Crown Allometry and Growing Space Efficiency of Norway Spruce (*Picea abies* [L.] Karst.) and European Beech (*Fagus sylvatica* L.) in Pure and Mixed Stands

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Abstract: In pure and mixed stands of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) we have analyzed crown allometry and growing space efficiency at the tree level and have scaled this from tree level to stand level production. Allometry is quantified by the ratio A between the relative growth rates of laterally and vertically oriented tree dimensions. Efficiency parameters, EOC for efficiency in space occupation, EEX for efficiency in space exploitation, and EBI for efficiency in biomass investment, were evaluated, based on quantity and quality of growing space and were measured using crown size and competition index. The evaluation reveals why pure stands of spruce are preferred by foresters, even though the natural vegetation would be dominated by beech. Spruce occupies its share of resources intensively by means of tightly packed pillar-like crowns, whereas beech seizes resources extensively by means of a multi-layered, veil-like canopy. With a given relative biomass increment, beech achieves a 57% higher increment in crown projection area and a 127% higher increment in height due to its particular capacity of lateral and vertical expansion. Beech trees are approximately 60% more efficient in space occupation than spruce trees, however, on average, they are about 70% less efficient in space exploitation. As a vertical fast growing tree, spruce is efficient in space exploitation under constant conditions, but far more susceptible to disturbances and less well equipped to overcome them when compared with beech. Beech is weaker in terms of space exploitation, while being superior in space occupation, where it encircles competitors and fills gaps after disturbances, which is a successful long-term strategy. A mixture of the two species reduces stand level production by 24% in comparison to a pure spruce stand, however, when considering enhanced stabilization of the whole stand and risk distribution in the long term, the mixed stand may exceed the production level of pure spruce stands. EEX reflects a strong ontogenetic drift and competition effect that should be considered when scaling from tree to stand level production.

Key words: Crown allometry, growing space efficiency, Norway spruce, European beech, mixed stand, competition index, scaling from tree to stand level.

Introduction

The vigour of trees and stands is usually rated in terms of the biomass growth per area unit, which is referred to as growing space efficiency (Assmann, 1961; Mayer, 1958; Sterba and Amateis, 1998). This approach is rather anthropocentric and well adapted to tell more from less productive species within a given growth period (Körner, 2005; Webster and Lorimer, 2003). Growing space efficiency, however, is not suited to assess a species' long-term performance regarding vigour, production, and reproduction. Norway spruce trees – as for many gymnosperms – invest biomass mainly in their central trunk (Niklas, 1994, p.173–174). Spruce trees are packed more tightly together and occupy less growing space than angiosperms such as European beech. Therefore, on many sites, spruce trees are considerably more efficient in utilizing growing space (Kennel, 1965; Petri, 1966). However, efficient growers, such as Norway spruce, may not be part of a natural plant community and may not be strong competitors on a particular site. On many sites in the flatlands of Central Europe spruce achieves superior growing space efficiency only if it is established artificially and tended by silviculturists (Kölling et al., 2005). Despite its superior growing space efficiency, spruce would be out-competed by European beech under natural conditions (Lüpke and Spellmann, 1999). Obviously, inefficient growers in terms of growing space efficiency must have traits to outcompete the fast growers, when a stand is not maintained by foresters.

Low growing space efficiency of a species due to its lateral crown expansion and space consuming can lead to success under a disturbance regime and during the regeneration phase. For example, beech is less efficient in growing space exploitation due to its high biomass investment in space-consuming horizontal branches, but somehow it is omnipresent in the canopy and always ready to fill and utilize gaps in the canopy after disturbances (Leuschner, 1998). Therefore, we note a trade-off between a species' efficiency in terms of growing space occupation and growing space exploitation. While the latter trait is useful to out-compete other species under steady-state conditions, the former has advantages when disturbance events take place, such as wind throw, ice breakage, and bark beetle attacks (Dhôte, 2004). In a changing and unpredictable environment, foresters frequently combine both strategies – highly efficient, strictly vertical growers with less efficient, more lateral growers – in mixed stands. However, to
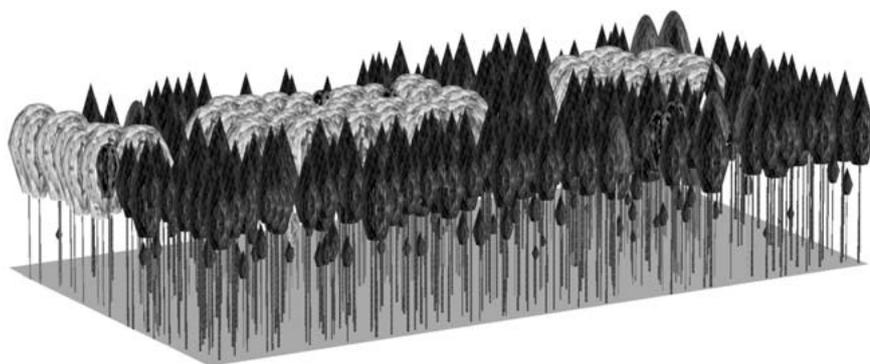
Table 1 Characteristics (n = sample size, mean = arithmetic mean, SDev = standard deviation) of sample trees categorized by species (survey in autumn 1994). Abbreviations: d = diameter at breast height, h = tree height, w = aboveground biomass, p = crown projection area, CI = competition index, Δd = mean annual diameter increment, Δh = mean annual height increment, Δw = biomass increment, Δp = increment of crown projection area

Attribute/unit	Age (y)	d (cm)	h (m)	w (kg)	p (m^2)	CI –	Δd (cm y^{-1})	Δh (m y^{-1})	Δw (kg y^{-1})	Δp (m^2 y^{-1})
Norway spruce										
n	4	252	41	252	104	252	252	41	252	104
Mean	42	24.9	25.0	311.9	13.1	1.4	0.4	0.2	16.8	0.7
SDev (±)	2	7.8	2.2	239.0	5.9	1.4	0.3	0.2	16.2	0.7
European beech										
n	4	142	41	142	79	142	142	40	142	79
Mean	52	20.7	23.4	301.5	23.1	3.3	0.2	0.3	10.0	0.6
SDev (±)	4	7.4	1.5	256.9	19.5	3.9	0.2	0.3	13.4	1.7

take advantage of different species' strategies in mixed stands, we need to understand their individual traits (Mielikäinen, 1985).

In order to reveal their individual traits and solve the contradiction between occupation and exploitation of growing space, we have analyzed an unmanaged middle-aged stand of spruce and beech in South Germany. The proportion of spruce and beech in German forests amounts to 50%. More than 10% of forests currently contain a mixture of spruce/beech, and this is increasing due to transformation from pure to mixed stands. The analyzed stand "Kranzberg Forest" is the central experiment of SFB 607 (Matyssek et al., 2002) and part of a six-plot chronosequence (Pretzsch et al., 1998). The following set of parameters was examined:
1. Allometry of crown form at tree level,
2. efficiency in space exploitation, space occupation, and biomass investment at tree level,
3. efficiency parameters at stand level, and
4. up-scaling from tree to stand level production.

This report is focused on the growth period between 1994 and 1999, before O$_3$ fumigation was started in 2000, and CO$_2$ pulse emission in 2005. It serves as the baseline for forthcoming reports on the impact of fumigation on tree and stand level production in "Kranzberg Forest".

