experimental plots were established in each stand in March 2009. The plots were 100 cm in radius and contained around 40 trees each. The plots were randomly positioned within each stand, but at a distance of at least 5 canopy heights from each other. All trees within

each plot (PlotTrees thereafter) were tagged. Height and diameter d_0 (diameter at ground level) of all tagged trees were measured in September of 2009, 2010 and 2011.

During late summer 2011, 40 beech and 40 spruce trees were selected just outside the experimental plots and their foliage sampled from upper, middle and lower crown sections (FolTrees thereafter). Ten trees each were selected from the following four crown classes within the canopy: dominant, co-dominant, intermediate and overtopped (Kraft, 1884). Care was taken to cover the entire diameter distribution found in experimental plots. Then, three leaves were randomly selected and taken from each crown section of beech trees (9 leaves per tree). In spruce, 30 needles were collected from each crown section and in each of the following age cohorts (by year of needle set): 2011, 2010, 2009, 2008 and, rarely, 2007. All foliage samples were scanned on a flatbed scanner (EPSON Expression 10000), oven-dried and weighed. Leaf area of sampled foliage was established by WinFOLIA (Regent Instruments Inc., Quebec). Specific leaf area (SLA) of individual leaves or needles was calculated as a ratio of foliage area and dry mass.

A further 80 beech and 100 spruce trees were selected from each stand for destructive sampling in early September 2011 (BiomTrees thereafter). All tree compartments with the exception of fine roots thinner than 2 mm were harvested. Slightly fewer beech trees were sampled as the population of this species was more uniform in size than spruce. Height and d_0 of all sampled trees were established prior to destructive sampling. Harvested trees were divided into foliage and other (woody) compartments, dried until constant weight and weighed. Out of the 100 harvested spruce trees, 30 were randomly selected to establish the contribution of needle cohorts to total needle mass. All needles found on these trees were collected, divided to 5 cohorts (2011 through 2007), dried and weighed

Stocking density and size distribution data from experimental plots were used for inter-specific comparisons between beech and spruce stands. Foliage size distribution data formed the basis

for characterisation of vertical leaf size profiles of the canopy. Data on biomass compartment and foliage characteristics gathered outside experimental plots were used for biomass model parameterisations.

Estimations of biomass equations, LA and LAI

Dry weight data of biomass compartments measured in BiomTrees were used to construct biomass equations after Pajtik *et al.* (2008). The following model was used to estimate dry weights of stems, branches, coarse roots and foliage of individual trees:

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

Where W_i is dry biomass of a tree component i , d_0 is stem diameter at base, b_0 and b_1 are coefficients to be estimated and λ is logarithmic transformation bias. Site-specific biomass equation parameters are listed in Table 2.

Specific leaf area (SLA) of foliage taken from FolTrees was calculated as the ratio between projected leaf area of foliage sample and its dry mass. Once the relationship between foliage biomass and tree size has been established, total leaf area of an individual tree (LA) dependent on d_0 can be calculated as follows:

$$LA = SLA * (e^{(b_0 + b_1 \ln d_0)} \lambda) \quad (2)$$

Where LA is total leaf area per tree, SLA is specific leaf area in m^2g^{-1} , b_0 and b_1 are site-specific coefficients of leaf biomass equation (1), d_0 is stem diameter at the base and λ is logarithmic transformation bias.

In each circular permanent experimental plot, we calculated LAI by dividing the sum of LA of all PlotTrees found within the plot by its area:

$$LAI_j = \frac{\sum_{i=1}^n LA_{ij}}{S_j} \quad (3)$$

where n is the number of trees within a plot, LA_{ij} is the leaf area of i -th tree on j -th plot, and S_j is the area of the j -th plot. This calculation is fairly straightforward in European beech due to the presence of a single cohort of leaves. In Norway spruce, however, the variation of SLA in needle cohorts was also taken into account. For each needle cohort, LA of needles from all trees present within a permanent plot can be calculated as follows:

$$LA_{jk} = \sum_{i=1}^n (W_i * P_k * SLA_k) \quad (4)$$

where n is the number of trees within a plot, W_i is the dry needle biomass of i -th tree, P_k is the proportion of k -th cohort from the total and SLA_k is the specific leaf area of the k -th needle cohort. Mean SLA for the entire vertical profile of the canopy was used for each cohort. Based on an analysis of trees harvested at the site, we established that P_k in spruce is stable and independent of d_0 (Supplementary Figure S1), therefore mean values of P_k were used across all diameter classes. LA of all spruce trees found within each plot was then obtained by summing up leaf areas of the five needle cohorts.

