

Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings

Any Mary Petrițan · Burghard von Lüpke ·
Ion Catalin Petrițan

Received: 31 January 2008 / Revised: 13 October 2008 / Accepted: 12 November 2008 / Published online: 12 December 2008
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Abstract In a field study, we measured saplings of beech, ash and maple growing in a fairly even-aged mixed-species thicket established by natural regeneration beneath a patchy shelterwood canopy with 3–60% of above canopy radiation reaching the saplings. Under low light conditions, maple and ash showed a slight lead in recent annual length increment compared with beech. With increasing light, ash and maple constantly gained superiority in length increment, whereas beech approached an asymptotic value above 35% light. A suite of architectural and leaf morphological attributes indicated a more pronounced ability of beech to adapt to shade than ash and maple. Beech displayed its leaves along the entire tree height (with a concentration in the middle crown), yielding a higher live crown ratio than ash and maple. It allocated biomass preferentially to radial growth which resulted in low height to diameter ratios, and expressed marked plagiotropic growth in shade indicating a horizontal light-foraging strategy. In addition, beech exhibited the highest specific

leaf area, a greater total leaf area per unit tree height, a slightly greater leaf area index, and a greater plasticity to light in total leaf area. Ash and maple presented a “gap species” growth strategy, characterized by a marked and constant response in growth rates to increasing light and an inability to strongly reduce their growth rates in deep shade. In shade, they showed some plasticity in displaying most of their leaf area at the top of the crown to minimize self-shading and to enhance light interception. Through this, particularly, maple developed an “umbrella” like crown. These species-specific responses may be used for controlling the development of mixed-species regeneration in shelterwood systems.

Keywords Shade tolerance · Juvenile growth · Mixed species broad leaf stand · Tree architecture · Leaf morphology · Light availability

Introduction

Among the various growth factors, light plays an outstanding role in forests, at least on mesic sites in temperate regions (Kimmins 1997), and it can easily be manipulated by silvicultural means (Röhrig et al. 2006). Although we regard light, the most important growth factor in the study to be described hereafter, we are aware that variations in light intensity beneath a forest canopy are associated regularly and to a mostly unknown extent with changes in other resources like soil, water and nutrients (Kimmins 1997). In forestry practice, the traditional shade tolerance classification of tree species does not differentiate between effects of these multiple resources. Therefore, the term ‘understorey tolerance’ actually would be more appropriate, but in the following we retain the term ‘shade tolerance’,

Communicated by R. Matyssek.

A. M. Petrițan (✉) · B. von Lüpke · I. C. Petrițan
Department of Silviculture and Forest Ecology of the Temperate
Zones, Georg-August University Göttingen,
Büsgenweg 1, 37077 Göttingen, Germany
e-mail: apetrit@gwdg.de

A. M. Petrițan
Department of Silviculture and Forest Ecology,
Institute of Forest Research and Management,
Closca 13, 500040 Brasov, Romania

I. C. Petrițan
Department of Forest Management, Transilvania University
Brasov, Sirul Beethoven 1, 500123 Brasov, Romania

because it is well introduced and widely used (Röhrig et al. 2006).

An understanding of how different tree species react to changing light conditions is fundamental for the silvicultural concept of ‘continuous-cover forestry’, which is adopted by many forest owners in central Europe. This concept is characterized by forest regenerations growing as long as possible beneath an overstory canopy (Schütz 1999; Pommerening 2002). Juvenile trees have to cope with more or less shady conditions. Shade-tolerant species, above all European beech (*Fagus sylvatica* L.), are well adapted to this situation and increase in competitiveness, whereas less shade-tolerant species among which are many valuable timber species are put at a disadvantage. They need more light especially in mixture with beech than is available in many stands under the regime of continuous-cover forestry. Achieving a light environment which is optimal for growth and survival of the wanted tree species requires species-specific knowledge of even subtle differences in responsive behavior to available light. Although some scientific investigations on young saplings of beech and ash (Wagner 1999), planted oaks (von Lüpke and Hauskeller-Bullerjahn 2004), beech and *Quercus pubescens* (Kunstler et al. 2005), beech, maple and ash (Bonosi 2006), and beech, *Abies alba* and *Picea abies* (Stancioiu and O’Hara 2006b) are published, they are not sufficient for practical silvicultural decisions in Central Europe. Therefore, many foresters still rely on empirical observations.

To fill this gap, we carried out the following investigation in addition to a companion study (Petrişan et al. 2007). In both studies, the objects were mixed-species thickets of maple (*Acer pseudoplatanus* L.), ash (*Fraxinus excelsior* L.) and beech from natural regeneration, growing underneath a beech shelterwood of variable canopy densities. This type of mixture is widespread and important in Germany on sites well supplied with nutrients and water. The general silvicultural aim in these stands is to have about 40–60% beech and 60–40% ash, maple and other valuable hardwood species in adult stands (Wagenhoff 1974). To reach this goal, the admixed maple and ash need a sufficient lead in juvenile height growth enabling them to hold ground on the long run against the increasingly competitive beech (Züge 1986). In the past, this was achieved by a uniform shelterwood, in which overstory trees were gradually removed over a short period of 10–15 years. However, this treatment put beech at a disadvantage due to heavy competition of the overtopping ashes and maples during the early development phases. As a result, the proportion of beech often decreased too much endangering its maintenance as a species of prime importance on these sites (Wagner 1999).

On the other hand, the shift to continuous-cover silviculture favored beech to a great extent, and put the admixed

species at a disadvantage. To solve this problem, an appropriate control of the canopy density of the shelterwood is needed, in order to provide enough light for the more light demanding species in mixture. It is common silvicultural knowledge that such appropriate canopy treatment consists of an irregular shelterwood creating heterogeneous light conditions in space and time (Röhrig et al. 2006).

Our first study (Petrişan et al. 2007) focused on a quantitative determination of shade tolerance of the three species based on mortality rates under low light and length growth rates under high light. According to this study, beech could be ranked as shade-tolerant, and maple and ash as mid-tolerant. The study on hand is partly a replication of the foregoing, but the main focus being now on leaf morphology and plant architecture. Besides, it covers a larger light gradient (up to about 60% of full light instead of maximal 33% in the first study).

The ability of juvenile trees to adapt their morphological and architectural traits to various light levels is an important species-specific characteristic (Messier et al. 1999). Plants have evolved different life-history strategies to optimize their fitness in different light conditions (Kunstler et al. 2005). Both, growth responses and plant architecture characteristics, have been used to estimate the shade tolerance of trees (among others: Canham 1988; Chen et al. 1996; Beaudet and Messier 1998; Messier and Nikinmaa 2000; Delagranges et al. 2004; Kunstler et al. 2005; Bonosi 2006; Stancioiu and O’Hara 2006a, b). Results are inconsistent: some studies suggested shade-tolerant species generally being more plastic than less tolerant ones (Canham 1988; Chen et al. 1996), others do not indicate any such relationship (Messier and Nikinmaa 2000; Paquette et al. 2007).