Materials and Methods

Study area

The approximately 60-year-old mixed spruce/beech stand FRE 813/1 (11°39′42″E, 48°25′12″N) is located in the ecological region "Oberbayerisches Tertiärhügelland" in South Bavaria near Freising, 35 km northeast of Munich. The stand is situated 490 m above sea level with an north-facing inclination of 1.8°C. Mean annual temperature is 7.0 to 7.5°C and precipitation 730 to 890 mm per annum. The corresponding temperature and rainfall during the vegetation period were 14.0 to 15.0°C and 410 to 520 mm. The prevailing parabrown soil, based on loess, tends to pseudo-gley. Natural vegetation would be a *Galio-odorati-Fagetum,* dominated by European beech.

The 0.5-ha plot comprises parts where the considered species occur in pure or mixed stands (Fig. **1**). The following characteristics reflect the site's outstanding growing conditions and refer to the total stand (Norway spruce, European beech) at the beginning of the analyzed period in 1994: 876 (540, 336) trees ha^{-1}, mean height 23.6 m (24.1 m, 22.9 m), quadratic mean diameter 23.4 cm (25.0 cm, 20.9 cm), volume of growing stock 452 m^3 ha^{-1} (319 m^3 ha^{-1}, 133 m^3 ha^{-1}), volume increment 22.0 m^3 ha^{-1} y^{-1} (17.5 m^3 ha^{-1} y^{-1}, 4.5 m^3 ha^{-1} y^{-1}). Volume indicates merchantable wood above 7 cm in diameter at the thinner end. For further information, see Table **1** and Pretzsch et al. (1998).

Measurements at tree and stand level

In autumn 1994, the 0.5-ha plot was inventoried for the first time. Tree age was determined by ring analyses from increment cores, stem co-ordinates were measured by theodolite (LEICA TC500), diameter at breast height utilized girth tapes, tree height and height of the crown base were measured with a clinometer (LEDHA GEO), and 8 crown radii per tree (N, NE, …, SW) were measured using an optical plumbing instrument, type biritz + hatzl™. This standard procedure was repeated in autumn 1999 and is described in detail by Pretzsch (2002, pp. 85–97). As in 1994, only co-ordinates, diameters, and crown radii were measured completely and all other features were recorded by sub-sampling n trees per variable (Table **1**).

Mean values and standard deviation of diameter and crown projection area are based on 100 recordings, whereas fewer height measurements were taken. Calculation for the crown projection area $p = \bar{r}^2\pi$ is based on the quadratic mean radius

$$\bar{r} = \sqrt{(r_1{}^2 + r_2{}^2 + \ldots + r_8{}^2)/8}.$$

Crown extension is required for evaluation of the tree competition index and was calculated by species-specific crown shape functions, depending on crown length and crown radius (Pretzsch, 2002, p. 208). For the latter evaluation, we derived tree height, h, and height of crown base, hcb, for trees via regression using $h = 1.3 + (0.3092 + 1.0829/d)^{-3.0}$ and $hcb = -0.0059\,d^2 + 0.4513\,d + 3.8195$ for spruce, and $h = 1.3 + (0.3423 + 0.3538/d)^{-3.0}$ and $hcb = -0.0263\,d^2 + 1.2151\,d$ for beech. For biomass estimation "w", we applied allometric functions for spruce $w = 0.044\,d^{2.659}$, and for beech $w = 0.114\,d^{2.503}$ which had been developed elsewhere (Grote et al., 2003; Pretzsch, 2005a). Biomass increment Δw is the difference between the two successive surveys, divided by a period length of 5 years ($\Delta w = [w_{1999} - w_{1994}]/5$). According to the specific function, we chose optimal subsets from the database, which comprised the maximum of available measurements for the particular relationship (Table **1**). For scaling from tree to stand level production, we select a 440-m² subplot with pure spruce, a 324-m² subplot with pure beech, and a 900-m² mixed spruce-beech subplot.

Detection of biomass allocation and crown allometry

The allocation of absorbed resources within an organism can be described by the allometric relationship between y and x:

$$\frac{dy/y}{dx/x} = A, \tag{1}$$

where dy, dx = increment, y, x = body size of y and x, and A = allometric coefficient. The latter represents the relationship between relative growth rate of a defined organ "y" and the relative growth rate of any other body part or of the entire body. The physiological interpretation of Equation (1) is that allocation of resources depends on the current size of the organs and A is the distribution key between organs y and x (Bertalanffy, 1951, pp. 311–315). For example, if A = 1.5, a 1% increase in x is coupled with a 1.5% increase in y. The integral of Equation (1) is $y = kx^A$, where k is the integration constant and exponent A is the allometric coefficient. The latter describes the slope of $\ln(y) = \ln(k) + A\ln(x)$, when plotted on a ln-ln scale. The value pairs y_i, y_{i+1}, and x_i, x_{i+1} from consecutive surveys of the plots are used to calculate the proportion of matter allocation between y and x in specific periods:

$$A = \frac{\ln(y_{i+1}) - \ln(y_i)}{\ln(x_{i+1}) - \ln(x_i)} = \frac{\ln(y_{i+1}/y_i)}{\ln(x_{i+1}/x_i)}. \tag{2}$$

Equation (2) is used for scrutiny of allocation patterns of Norway spruce and European beech in terms of: p = crown projection area, w = aboveground biomass, h = tree height, d = diameter at breast height, b = diameter of crown. The ratios $A_{p,w} = \ln(p_2/p_1)/\ln(w_2/w_1)$, $A_{h,w} = \ln(h_2/h_1)/\ln(w_2/w_1)$, and $A_{d,w} = \ln(d_2/d_1)/\ln(w_2/w_1)$ reflect the tendency of the trees to combine a given relative biomass growth with lateral crown expansion, height growth, or diameter growth. The higher the values of $A_{p,w}$ or $A_{h,w}$, the more pronounced is the ability to expand laterally and vertically, and vice versa. The ratios $A_{h,d} = \ln(h_2/h_1)/\ln(d_2/d_1)$ and $A_{b,d} = \ln(b_2/b_1)/\ln(d_2/d_1)$ also indicate the respective horizontal and the vertical expansion capacity. In these cases, however, relative diameter growth is the denominator.

Ratios for growing space efficiency

Efficiency parameters define biomass or growth with reference to available resources. While biomass or growth are easily evaluated from successive inventories, resources R, which are available to and utilized by a tree, are difficult to measure directly in an adult forest stand. Instead, growing space is used as a surrogate for R. Common approaches quantify growing space in terms of crown projection area (Assmann, 1961; Sterba and Amateis, 1998; Webster and Lorimer, 2003).

In order to examine the species space sequestration in a given period, we used the following parameters: p = crown projection area at the beginning of a growth period (in m²), w = aboveground tree biomass at the beginning of a growth period (in kg), and $\Delta w = w_2 - w_1$ mean annual biomass increment in the respective growth period (in kg) for evaluation of the

efficiency in space occupation
$$EOC = p/w, \tag{3}$$

efficiency in space exploitation
$$EEX = \Delta w/p, \text{ and} \tag{4}$$

efficiency in biomass investment
$$EBI = \Delta w/w = EOC\,EEX. \tag{5}$$

In order to distinguish between efficiency parameters EOC, EEX, EBI (Formulas 3 to 5) for tree and stand level, we refer to the latter in the "Results" section as EOC_{Stand}, EEX_{Stand}, EBI_{Stand} (Formulas 8–10; Table **5**). Even though the complete evaluation was also undertaken for efficiency parameters related to crown volume c (in m³) and growing space, according to volume s of the imaginary cube with basal p and height h ($s = p \cdot h$, in m³), the subsequent report is restricted to area-related parameters (EOC). The efficiency parameters calculated on the basis of crown volume c and growing space s did not contribute further insights or provide answers to the questions raised.