Data analysis

All stand-level observations were averaged to plot level (N=5), differences between species were compared by one-way ANOVA and considered significant at $P < 0.05$. All variables were checked for the homogeneity of variance (Levene's test) and normality of distribution (D'Agostino and Pearson Test). Repeated measures ANOVA was used to compare the development of LAI in the two stands over the period of observation. Two-way ANOVA was used to assess the effect of species and canopy position on SLA, followed by Tukey's multiple comparison test. Data were log-transformed where they did not satisfy ANOVA assumptions. Linear or exponential equations were fitted to individual tree data where appropriate, using least squares fit. Model parameters were assessed for differences between species (stem increment per unit leaf mass) or from specific value (needle cohort contribution to total) by extra sum-of-squares F test.

Results

Although very similar in age, the two studied ecosystems did differ in several standard forest stand characteristics (Table 1). Beech trees were significantly taller than spruce, while spruce trees had a larger diameter at base, resulting in a significantly larger height/diameter ratio in beech than in spruce. The difference in height to diameter ratio between the two species is evident throughout the diameter size distribution (Supplementary Figure S2). On the other hand, there was no difference in the number of trees per unit area, mean stem volume and basal area.

Measurements of foliage collected from 40 beech and 40 spruce FolTrees reveal that individual leaf size is far more conservative in spruce than in beech (coefficient of variance 0.29 and 0.53 respectively, Figure 1). Within the stem diameter distribution present in the stands at the time of measurement, beech leaf area increases by 83% from the 25th to the 75th d₀ percentile. In spruce, however, the comparable increase in individual needle area is only 38%. Similarly, the

spread of leaf size between leaves collected at the top and bottom of the canopy represents 84% of mean leaf size at mean d_0 in beech, but only 28% in spruce.

Analogous to foliage area, we observed how SLA is affected by tree size and foliage position within the canopy (Figure 2). The highest values for both species were recorded in overtopped trees growing underneath the main canopy. In contrast to leaf area, we did not observe such a strong effect of d_0 on the differentiation of SLA values between the two species. The spread of mean SLA at the top and bottom of the canopy represents 43% of mean SLA in beech and 33% in spruce. SLA of foliage growing in the middle of the canopy on the mean tree was $273 \text{ cm}^2.\text{g}^{-1}$ in beech and $87 \text{ cm}^2.\text{g}^{-1}$ in spruce.

Ten beech and ten spruce FolTrees were selected from each of the four crown classes considered in this study to evaluate the effect of tree size on SLA (Figure 3). We observed no difference between the two species in the effect of crown class on SLA. Dominant and co-dominant trees show the same SLA in beech ($p=0.812$) and in spruce ($p=0.986$). Intermediate and suppressed trees, however, have higher SLA than dominant trees in both species ($p<0.001$). Foliage position within an individual tree crown does not affect SLA in overtopped trees in beech ($p=0.856$) or spruce ($p>0.999$), trees in other canopy classes however do show a significant effect of foliage position on SLA ($p<0.026$).

Destructively sampled BiomTrees were used to construct biomass equations linking biomass compartments to diameter at base (Supplementary Table 1). Figure 4A shows total foliage mass of beech and spruce trees across the diameter distribution observed in this study. It is clear that spruce trees of the same size support more foliage mass than beech trees. At the same time, beech foliage has greater SLA in all tree sizes under investigation (Figure 4B). Using data for

whole tree foliage mass in combination with mean SLA, we observe that there is very little difference in whole tree leaf area between beech and spruce trees (Figure 4C).

The observed similarity of whole tree leaf area of beech and spruce trees was reflected in calculated LAI. As already mentioned, basal area and tree density did not differ between the two stands. Coupled with very similar total leaf area of individual trees, it is not surprising that LAI did not differ between beech and spruce ($p=0.865$, Figure 5). From 2009 through 2011, modelled LAI increased from 11.4 to 14.9 m^2m^{-2} in beech and 10.3 to 14.2 m^2m^{-2} in spruce.