Generally, these opposing results may partially be explained by the use of different metrics for adaptive features and/or of different methods to determine plasticity. Whatever the reasons are, the situation is not satisfactory and justifies additional research. Our study shall contribute further in filling this knowledge gap for three important tree species in central Europe, with the main focus on utilization of the results in practical forestry. Thus, our main objectives are:

- to describe species-specific patterns of morphological, architectural, and growth responses to changing light levels (or to be more exact: “overstory density levels”)
- to compare the adaptive capacity between the three species, and to compare it with their shade tolerance ranking, and
- to give recommendations for mixed-species management

Our study design is similar to that of the above mentioned companion study (Petrişan et al. 2007). As we were

mainly interested in comparing the three species in a more or less even-aged stand representing a typical situation in practical silviculture, we accepted (1) a close correlation between light availability and tree height (i.e. a fully closed overstory canopy resulted in low light in the understory, retarded sapling growth and small heights, and vice versa under open canopy conditions), and (2) a highly competitive situation within the thicket. We have to assume that both size and competition affected growth and morphology of our sample trees as we know from some investigations (Messier and Nikinmaa 2000; Claveau et al. 2002; Delagranges et al. 2004). But we ensured by adequate sampling that we were able to detect interspecific differences at a given light level by comparing saplings with same sizes and similar competitive situation.

Materials and methods

Study site

The study was carried out in a mixed deciduous stand with an overstory of 120-year-old beech and some trees of hornbeam (*Carpinus betulus*), ash, maple, Norway maple (*Acer platanoides*), and sessile oak (*Quercus petraea*), located in the community forest Wibbecke, near Göttingen (Lower Saxony, Germany, 10°02'11"E, 51°34'46"N). The site is characterized by a shallow limestone plateau with rendzina soils and haplic luvisols, rich in nutrient supply, but rather poor in water supply during dry periods in summer. The altitude above sea level ranges from 151 to 200 m, the mean annual rainfall is 780 mm (370 mm in the growing season), and the average annual temperature is 7.8°C. Within the last 10 years, neither silvicultural interventions nor natural disturbances occurred. We therefore assume fairly stable canopy conditions in the overstory for the last years. The canopy closure is patchy, ranging from fully closed parts to large gaps. Thus, it provides a broad gradient of light conditions in the understory. The regeneration layer is now in the thicket growth phase with >20,000 saplings per hectare and a top height of 6–8 m.

Sapling measurements

Samples were collected in 2006 from 129 randomly selected individual trees (43 maple, 41 beech and 45 ash trees), free of apparent damage, growing under a wide gradient of light conditions. For every sapling, the following data were recorded: total height, total length, crown length, two crown diameters at the height of the maximal crown width (in N–S and W–E orientation), all to the nearest centimeter; length of the last five annual terminal shoot increments; and diameter at 10 cm above ground, both to the nearest

millimeter. The base of the crown was defined as the height of the lowest leaf-bearing branch. After cutting the saplings, a stem disc was taken from 10 cm above ground for determining age and radial growth. The discs were sanded (grit size 400), and the width of the last five annual rings were measured in two perpendicular directions. The final values were calculated as arithmetic means of the two perpendicular measurements.

Light availability was quantified by taking a hemispherical photo just above the uppermost leaves of every sampled sapling in mid-summer with a Nikon digital camera with fisheye lens and a self-leveling mount. Photos were processed with the Winscanopy software (Regents Instruments Inc., Sainte-Foy, Québec 2003). As a measure of light intensity, we used the indirect site factor (ISF) in percent of above canopy light, which is based on diffuse radiation. Under our conditions, this measure proved as a reliable proxy of total growing season's photosynthetically active radiation as ISF and total site factor (including diffuse and direct radiation) were strongly correlated with $R^2 = 0.94$ and $p < 0.001$.

Each sapling was divided into five horizontal layers of equal height (=1/5 of total length). A subsample of 50 randomly chosen leaves per layer (when the number was less, we took all leaves) was used for leaf area measurements with the LI-3100 Area Meter (LI-COR, Inc. 1987) and subsequent drying (at 70°C for 3 days) and weighing. For all other leaves, only dry weights were determined. Using the ratio of leaf weight to leaf area of the subsamples, we calculated for each layer the area of the rest of the leaves. The sum of the leaf areas of the individual layers made up the total leaf area of the sapling. Mean leaf area (MLA in cm² per leaf) and specific leaf area (SLA in cm² g⁻¹ leaf dry weight) were also determined on layer and total plant level. Finally, two ratios were computed to characterize the leaf display: (1) Leaf area index, as ratio of total leaf area to projected crown area (LAI in cm² cm⁻²). For the projected crown area, we computed an ellipse area (the product of the two crown diameters with π , divided by 4, similar to Perry et al. 1993 and Paquette et al. 2007), (2) efficiency of leaf display, as ratio of total leaf area to tree height (ELD, cm² cm⁻¹). It is a simplified version of a ratio used by Paquette et al. (2007) and describes the density of leaf arrangement. The higher the value, the more leaf area a sapling can display per unit of height, and the more efficient it utilizes the support tissue of the stem.

Morphological and architectural traits were described by the following indices: Live crown ratio (crown length relative to total sapling length: LCR in cm cm⁻¹); ratio of crown length to mean crown diameter (RCLD in cm cm⁻¹), and ratio of height to stem diameter at 10 cm above ground (H/D in cm cm⁻¹).

To analyze the plagiotropy of saplings, we used the inclination angle of the main stem from the vertical [$\alpha = 90^\circ - \arcsin(\text{height length}^{-1})$], see Schmitt et al. (1995). Finally, we computed an index of investment into height growth per unit of basal area growth as ratio of annual terminal length increment to annual basal area increment (LBAR in cm mm^{-2}). We used basal area increment instead of diameter increment, because it better describes the biomass investment into stem growth. This ratio should allow discerning growth strategies with preferred height growth (as in gap species) from those giving diameter growth priorities (as in understory-species, King 1991).

Data analysis

Light-growth and light-morphological functions for the tree species were developed using linear and nonlinear models based on the least squares method. As growth variables we used the annual radial and terminal leader length growth as averages over the last 5 years. The following growth models were compared: the logistic growth model, the Michaelis–Menten model, the Gompertz model and the Chapman–Richard’s model. To choose the best model, we examined two statistical criteria: the coefficient of determination (R^2), which shows the proportion of the total variance explained by the model, and the modified Akaike information criterion (AIC_c), which is an index to select the best model based on minimizing the Kullback–Liebler distance (Anderson et al. 2000). It represents the information loss when the subject model is used to approximate the true model, and therefore the minimum AIC_c implies the best fit.

The response of morphological variables to variation in light availability was examined by linear regression analysis for each species. The independent variable, % ISF, was transformed to its natural logarithm when necessary to comply with the requirements of normality and homoscedasticity (see also Beaudet and Messier 1998).

The difference between tree species depending on light was tested by an analysis of covariance (ANCOVA), considering species as the main factor and ISF as the continuous covariate. Data of the covariables were transformed when necessary to reach residue normality and variance homogeneity needed for the analyses. In case the ANCOVA yielded a significant species effect, we examined the differences between species mean values by Scheffé’s post-hoc test.

When the data did not comply with the requirements of parametric test methods, we used non-parametric tests (Kruskal–Wallis test, Wilcoxon-pair test, and Mann–Whitney U Test). All data analyses were performed using Statistica 7.1 (StatSoft, Inc., USA).

