



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

Article

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

3
4 **Bohdan Konôpka^{1,2}, Jozef Pajtík^{1,2}, Róbert Marušák², Michal Bošela^{2,3}, Martin**
5 **Lukac^{2,4,*}**

6 ¹National Forest Centre, T. G. Masaryka 2175/22, 960 92 Zvolen, Slovak Republic

7 ²Czech University of Life Sciences in Prague, Kamýcká 129, 165 21 Praha 6 - Suchbát, Czech Republic

8 ³ Faculty of Forestry, Technical University in Zvolen, T.G.Masaryka 24, 960 53 Zvolen, Slovak Republic

9 ⁴School of Agriculture, Policy and Development, University of Reading, RG6 6AR, UK

10 *corresponding author, m.lukac@reading.ac.uk

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12 *structure*

13
14 **Abstract**

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

29

30 **Introduction**

31

32 Competition for light and resulting mortality are the most critical processes driving
33 development of young forest stands (King, 1990). As the canopy closes, in particular in stands
34 originating from natural regeneration, tree height relative to neighbours, but also position
35 within a crown dictate light availability to foliage (Niinemets *et al.*, 2001; Richardson *et al.*,
36 2001). Leaves and needles are the only tissues with the capacity to capture energy and thus
37 drive forest growth. Foliage responds very sensitively to growth conditions within a stand and
38 has been shown to adapt its morphology (Bussotti *et al.*, 2000), structure (Kull *et al.*, 1999)
39 and metabolism (Hallik *et al.*, 2009) in response to light intensity.

40

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

54

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

68

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

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

82

83 Allometric relations are frequently used to assess biomass partitioning to various pools in
84 forests (Claesson *et al.*, 2001; Wirth *et al.*, 2004; Fehrmann and Kleinn, 2006; Cienciala *et al.*,
85 2008; Pajtk *et al.*, 2011). In general, biomass contained in a particular tree compartment can
86 be predicted by an allometric equation usually using tree height or diameter (at breast height,
87 *i.e.* DBH) as predictor variables (West *et al.*, 2009). Estimates of foliage biomass in young
88 beech and spruce stands were put forward by Kantor *et al.* (2009), whilst Xiao and Ceulemans
89 (2004) established allometric equations for foliage at both branch and tree levels in young
90 Scots pine. The latter study attempted to consider the vertical position of a whorl as one of the
91 independent variables predicting foliage biomass. Having said that, biomass allometric
92 equations by definition predict only foliage mass and do not offer any information about
93 foliage area. Since leaf area and its stratification is key determinant of forest stand
94 productivity, this paper aims to link allometric relations to foliage area and stand LAI.
95 Developing stands of pure *Fagus sylvatica* L. (beech) and pure *Picea abies* Karst. (spruce)
96 with fully closed canopy are contrasted and their growth performance compared.

97

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

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

110

111 **Materials and methods**

112 *Site description*

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

124

125 *Size distribution, biomass and foliage sampling*

126 Five circular experimental plots were established in each stand in March 2009. The plots were
127 100 cm in radius and contained around 40 trees each. The plots were randomly positioned
128 within each stand, but at a distance of at least 5 canopy heights from each other. All trees within

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

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

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

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

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

157

158 *Estimations of biomass equations, LA and LAI*

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

162

$$163 \quad W_i = e^{(b_0 + b_1 \ln d_0)} \lambda \quad (1)$$

164

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

168

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

173

$$174 \quad LA = SLA * (e^{(b_0 + b_1 \ln d_0)} \lambda) \quad (2)$$

175

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

179

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

182

$$183 \quad LAI_j = \frac{\sum_{i=1}^n LA_{ij}}{S_j} \quad (3)$$

184 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
185 is the area of the j -th plot. This calculation is fairly straightforward in European beech due to
186 the presence of a single cohort of leaves. In Norway spruce, however, the variation of SLA in
187 needle cohorts was also taken into account. For each needle cohort, LA of needles from all
188 trees present within a permanent plot can be calculated as follows:

