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## Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania

Received: 24 September 2004 / Accepted: 9 May 2005 / Published online: 6 September 2005  
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**Abstract** Growth of regenerating trees in different light environments was studied for the mountainous, mixed-species forests in the Carpathian Mountains of Romania. The primary species in these mixtures were silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst). Seedlings/saplings of these species were selected and measured in different stands from two different geographical locations. Regenerating trees were measured for height and diameter growth during the summer of 2002. For each seedling/sapling, percentage of above canopy light (PACL) and stand basal area (BA) were used to assess available and occupied growing space respectively. Regeneration growth was compared against these two variables and regression relationships were developed. Using these models, we predicted the dynamics of regeneration as both growth and species composition. Our results showed that in low-light environments (PACL < 20–35%; BA > 30 m<sup>2</sup>/ha), shade tolerant fir and beech clearly outcompeted the spruce. Therefore, in dense stands, spruce could be eliminated by the shade tolerant species. For intermediate levels of cover (PACL = 35–70%; BA = 15–35 m<sup>2</sup>/ha) the spruce grew at comparable rates as the beech and fir. All three species showed similar growth rates in open conditions (PACL > 80–90%; BA < 15–20 m<sup>2</sup>/ha) with the spruce having a tendency to outgrow the others. However, in terms of establishment, such conditions favor spruce and inhibit fir and beech.

**Keywords** *Abies alba* · *Picea abies* · *Fagus sylvatica* · Multiaged · Uneven-aged · Mixed species stands · Single tree selection · Regeneration growth

### Introduction

Forests as dynamic systems are subject to continuous change. Over time they move through different developmental stages, characterized by different structures and processes (Oliver and Larson 1996). When growing space is fully occupied, the biomass in the understory is inversely correlated with the biomass of the overstory (Lieffers 1999). Any changes in the overstory are accompanied by changes in the understory light regime directly influencing regeneration at the forest floor (Emborg 1998). To obtain a mixed composition and vigorous regeneration, management can control the amount, position and type of overstory vegetation that intercepts the incoming light and competes for ground resources (Lieffers 1999).

The beech–conifer mixed species forests in this study are temperate complex ecosystems situated in Romania's mountain region (800–1300 m altitude). Dominant species of these forests are silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* (L.) Karst) and European beech (*Fagus sylvatica* L.) which are commonly found as mixtures of two or three species. Among these, fir and beech are considered extremely shade tolerant while spruce is considered intermediate (Stanescu et al. 1997).

Each of these species has different resource requirements and regeneration abilities. The seedlings of silver fir and European beech are able to tolerate both lateral and vertical shade. Seedling survival of these species is dependent on overstory protection, as early and late frosts as well as strong insolation apparently limit their regeneration in more open areas (Negulescu and Ciunac 1959; Haralamb 1967; Stanescu et al. 1997; Savill 1991; Evans 1984; Padraic et al. 1998). Alternatively, seedlings of Norway spruce, the third species in these mixtures,

Communicated by Jürgen Bauhus

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grow better in more open environments with just lateral shade (Haralamb 1967; Stanescu et al. 1997).

Even though, resource needs are essentially the same for all species (light, water and nutrients, etc.), among the key resources, light plays a major role (Brunner 1993; Finzi and Canham 2000). However, the ability to survive in limiting conditions and the patterns of photosynthate allocation to the different parts of a tree vary greatly among different species (Beaudet and Messier 1998). Such differences in allocation to growth lead to differences in tree architecture, providing competitive advantages to certain species in a given environment. As a result of these competitive gains, diverse patterns of stand development could evolve (Oliver and Larson 1996).

In Romania, current management guidelines for regenerating beech–conifer mixed stands are based mostly on size of the canopy opening or percents of standing volume that needs to be harvested. Studies and information regarding regeneration growth as a function of both light and basal area (and the correlation between the two) are scarce. To improve the current knowledge about managing these forests, the present study had the following three objectives:

1. To quantify the regeneration growth for each of these three species in mixed forests. Specifically, height and volume growth of understory trees were quantified for each of the three dominant species growing in similar conditions.
2. We quantified and compared differences in height and diameter growth among subject species, to assess the dynamics of natural regeneration in these stands along a gradient of growing space (light and basal area).
3. To develop management recommendations for mixed species composition and multiaged structures in these stands.

## Materials and methods

### Study area

The study was located in the Carpathian Mountains of Romania, within the natural range of the temperate, mixed beech–conifer forests. Study sites were established on state forest managed by the National Forest Administration at two different locations: Poiana Rusca Mountains (Rusca Montana Forest District at 45°39'22"N and 22°22'30"E) and Retezat Mountains (Retezat National Park and Retezat Forest District at 45°19'05" N 22°45'14"E). General data for sampled regeneration and overstory trees are presented in Table 1. Information about site, climate, stand structure and management history was obtained from the management plans of the two forest districts.

Geologic substrates are slightly different between the two locations: at Rusca Montana it is metamorphic (marble, paragneiss and schist), while at Retezat the substrate is mostly igneous (volcanic) with some metamorphic components (schist). Soil depth was greater at Rusca Montana with ground vegetation represented mostly by blackberry (*Rubus hirtus* Waldst. & Kit.) (i.e., lower acidity). At Retezat, wood sorrel (*Oxalis acetosella* L.) on shallow soils with rocks at surface covered by green mosses shows potential for higher acidity.

Altitude ranged from around 800–1,300 m (the natural range for these mixed forests). The climate is temperate–continental with wet and cool summers and cold winters with high precipitation (most of it being snow). Annual average temperature is approximately 8–9°C and annual average precipitation around 700–1,400 mm. A large range of slopes (2–45%), aspects (N, N–E, S, S–E, S–W, E, W), and crown cover (from open conditions to completely closed stands) was represented in the study.