Quantification of inter-tree competition

The quantification of the multivariate resource supply, R (light, nutrients, water, etc.), merely by the surrogate variable "crown projection area" seems to be questionable. Especially in approaches to multi-layered stands, which only use the size of the projection area, and are hardly representative of R. For example, the fact that sunlight does not come vertically from above but is absorbed or modified when passing through canopy layers, calls two-dimensional concepts into question. If R can be quantified by growing space approaches, then the crown position in the canopy (access to light) should be considered in addition to its occupied area.

In order to quantify the vertical aspect of access to resources, we have applied the competition index concept, which is frequently used in individual tree models to quantify inter-tree competition for each tree (Bachmann, 1998; Biging and Dobbertin, 1992; Pretzsch, 2002, pp. 264–274). Competition index CI (Formula 6) is calculated in two steps: determination of competitor trees and actual determination of relative competition. The competitors of a particular tree are identified from the application of a virtual reverse cone (Fig. **2**). The axis of this cone is equal to the tree axis and its vertex is placed within the crown of the tree. The relative height within the crown and the angle of the vertex are species-specific. Any tree whose apex is inside this virtual cone is regarded as a competitor. For any competitor, the angle between the insertion point of the cone and the top of the competitor tree is determined. This angle is weighted by the relation between the crown cross-sectional areas (CCA) of the competitor and the respective tree. These areas are calculated according to the respective crown models (Pretzsch, 2002, p. 208), either at the height of the cone vertex, where the cone vertex is above the maximum crown width, or in the height of maximum crown width, if the vertex is below. In addition, the angle β is also multiplied by a species-specific light transmission coefficient, according to Pretzsch (2001, p. 220). The competition index is defined as the sum of all competitor contributions

$$CI_i = \sum_{j=1}^{n} \beta_j \cdot \frac{CCA_j}{CCA_i} \cdot TM(j) \tag{6}$$

where CI_i = competition index for tree i, β_j = angle between cone vertex and apex of competitor j, CCA_j, CCA_i = crown cross-sectional area of trees j and i, respectively, TM_j = species-specific light transmission coefficient for tree j, n = number of competitors of tree i.

Model for analysis of crown efficiency

Both variables p and CI are applied as independent variables in a model that elucidates the dependency of crown efficiency from lateral expansion and vertical position of a crown. Space occupation efficiency, EOC, is analyzed by species, depending on crown size p and competition index CI using the equation

$$\ln(EOC) = a + b\ln(CI+1) + c\ln(p). \tag{7}$$

Efficiency in space exploitation, EEX, and biomass investment, EBI, are scrutinized in the same way. The addition of 1.0 to CI values prevents the term $\ln(CI+1)$ from becoming undefined when CI = 0. The antilogarithm of Equation 7 (EOC =
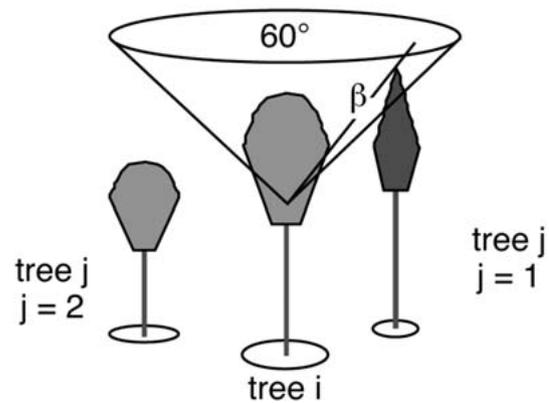

Fig. 2 Principle for determining competitors for calculation of the competition index, CI (adapted from Pretzsch, 2002, p. 219).

$e^a [CI+1]^b p^c$) reveals an allometric relationship between efficiency parameters and tree attributes implied in the Results section for scaling from tree to stand level. For this and all subsequent evaluations we apply SPSS (Version 11.5).

Results

Allocation pattern and allometry of Norway spruce and European beech

For the considered period from 1994 to 1999, Fig. **3** displays the allometric relationship between increment of crown projection area and increment of biomass (above) and height increment and increment of biomass (below) in a ln-ln grid. The straight lines serve as a reference and display the expected allometry under geometric similarity ($A_{p,w}$ = 2/3, $A_{h,w}$ = 1/3, respectively). Both species show an unambiguous deviation from geometric similarity and tendency to lateral expansion. However, beech (right) exceeds spruce in this tendency and shows greater variation (left). Allometry $A_{h,w}$ is closer to geometric similarity but, again, beech differs from spruce in its propensity to achieve considerable height increment with a relatively low biomass input. Fig. **3** (left) reflects steep slopes for small-sized spruce trees, however, it also shows a remarkable flattening of the slope for dominant trees with high growth rates. For beech, in comparison, Fig. **3** (right) has steep slopes for all sizes and growth rates, and reflects European beech's ability to occupy space efficiently by vigorous lateral and vertical crown expansion. Comparison with the reference line for similarity with intercepts 0.5 to 2.5 underlines the trend in beech to higher variation and steepness.

The allometric parameter A reflects the trees' tendency to alter shape. Ratios $A_{p,w}$ and $A_{h,w}$ of beech are about 57% and 127%, respectively, higher than for spruce and provide evidence for beech's higher capacity to expand the crown laterally or vertically (Table **2**). The same applies for the ratios of $A_{h,d}$ and $A_{b,d}$; beech exceeds spruce by, respectively, 143% and 56%. In all cases, the value of A for spruce is significantly different from that of beech.
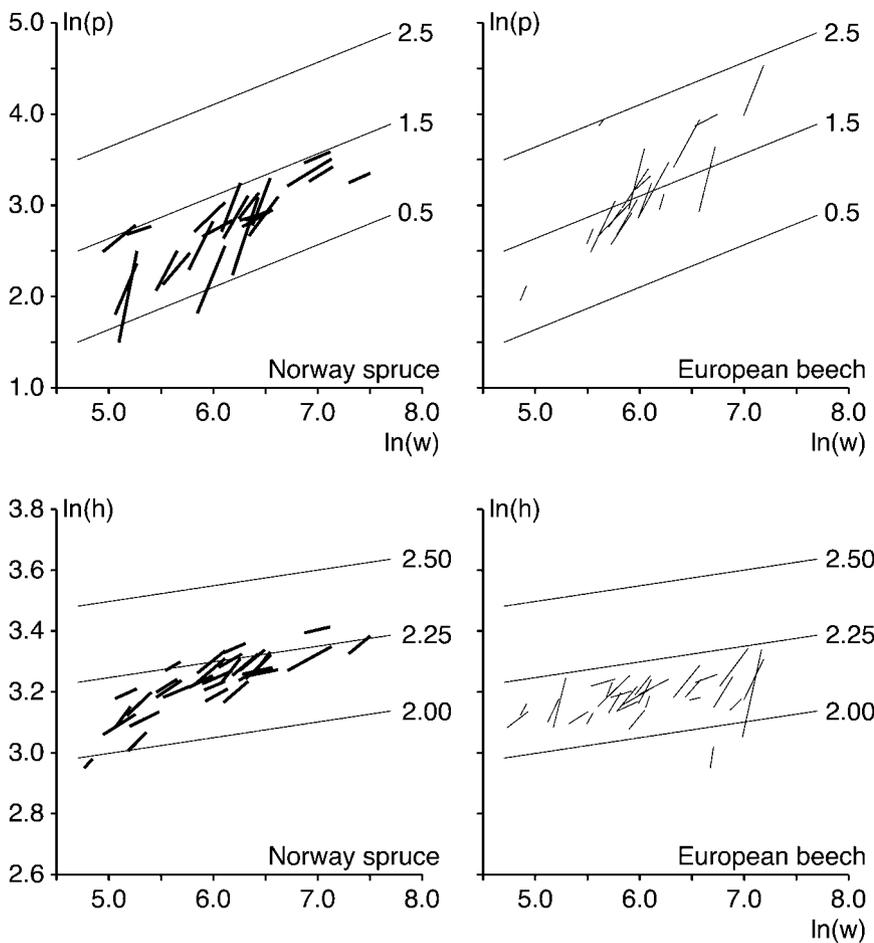
Fig. 3 Allometric relationship between increment of crown projection area Δp and biomass Δw (above) and increment of height Δh and biomass Δw (below) for Norway spruce (left) and European beech (right) in a ln-ln grid (for the growth period 1994–1999). Straight lines $\ln(p) = k' + 2/3 \ln(w)$ (above) and $\ln(h) = k' + 1/3 \ln(w)$ (below) with $k' = 0.5...2.5$ are the expected allometry under geometric similarity ($A_{p,w} = 2/3$, $A_{h,w} = 1/3$).