189

$$190 \quad LA_{jk} = \sum_{i=1}^n (W_i * P_k * SLA_k) \quad (4)$$

191

192 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
193 proportion of k -th cohort from the total and SLA_k is the specific leaf area of the k -th needle
194 cohort. Mean SLA for the entire vertical profile of the canopy was used for each cohort. Based
195 on an analysis of trees harvested at the site, we established that P_k in spruce is stable and
196 independent of d_0 (Supplementary Figure S1), therefore mean values of P_k were used across
197 all diameter classes. LA of all spruce trees found within each plot was then obtained by
198 summing up leaf areas of the five needle cohorts.

199

200 ***Data analysis***

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

212 **Results**

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

219
220 Measurements of foliage collected from 40 beech and 40 spruce FolTrees reveal that individual
221 leaf size is far more conservative in spruce than in beech (coefficient of variance 0.29 and 0.53
222 respectively, Figure 1). Within the stem diameter distribution present in the stands at the time
223 of measurement, beech leaf area increases by 83% from the 25th to the 75th d₀ percentile. In
224 spruce, however, the comparable increase in individual needle area is only 38%. Similarly, the

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

227

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

235

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

244

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

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

252

253 The observed similarity of whole tree leaf area of beech and spruce trees was reflected in
254 calculated LAI. As already mentioned, basal area and tree density did not differ between the
255 two stands. Coupled with very similar total leaf area of individual trees, it is not surprising that
256 LAI did not differ between beech and spruce ($p=0.865$, Figure 5). From 2009 through 2011,
257 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.

258

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

275

276 **Discussion**

277

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

286

287 ***Leaf level***

288 Individual leaves with the largest area were always found at the top of the canopy, both in beech
289 and in spruce. Leaves and needles were progressively smaller with increasing canopy depth,
290 this differentiation of single leaf size appears to be stronger in beech than in spruce. Shorter
291 trees had smaller leaves than taller trees, owing to the shading of their entire crowns by taller
292 trees. Contrasting evidence exists on the effect of shading on individual leaf size. Our results in
293 beech are in disagreement those of Barna *et al.* (2004) and Tognetti *et al.* (1998) who found
294 that the size of foliage increased with shading, but correspond with the study by Carnham
295 (1988) who found larger leaf size at high light levels in *Acer saccharum* Marsh. and *Fagus*
296 *grandiflora* Ehrh. Similarly, Niinemetz and Kull (1995) found no effect of irradiance on
297 projected needle area in spruce and Gebauer *et al.* (2011) indicate that needle size increases
298 with light intensity in most but not all of the 57 spruce provenances they compared. The wide
299 variation in the relationship between leaf size and light intensity points to substantial plasticity

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

304

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

320

321 *Tree level*

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

325 spruce foliage mass shows that the two species invest exactly the same amount of resource to
326 building their photosynthetic apparatus in a given year. Considering the effect of shading on
327 SLA, mean SLA per tree is far larger in small (overtopped) trees, but approximates to that of
328 spruce in larger (dominant) individuals. Higher SLA of shaded foliage in young beech stands
329 was recorded by Closa *et al.* (2010). Barna (2004) showed lower values of SLA in dominant
330 and co-dominant beech trees than in subdominant individuals. Our observations of beech SLA
331 are in the same range as those of Barna (2004) who report 120 to 460 cm².g⁻¹, Closa *et al.*
332 (2010) with values between 180 – 480 cm².g⁻¹, and those of Leuschner *et al.* (2006) who
333 report a range between 190-240 cm².g⁻¹. As for the SLA of spruce needles, our values are
334 higher than those of Heger and Sterba (1985) who found SLA of 30-70 cm².g⁻¹ in a 17-year-
335 old stand, however the needles in the upper and middle part of the largest trees in our study
336 were inside this range. Taken together, the observed contrasting trends of leaf area per tree
337 and SLA mean that there is little difference in total leaf area per tree between beech and
338 spruce trees of the same size. Despite one being conifer and the other broadleaf, beech and
339 spruce trees of the same diameter class support nearly identical leaf area.