Finally, biomass equations and data describing foliage cover in both species were used to compare wood production efficiency expressed as wood mass produced per unit foliage mass or unit foliage area. Taller trees were always more efficient in using unit foliage to produce unit stem biomass (Figure 6). The slope of linear regressions describing the relationship between foliage efficiency and tree height of all trees measured in permanent plots was always positive and significantly different from zero ($P<0.0001$). Interestingly, as the stands grew older, the advantage of dominant and co-dominant trees in terms of wood production efficiency was slowly eroding – but only in beech. A tree 1 m taller than its competitors produced 0.63 more grams of stem wood per gram foliage in 2009, but this advantage in foliage productivity decreased to 0.33 g g^{-1} in 2011 ($P=0.0007$). This decrease was not evident in spruce, where the slope of the linear regression was 0.11 in 2009 and 0.09 in 2011 ($P=0.304$). Similar to foliage mass, we observed the same dynamic when plotting the stem production efficiency expressed per unit of foliage area against tree height; a decrease of regression slope from 36.3 g of stem mass per metre square of foliage for every metre of height in 2009 to 22.7 in 2011 in beech ($P<0.0001$). In spruce, the slope did not change over the period of observation; 19.2 $\text{g m}^{-2} \text{m}^{-1}$ in 2009 and 10.1 $\text{g m}^{-2} \text{m}^{-1}$ in 2011 ($P=0.424$).

Discussion

Both stands considered in this study originate from natural regeneration following the removal of original tall forest. It is to be expected that not all trees are of the same age, however we established that the cohort of trees currently growing on the site is between 12 and 14 years old. The stands were dense, at the time of the study there was no difference in the number of trees per hectare. Beech trees were marginally taller, while spruce trees had thicker stems at the base. However, there was no difference in basal area, leading us to the assertion that any differences in foliage characteristics are due to differences in genetics and growth habit, rather than because of different tree size or stocking density and resulting competition.

Leaf level

Individual leaves with the largest area were always found at the top of the canopy, both in beech and in spruce. Leaves and needles were progressively smaller with increasing canopy depth, this differentiation of single leaf size appears to be stronger in beech than in spruce. Shorter trees had smaller leaves than taller trees, owing to the shading of their entire crowns by taller trees. Contrasting evidence exists on the effect of shading on individual leaf size. Our results in beech are in disagreement those of Barna *et al.* (2004) and Tognetti *et al.* (1998) who found that the size of foliage increased with shading, but correspond with the study by Carnham (1988) who found larger leaf size at high light levels in *Acer saccharum* Marsh. and *Fagus grandiflora* Ehrh. Similarly, Niinemetz and Kull (1995) found no effect of irradiance on projected needle area in spruce and Gebauer *et al.* (2011) indicate that needle size increases with light intensity in most but not all of the 57 spruce provenances they compared. The wide variation in the relationship between leaf size and light intensity points to substantial plasticity

in both species considered in this study. In general, Dombroskie *et al.* (2012) propose that smaller leaves are favoured under low light exposure because they minimize overlap of closely spaced adjacent leaves and they are subject to a trade-off of selection favouring high number/low size strategy which in turn maximizes the size of the reserve bud bank .

SLA, calculated as leaf area per unit mass, was found to be the smallest at the top of the canopy in full light conditions and increases with shading both in beech and in spruce. Larger SLA with increasing shading is likely an adaptation for more efficient light interception in low light conditions (Niinemets *et al.*, 2001). SLA was found to be greatest at the bottom compared to the top of the crown in 13- to 82-year-old Norway spruce (Merilo *et al.*, 2009) and in spruce, beech and fir seedlings (Stancioiu and O'hara, 2006). In this study, both beech and spruce show the same decreasing trend, graphs in Figure 2 indicate that leaf and needle SLA will decrease further as the stands mature before stabilising. Significant differences in SLA between socio-ecological classes of trees within the canopy were found. Dominant, co-dominant and intermediate crown have shown strong effect of crown depth on SLA. Foliage SLA of overtopped trees, owing to growth in shade conditions, did not differ between the top and the bottom parts of tree crowns. The optimal partitioning theory suggests that a plant invests primarily to those compartments which are crucial for acquiring the most limiting resource (Niklas, 2004). Maximum available light must be captured by overtopped trees, leading to construction of large foliage area with minimum mass investment.

Tree level

As expected, beech trees had substantially smaller foliage mass than spruce trees of comparable size. However, we have established that the latest cohort of spruce needles constituted only 34% of the total needle mass. Comparing only the current year beech and

spruce foliage mass shows that the two species invest exactly the same amount of resource to building their photosynthetic apparatus in a given year. Considering the effect of shading on SLA, mean SLA per tree is far larger in small (overtopped) trees, but approximates to that of spruce in larger (dominant) individuals. Higher SLA of shaded foliage in young beech stands was recorded by Closa *et al.* (2010). Barna (2004) showed lower values of SLA in dominant and co-dominant beech trees than in subdominant individuals. Our observations of beech SLA are in the same range as those of Barna (2004) who report 120 to 460 cm².g⁻¹, Closa *et al.* (2010) with values between 180 – 480 cm².g⁻¹, and those of Leuschner *et al.* (2006) who report a range between 190-240 cm².g⁻¹. As for the SLA of spruce needles, our values are higher than those of Heger and Sterba (1985) who found SLA of 30-70 cm².g⁻¹ in a 17-year-old stand, however the needles in the upper and middle part of the largest trees in our study were inside this range. Taken together, the observed contrasting trends of leaf area per tree and SLA mean that there is little difference in total leaf area per tree between beech and spruce trees of the same size. Despite one being conifer and the other broadleaf, beech and spruce trees of the same diameter class support nearly identical leaf area.