**Table 1** General data for understory and overstory trees sampled in the study

Species	Overstory/ understory	Sample size (n)	$H_{TOT}$ (m)	$H_{BLC}$ (m)	Diameter (cm)	Age (years)	PACL (%)
European beech	Overstory (RM)	18	32.2–44.8	5.6–21.2	33.7–94.0	121–190	-
	Overstory (RT)	9	18.8–34.1	1.5–14.9	23.1–99.5	107–244	-
	Understory (RM)	39	0.46–5.43	0.07–0.58	0.79–10.00	8–23	1.14–98.66
	Understory (RT)	16	0.81–3.76	0.06–0.32	1.09–6.50	11–40	3.43–75.84
Silver fir	Overstory (RM)	12	35.4–47.9	3.3–21.9	42.6–98.5	72–350	-
	Overstory (RT)	11	19.2–48.1	2.2–24.8	24.3–131.3	89–142	-
	Understory (RM)	30	0.45–4.54	0.01–0.62	1.64–10.10	9–37	1.17–99.42
	Understory (RT)	20	0.67–4.05	0.05–0.51	2.00–8.30	13–36	5.63–97.68
Norway spruce	Overstory (RM)	10	20.60–41.30	4.30–20.90	25.70–65.40	112–180	-
	Overstory (RT)	-	-	-	-	-	-
	Understory (RM)	3	1.88–2.72	0.04–0.19	4.5–7.1	9–17	51.16–100.00
	Understory (RT)	37	1.19–3.96	0.04–0.70	2.5–10.1	10–65	2.85–100.00

Diameter, in centimeters, refers to diameter at the base of the tree for regeneration trees and to diameter at breast height for overstory trees

PACL percent of above canopy light;  $n$  number of trees; RM Rusca Montana; RT Retezat;  $H_{TOT}$  total height in meters;  $H_{BLC}$  height to the base of the live crown in meters

## Understory tree measures

During the summer of 2002, a total of 145 naturally regenerated seedlings/saplings of the subject species were sampled in eight different stands with mixed regeneration and diverse canopy cover conditions (three stands at Rusca Montana, ranging from 19.1 to 44.4 ha and 5 stands at Retezat, ranging from 0.8 to 9.3 ha). We sampled regeneration trees between  $\approx 0.5$  and 5.0 m tall. Trees smaller than 0.5 m were considered to be more affected by soil resources than light while taller trees were difficult to measure. Understory trees under no apparent competition for light from other similar size vegetation and with no apparent damage were sampled. To avoid any possible competition from above for light due to other understory vegetation, the chosen tree was the tallest in its clump (if it was growing in a clump). The next tree was at a distance large enough (more than one height at least) and was again the tallest in its clump/neighborhood. Written records about stand management history, evidence of no other recent canopy disturbance and small variation in annual height increment of individual trees were used to ensure that growing conditions for each sampled tree were relatively uniform for the last 3–5 years.

Understory tree measurements included total size (height and diameter) and annual growth as an average for the last three growing seasons. Working with relatively small trees, to account for potential variability among years we used growth measures over the last 3 growing seasons only. Height growth was measured to the nearest millimeter with a metric tape. Destructive sampling was used to measure diameter growth. Stem disks were cut at the root collar and at base of the live crown, the bark was removed and disks were carefully sanded and scanned (400 dpi resolution). On all disks, for growth measures, the area for the last 3 years was delineated using Adobe Photoshop and measured (in  $\text{mm}^2$ ) using Winseedle software (Regent Instruments—Quebec, Canada). To determine age, annual rings on basal disks and increment cores or scanned images in some cases, were counted using a stereomicroscope.

Particularly for beech, growth rings are very hard to distinguish on fresh (untreated) material. As a result, for this species, both age and growth analysis disks were treated first with phloroglucinol and hydrochloric acid (Patterson 1957). Disks were then sanded with fine grit sandpaper. For a very few small seedlings, rings were still not apparent and disks were sent to Rocky Mountain Tree-Ring Research, Inc. (Ft. Collins, Colorado, USA). In this case, ring widths were measured using a sliding stage micrometer. Cross-dating and measurement accuracy were assessed using COFECHA (Holmes, 1983).

Volume of individual tree stems was computed using height and cross-sectional area. For trees that had the crown base close to the ground the same disk was considered for both base of the tree and base of the live

crown, and stem form was assumed to be a cone. For trees with separate disks for base of tree and crown base, the part of the stem below crown base was assumed to be a truncated cone, and the part above to a cone. The sum of these two parts would give us the total stem volume. For analysis, we used the annual volume increment computed as the average growth for the last 3 growing seasons.

For diameter growth measurements, regeneration trees at Rusca Montana were harvested during the second half of July. At that time, the growing season had not ceased yet, and the growth ring for 2003 was not completed. This should be considered as a potential source of variability in the diameter growth data set.

## Overstory tree measures

At each study site where regeneration trees were sampled, stand age and size structure were assessed. Diameter at breast height (DBH) was measured with a tape to the nearest millimeter. Overstory trees of different sizes for each species were cored to determine age structure. Total height and crown base for these trees were measured to the nearest decimeter with a Vertex III hypsometer (Haglof, Sweden). The base of the crown was considered where the lowest living, vigorous branch occurred.

The overstory canopy structure was assessed using a crown stratification procedure developed by Latham et al. (1998). This method assumes competition, for light acquisition is greatest in the top 60% of the tree crown. The cut-off point for the first stratum is therefore at the base of this portion of the crown for the tallest tree (with the longest crown). All trees that reach this height are in the same stratum. Trees below this cut-off point are in the next stratum. Lower strata are determined in a similar manner.

## Growing space measurements

The light that penetrates the overstory and reaches a regenerating tree is very often the most important limiting factor for growth. However, light represents only one resource and is rather difficult to estimate or measure. Alternatively, stand basal area is often used to assess stand density and competition. At the tree level, this measure is less precise than light but it represents effects of past competition related to both above- and below-ground factors. Both percentage of the above canopy light and overstory basal area were used as surrogates for the available and occupied growing space of sampled regenerating trees.