340

341 ***Stand level***

342 Reflecting foliage area per tree and stand density, LAI indicates the potential of forest
343 stands to utilise incident radiation to produce biomass. Stand LAI was steadily increasing during
344 the period of observation, reaching approximately 15 m².m⁻² in 2011. Most studies indicate LAI
345 in a variety of forest tree species below 10 m².m⁻² (*e.g.* (Bréda, 2003; Leuschner *et al.*, 2006),
346 but higher values are also reported, albeit considered as extreme (*e.g.* (Ford, 1982; Albrektson,
347 1984; Bolstad and Gower, 1990). Waring and Schlesinger (1985) posit that very dense foliage
348 can be found in some coniferous forests, exceptionally reaching LAI values as high as 20 m².m⁻²
349 ². Nock *et al.* (2008) found a relationship between tree size and LAI in *Acer saccharum* and

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

358

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

372

373 **Conclusion**

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

382

383 **References**

384

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523 **Tables**

524

525 **Table 1** Stand characteristics for European beech and Norway spruce in November 2011,526 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

527 * Stem diameter and basal area measured at ground level

528

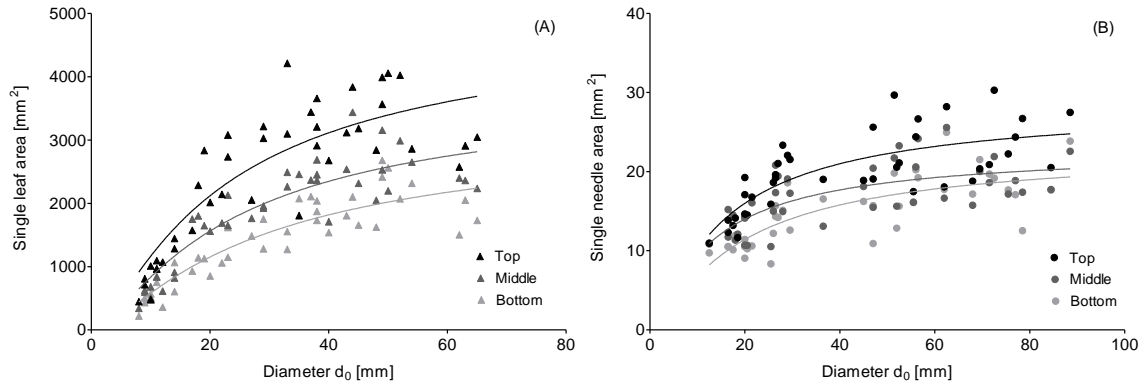
529 **Table 2** Site-specific biomass equation parameters for European beech (*Fagus sylvatica*) and
 530 Norway spruce (*Picea abies*). Diameter at based is used as the single predictor in all models
 531 estimating compartment biomass.

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)
Spruce	Needles	-3.079 (0.171) < 0.001	2.432 (0.054) < 0.001	0.964	0.106	1.053 (0.366)
	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)

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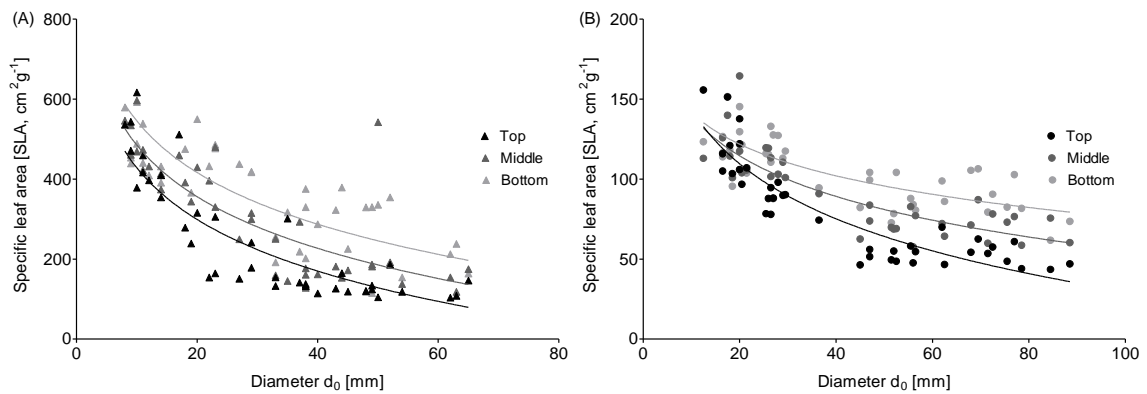
533 **Figures**