Growing space efficiency of Norway spruce and European beech

In order to display the effect of both quantity and quality of growing space on the efficiency parameters (Equations [3]-[5]), we placed the 104 trees of spruce and 79 trees of beech in a 3 × 3 matrix, depending on crown size and competition index (Table **3**). Size classes were $p < 10\,m^2$, $10-16\,m^2$, $> 16\,m^2$ and CI classes were CI < 1, 1 – 2, CI > 2.

A comparison of overall mean values of EOC (Table **3**, bold numbers) between spruce (0.069 $m^2\,kg^{-1}$) and beech (0.108 $m^2\,kg^{-1}$) shows that the latter develops, on average, 57% more crown projection area with the same amount of biomass. Beech increases its intrusion concerning EOC especially in the upper canopy where there is good access to resources. On the other hand, EEX of spruce (1.321 kg m^{-2} y^{-1}) is about three times the EEX of beech (0.425 kg m^{-2} y^{-1}). EEX is maximal when trees have small crowns and CI is low. With increasing p efficiency in space exploitation by spruce and beech, it decreases considerably. Despite differences in crown size, EEX diminishes even more steeply with competition. EBI multiplied by 100 represents the percentage of biomass increment, which amounts to 5.0% and 2.8%, on average, for spruce and beech, respectively. Thus, spruce achieves approximately twice the efficiency in biomass investment to beech, and this relation

between the species persists in all strata (Table **3**). EBI decreases clearly from small to tall crowns and from trees with good access to light to those having reduced access to light.

Modelling crown efficiency of Norway spruce and European beech

Table **4** and Figs. **4,5** display the relationships between the considered crown efficiency parameters and tree attributes CI and p. EOC increases when crown projection area and competition increase. Spruce trees and beech trees in the understorey (CI = 2.5) occupy considerably more growing space for a given amount of biomass than dominant trees (CI = 0.5) of the same size. While this tendency is similar for both species, their level of EOC and range of crown size differs considerably. Spruce trees with small crowns are more efficient than beech trees of the same size. However, this apparent superiority of spruce is not relevant at the stand level. Solid parts of the curves in Fig. **4** represent the ranges covered by the observations and show that spruce trees dominate in small size classes with low EOC values, whereas beech trees achieve twice the size of spruce trees and achieve high EOC values.

Table 2 Comparison of allometric coefficients $A_{y,x} = \ln(y_{i+1}/y_i)/\ln(x_{i+1}/x_i)$ of individual trees for Norway spruce and European beech. Based on the successive surveys in 1994 and 1999, the relations $p \propto w^A$, $h \propto w^A$, $d \propto w^A$, $h \propto d^A$, and $b \propto d^A$ are analysed. p = crown projection area, w = biomass, h = height, d = tree diameter, and b = crown diameter

	$A_{p,w}$	$A_{h,w}$	$A_{d,w}$	$A_{h,d}$	$A_{b,d}$
Geometrical similitude	0.66	0.33	0.33	1.00	1.00
Norway spruce					
n	23	24	26	24	22
Mean	1.42	0.22	0.37	0.60	1.81
SE (±)	0.22	0.02	0.01	0.06	0.28
European beech					
n	19	23	28	24	19
Mean	2.23	0.50	0.40	1.46	2.82
SE (±)	0.28	0.08	0.01	0.27	0.35
Norway spruce vs. European beech					
df 1, df 2	1, 41	1, 46	1, 53	1, 47	1, 40
F-value	5.42	11.93	610.28	9.44	5.28
p-tail	0.025	0.001	0.000	0.004	0.027

Table 3 Efficiency in space occupation EOC (m^2 kg^{-1}), space exploitation EEX (kg m^{-2} y^{-1}), and biomass investment EBI (kg kg^{-1}) for Norway spruce and European beech, by crown size classes ($p < 10$ m^2, $10 - 16$ m^2, > 16 m^2) and CI classes ($CI < 1$, $1 - 2$, > 2). For explanation of efficiency parameters see Formulas 3 to 5

	n	EOC (m^2 kg^{-1}) p-class (m^2)				EEX (kg m^{-2} y^{-1}) p-class (m^2)				EBI (kg kg^{-1}) p-class (m^2)			
		< 10	10 – 16	> 16	Mean	< 10	10 – 16	> 16	Mean	< 10	10 – 16	> 16	Mean
Norway spruce													
CI < 1	63	0.027	0.044	0.040	0.040	2.348	1.584	1.788	1.781	0.059	0.061	0.065	0.062
CI = 1 – 2	24	0.044	0.067	–	0.055	1.123	0.773	–	0.963	0.046	0.040	–	0.043
CI > 2	17	0.188	0.236	–	0.199	0.149	0.038	–	0.123	0.018	0.007	–	0.015
Mean	104	0.093	0.068	0.040	**0.069**	1.076	1.224	1.788	**1.321**	0.039	0.051	0.065	**0.050**
SDev (±)		0.114	0.069	0.014	0.082	1.024	0.778	0.884	0.931	0.023	0.024	0.024	0.026
European beech													
CI < 1	22	–	–	0.073	0.073	–	–	0.554	0.554	–	–	0.035	0.035
CI = 1 – 2	22	0.040	0.051	0.087	0.068	1.097	0.690	0.504	0.606	0.042	0.033	0.037	0.035
CI > 2	35	0.134	0.207	0.153	0.155	0.105	0.301	0.513	0.231	0.012	0.024	0.038	0.020
Mean	79	0.125	0.122	0.091	**0.108**	0.195	0.472	0.534	**0.425**	0.015	0.028	0.036	**0.028**
SDev (±)		0.075	0.144	0.071	0.094	0.343	0.430	0.420	0.423	0.017	0.022	0.023	0.023