Stand level

Reflecting foliage area per tree and stand density, LAI indicates the potential of forest stands to utilise incident radiation to produce biomass. Stand LAI was steadily increasing during the period of observation, reaching approximately 15 m².m⁻² in 2011. Most studies indicate LAI in a variety of forest tree species below 10 m².m⁻² (*e.g.* (Bréda, 2003; Leuschner *et al.*, 2006), but higher values are also reported, albeit considered as extreme (*e.g.* (Ford, 1982; Albrektson, 1984; Bolstad and Gower, 1990). Waring and Schlesinger (1985) posit that very dense foliage can be found in some coniferous forests, exceptionally reaching LAI values as high as 20 m².m⁻². Nock *et al.* (2008) found a relationship between tree size and LAI in *Acer saccharum* and

Betula alleghaniensis, trees with DBH of 30 cm had LAI of 7.5 and 8.5 m².m⁻², but trees with DBH of 70 cm showed LAI of 4.0 and 6.0 m².m⁻² in *Acer* and *Betula*, respectively. There are several reasons why we observed very high LAI values; methodological, ontogenetic and possibly climatic. The diameter-based allometric method of LAI estimation has been reported to show values higher than other methods (Marshall and Waring, 1986). The aggrading nature of our naturally regenerated stands may have caused the increasing LAI, which may reverse in the future as the stands age and self-thin. Finally, the exposition of the site is south-westerly, providing optimal insolation for these young stands.

Wood production efficiency, expressed as unit stem increase per unit foliage, did differ between beech and spruce. Stem increment per unit leaf mass was far higher in beech compared to spruce, driven by retention of older needle cohorts in spruce which increases foliage mass. Dominant beech trees had significantly higher efficiency than overtopped trees, this advantage of taller trees was not as evident in spruce. A possible explanation for this difference can be that needle-shaped leaves can be arranged in a pattern that bounces the incoming radiation over a larger number of leaves deeper in the canopy (Sprugel, 1989). This effects increases photosynthesis of overtopped spruce trees by reducing the energy wastage that occurs when light falls on horizontally positioned beech leaves at the top of the canopy that are already light-saturated. However, when plotted against leaf area, wood production efficiency did not differ between the two species. This suggests that it is higher leaf thickness (Aranda *et al.*, 2004) rather than leaf area at the top of the canopy that confers stem growth advantage in dominant beech trees.

Conclusion

Stands of beech and spruce around Central Europe occur as monospecific stands, but also as various mixtures of the two species. This study compared the development of foliage and canopy in the two species, with the view of contrasting their light utilisation strategies. Leaf area per tree, stand LAI and stem increment per unit leaf area were found not to differ between beech and spruce in our stands, suggesting that stands of both species are utilising close to maximum available light energy. We found that morphology of beech foliage is more plastic than that of spruce, possibly contributing to the competitive advantage of beech in locations where the two species co-occur.

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Tables

Table 1 Stand characteristics for European beech and Norway spruce in November 2011, approximately 13 years after natural regeneration (means \pm se, p values at N=5).

	European beech	Norway spruce	d.f./F	P
Number of trees (ths. ha ⁻¹)	124.3 \pm 11.6	99.4 \pm 6.6	1/3.45	0.100
Mean tree height (cm)	295.3 \pm 22.2	213.0 \pm 5.3	1/13.63	0.006
Mean diameter d ₀ * (cm)	2.42 \pm 0.11	3.19 \pm 0.11	1/25.57	0.001
H/D ratio (cm.cm ⁻¹)	125.9 \pm 8.5	76.3 \pm 2.5	1/31.50	0.001
Mean stem volume (cm ³)	526.6 \pm 56.7	645.9 \pm 34.5	1/3.22	0.110
Basal area d ₀ * (m ² .ha ⁻¹)	356.2 \pm 35.5	334.6 \pm 28.5	1/0.22	0.648

* Stem diameter and basal area measured at ground level

Table 2 Site-specific biomass equation parameters for European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*). Diameter at based is used as the single predictor in all models estimating compartment biomass.