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



537

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

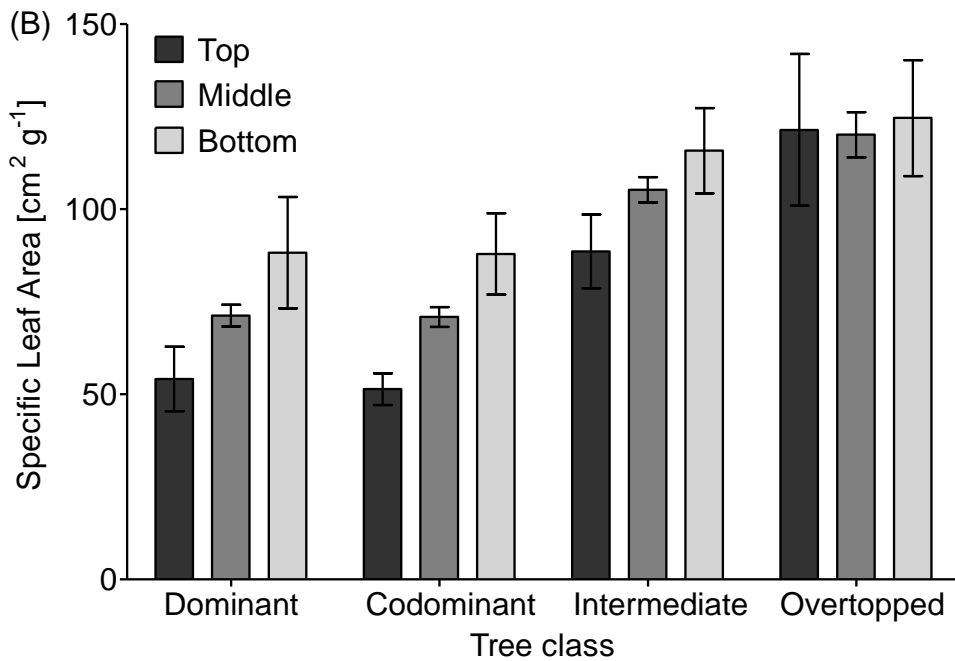
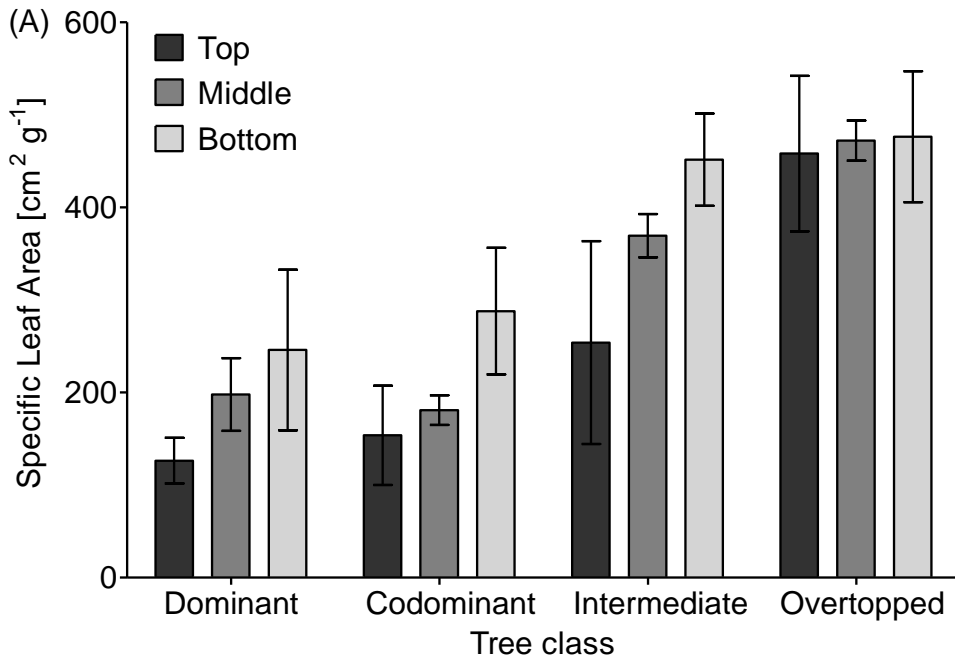