Table 4 Species-specific regressions for efficiency in space occupation EOC (m^2 kg^{-1}), efficiency in space exploitation EEX (kg m^{-2} y^{-1}), and efficiency in biomass investment EBI (kg kg^{-1}) in relation to competition index CI and crown projection area p (m^2). All regressions and regression coefficients are highly significant ($p < 0.001$)

	n	Equation	R^2	*p*-tail
Norway spruce	104	$\ln(EOC) = -5.97 + 1.76\ln(CI+1) + 0.71\ln(p)$	0.78	0.000
	104	$\ln(EEX) = 4.02 - 3.05\ln(CI+1) - 0.84\ln(p)$	0.85	0.000
	104	$\ln(EBI) = -2.33 - 1.21\ln(CI+1)$	0.58	0.000
European beech	79	$\ln(EOC) = -5.88 + 1.12\ln(CI+1) + 0.73\ln(p)$	0.85	0.000
	79	$\ln(EEX) = 2.53 - 1.64\ln(CI+1) - 0.69\ln(p)$	0.85	0.000
	79	$\ln(EBI) = -3.21 - 0.55\ln(CI+1)$	0.21	0.000
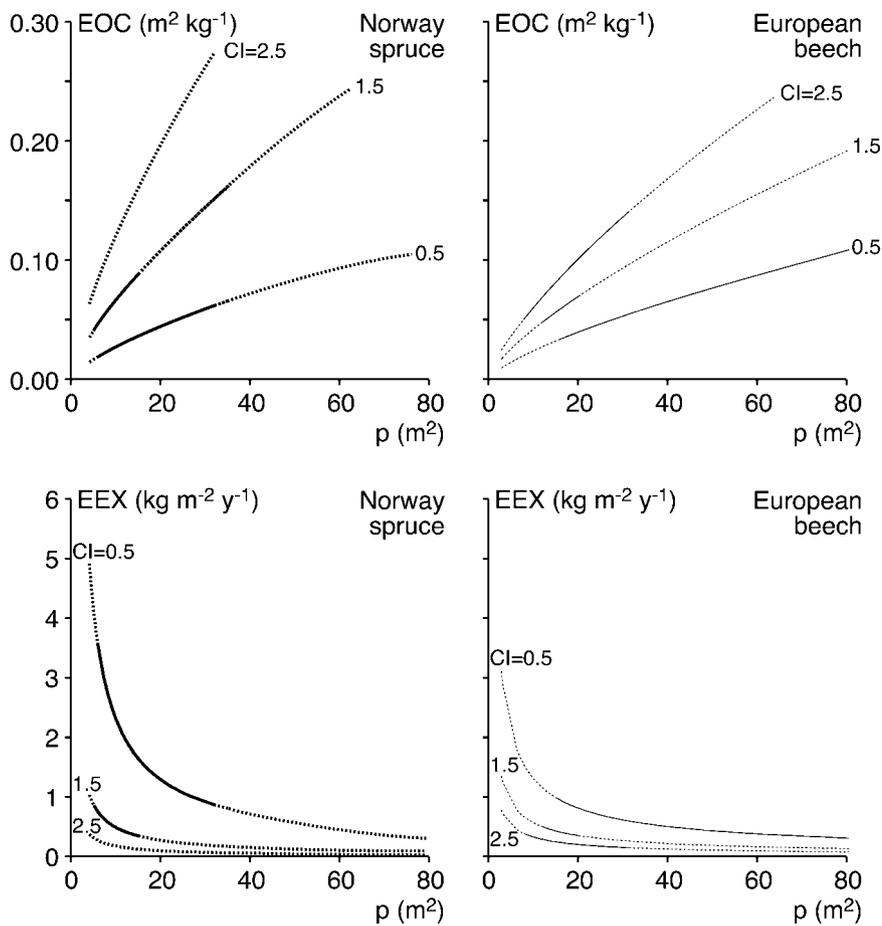
Fig. 4 Efficiency in space occupation EOC (m^2 kg^{-1}) (above) and in space exploitation EEX (kg m^{-2} y^{-1}) (below) for Norway spruce (left) and European beech (right) in relation to competition index CI and crown projection area p (m^2). Solid parts of the curves represent ranges covered by the observations.
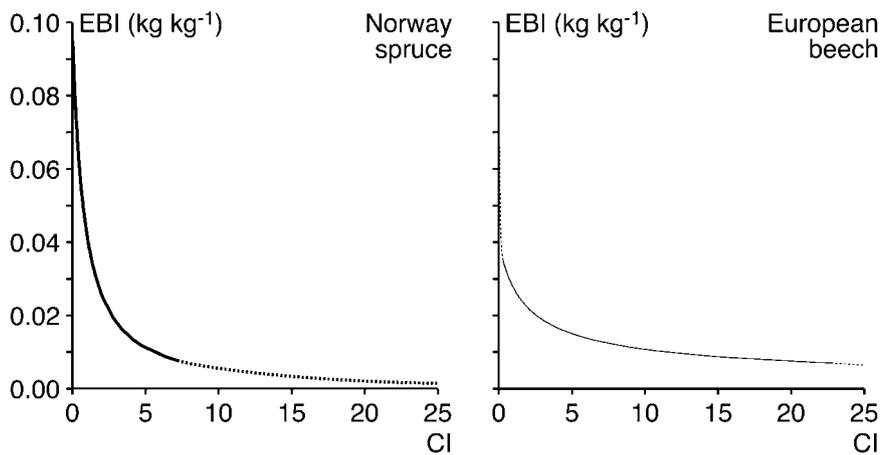
Fig. 5 Efficiency of biomass investment EBI (kg kg^{-1}) for Norway spruce (left) and European beech (right) in relation to competition CI. Solid parts of the curves represent ranges covered by the observations.

EEX is maximal when small crowns have access to the upper canopy layer, but decreases exponentially with increasing crown size and CI. Absolute EEX of the dominant spruce trees is considerable higher in comparison to beech. Though the exponents – 3.05 vs. – 1.64 for CI and – 0.84 vs. – 0.69 for crown size (Table **4**) reflect the fact that the EEX of spruce decreases more steeply than that of beech when size and CI rise. Therefore, in comparison to spruce, beech is more efficient in occu-

pying space and takes only one third of the efficiency in exploiting the occupied space. Size seems to be an ambivalent characteristic of a tree. On the one hand, it ensures privileged access to light and prevents competitors from accessing limited resources. On the other hand, size boosts energy consumption for maintenance, so that size growth is inevitably coupled with a decline in EEX.

Table 5 Stand level characteristics for Norway spruce and European beech in pure stands and mixed stands (growth period 1994–1999). Crown cover and biomass proportions in the mixture are given in percentages and printed in italics. Self-thinning is reflected by slope r = ΔN/N / Δd/d, i.e., the ratio between the change in stem number N and diameter d during the growth period. As the reference area for the species in the mixed stand is questionable, EOC_{Stand} and EBI_{Stand} are replaced by "–" in those cases

	Crown cover ratio CR (ha ha⁻¹)		Self-thin-ning slope r (% %⁻¹)	Biomass w_{Stand} (t ha⁻¹)		Biomass growth Δw_{Stand} (t ha⁻¹ y⁻¹)		EOC_{Stand} (m² kg⁻¹)	EEX_{Stand} (kg m⁻² y⁻¹)	EBI_{Stand} (kg kg⁻¹)
Norway spruce, pure	1.10		– 0.437	235.2		14.84		0.0425	1.48	0.06
European beech, pure	1.75		– 1.358	268.2		7.52		0.0373	0.75	0.03
Norway spruce, mixed	0.49	*26%*	– 0.656	136.2	*47%*	7.18	*64%*	–	–	0.05
European beech, mixed	1.39	*74%*	– 1.240	154.6	*53%*	4.03	*36%*	–	–	0.03
Total, mixed	1.88	*100%*		290.9	*100%*	11.21	*100%*	0.0344	1.12	0.04

EBI was found to be independent of crown projection area but was dependent on CI. The different increment percentage of spruce and beech trees is reflected in the respective equations in Table **4**: $e^{-2.33} = 0.097$ kg kg⁻¹ (spruce) and $e^{-3.21} = 0.040$ kg kg⁻¹ (beech) reflect EBI when CI = 0 and reveal that the efficiency of spruce amounts to 243% that of beech. However, if competition increases, the spruce EBI decreases with an exponent of – 1.21 while that of beech only changes with an exponent of – 0.55. Beech occupies space with lower biomass investment in the understorey, but exploits it more efficiently than spruce due to its shade tolerance. For an explanation of the preceding analysis of regression coefficients in Table **4**, see the section "Model for analysis of crown efficiency".