For light measurements we followed a procedure developed by Parent and Messier (1996) and verified for mixed species stands with irregular canopies (Messier and Parent 1997; Gendron et al. 1998). This method requires completely overcast and homogenous sky con-

ditions with the solar disk invisible. Under such weather conditions most of the incoming light is diffuse and a single instantaneous point measurement of light is sufficient to estimate the mean daily percentage of the photosynthetic photon flux density (PPFD) for that microsite.

In our study, light environment was computed as the percentage of above canopy light (PACL) that reaches the tip of a seedling/sapling. Light in this context means only the photosynthetic active radiation (PAR) measured as PPFD in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . PACL represents the ratio of two measurements: one below the canopy and one above the canopy.

Within the study area, large openings (around 0.5 ha at Rusca and 0.3–1.0 ha at Retezat) were used to measure the light regime as a surrogate for above the canopy reading. For these measurements, an AccuPAR ceptometer (Model PAR-80, Decagon Devices, Inc., Washington-USA) having a probe with 80 light sensors was used. To measure the below canopy light, at the tip of each regeneration tree, a Li-250 light meter with a Li-190SA quantum sensor attached (LI-COR, Inc., Nebraska-USA) was used. For small trees the sensor was placed on a metal ruler, while for taller trees the sensor was attached to a height pole. In both cases a leveling fixture was used to ensure a horizontal sensor and measure accurate readings. Exact time (hours-minutes-seconds) was recorded for each individual measurement (i.e., tree).

To ensure the compatibility of the readings taken by the sensors of the different instruments in open and under canopy, an external quantum sensor (Li-190SA, LI-COR) was attached to the ceptometer and placed next to the middle of the probe during measurements. Simultaneous readings taken by both sensors (AccuPAR probe and Li-190SA) in the same light environment were compared. The AccuPAR readings were almost always greater but differences were between 0 and 11.69%, although the average was 3.7% while the median only 2.5%. The larger differences could be due to the fact that AccuPAR readings represent an average of 80 sensors

while the Li-Cor is a single sensor reading. The readings of Li-Cor also tended to drift away if the sensor was not repeatedly matched to the AccuPAR sensors. Therefore, above canopy readings data collected with the ceptometer were used. Finally, after matching the two clocks, we were able to compare light measurements (below and above canopy) and to compute PACL values.

Basal area of overstory trees in the surrounding stand was determined for each regenerating tree using point sampling. A prism with a 20 basal area factor (BAF in  $\text{ft}^2/\text{ac}$ ) was used because it provided the requisite 5–12 trees per sampling point (Avery and Burkhart 2002). For analysis, basal area readings were converted to metric units ( $\text{m}^2/\text{ha}$ ).

## Analysis

Data analysis was performed using S-Plus 6.0 statistical software package. For both height and volume, growth was expressed as a ratio of annual growth to total tree size (i.e., relative annual growth). This relative measure avoided biases associated with comparing growth for trees of different sizes. Growth of individual trees was assessed in relationship to both growing space surrogates. Linear and nonlinear models based on the least squares method were used to regress growth as a function of these two variables. Confidence intervals were computed assuming errors are normally distributed and were used to compare among species (if they crossed, species were considered not to be different). When basal area was the explanatory variable, two different procedures were used to estimate growth: direct and indirect. For the direct (empirical) procedure, we chose the best fit for data at hand (see below). For the indirect (predicted) procedure, we expressed light as a function of basal area and afterwards we implemented this formula into the growth-light equations (also established in this study). Growth estimates using these two procedures were also compared.

**Table 2** Equation forms and biological implications for the a priori set of models used in analysis

Model	Form	Biological implications
Linear	$Y = a + b * X$	Linear increase or decrease in the response variable (growth, light) over entire range of the explanatory variable (light, basal area)
Quadratic	$Y = a + b * X + c * X^2$	Growth increases with light to a certain point, peaks and then decreases due to possible inhibition
Saturating (Weibull)	$Y = 1 - e^{-a * X^b}$	Growth increases with light to a certain level and then saturates. Any increase in light above this threshold has no additional effect on growth
Saturating (Chapman-Richard's)	$Y = a * (1 - e^{-b * X})^c$	
Saturating (Michaelis–Menten)	$Y = \frac{a * X}{b + X}$	
Saturating (Logistic)	$Y = \frac{a}{1 + e^{-c * X}}$	
Exponential	$Y = a * e^{b * X}$	Growth and light decrease at a decreasing rate with increasing stand density (i.e., increasing basal area)
Gaussian	$Y = a * e^{-\frac{(b - X)^2}{2 * c^2}}$	Possible saturation or inhibition of growth in open conditions, followed by a decrease at a decreasing rate with increasing basal area

**Table 3** Model selection and comparison for growth versus light regressions (for saturating models, only the best one is presented here)

Regression (Y vs. X)	Species	Model and rank	$K_i$	$AIC_{ci}$	$\Delta_i$	$w_i$	$w_1/w_i$
Height versus light	Beech	1. Logistic	3	-363.4	0.0	0.33	-
		2. Quadratic	3	-358.2	5.2	0.02	13.6
		3. Linear	2	-352.4	11.0	0.00	242.8
	Fir	1. Quadratic	3	-355.6	0.0	0.64	-
		2. Logistic	3	-353.4	2.1	0.22	2.9
		3. Linear	2	-341.4	14.1	0.00	1,177.5
	Spruce	1. Weibull	2	-291.5	0.0	0.46	-
		2. Quadratic	3	-289.2	2.3	0.14	3.2
		3. Linear	2	-284.8	6.7	0.02	28.8
Volume versus light	Beech	1. Weibull	2	-373.0	0.0	0.39	-
		2. Quadratic	3	-361.4	11.6	0.00	322.5
		3. Linear	2	-355.1	17.9	0.00	7,686
	Fir	1. Quadratic	3	-344.7	0.0	0.69	-
		2. Logistic	3	-342.9	1.8	0.27	2.5
		3. Linear	2	-319.0	25.7	0.00	383,074
	Spruce	1. Michaelis-Menten	2	-248.8	0.0	0.43	-
		2. Quadratic	3	-245.1	3.7	0.07	6.3
		3. Linear	2	-233.6	15.3	0.00	2,049.9

$K_i$  = number of parameters;  $AIC_{ci}$  = Akaike Information criterion (corrected);  $\Delta_i$  =  $AIC_{ci}$  differences ( $\Delta_i - \Delta_{min}$ );  $w_i$  = Akaike weights;  $w_1/w_i$  = weight ratio;  $w_1$  = weight for selected model (best fit);  $w_i$  = weight for model  $i$

To select the best model for data at hand, we used an information-theoretic method based on the Akaike Information Criterion (Anderson et al. 2000). To explain the possible biological relationships between tree growth and growing space, three different a priori hypotheses representing different families of curves were used for each explanatory variable (light or basal area). To model light as a function of basal area, two models were compared. Table 2 presents equation forms and biological implications for the models used with this method.