Results

General information about sampled saplings

Figure 1 shows the even distribution of the sampled saplings along the light gradient. As already mentioned in the introduction, there was a strong correlation between light and height, which could be fitted by linear regression lines with coefficients of determination between 0.82 and 0.91. There were no significant differences between the three species; the 95% confidence intervals are clearly overlapping. This is also shown in Table 1 giving means and ranges for attributes of the sampled saplings. The sample trees experienced almost the same light gradients with mean values of 24.1–26.3% ISF and extremes from 2.3 to 59.6% ISF, and possessed similar mean and extreme values for diameter, height and age. The small differences between species were not significant (Kruskal–Wallis H Test, $p > 0.05$).

Response of tree growth to light

The strong correlation between sapling height and light availability did not allow separating the effects of the two factors, light and size, on growth rates. However, for the sake of simplicity, we address in the following description of the results mainly the factor light, keeping in mind that an increase in light is always concomitant with an increase in size.

The relationship between growth and light availability could generally best fitted by a logistic model (Fig. 2). Light availability explained more than 80% of the variation in length growth and more than 70% in radial growth (Table 2).

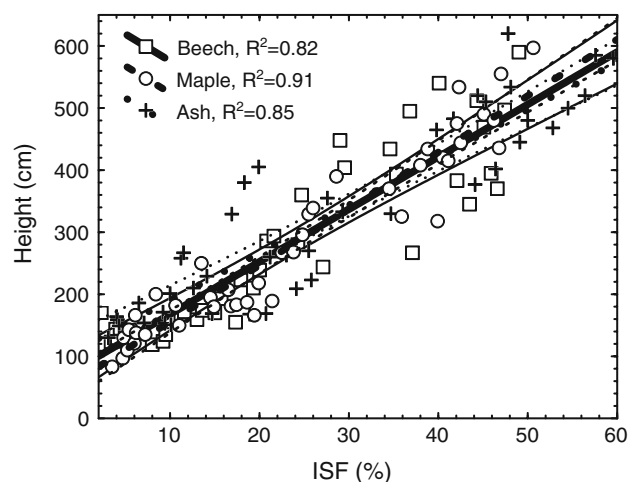
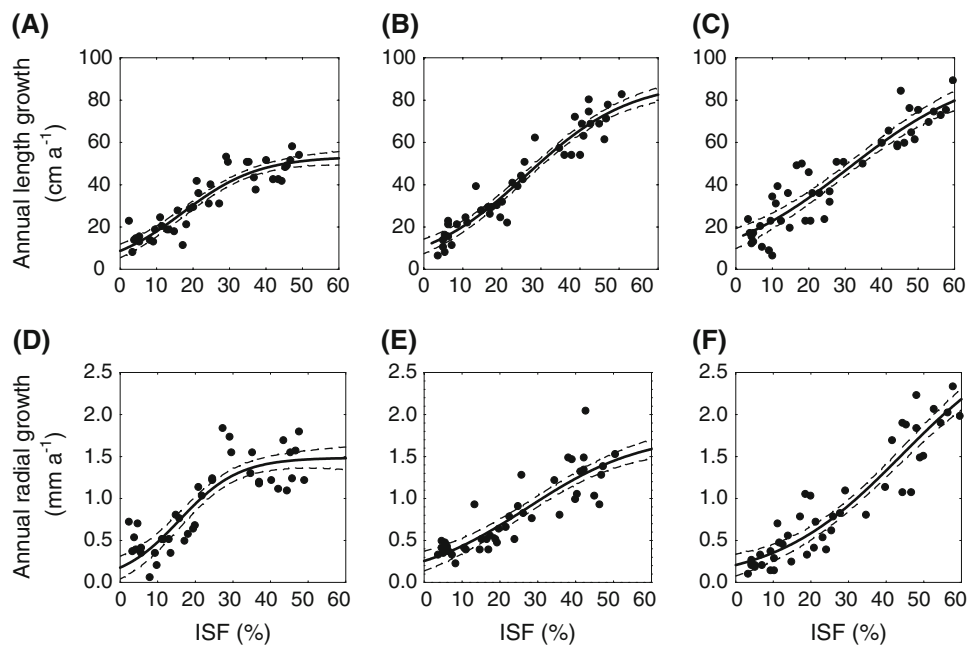


Fig. 1 Height of the sample trees in relation to light (ISF in % of above canopy light). Bold lines give the linear regression lines, normal lines, the 95% confidence intervals

Table 1 General data for sampled saplings

Species	<i>n</i>	Indirect site factor (% of above canopy)	Diameter (mm)	Height (cm)	Age
Beech	41	24.1 (2.3–53.1)	19.7 (5.0–55.0)	285.1 (119.0–590.0)	14 (7–25)
Maple	43	24.1 (3.5–50.6)	16.6 (5.0–38.0)	283.7 (83.0–597.0)	13 (6–19)
Ash	45	26.3 (3.1–59.6)	18.2 (5.0–37.0)	315.7 (130.0–620.0)	14 (9–19)

Fig. 2 Scatterplots and fitted regression lines of the mean last 5 years' length (a–c) and radial (d–f) increment on indirect site factor (ISF % of above canopy light) for beech (a, d), maple (b, e) and ash (c, f). The broken lines represent 95% confidence intervals



Length growth at low light levels (determined as the slope of the regression line at zero ISF, see S_0 in Table 3) was similar for all three species. In high light, greater differences appeared between species: ash had the strongest increase (measured as slope of the regression line at 60% ISF = S_{60} , see Table 3) with $S_{60} = 0.733$, while beech had the lowest value of 0.082, and maple presented an intermediate position with 0.455. Looking at the absolute values, in deep shade with 5% ISF, beech achieved the lowest growth rate of 13 cm, maple 15 cm (or 115% of beech), and ash 18 cm (or 138% of beech). The less shade-tolerant species thus had a slight advantage even in deep

shade. Under high light with 50% ISF, this growth lead increased to 149 and 145%, respectively (or in absolute figures: beech 51, maple 76, ash 71 cm).

Table 2 Annual length and radial growth (as mean values of the last 5 years) depending on indirect site factor (ISF, in % of above canopy light): logistic model ($y = a/(1 + \exp(b - c \times x))$)

Regression (Y vs. X)	Species	R^2	Parameters of the logistic model		
			<i>a</i>	<i>b</i>	<i>c</i>
Length growth versus light	Beech	0.84	53.3735	1.6323	0.0955
	Maple	0.92	89.1359	1.9765	0.0752
	Ash	0.85	95.5290	1.7138	0.0555
Radial growth versus light	Beech	0.73	1.4853	2.0007	0.1266
	Maple	0.75	1.773	1.7825	0.0655
	Ash	0.87	3.0378	2.6147	0.0592

The point of inflection of the response curve was at 17.1% full sunlight for beech, 26.3% for maple, and 30.9% for ash (*x*-values of PI in Table 3). At these light levels, all studied species reached about half of their maximal length growth (ISF at 50% G_{max} in Table 3) which was for maple and ash about 150 or 170% of beech growth (*y*-values of PI in Table 3). With increasing light, beech reached sooner the point of inflection and showed a more pronounced asymptotic growth pattern with lower maximal growth rates than maple and ash (53 $cm a^{-1}$, but 89 for maple and 96 for ash, see A in Table 3).

The slope of the radial growth response function of ash at zero light was lower than that of beech and maple, whereas the slope at high light (ISF = 60%) was the highest (Table 3). Looking again at the absolute values, in deep shade with 5% ISF, beech and maple achieved a slightly greater radial growth rate of 0.30 and 0.33 mm, respectively, than ash with 0.27 mm. Under high light of 50% ISF, ash (1.78 mm) outgrew beech (1.47) and maple (1.45) which was a smaller difference than in length growth.