It should be stressed that, when interpreting these parameters at tree level, they relate growth to crown projection area of the tree. Hence, interactions between tree crowns that are tightly packed may modify the efficiency at stand level.

Stand level production

Crown cover ratios CR (ha ha⁻¹) and biomass of growing stock w_{Stand} (t ha⁻¹) on the subplots (Table **5**) suggest the following ranking: spruce/beech > beech > spruce. In relation to biomass growth from 1994 to 1999 at stand level Δw_{Stand} (t ha⁻¹ y⁻¹), the subplots differ in ranking: spruce > spruce/beech > beech. Data for tree level, efficiency parameters at stand level EOC_{Stand} (m² kg⁻¹), EEX_{Stand} (kg m⁻² y⁻¹), and EBI_{Stand} (kg kg⁻¹) are reported in Table **5**. Fig. **6** displays how the total values in Table **5** are spread over the 3 × 3 matrix of crown sizes and competition indices (size classes p < 10 m², 10–16 m², > 16 m², CI classes CI < 1, 1–2, > 2). It reveals the sequestration of space by species in pure stands and their interaction in mixed stands. For spruce, the crown projection area p_{Stand} is lowest (1.10 ha ha⁻¹) and distributes at a ratio of 73:16:11 in percentage terms over the classes CI < 1, 1–2, > 2 (Fig. **6**, above). The corresponding distribution for beech (1.75 ha ha⁻¹) is 32:33:35 in percentage terms, and for spruce/beech (1.88 ha ha⁻¹) it is 55:20:25. In other words, beech develops considerably more crown projection area and expands into a multi-layered canopy. On all three subplots in Fig. **6**, the predominate portion of the total crown projection area comes from p class > 16 m². The same tendency is found for the distribution of biomass per unit area w_{Stand} over the 3 × 3 matrix (Fig. **6**, middle). Again, in pure and mixed stands, spruce is concentrated in the upper canopy, while the

presence of beech in the different strata of light supply is more balanced.

The biomass growth per stand area, Δw_{Stand}, for pure spruce stands is highest (14.84 t ha⁻¹ y⁻¹) and represents 83:13:4 in percentage terms over the classes CI < 1, 1–2, > 2, respectively (Fig. **6**, below). The corresponding distribution is 40:37:23 in percentage terms for beech stands (7.52 t ha⁻¹ y⁻¹) and 68:16:16 in percentage terms for mixed spruce/beech stands (11.21 t ha⁻¹ y⁻¹). The considerably higher biomass growth of pure spruce compared to beech (about 2:1) underlines the tendency of beech to occupy much space and require higher inputs for comparably lower gains in terms of biomass growth (Fig. **6**, below). In mixed stands, spruce concentrates resource use more on a highly efficient upper canopy, whereas beech becomes less dominant in the lower canopy strata where light is limited. So, in the pure stand, 88% of the stand biomass growth is achieved by 72% of the projection area of class CI < 1 (≈ 1:1). In mixed stands, 60% of the stand biomass growth is produced by 21% of the projection area of class CI < 1 (≈ 3:1).

In order to compare the pattern of different stand types in terms of space sequestration and exploitation, we applied Kendall's test of concordance with similarity measurements W, the test statistic T_w, and the χ^2 test (Bortz et al., 1990, pp. 465). W ranges between 0 = maximum discordance and 1 = maximum similarity. The zero hypothesis is that the three subplots, spruce, beech, and spruce/beech, differ in terms of the portion of the crown projected area p_{Stand}, biomass of growing stock w_{Stand}, and biomass growth Δw_{Stand} in the 3 × 3 matrix, as depicted in Fig. **6** (top down).

Spruce has the same pattern of biomass allocation (W = 0.98, T_w = 15.73, df 8, n = 9, $p < 0.05$) in pure and mixed stands. The same pattern applies for biomass growth of spruce and even values for crown projection area stay rather stable (W = 0.95, T_w = 15.19, df 8, n = 9, $p < 0.10$). In contrast, the comparison between stands of pure spruce and pure beech (W = 0.58, n.s.), as well as between pure beech and beech in mixed stands (W = 0.83, n.s.), reveals significant differences in the spatial allocation of crown projection area, biomass, and biomass growth.
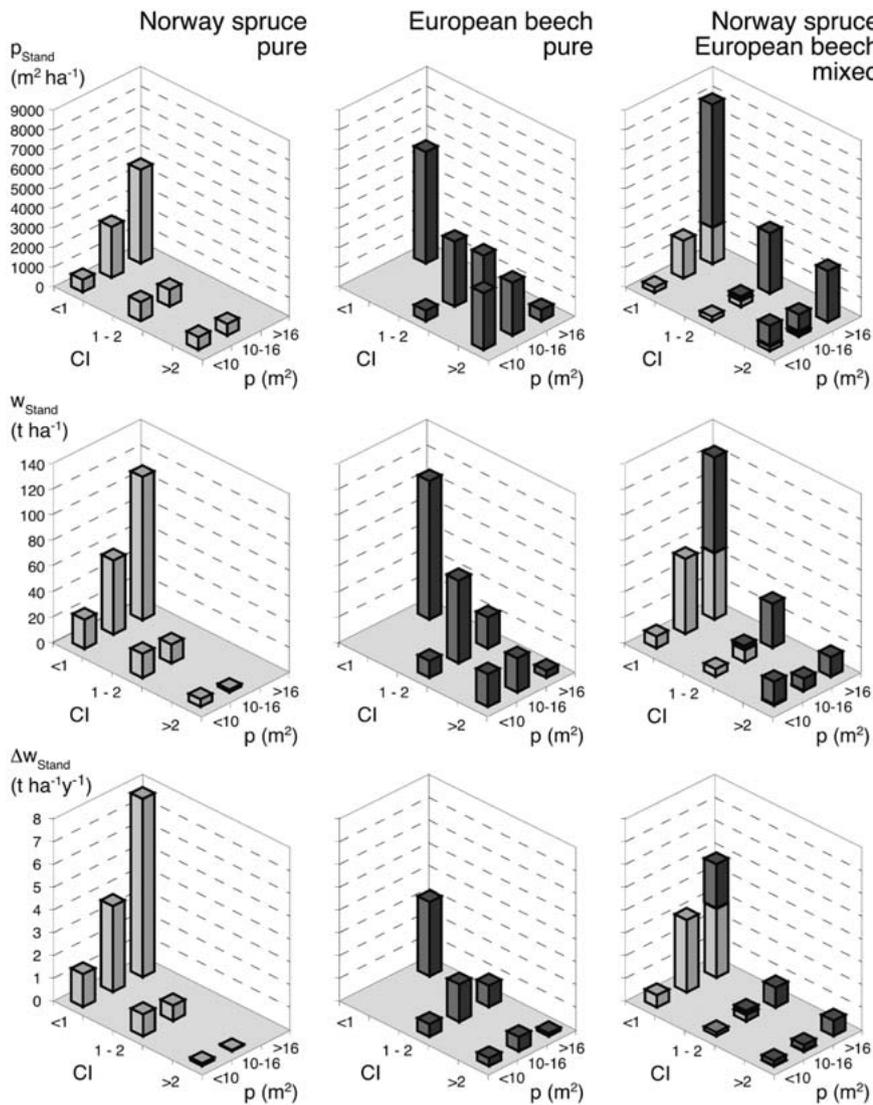
Fig. 6 Crown projection area p_{Stand} (m^2 ha^{-1}) (above), biomass of growing stock w_{Stand} (t ha^{-1}) (middle), and biomass growth Δw_{Stand} (t ha^{-1} y^{-1}) (below) for pure Norway spruce (left), European beech (middle), and mixed Norway spruce/European beech (right) divided into crown size classes (p) and competition classes (CI). Light columns represent Norway spruce, dark columns represent European beech.