To rank models in the a priori set and to account for small sample sizes ( $n/K < 40$ , where  $n$  = sample size and

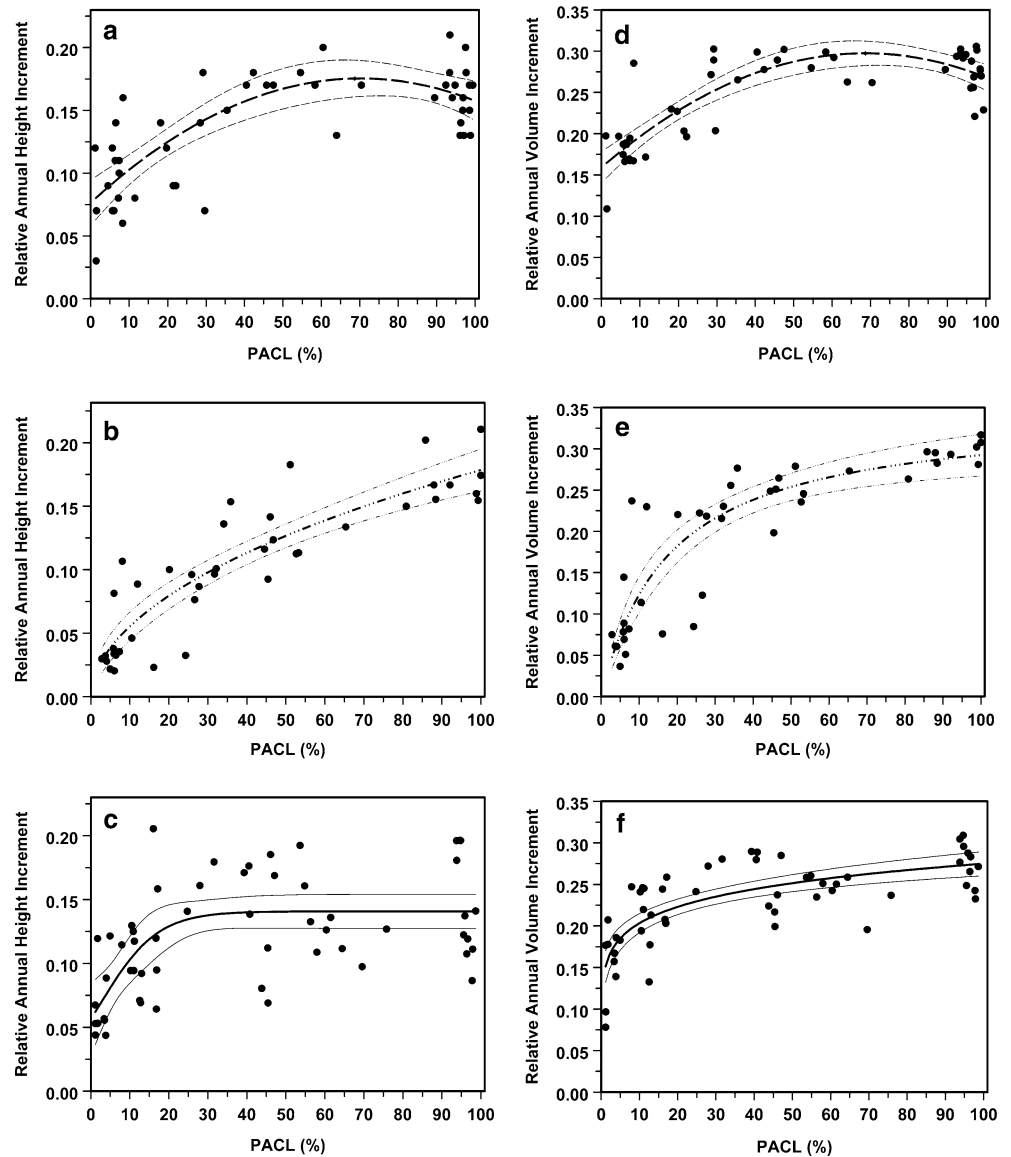
$K$  = the number of model parameters), we computed the modified form for the Akaike Information Criterion ( $AIC_c$ ) (Burnham and Anderson 1998). This parameter represents the information loss when the subject model is used to approximate the true model and therefore the minimum  $AIC_c$  implies the best fit. To assess the differences between best fit and the rest of the models, the likelihood of a given model data (Akaike weight— $w_i$ ) was computed (Anderson et al. 2000). Next, the highest likelihood, the one with the best fit ( $w_1$ ), was compared against the likelihood of the other models ( $w_i$ ). A high value of the ratio ( $w_1/w_i$ ) indicates different likelihood for the models, given the data.