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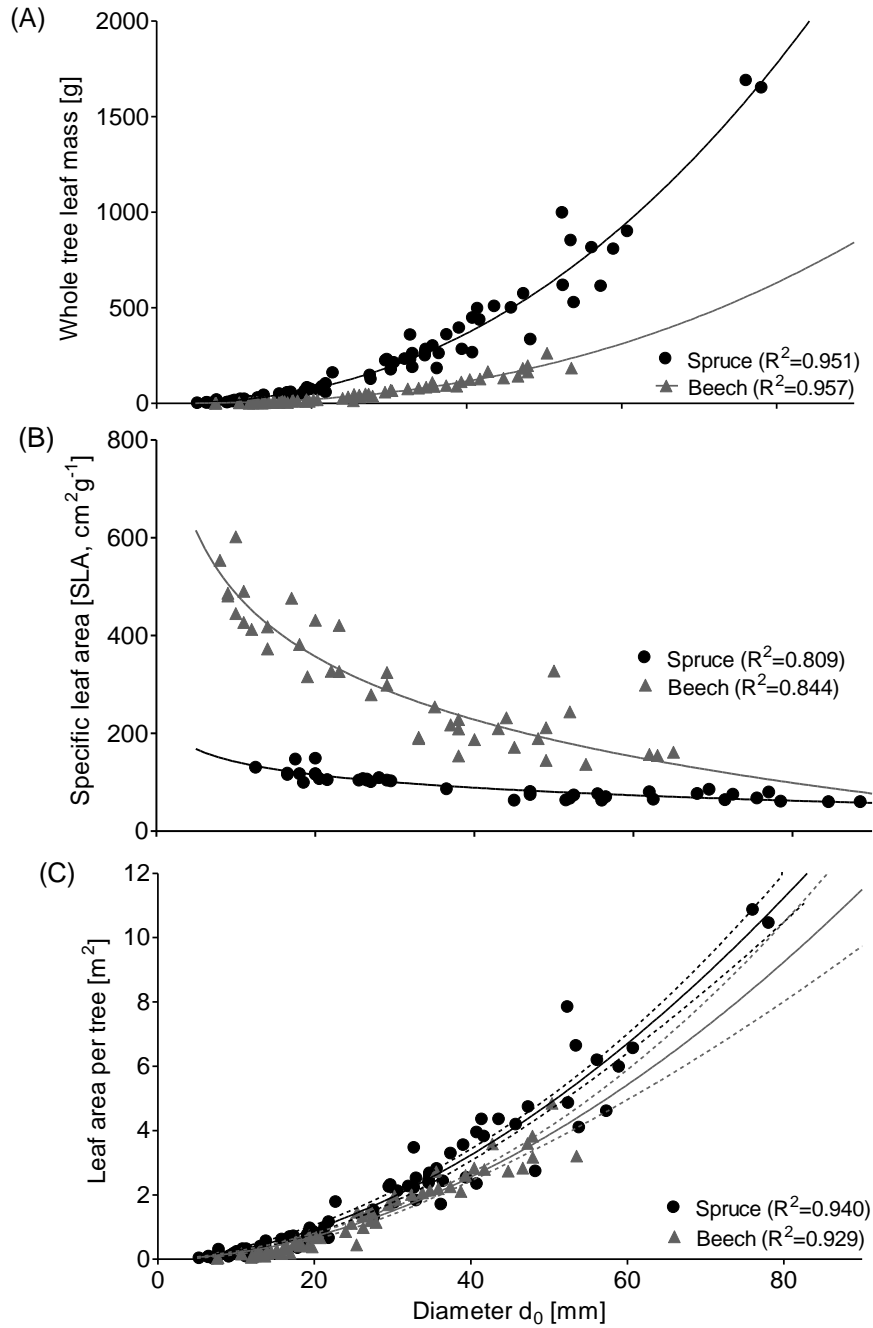
543