Scaling from tree to stand level production

For the subset plots of pure spruce, pure beech, and mixed spruce/beech, exploitation efficiency EEX was calculated for both tree levels in the form of annual biomass growth per crown projection area (kg m^{-2} y^{-1}) (Table **4**, Fig. **4**), and for stand level as annual biomass growth per hectare (t ha^{-1}) (Table **5**). Subsequently, the former was called EEX_{Tree}, the latter EEX_{Stand}, and both are presented in kg m^{-2} y^{-1}. By comparison of EEX_{Tree} and EEX_{Stand}, problems become apparent when scaling from tree to stand level ($EEX_{Tree} \rightarrow EEX_{Stand}$). The crucial questions of whether the detected growing space efficiency at tree level is equivalent to that at stand level, and how the latter can be derived from the former, can be answered using the following equation

$$EEX_{Tree} = k\,EEX_{Stand}. \tag{8}$$

Factor k is 1.0 if tree level equals stand level production. In all other cases, k reflects the required adjustment when stand level production should be derived from tree level production.

Rearranging Equation 8 and inserting Formula 7, after calculating the delogarithm, leads to

$$k = EEX_{Tree}/EEX_{Stand} = e^a(CI+1)^b\,p^c/EEX_{Stand} \tag{9}$$

and reflects the fact that k depends on the competition index CI and crown size p. Table **6** displays k values for different combinations of competition indices, CI, and crown projection areas, p, and is based on the species-specific parameters a, b, c, and EEX_{Stand}. That means that, assuming that a given tree has a small crown (p = 10 m^2) and is predominant (CI = 0.5), then, for spruce, the biomass increment per unit area EEX_{Tree} will be 158 % of the stand level production EEX_{Stand} and 175 % in the case of beech. Table **6** reflects the expected bias in the case of an uncorrected projection from tree to stand level. In comparison, the reciprocal value of k enables an unbiased upscaling from tree to stand level:

$$EEX_{Stand} = EEX_{Tree}/k. \tag{10}$$

Table 6 Factor k for scaling from tree to stand level production ($EEX_{Stand} = EEX_{Tree}/k$), while k is tabulated in relation to crown projection area p and competition index CI for Norway spruce and European beech (Formula 9)

	p				
	$10\,m^2$	$20\,m^2$	$30\,m^2$	$40\,m^2$	$50\,m^2$
Norway spruce					
CI = 0.5	1.58	0.88	0.63	0.49	0.41
CI = 1.5	0.33	0.19	0.13	0.10	0.09
CI = 2.5	0.12	0.07	0.05	0.04	0.03
European beech					
CI = 0.5	1.75	1.09	0.82	0.67	0.58
CI = 1.5	0.76	0.47	0.36	0.29	0.25
CI = 2.5	0.44	0.27	0.20	0.17	0.14

Discussion

Using the introduced characteristics A, EOC, EEX, and EBI, we are now equipped to analyze the species growth at both tree and stand level and to solve the apparent contradiction between space occupation and exploitation. The particular spatial and temporal dimension of forests provides a unique opportunity to track tree growth from individual plants to stand level. Comparable insight into herbaceous stands would require a reduction in size by a factor in the region of 10 or 100 like Alice did in Wonderland. Harper (1977, p. 280) states "… it is rarely possible to count survivors accurately without greatly disturbing them and the structure of their canopy".

Species-specific allometry

Allometry at the level of the individual tree provides a key for understanding space occupation. While recently Enquist and Niklas (2001) and West et al. (1997) posed general allometric scaling laws, Table **2** and Fig. **3** reveal considerable species-specific differences in terms of mean value and variation in individual tree allometry. Allometry coefficients, A, reflect the capacity to expand within a given biomass increment. Scaling parameters for geometric similarity serve as a reference for interpretation of the observed A values (Table **2**). If a plant kept its initial shape by proportionally increasing all its linear dimensions (height h, stem diameter d), then this would result in $h \propto d^A$, $b \propto d^A$ with A = 1. In this case, $ba \propto d^2$, $p \propto d^2$ would apply for the relationships between diameter d and basal area ba, or diameter and crown projection area p, whereas $w \propto d^3$ results for the relationship between diameter and biomass w. From $p \propto d^2$ and $w \propto d^3$ follows $p \propto w^{2/3}$, from $h \propto d$ and $w \propto d^3$ follows $p \propto w^{1/3}$, and $w \propto d^3$ is equivalent to $d \propto w^{1/3}$.

The fact that beech especially exceeds these naive scaling coefficients A of geometric similarity, indicates its tendency to enhance crown extension within a given biomass. Beech couples a 1% increase in biomass with a 2.28% increase in crown projection area and a 0.5% increase in height, which gives a surplus of 57% and 127%, when compared to spruce (Table **2**, $A_{p,w}$ and $A_{h,w}$). A 1% increase in diameter in beech is coupled with a 1.46% increase in height and a 2.82% increase in crown diameter, which is 143%, and 56%, respectively, higher than in spruce

($A_{h,d}$, $A_{b,d}$). In addition, the up to four-fold standard errors for beech underline its higher crown elasticity.

For scaling height with respect to diameter, McMahon and Kronauer (1976) suggested two model approaches: a model of stress similarity $h \propto d^{1/2}$ and a model of elastic similarity $h \propto d^{2/3}$. However, observed $A_{h,d}$ underlines that Norway spruce ($A_{h,d} = 0.60 \pm 0.06$) approaches 2/3 and European beech ($A_{h,d} = 1.46 \pm 0.27$) exceeds both thresholds; in other words, beech tends strongly to top heaviness. Compared to Niklas (1994, pp. 173 – 174), $A_{b,d}$ for both species indicates an enhanced crown diameter growth with respect to stem diameter. Nevertheless, as Niklas (1994, p. 174) states, slopes are steeper for angiosperms than for gymnosperms, $A_{b,d}$ has an approximately 50% steeper slope for beech in comparison to spruce. The latter suggests that beech, an angiosperm, invests a higher portion of its biomass in the formation of horizontal branches, whereas spruce, a gymnosperm, invests more into its central trunk instead of into wide branches. With 1% biomass investment beech produces only an 8% more diameter increment when compared to spruce, and both species differ least in $A_{d,w}$. These individual species' peculiarities should not be ignored in favour of a questionable general scaling law (Kozlowski and Konarzewski, 2004; Pretzsch, 2005 a; Zeide, 1987). It is a rather promising research perspective to detect species-specific allometry, which ranges from aboveground to belowground (Bolte et al., 2004) and from tree level to stand level (Stoll et al., 2002; Weller, 1987).