**Table 4** Model selection and comparison for growth versus basal area and light versus basal area regressions (for saturating models, only the best one is presented here)

Regression (Y vs. X)	Species	Model and rank	$K_i$	$AIC_{ci}$	$\Delta_i$	$w_i$	$w_1/w_i$
Height versus basal area	Beech	1. Linear	2	-357.99	0	0.70	-
		2. Gaussian Model	3	-356.00	1.99	0.26	2.71
		3. Exponential	2	-352.30	5.69	0.04	17.20
	Fir	1. Exponential	2	-335.02	0	0.45	-
		2. Linear	2	-334.75	0.27	0.40	1.14
		3. Gaussian Model	3	-332.80	2.22	0.15	3.03
	Spruce	1. Exponential	2	-283.07	0	0.40	-
		2. Linear	2	-282.64	0.43	0.32	1.24
		3. Gaussian Model	3	-282.32	0.75	0.28	1.46
Volume versus basal area	Beech	1. Linear	2	-356.76	0	0.44	-
		2. Exponential	2	-356.65	0.11	0.42	1.06
		3. Gaussian Model	3	-354.45	2.31	0.14	3.17
	Fir	1. Linear	2	-319.92	0	0.41	-
		2. Gaussian Model	3	-319.52	0.41	0.34	1.22
		3. Exponential	2	-318.92	1.00	0.25	1.65
	Spruce	1. Linear	2	-251.29	0	0.53	-
		2. Gaussian Model	3	-250.98	0.31	0.46	1.17
		3. Exponential	2	-243.32	7.96	0.01	53.62
Light versus basal area	2	1. Exponential	2	610.95	0	0.85	-
		2. Linear	2	759.42	148.4	5.8E-33	1.7E+32

$K_i$  = number of parameters;  $AIC_{ci}$  = Akaike Information criterion (corrected);  $\Delta_i$  =  $AIC_{ci}$  differences ( $\Delta_i - \Delta_{min}$ );  $w_i$  = Akaike weights;  $w_1/w_i$  = weight ratio;  $w_1$  = weight for selected model (best fit);  $w_i$  = weight for model  $i$

**Fig. 1** Scatter plots and nonlinear regression models for relative annual height (a silver fir; b Norway spruce; c European beech) and relative annual volume growth (d silver fir; e Norway spruce; f European beech) as a function of light (*PACL* percentage of above canopy light; *thin lines* represent the 95% confidence intervals)



The statistical results for this method were reported as suggested by Anderson et al. (2001) and are presented in Tables 3 and 4. The Akaike Information Criterion was used to discriminate among models belonging to different families of curves and not necessarily among models within the same family of curves. Therefore, for growth–light models, only the best-fit model among the saturating curves was presented in the tables with results.

## Results

### Stand structure

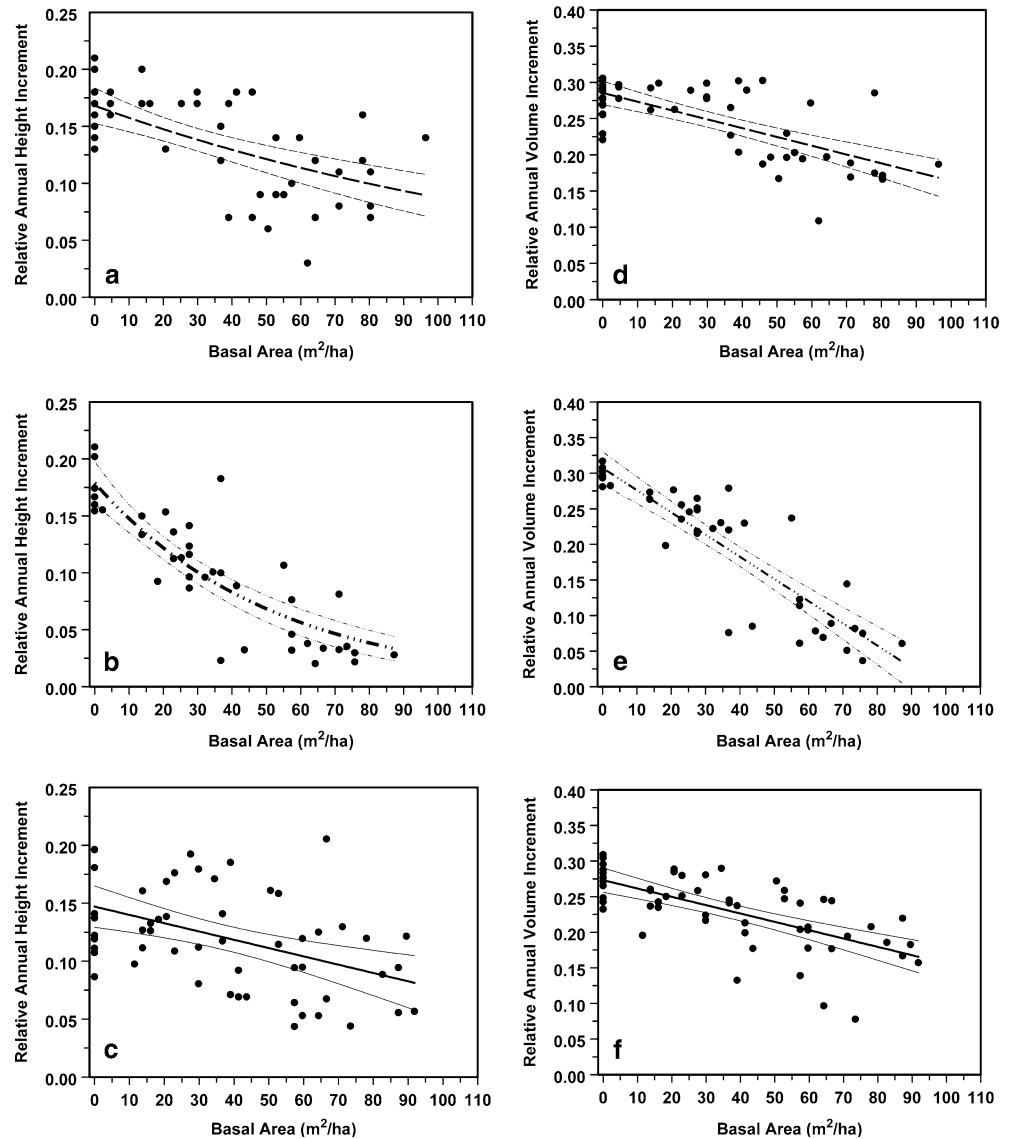
Although the range in height, diameter and age was rather large at each location (Table 1), the overstory of sampled stands included one or two cohorts. A very few

old (244–350 years) remnant trees were found at both Rusca Montana and Retezat but were not considered to represent a separate cohort (age class). Often, for sampled overstory trees, large differences in DBH and/or total height did not reflect the presence of two separate age classes but only different size classes.