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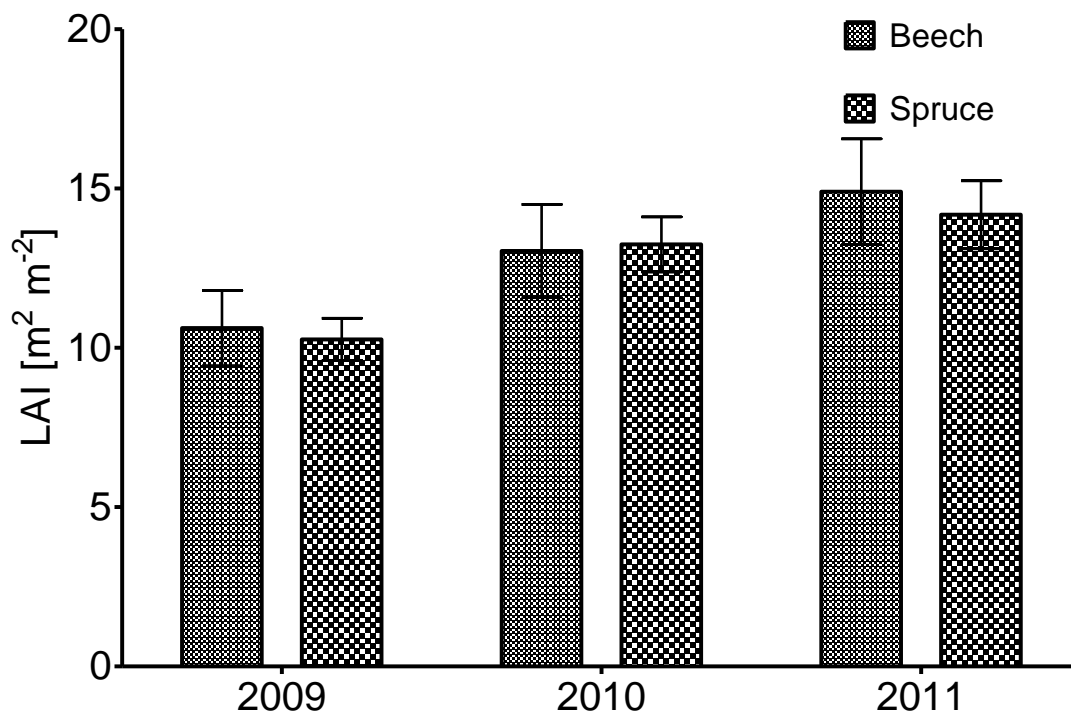
548 **Figure 4** Whole tree foliage mass (A), specific leaf area (B) and whole tree leaf area (C) of naturally
549 regenerated European beech and Norway spruce trees. Dotted lines in pane C represent 95% confidence
550 interval of fitted line.