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

Figures

Figure 1 Single leaf and needle area at three different canopy levels in European beech (A) and Norway spruce (B). Solid lines represent best fit models for top, middle and bottom of individual tree crown.

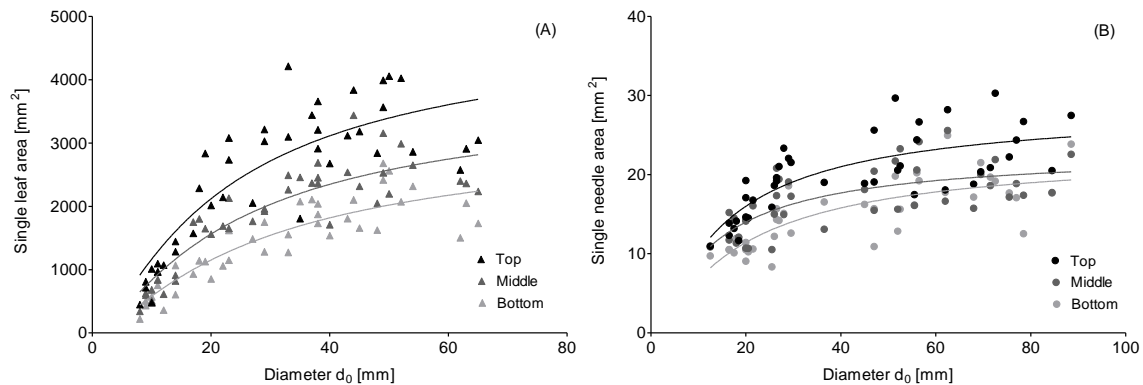
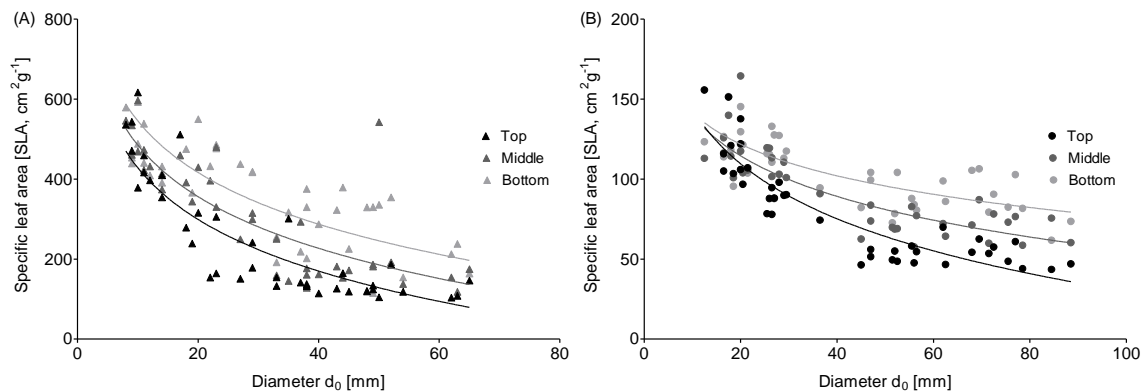
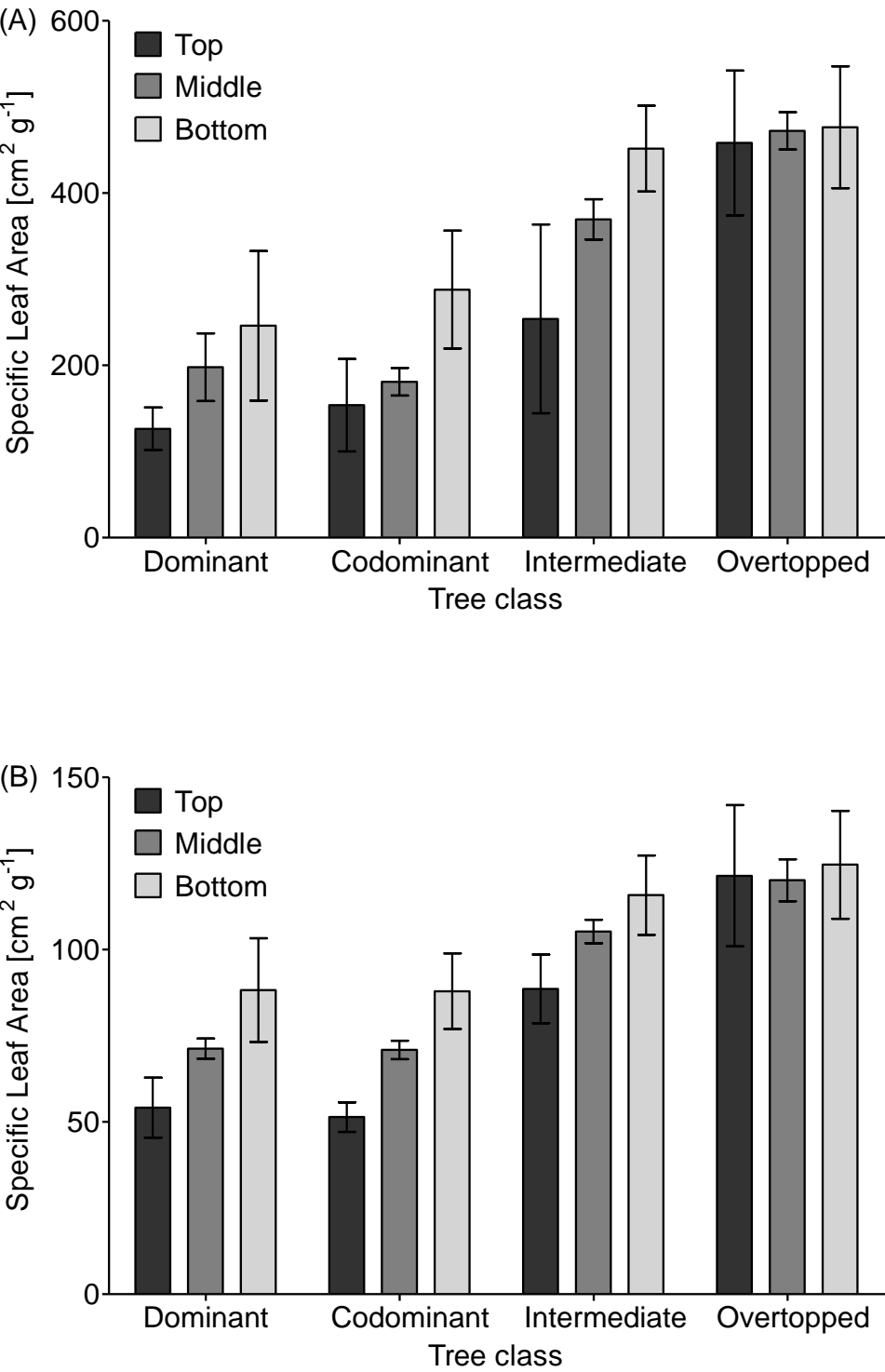