In terms of vertical structure, some variation in total height was encountered at both locations (Retezat and Rusca Montana). All stands at Rusca Montana were classified as a single canopy overstory using the crown stratification method proposed by Latham et al. (1998). This situation is not uncommon as these stands were managed with even-aged methods.

At the other location (Retezat), management in the study area was less intensive (sanitation cuttings and transformation to uneven-aged structures) and therefore, overstory canopies were more complex. Variation in total height was greater here (Table 1) and two different canopy strata in the overstory were identified.

**Fig. 2** Scatter plots and empirical (direct) nonlinear regression models for relative annual height (a silver fir; b Norway spruce; c European beech) and relative annual volume growth (d silver fir; e Norway spruce; f European beech) as a function of stand basal area. (*thin lines* represent the 95% confidence intervals)



#### Relative regeneration growth versus light

Each of the subject species showed similar trends in relative annual growth for both height and volume (Fig. 1). A saturating trend provided the best fit for both spruce and beech. However, for both relative growth measures, the difference in likelihood to the second best fit (a quadratic function) for spruce was rather small (Table 3). For silver fir, a quadratic model represented the best fit for both height and volume, although a saturating model (logistic) had a very similar likelihood in both cases (Table 3). Values of regression coefficients and goodness of fit for final models are presented in Table 5.

#### Relative regeneration growth versus basal area: direct (empirical) method

A linear decreasing function was the best fit for volume growth and overstorey basal area for all three species

(Fig. 2). For height growth, the exponential decreasing model explained best the trend for both conifers, while a linear model was the best fit for beech (Fig. 2). However, for both height and volume, the other model types generally had very similar likelihood (ratio of weights was very small). Comparisons among the three different categories of curves are presented in Table 4. Final regression models selected for analysis are presented in Table 5.

#### Relative regeneration growth versus basal area: indirect (predicted) method

An exponential decreasing curve provided the best model for light (PACL) with increasing basal area (Table 2). The linear model had a very small likelihood given the data ( $w_1/w_i = 1.7E+32$ , see Table 4) and could be considered an inappropriate fit to this relationship. Coefficients and residual mean square error for the best fit are presented in Table 5.

**Table 5** Regression models (best fit) selected using Akaike Information Criterion (RMSE = residual mean squared error)

Regression (Y vs. X)	Species	Model	Coefficients			RMSE
			<i>a</i>	<i>b</i>	<i>c</i>	
Height versus light	Beech	Logistic	0.1408	0.3968	0.1396	0.0356
	Fir	Quadratic	0.0765	0.0028	-0.00002	0.0284
	Spruce	Weibull	0.0165	0.5384	-	0.0254
Volume versus light	Beech	Weibull	0.1607	0.1506	-	0.0330
	Fir	Quadratic	0.1591	0.0040	-0.00003	0.0287
	Spruce	Michaelis–Menten	0.3447	17.9184	-	0.0433
Height versus basal area	Beech	Linear	0.1471	-0.0007	-	0.0398
	Fir	Exponential	0.1681	-0.0065	-	0.0343
	Spruce	Exponential	0.1790	-0.0192	-	0.0282
Volume versus basal area	Beech	Linear	0.2731	-0.0012	-	0.0383
	Fir	Linear	0.2853	-0.0012	-	0.0374
	Spruce	Linear	0.3072	-0.0031	-	0.0420
Light versus basal area		Exponential	97.6686	-0.0331	-	8.1627

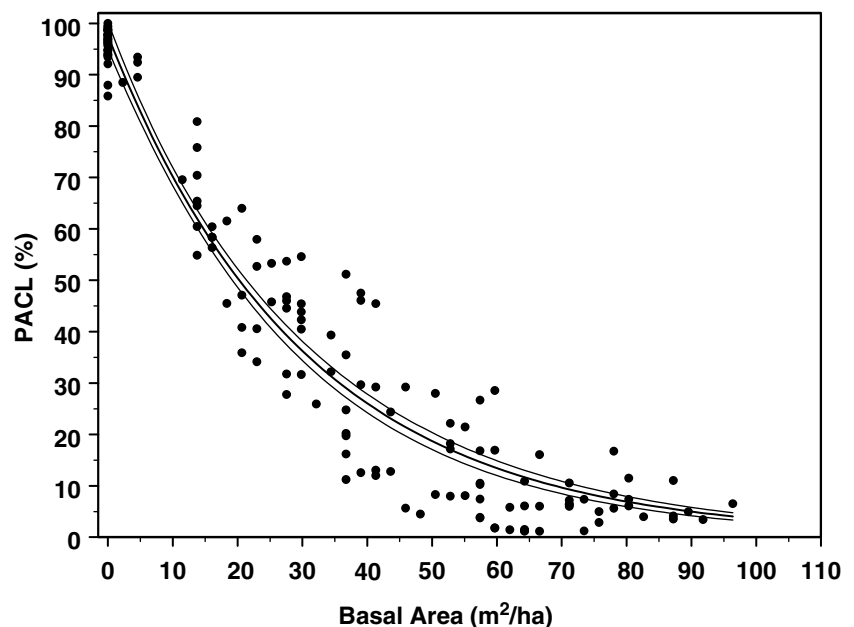
According to the exponential model, a marked decrease in PACL from 100% down to 15–25% occurs with an increase in basal area from 0 to  $\approx 40$ –50 m<sup>2</sup>/ha (Fig. 3). Thereafter, the decrease is moderate, with PACL reaching values close to 0 when basal area is around 100 m<sup>2</sup>/ha. This equation was included in the previously considered light–growth models for each species and used to predict growth over the range of basal area values encountered in the study. Growth estimates using this method were compared to those obtained with the direct method and the differences between them are presented in Fig. 4 and Table 6.