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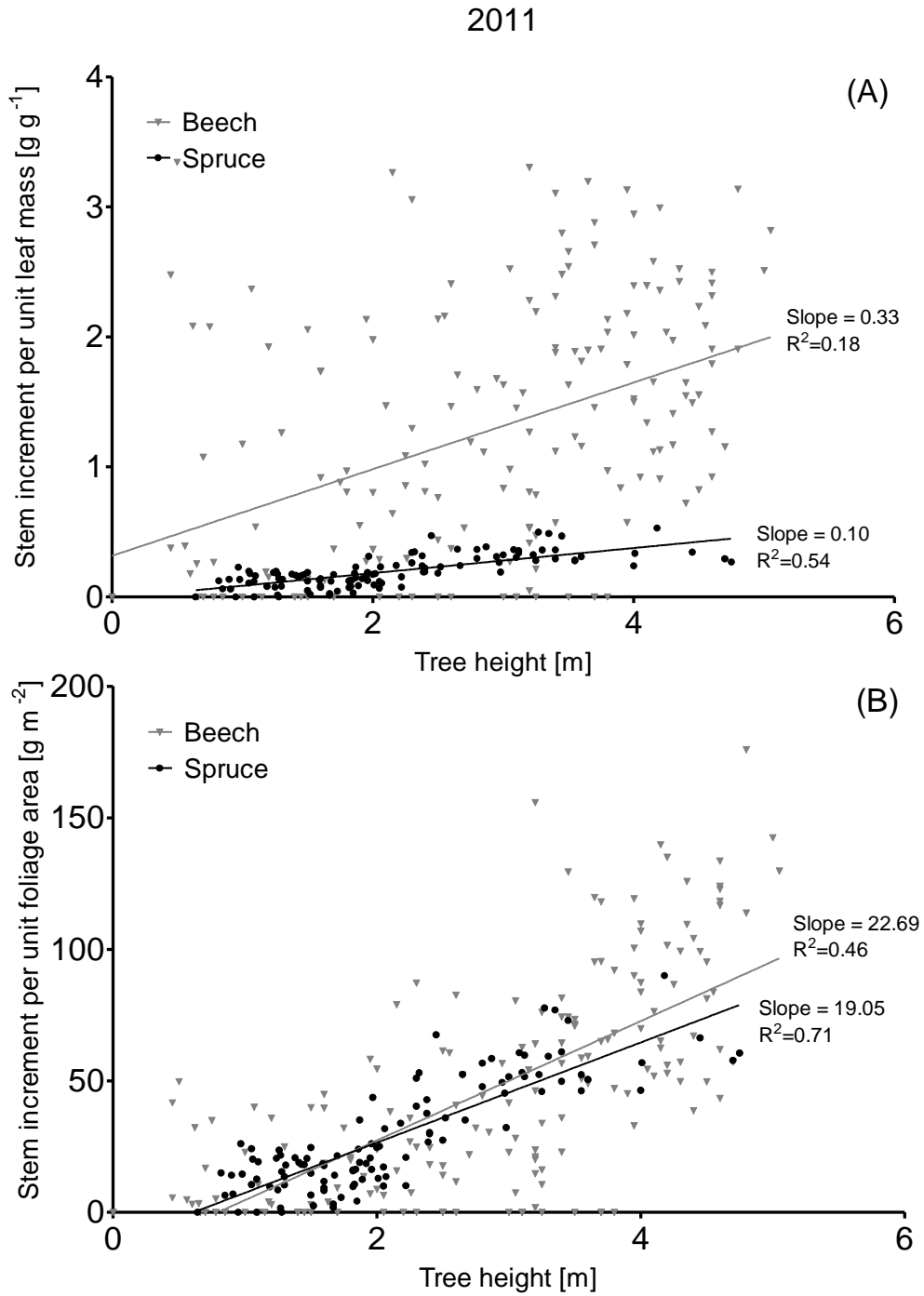
553 **Figure 5** Leaf Area Index (LAI) in naturally regenerated stands of European beech and Norway spruce
554 trees measured in permanent plots (mean \pm SD, N=5).



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556

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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