The point of inflection was for beech at 15.8% full sunlight and 0.74 $mm a^{-1}$ radial growth, the lowest values

Table 3 Characteristics of the logistic light—length and light—radial growth response curves

Species	S_0	S_{60}	PI		ISF at 50% G_{\max}	A
			x	y		
Light-length increment						
Beech	0.697	0.082	17.08	26.68	18.87	53.378
Maple	0.716	0.455	26.27	44.55	24.44	89.139
Ash	0.685	0.733	30.83	47.80	28.52	95.541
Light-radial increment						
Beech	0.019	0.0007	15.81	0.743	19.65	1.485
Maple	0.014	0.011	27.21	0.886	32.02	1.773
Ash	0.011	0.036	44.16	1.518	36.26	3.037

Length growth refers to annual length increment, radial growth to radial increment (=annual ring width) of the stem axis 10 cm above ground, both as mean values of the last 5 years

S_0 and S_{60} are slopes of the curve at indirect site factor (ISF) = 0 and 60%, respectively; PI is the point of inflection (x -axis = ISF and y -axis = length or radial growth increment); ISF at 50% G_{\max} is the ISF value at 50% of the maximum length or radial growth; and A is the asymptotic length or radial growth at maximum light (60% ISF, a in Table 2)

of the three species, followed by maple with 27.2% light and 0.89 mm a^{-1} , and ash presenting the highest values with 44.2% light and 1.52 mm a^{-1} .

In this regard, as well as looking at the light level at which each species reached half of its maximal radial growth, the species differed more distinctly than in length growth. The growth pattern of beech, which is characterized by fairly low light values at the point of inflection and at the point of reaching half of the maximal growth rate (x -value of PI, and ISF at 50% G_{\max} , see Table 3), and by a relatively low asymptotic growth rate, was even more pronounced with radial growth than with length growth. In addition, the growth pattern of ash with its strong increase with light appeared more clearly in radial growth.

The response of maple's radial growth resembled beech, whereas terminal length growth was closer to ash. Looking at the high light values (at 60% ISF), maple reached a radial growth of 119% of the respective beech value, but ash showed more than double of beech (205%). This clearly differs from length growth with maple and ash reaching fairly similar rates of 167% and 179%, respectively, of the beech value.

Response of crown architecture to light

All three species extended *crown length and crown width* significantly ($p < 0.05$) with increasing light. Beech showed the longest and widest crown, maple the smallest and most slender for a given light level.

A linear regression with the natural logarithm of ISF as independent variable proved to be the best fit for all parameters to be described hereafter.

Live crown ratio (LCR) showed a weak, but only in the case of maple significant increase ($p < 0.05$) with light (Table 4, Fig. 3a). Significant differences between mean LCR values of all three species could be detected ($p < 0.05$, Scheffé-test), with beech showing the highest value (0.69), followed by ash (0.56), and maple (0.44) having the smallest.

In low light, the *ratio crown length/crown diameter (RCLD)* increased until 20–30% ISF for all species (steeply in maple, less in beech and ash), while in high light (ISF > 30%), it approached slowly a common asymptotic value (Fig. 3b). However, this trend proved to be significant only for maple (see Table 4). No significant differences between species mean values were detectable ($p > 0.05$, Scheffé-test). Maple seemed to be more responsive in this respect (the greatest slope: 0.28 and the largest range: 0.18–3.7) than beech (0.13 and 0.97–2.5) and ash (0.03 and 0.17–2.8).

The *angle of the inclination of the main stem to the vertical (SIV)* decreased significantly with increasing light: pronounced in beech, to a lesser degree in ash and weakly in maple ($p < 0.05$, Table 4 and Fig. 3c). The correlation with light proved to be fairly strong for beech ($R^2 = 0.55$), moderate for ash ($R^2 = 0.37$), and very poor for maple ($R^2 = 0.05$, Table 4).

The analysis of differences among species for the logarithmic fits led to a significant difference between beech and the other two species ($p < 0.05$, Scheffé-test), but not between maple and ash.

Slenderness coefficient (height to diameter ratio, H/D) decreased significantly with increasing light ($p < 0.05$, see Table 4 and Fig. 3d) in all species, stronger in ash and beech, and weaker in maple. A significant difference among species was found between beech and the other two ($p < 0.05$), whereas ash and maple did not differ significantly ($p = 0.59$, Scheffé-test). Across the entire light gradient beech showed the least slenderness, which can be seen as an indicator for higher stability against mechanical impacts like snowbreak.

The *length to basal area growth ratio (LBAR)* decreased significantly with light for all three species (see Table 4 and Fig. 3e). Beech tended to invest more in basal area under low light conditions, but differences between species were not significant.

Response of leaf characteristics to light

Total leaf area (TLA) showed a distinct response to increasing light availability, stronger in beech than in ash and maple (Fig. 4a). Significant differences among species were found between beech and the other two species

Table 4 Model parameters and statistics describing the relationships between light (ISF) and the following dependent variables: live crown ratio (LCR), ratio crown length/crown diameter (RCLD), main stem inclination to the vertical (SIV), height to diameter ratio (H/D), and length to basal area growth ratio (LBAR)

Model	Species	Regression model coefficients						R^2
		a	SE_a	p_a	b	SE_b	p_b	
LCR = $a + b \ln(\text{ISF})$	Beech	0.593	0.077	<0.01	0.034	0.025	0.18	0.04
	Maple	0.199	0.088	<0.01	0.084	0.029	<0.01	0.17
	Ash	0.464	0.089	<0.01	0.032	0.029	0.27	0.03
RCLD = $a + b \ln(\text{ISF})$	Beech	1.405	0.227	<0.01	0.131	0.074	0.09	0.08
	Maple	0.832	0.393	<0.05	0.286	0.129	<0.05	0.11
	Ash	1.721	0.311	<0.01	0.034	0.099	0.73	0.01
SIV = $a + b \ln(\text{ISF})$	Beech	37.124	3.521	<0.01	-8.023	1.168	<0.01	0.55
	Maple	15.496	3.827	<0.01	-1.924	1.264	0.14	0.05
	Ash	23.063	3.209	<0.01	-5.234	1.040	<0.01	0.37
H/D = $a + b \ln(\text{ISF})$	Beech	218.189	5.872	<0.01	-21.165	5.264	<0.01	0.29
	Maple	212.363	14.491	<0.01	-11.646	4.786	<0.05	0.13
	Ash	249.888	14.372	<0.01	-22.159	4.658	<0.01	0.34
LBAR = $a + b \ln(\text{ISF})$	Beech	2.357	0.439	<0.01	-0.419	0.145	<0.01	0.18
	Maple	3.385	0.431	<0.01	-0.693	0.142	<0.01	0.37
	Ash	3.273	0.443	<0.01	-0.704	0.142	<0.01	0.37

In all cases, the linear regression of the dependent variables to the natural logarithm of ISF produced the best fit

a, b coefficients of tested models; SE_a, SE_b the standard errors of determined coefficients

p_a, p_b testing of coefficients' significance (probability); R^2 coefficient of determination

($p < 0.05$, Scheffé-test). Beech possessed a higher total leaf area across the entire light gradient.