## Discussion

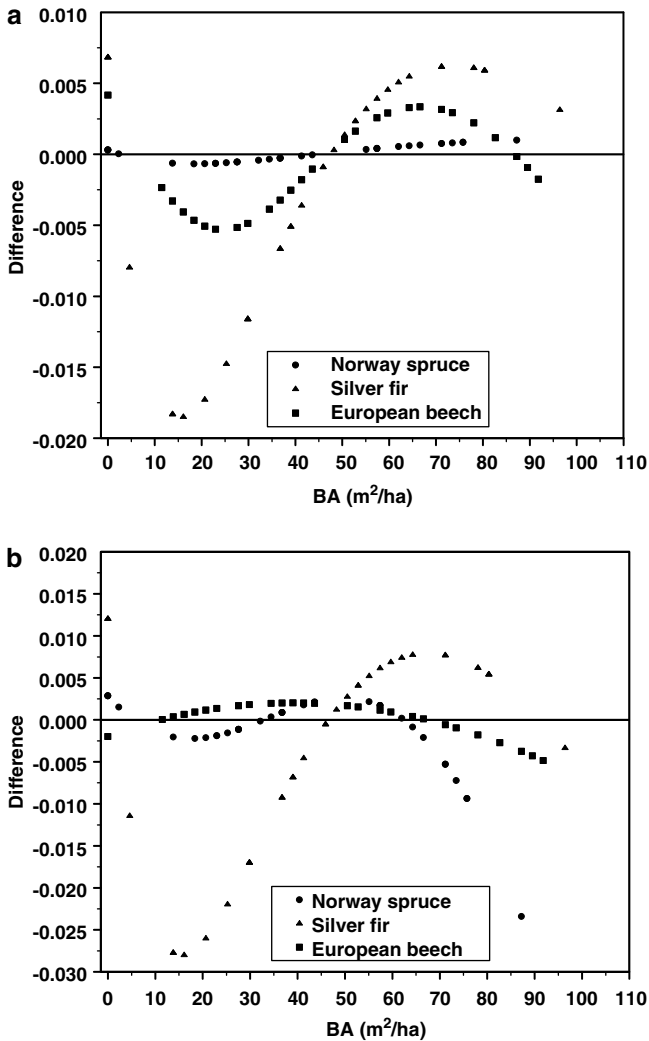
A decreasing exponential equation provided the best relationship between light and basal area of our stands

as has been reported for these species by Brunner (1993). The slow reduction in PACL above basal areas of 40–50 m<sup>2</sup>/ha (Fig. 3) shows that each additional unit of basal area above this threshold would have less effect on reducing light penetration than at lower basal areas. This could be explained by the fact that above a certain level of basal area, stands reach canopy closure and an increase in basal area is only due to an increase of the stem size and not necessarily crown size (and therefore cover). Wellner (1948) and Jackson and Harper (1995) reported such inverse relationships between illumination and increasing basal area as well. Barnes et al. (1997) found that the shape of this relationship would vary for different canopy structures and composition. The larger spread of data points when basal area is the explanatory variable implies that, at the individual tree level, it is a less precise indicator of growth than light. Basal area does not represent crown form and size (i.e., cover) or

**Fig. 3** Scatter plot and nonlinear regression model for light (PACL) as a function of basal area. (*thin lines* represent 95% confidence intervals)



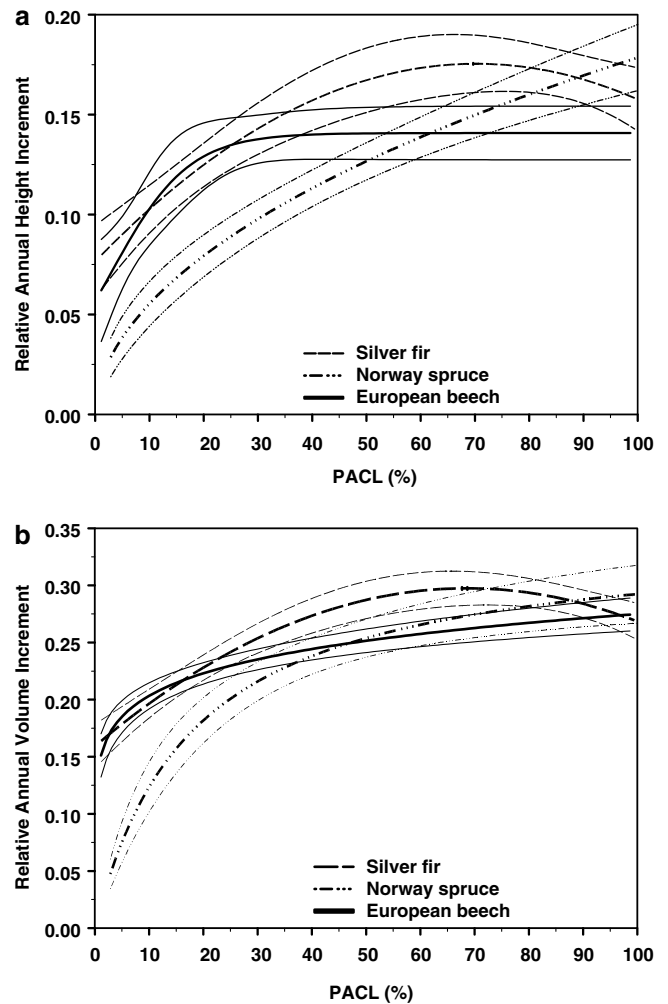




**Fig. 4** Differences between estimates of direct (empirical) and indirect (prediction) methods for relative growth (a height; b volume) along the range in basal area

tree distribution around the subject seedlings (spatially uniform or not uniform competition) (Canham et al. 1994).