Figure 2 Specific leaf area at three different canopy levels in European beech (A) and Norway spruce (B). Solid lines represent best fit models for top, middle and bottom of individual tree crown.

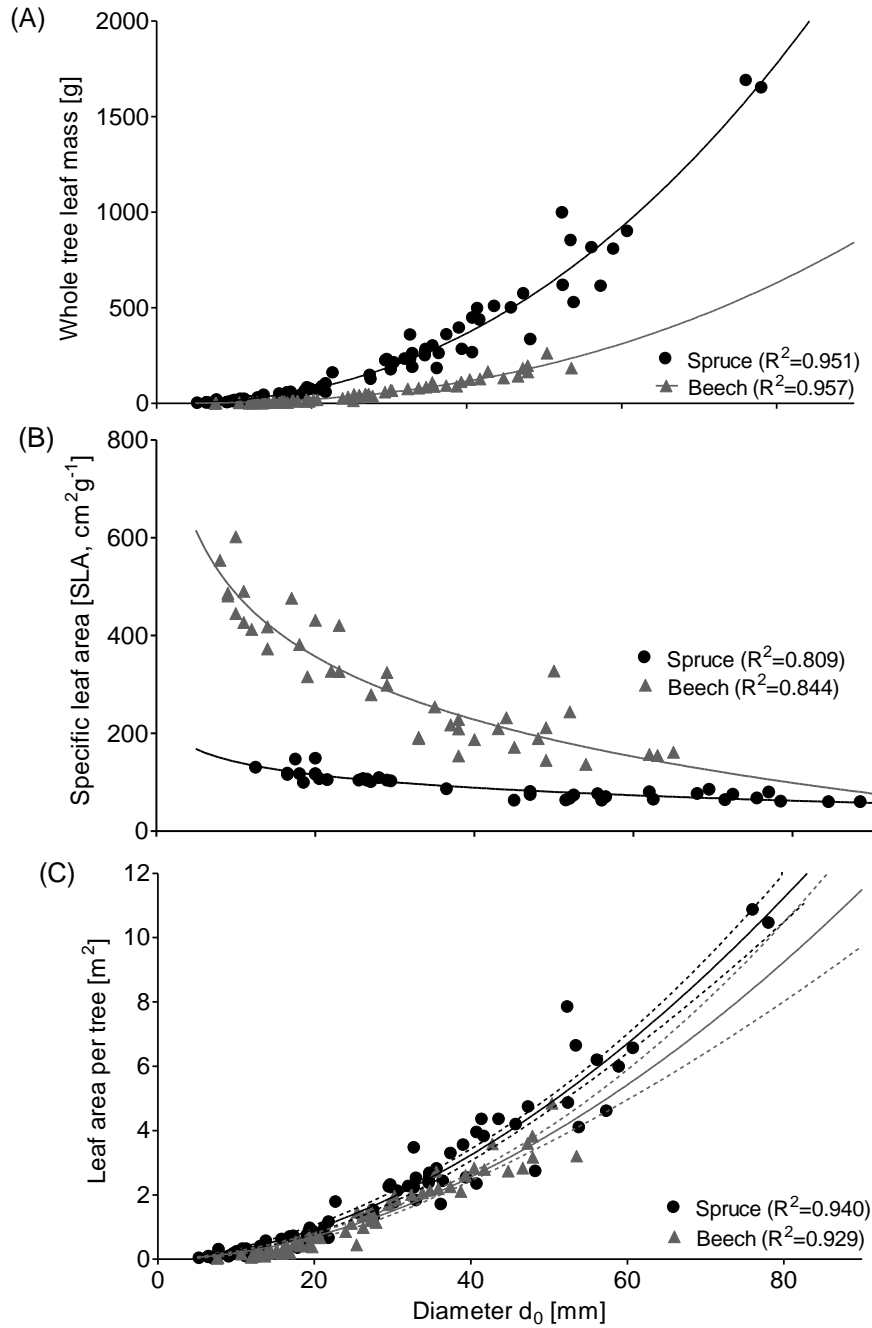


544 **Figure 3** Specific leaf area of European beech (A) and Norway spruce (B) foliage as affected by