Mean leaf area (MLA) rose with increasing ISF with all species ($p < 0.05$, Table 5, Fig. 4b). Significant differences were found between all three species, with beech showing the smallest value, ash the largest and maple in between ($p < 0.05$, Scheffé-test). Ash had the most variable mean leaf area with a coefficient of variation of 44%, maple the least with 24% and beech an intermediate variability with 37%.

In all three species, specific leaf area (SLA) showed a similar, strong negative response to increasing light availability (Fig. 4c) with coefficients of determination between 0.74 and 0.81 (Table 5). The statistical analysis revealed a significant species effect ($p < 0.05$). Across the whole light gradient, beech had a significantly higher specific leaf area than maple and ash. The latter two species did not differ significantly (Scheffé-test).

Leaf area index (LAI) significantly increased with light in all species ($p < 0.05$, Table 5, Fig. 4d), but in comparison with TLA, this rise slowed down with increasing light and almost approached an asymptotic value. No significant differences among species were detected ($p > 0.37$, Scheffé-test).

With increasing light, the efficiency of leaf display (ELD) increased in a species-specific manner (Fig. 4e, Table 5). In beech, it rose steeply to $85 \text{ cm}^2 \text{ cm}^{-1}$ (at 60%

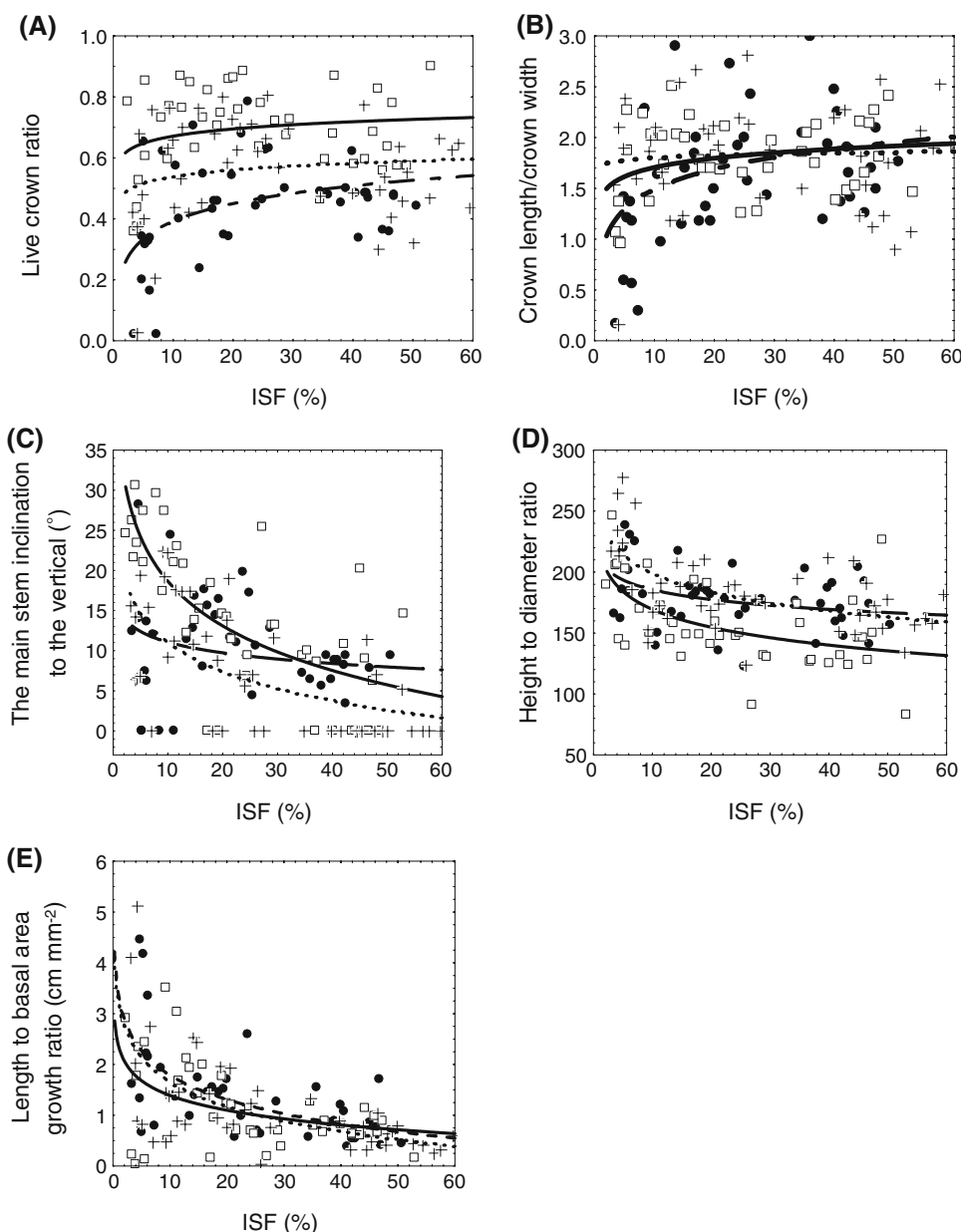
ISF) and exceeded the two other species across the entire light gradient. Next was ash with a clearly less steep rise up to $51 \text{ cm}^2 \text{ cm}^{-1}$, and least maple with a gentle rise and a maximum of $34 \text{ cm}^2 \text{ cm}^{-1}$. Mean values differed significantly between beech at one side ($49 \text{ cm}^2 \text{ cm}^{-1}$) and ash and maple at the other side (29 and $21 \text{ cm}^2 \text{ cm}^{-1}$, respectively; $p < 0.05$, Scheffé-test). The slope of the linear regression with the natural logarithm of ISF (see parameter b in Table 5) can be seen as a quantitative measure for the plasticity of this attribute. Beech exhibited the highest slope ($b = 29.08$), and surpassed ash ($b = 18.83$) and maple ($b = 11.63$).

Vertical distribution of leaf characteristics

The subdivision of the sapling crowns into five layers enabled us to look at the variability of some leaf characteristics within the crown. The light measures given above represented the light availability at the top layer (abbreviated as S5 in the following). From there to the bottom layer (S1), light availability decreased sharply, but unfortunately we cannot provide measured values.

Parallel to the above shown increase of MLA of the total crown with increasing light (Fig. 4b), we found a similar increase from bottom to top layer (Fig. 5a). Again this effect was more pronounced in ash and maple than in beech. Ash and maple leaves in the top layer were 6.4- and

Fig. 3 Scatterplots and fitted regression lines of live crown ratio LCR (a), crown length/crown diameter RCLD (b), main stem inclination to the vertical SIV (c), height to diameter ratio H/D (d), and length to basal area growth ratio LBAR (e), as a function of light (ISF). Beech (*open squares and solid lines*), maple (*solid circles and long-dashed broken lines*), ash (*crosses and short-dashed broken lines*)



8.9-fold larger than in the bottom layer, whereas in beech the increase was only 1.9-fold.

Specific leaf area clearly increased from the top layer to the bottom layer (Fig. 5b) which again paralleled the variation of the whole crown values along the light gradient (see Fig. 4c).