Trade-off between occupation and exploitation of growing space

Concerning occupation and exploitation of growing space, spruce is 100% more efficient in terms of growth per crown projection area and growth per stand area, compared with other species with similar site conditions. For this reason, foresters prefer spruce to beech and establish pure spruce stands or mixed spruce/beech stands. Nevertheless, the natural forest association in the study site would consist mainly of *Fagus sylvatica* and *Quercus robur,* but not *Picea abies.* Therefore, beech must have some other attributes that compensate for its inferior efficiency in space exploitation. Through superior efficiency in lateral crown expansion and space occupation, beech is able to maintain a multi-layered canopy that holds back competitors from the understorey; it fills gaps in the canopy immediately after self-thinning processes within the stand, and is elastic enough to occupy gaps after disturbance events within the canopy caused by windthrow or bark beetle attacks (Pretzsch, 2005 b). Beech can tightly encircle and deeply penetrate the shade crowns of spruce (Pretzsch, 2002, p. 287). In addition, when precipitation is limited, so too is the growth of spruce and hence its access to light, and this is more apparent for spruce than for beech (Pretzsch, 2004).

Application of Zeide's (1985) measure for self-tolerance, $r = \Delta N/N/\Delta d/d$, in reference to central European species confirms the low self-tolerance of beech and its space-consuming investment strategy (Pretzsch and Biber, 2005). An increase in mean diameter of 1% causes a decrease in stem number of 1.69% in beech stands and 1.47% in spruce stands. Thus, self-thinning of beech is about 15% more rigorous when compared to that in spruce. For r in mixed stands, beech has a higher self-tolerance than spruce; large expansion abilities under intra-

specific conditions evidently guarantee more assertive power in a mixed stand. For the observation period 1994–1999, Table **5** (second column) reveals a more rigorous self-thinning process in pure beech stand ($r = -1.358$) in comparison to pure spruce stands ($r = -0.437$). In mixed stands, alien thinning accelerates the decline in spruce by 50% but slows down the decline in beech by 10%.

The strategy of beech seems to be to build on risk distribution, while spruce's pillar-like crowns with high growing space efficiency and low efficiency in space occupation reflects a strategy of risk concentration. We assume that the successful allometry of beech developed through via co-evolution, i.e., by adapting to the more ancient gymnosperms. In the long term, and especially during disturbances, at a given site, the strategy of beech appears more successful in terms of population dynamics. Thus, superior growing space efficiency seems to be a prerequisite but is not a sufficient trait for success within a stand and in terms of population dynamics. Nevertheless, the comparison between cultivation of spruce versus beech provides a classic example that superiority in the short term is unlikely to be sustainable and superior in the long term.

Pure versus mixed species stands

The relationship between the efficiency of spruce and beech in terms of space exploitation EEX_{Stand} is approximately $2:1$ for pure stands and becomes even more apparent in mixed stands. Based on the biomass of growing stock, the mixture proportions are 0.47 for spruce and 0.53 for beech (Table **5**). When assuming that the two species grow the same way in mixture as they in a pure stand, we would expect 0.47 14.84 (t ha^{-1} y^{-1}) = 6.95 (t ha^{-1} y^{-1}) for spruce and 0.53 7.52 (t ha^{-1} y^{-1}) = 4.01 (t ha^{-1} y^{-1}) for beech, i.e. 10.95 (t ha^{-1} y^{-1}) in total. The total expected value matches the observed values remarkably well (– 2%). However, the reported biomass increment per ha in mixtures requires considerably more biomass investment (290.9 t ha^{-1} in mixed stand versus 235.2 t ha^{-1} in a pure spruce, or 268.2 t ha^{-1} in a pure beech stand). With the far higher productivity of spruce stands, the admixture of other species usually causes a decrease in productivity, since losses from the substitution of a superior species by an inferior species cannot be compensated for by any beneficial interactions between species in the mixture. This implies that almost any admixture to the more productive pure spruce stand would lead to lower yields. In our particular case, the biomass growth of the pure spruce stand amounts to 14.84 t ha^{-1} y^{-1} whereas the mixed stand produces only 11.21 t ha^{-1} y^{-1}, which is equivalent to a growth reduction of 24% (Table **5**). The superiority of pure spruce stands explains the increases in their cultivation in the past (Pretzsch, 2004).

Supposing that both species would perform with the same efficiency in biomass investment EBI_{Stand} in a mixed stand as well as in a pure stand, then we would expect 136.2 t ha^{-1} 0.0631 = 8.5942 t ha^{-1} for spruce and 154.6 t ha^{-1} 0.0280 = 4.3288 t ha^{-1} for beech. However, the observed growth is 7 to 16% lower than expected (7.18 t ha^{-1} y^{-1} and 4.03 t ha^{-1} y^{-1}, respectively). Depending on whether site conditions have favourable or unfavourable effects on either spruce or beech, these values will approach those in the pure spruce or pure beech stands. In all available studies, however, mixed stands of spruce and beech are intermediate between the corresponding pure stand values as far as productivity is concerned (Kennel, 1965; Pretzsch, 2004; Wiedemann, 1942, 1943).

Scaling from tree to stand level production

The combination of tree and stand level characteristics has implications for up-scaling from tree to stand. Similar to all other complex open-air experiments with adult trees, between 2000–2005, free air ozone and CO_2 fumigation of the stand was restricted to a sample of 10 spruce trees and 10 beech trees for technical and financial reasons (Matyssek et al., 2002; Reitmayer et al., 2002). However, using Table **6** and Formulas 8 to 10, we can now project the results from these small sample size tree experiments to stand level production.

As biomass growth per unit area is strongly determined by tree size and even more strongly by the crown hierarchical position in the canopy, projections from tree to stand level require adjustment by factor k^{-1} (Formula 8). EEX of small crowns in the upper canopy amounts to approximately 300% of stand level production. Wide crowns in subordinate positions produce a negligible fractional amount of the stand's biomass growth per area unit. This tendency is much more pronounced in the case of spruce than in the case of beech. EEX of spruce decreases by $(CI+1)^{-3.05}$ and $p^{-0.84}$ when the competition index or size increases (Table **4**). With reference to this, the decrease in EEX of beech by $(CI+1)^{-1.64}$ and $p^{-0.69}$ is considerable less. The high productivity of trees with small crowns and dominant trees, especially in spruce stands, may lead to a serious risk of bias when their EEX is projected to the stand level without correction. Using Equation 9, we can extrapolate to the ideal size of a tree in the upper canopy ($CI = 0.5$) in order to guarantee an unbiased projection to stand level. In this case, the following formula applies: $EEX_{Stand} = e^a (CI+1)^b p^c$ or $p = EEX_{Stand}^{1/c} e^{-a/c} (CI+1)^{-b/c}$. Inserting $CI = 0.5$ and $EEX_{Stand} = 1.484$ kg m^{-2} y^{-1} for spruce and 0.752 kg m^{-2} y^{-1} for beech results in 17.18 m^2 and 22.56 m^2, respectively. In summary, a predominant spruce tree with a $CI = 0.5$ and crown size of $p = 17.18$ m^2 is suitable for unbiased upscaling from tree to stand level. In all other cases, a projection from tree to stand level requires a correction in the dependence of p and CI using Formula (9).

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