 545 canopy position and socio-ecological status of individual trees (cm^2g^{-1} , $N=10$ in each class, mean \pm
 546 sd).

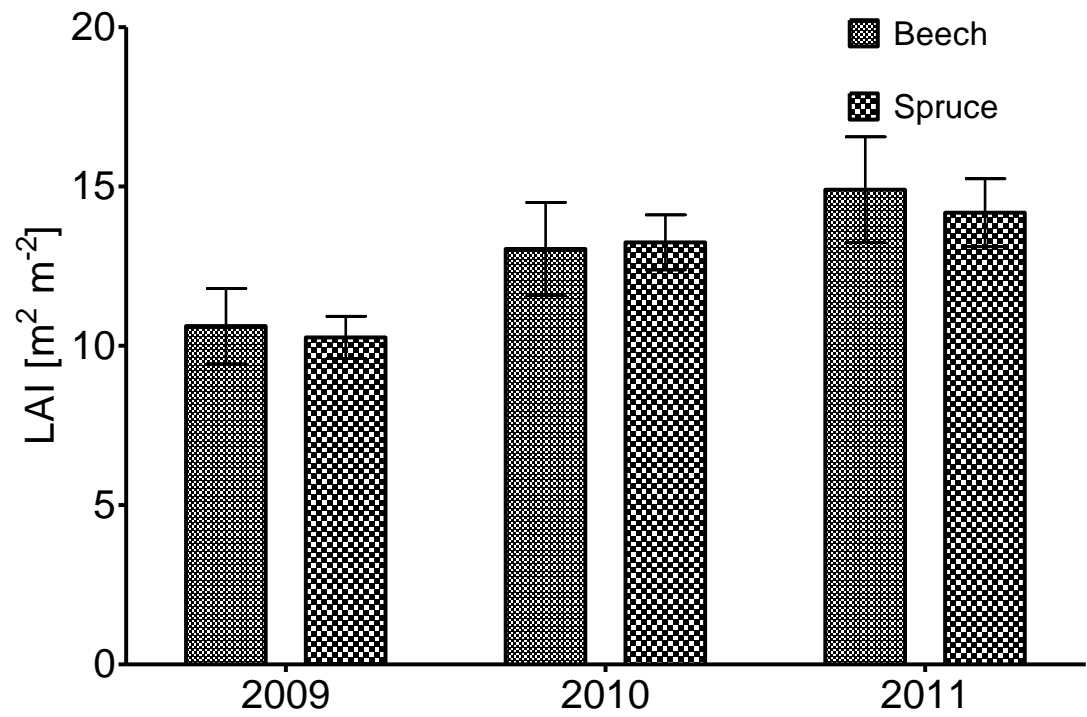


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Figure 4 Whole tree foliage mass (A), specific leaf area (B) and whole tree leaf area (C) of naturally regenerated European beech and Norway spruce trees. Dotted lines in pane C represent 95% confidence interval of fitted line.