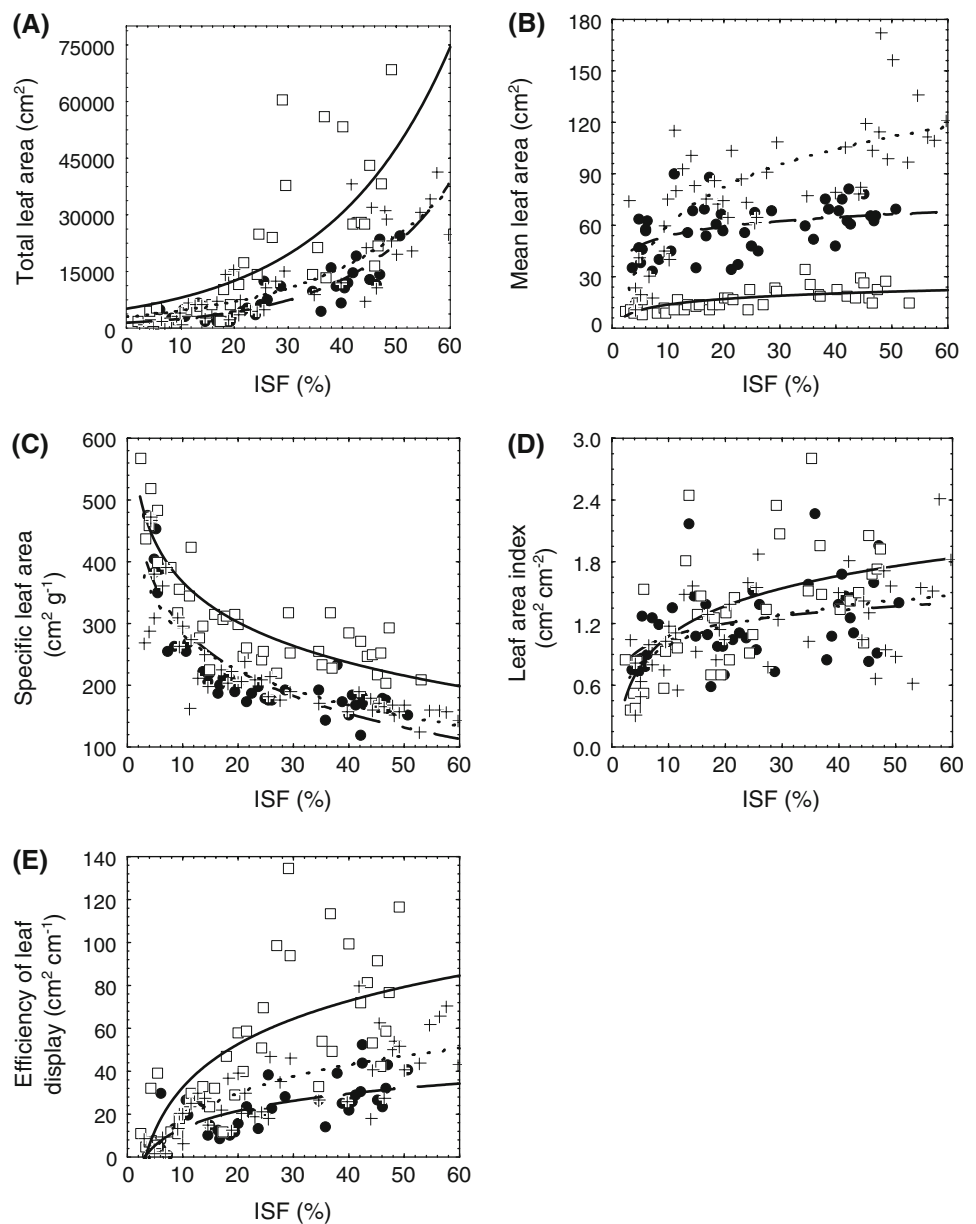
Beech displayed more than two-thirds of its TLA in the middle crown between 41 and 80% of tree height (37% in S4 and 31% in S3) and only 16% each at the top and at the two bottom layers. Maple and ash showed a pattern clearly different from beech, but without significant differences between them. Both species concentrated the majority of their TLA (ca. 85%) at the top of the crown above 60% of tree height, and only ca. 15% in the three bottom crown layers (data not shown).

In order to check whether the vertical distribution of MLA and TLA varied with the light availability above the sapling's crown, we formed two subsamples representing our darkest and our brightest conditions: (1) saplings with <12% ISF, and (2) saplings with >35%. These threshold values ensued from the distribution of light values (see Fig. 1) and our endeavor for getting a large as possible difference in light conditions and for having 12–15 saplings per species in each subsample.

Mean leaf area retained the same pattern in both light classes with all three species having bigger leaves at the top crown and increasingly smaller leaves along the way down to the bottom crown.

Looking at the allocation of TLA (Fig. 6), beech obviously kept its distribution pattern almost unchanged

Fig. 4 Scatterplot and fitted regression lines of total leaf area (a), mean leaf area (b), specific leaf area (c), leaf area index (d) and efficiency of leaf display (e), as a function of light (ISF). Beech (*open squares and solid lines*), maple (*solid circle and long-dashed broken line*), ash (*crosses and short-dashed broken line*)



under both light environments, i.e. it concentrated the leaf area in the middle crown. However, maple and ash changed their distribution pattern. Under low light, they displayed (Fig. 6a) the biggest part of their leaf area at the top of the crown (with ca. 60% more total leaf area in S5 as in S4) to optimize light capture, while under high light the maximal proportion was found in the second upper layer (S4) between 61 and 80% of tree height (Fig. 6b). Under both light conditions, maple and ash had very few or no leaves in the two lowest layers. This pattern clearly contrasts that of beech, which had 15–20% of its TLA in the two lowest layers under both light environments.

Discussion

Growth as a function of light

Length growth of all three species in our study significantly increased with increasing light availability, as observed in numerous studies (Röhrig 1966; Huss and Stephani 1978; Suner and Röhrig 1980; Schmidt 1996; Wagner 1999; Horn 2002; Ammer 2003; Lüpke von and Hauskeller-Bullerjahn 2004; Kunstler et al. 2005; Stancioiu and O'Hara 2006a). Some studies confirm the traditional expectation that shade-tolerant species exhibit higher growth rates under low light conditions, and lower growth rates in high light

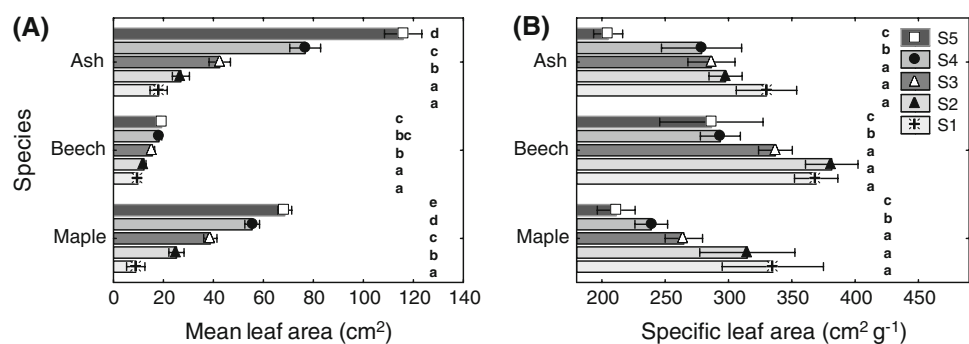
Table 5 Leaf characteristics in relation to light

Model	Species	Regression model coefficients						R^2
		a	SE_a	p_a	b	SE_b	p_b	
TLA = $a \exp(b \text{ISF})$	Beech	5,138.645	1,878.367	<0.01	0.045	0.009	<0.01	0.53
	Maple	1,423.215	413.593	<0.01	0.055	0.007	<0.01	0.75
	Ash	3,022.093	775.108	<0.01	0.042	0.005	<0.01	0.73
MLA = $a + b \ln(\text{ISF})$	Beech	2.966	2.551	0.25	4.695	0.846	<0.01	0.44
	Maple	35.513	7.777	<0.01	7.903	2.569	<0.01	0.19
	Ash	-13.918	12.359	0.27	32.099	4.006	<0.01	0.60
SLA = $a + b \ln(\text{ISF})$	Beech	584.329	23.772	<0.01	-94.235	7.951	<0.01	0.79
	Maple	524.908	23.829	<0.01	-100.58	7.811	<0.01	0.81
	Ash	470.676	23.147	<0.01	-81.959	7.502	<0.01	0.74
LAI = $a + b \ln(\text{ISF})$	Beech	0.103	0.264	0.70	0.423	0.089	<0.01	0.38
	Maple	0.652	0.220	<0.01	0.183	0.072	<0.05	0.14
	Ash	0.368	0.209	0.08	0.270	0.067	<0.01	0.29
ELD = $a + b \ln(\text{ISF})$	Beech	-34.493	13.148	<0.05	29.084	4.401	<0.01	0.53
	Maple	-13.332	5.073	<0.05	11.631	1.675	<0.01	0.54
	Ash	-26.439	6.463	<0.01	18.829	2.094	<0.01	0.65

Statistics are given for an exponential model in the case of total leaf area (TLA), and for logarithmic models in the cases of mean leaf area (MLA), specific leaf area (SLA), leaf area index (LAI), and efficiency of leaf display (ELD)

a , b coefficients; SE_a , SE_b standard errors of the respective coefficients; p_a , p_b probability of respective coefficients; R^2 coefficient of determination

Fig. 5 Vertical distribution of mean (a) and specific (b) leaf area on five vertical crown layers of equal widths (each 20% of tree height). *Box-plots* represent the mean values \pm SE. The significant differences between layers are marked by *letters* (Mann–Whitney U test, $p < 0.05$). *S1* is the lowest and *S5* the topmost layer

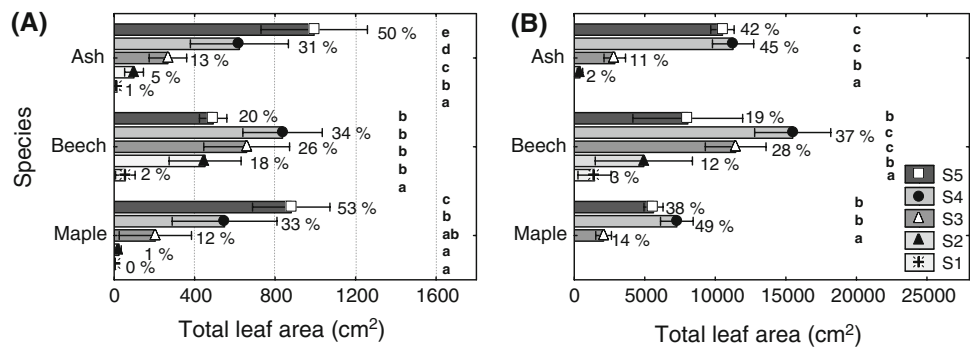


than shade-intolerant species (Pacala et al. 1994; Walters and Reich 1996; Gratzner et al. 2004 for most of their investigated species). In contrast, other studies have found that shade-intolerant species possessed higher growth rates at both low and high light conditions (Walters et al. 1993; Beaudet and Messier 1998). Our study supports these latter results. Even in deep shade, the shade-tolerant beech did not surpass ash and maple decisively in length growth. Under high light, it was considerably overtopped by the intermediate shade-tolerant ash and maple. This corresponds to results of Faust (1963), von Lüpke (1989), Schmidt (1996), and Petriřan et al. (2007) and corroborates the classification of ash and maple as gap specialists, having a strategy of preferentially favoring height growth,

by which they can win and maintain a dominant position relative to their neighbors and can reach the overstory before gap closure occurs (Runkle and Yetter 1987).

Under constantly low light conditions, like for instance beneath a closed overstory canopy, gap specialists incur the risk of investing much of their resources in height growth without gaining more light. Finally, they might die because of starvation (Messier et al. 1999). In contrast, shade-tolerant species can survive long periods in deep shade by strongly reducing their height growth (Messier et al. 1999). This corresponds with our findings of the first study (Petriřan et al. 2007), where we showed that the less tolerant species ash and maple had a higher mortality in low light than beech.

Fig. 6 Vertical allocation of total leaf area (absolute and relative values) into five crown layers (as in Fig. 5) under low light (<12% ISF) (a) and high light (>35% ISF) (b). Box-plots represent the mean values ± SE. The significant differences between layers are marked by letters (Wilcoxon-pair test, $p < 0.05$). S1 is the lowest and S5 the topmost layer



Response of plant crown architecture to light

Within the same light environment, shade-intolerant species should have lower LCR (Canham et al. 1994), as their lower branches are less able to use efficiently light and will die. In our study, beech as the most shade-tolerant species had the highest LCR along the entire light gradient, which can be interpreted as high tolerance to self-shading. This agrees with findings of Bonosi (2006) for the same species, and of Messier and Nikinmaa (2000) for sugar maple. With changing light, we found the greatest variation of LCR in maple, by this exhibiting the greatest plasticity in this trait, which concurs with Bonosi (2006).

Under limiting light conditions, a growth strategy that promotes lateral crown expansion and by this a decrease of the RCLD might be favorable in enabling saplings to minimize self-shading and to improve light interception (Canham 1988). A tendency to broader crowns in shade and no significant differences between species, which Beaudet and Messier (1998) and Stancioiu and O’Hara (2006b) reported, agrees with our results. Maple exhibited the highest plasticity in this trait with the smallest vertical crown extension in deep shade and a concentration of branches and leaves at the top, forming more pronounced ‘umbrella’ like crowns than beech and ash.

Another way to improve light capture under shade can be seen in an increased SIV or *plagiotropy* value (Kunstler et al. 2005). As in previous studies (Schmitt et al. 1995; Wagner 1999; Horn 2002; Stancioiu and O’Hara 2006b), beech exhibited the most pronounced plagiotropy in low light. Stem inclination of maple remained more or less unaffected in different light environments. Ash responded significantly like beech, but with generally lower absolute values.

Corresponding to results of Chen and Klinka (1998), Chan et al. (2002) and Gratzner et al. (2004), H/D decreased for our species with increasing light availability. Beech presented the smallest values in most cases with a mean of 156, while the two other species possessed higher values with means of 178 for maple and 184 for ash. This result concurs with work of Beaudet and Messier (1998) who

found that shade-tolerant species (sugar maple and American beech) had lower slenderness indexes than less shade-tolerant yellow birch. Nüsslein (1995) found for our species similar values in thicket stands in North-Bavaria.