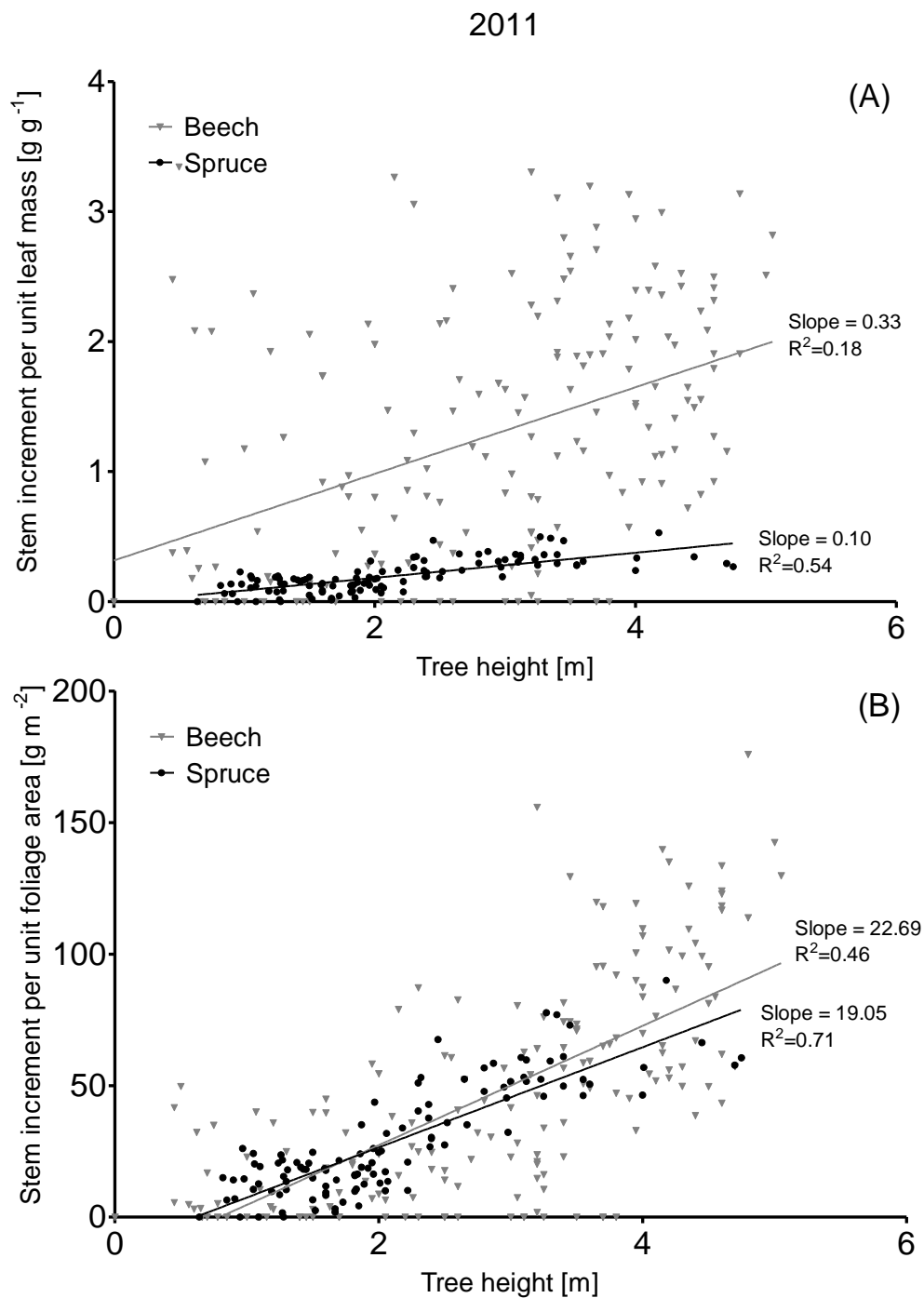
553 **Figure 5** Leaf Area Index (LAI) in naturally regenerated stands of European beech and Norway spruce
554 trees measured in permanent plots (mean \pm SD, N=5).



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557 **Figure 6** Stem mass increment per unit foliage mass (A) and area (B) plotted against stem height of
558 individual European beech and Norway spruce in 2011.



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