Length to basal area growth ratio (LBAR) reached the highest values under low light and decreased with increasing light in all three species. It means that with decreasing light length, growth was increasingly favored at the expense of lateral growth. This is in accordance with the general hierarchy of allocation of photosynthates with increasing shortage of resources, which attributes the least priority to diameter growth of stem and branches (Oliver and Larson 1996). In low light conditions, diameter growth will be reduced first, and only after that length growth (Kimmins 1997). This reaction was more pronounced in our two less shade-tolerant species. Beech could thus maintain relatively stronger axes in decreasing light which can be taken as an important prerequisite for leaf display and efficient light interception. This agrees with the opinion of Messier et al. (1999) that shade-tolerant species are better able to modify their shoot morphology to improve light interception in shaded environments by reducing or almost stopping their height growth.

To sum up, we can say that maple showed the greatest plasticity in crown shape (LCR and RCLD). Regarding the investment in vertical versus lateral growth (H/D and LBAR), ash possessed the greatest plasticity, which qualified it as a typical gap species. Beech in turn had the greatest plasticity in attributes which improve leaf display in shade, like plagiotropy (SIV) or a sturdier leaf support system (stem and branches, H/D and LBAR).

Leaf characteristics

Leaf area is generally considered to play a key role, as it is the main attribute controlling light interception (Bartelink 1997).

Total leaf area increased significantly with increasing light (and concomitantly with size) in all three species. Contrary to Bonosi (2006), in our study beech possessed a significantly greater TLA than ash and maple across the

entire light range despite smaller mean leaf area of single leaves. However, a comparison with the results of Bonosi is impeded by his study design that included different size and light ranges of the investigated species.

Looking at the vertical distribution of TLA within crowns across the whole light gradient, we found species-specific patterns, with beech displaying more than two-thirds of its TLA in the middle crown and maple, and ash, the great majority of their TLA at the top crown. This general pattern varied with light intensity in a species-specific way. While beech remained more or less unaffected, the less shade-tolerant ash and maple concentrated strongly their TLA at the tree top in deep shade. By this, light interception could be adapted to the sharp decrease in light intensity from tree top to bottom crown under these shady conditions (Niinemets 1996; Messier and Nikinmaa 2000; Voß 2005). Under bright conditions (35–60% ISF), ash and maple showed a changed distribution pattern with a greater proportion of TLA in lower crown layers. However, most leaf area is still displayed within the top two crown layers with a concentration in the second layer. This agrees with the observation of Voß (2005) in sessile oak saplings.

Mean leaf area increased with light in all three species. This corresponds with results of Beaudet and Messier (1998) and partially with those of Voß (2005). The vertical distribution of MLA within crowns confirms the positive effect of light on MLA of our species which is in agreement with results of Voß (2005) for sessile oak and of Paquette et al. (2007) for black cherry, *Quercus rubra* and sugar maple. Similar to Paquette et al. (2007), we found that our less shade-tolerant species showed a greater reduction of MLA from tree top to bottom crown than beech.

Higher specific leaf area under shadier conditions increases the efficiency of light interception by maximizing the leaf area per unit leaf biomass (Walters et al. 1993; Minotta and Pinzauti 1996; Niinemets 1996; Bartelink 1997; Beaudet and Messier 1998; Niinemets and Kull 1998; Messier and Nikinmaa 2000; Barthod and Epron 2005; Kunstler et al. 2005; Voß 2005; Bonosi 2006; Stancioiu and O'Hara 2006b). With increasing light availability, SLA of our three species decreased significantly, both across the overstorey light gradient and from tree top down to crown base.

Regarding the relationship between SLA and shade tolerance, some investigations (Chen et al. 1996; Niinemets and Kull 1998; King 2003; Barthod and Epron 2005; Kunstler et al. 2005; Bonosi 2006; Klooster et al. 2007) found that the higher the shade tolerance rank of the species, the more pronounced SLA increase. Others did not confirm this trend (DeLucia et al. 1998; Beaudet and Messier 1998; Stancioiu and O'Hara 2006b). Our findings support the first tendency, that shade-tolerant species have higher SLA values than less shade-tolerant ones.

We used two indexes, *leaf area index* and *efficiency of leaf display*, to describe how efficiently our species displayed their leaves. Both indexes increased significantly with light availability in all three species, which corresponds to findings of Beaudet and Messier (1998) and Paquette et al. (2007). Looking at the differences between species, Paquette et al. (2007) found that very shade-tolerant species had a significant greater LAI than less shade-tolerant species. But like Beaudet and Messier (1998), we could not detect significant differences between our species. Only a tendency appeared with beech, having a higher mean LAI (1.3) than maple (1.19) and ash (1.18), which indicates a greater ability of beech in tolerating self-shading.

Regarding the ELD per unit height, we observed significant differences between beech on one side and ash and maple on the other side. The two less shade-tolerant species showed clearly lower values than beech, both in shade and in high light, which agrees partly with findings of Beaudet and Messier (1998). All together, in our study beech showed a greater plasticity in leaf display and its efficiency than ash and maple.

Silvicultural conclusions

The results of this study support the silvicultural conclusions of the companion study (Petriřan et al. 2007), but now on the basis of a more thorough growth analysis including a wider light gradient up to about 60% ISF. The previous statement was confirmed in that more than 20% ISF is required to provide a clear lead in annual height growth for ash and maple in a natural regeneration of about 6–8 m top height. This height lead is needed to make provision for the decreasing growth of maple and ash beyond the pole stage, and for the constantly increasing height growth of beech (Züge 1986). As a long-term consequence, ash and maple may be reduced in numbers or even eliminated under shade with less than 20% ISF, a development which is greatly enforced in competition with beech.

The knowledge of how different the species respond to light is important for forest managers in controlling light conditions in accordance with the silvicultural goals. On the basis of the current results, we confirm the proposal of the companion study. It aims at regenerating stands which contain beech, ash and maple in significant proportions in the final overstorey. One promising way to reach this goal includes the following steps: The regeneration should start with a fairly dense shelterwood providing 5–10% of above canopy light at the forest floor. These dark conditions facilitate the establishment of beech, but ash and maple are able to regenerate as well. After having reached a well-established beech regeneration, which satisfactorily meets the silvicultural goal, the canopy should be opened in a way that provides sufficient light for a height growth lead

of maple and ash over beech. According to our results, this can be attained by at least 20–30% light above the regeneration layer. Following the rules of continuous-cover silviculture, this is best achieved by means of an irregular group selection cutting, because it creates heterogeneous light conditions which can satisfy the demands of ash and maple at open places with 20–30% ISF, while beech grows well everywhere. Thereafter, the gradual canopy opening should be continued mainly by enlarging the groups to ensure sufficient light for the necessary height lead of ash and maple.

Regarding stem quality, another practical conclusion can be derived from the observation that under light conditions below about 25% ISF, beech showed higher values of plagiotropic growth than ash and maple. For beech, this agrees with findings of Stancioiu and O'Hara (2006b), who reported frequent occurrence of plagiotropy below this light value, accompanied by poorer stem quality with more forked and crooked saplings. von Lüpke (2005) suggested in this regard a threshold light value of about 15% ISF. Thus, to meet a greater risk of poor stem forms in beech we suggest avoiding light conditions below 15–25% ISF for longer periods in advanced regeneration stages with top heights of more than 6–8 m.

Acknowledgments We thank Ulrike Westphal, Michael Unger and Martina Knaust from the Institute for Silviculture for their help with collecting the field data and performing the lab work. Two anonymous reviewers gave valuable advice for writing the manuscript.

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