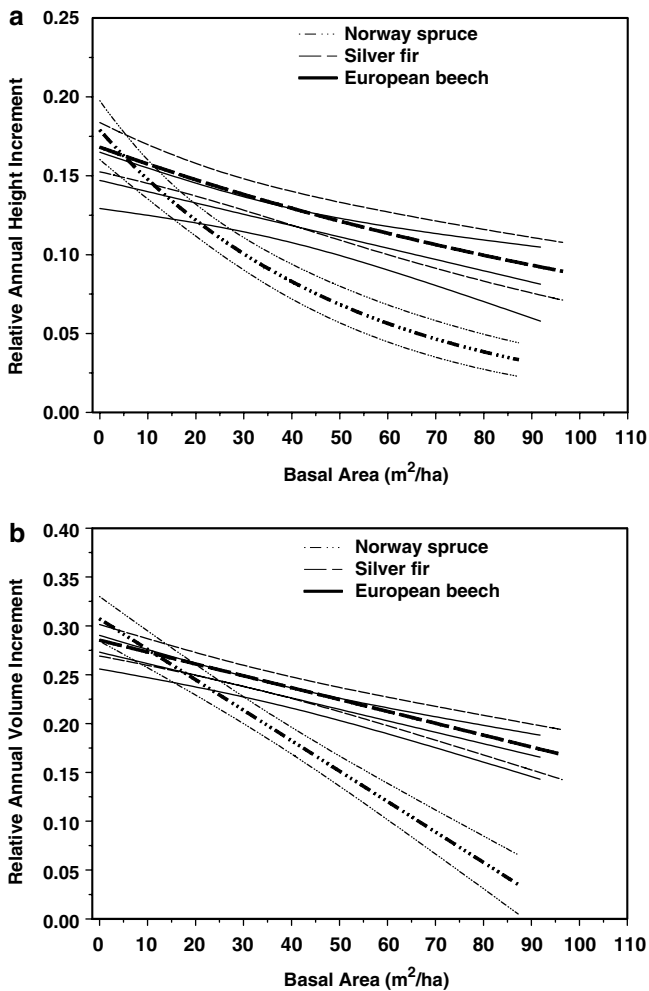
Between the two types of methods used for relative regeneration growth versus basal area, prediction models have a biological foundation as light is directly linked to photosynthesis (and therefore to biomass accumulation or growth). However, these indirect models are essentially a combination of two different equations, each one with its own coefficients and standard errors. Therefore, errors will propagate and RMSE will inflate. Alternatively, empirical models may have the advantage of a better fit (smaller RMSE) and also the advantage of explaining effects on growth of variables other than light (e.g., site). Considering these potential advantages and the fact that differences between the methods are relatively small (Fig. 4, Table 6), the empirical methods were considered more appropriate in this case.



**Fig. 5** Regression models for relative annual growth (a height; b volume) of all three species as a function of light (PACL); thin lines represent 95% confidence intervals

Compared to even-aged stands, growing space allocation in uneven-aged stands is usually not uniform (O'Hara 1996). Parts of the stand with closed canopy and intense competition in the understory may alternate spatially and temporally with thinned portions and gaps of different sizes and shapes. As a result, the behavior of fir, spruce and beech were analyzed over three separate intervals of available growing space (low, intermediate and high). To ease comparisons among different species and draw conclusions, growth–growing space regression models were combined together in Figs. 5 and 6. A 95% confidence interval was adopted to determine significant differences among species.

In dense stand conditions characterized by low levels of available growing space (PACL < 20–35%; BA > 30 m<sup>2</sup>/ha), growth of shade tolerant species (beech and fir) was clearly favored compared to the mid-tolerant spruce. In such conditions, beech and fir will grow into the main canopy while spruce is relegated to the lower strata. Although in the understory spruce is able to tol-



**Fig. 6** Empirical (direct) regression models for relative annual growth (a height; b volume) of all three species as a function of stand basal area. (thin lines represent 95% confidence intervals)

erate some shading, after long periods of suppression it has a lower ability to respond to release (Stanescu et al. 1997). Therefore, for previously established mixed regeneration, to maintain the spruce in the emerging canopy, cover should be reduced early and substantially. Beech has decurrent growth and its growing space has a strong influence on the form of the leader. Most stem forking and leaning stems occurred where PACL was below 20% (Stancioiu and O'Hara 2005, in press). Therefore, in such shaded conditions, beech should be released earlier than fir to avoid stem form damage.

For intermediate levels of canopy closure (PACL = 35–70%; BA = 15–35 m<sup>2</sup>/ha), spruce growth catches up with that of the more shade tolerant species. It shows a tendency to overgrow beech in height and volume towards the upper end of this growing space interval. In this intermediate shade, the mixture is maintained although fir seems to grow better than both spruce and beech. However, when compared to light (PACL = 35–70%), fir growth is significantly greater than only beech. When the independent variable is basal

area, for BA = 15–35 m<sup>2</sup>/ha, fir and beech have similar growth rates with fir growing significantly more than spruce for most of the interval.

In more open environments (PACL > 80–90%; BA < 15–20 m<sup>2</sup>/ha) all three species have similar growth rates. The decreasing trend for fir could represent possible growth inhibition of this very shade tolerant species in a high intensity light environment. Although, the mid-tolerant spruce seems to take advantage of the high light environment and to outgrow both beech and fir, the differences are not significant. Therefore, given the similar size and growth rates of regeneration of these species, the mixed composition will likely be maintained regardless of the possible inhibition (for fir) or early saturation of growth (for beech).

In a study carried out in the eastern Bavarian Alps (Brunner 1993; Brunner and Huss 1994), planted regeneration of these species behaved slightly different. In closed stands the spruce attained greater height than beech. In open conditions (clearcuts) fir grew less than spruce and beech which had comparable growth rates. For intermediate cover (shelterwood conditions) all three species were similar in height growth. However, the authors used linear models between height growth and light levels and did not sample the light interval between 35 and 90%.

Our results suggest that even though open space conditions may inhibit the regeneration establishment for fir and beech (Haralamb 1967; Stanescu et al. 1997; Savill 1991; Evans 1984; Padraic et al. 1998), growth rates for previously established seedlings of these species were not significantly lower than those of the more light-demanding spruce. Even in the case of a possible growth inhibition of fir in high light environments, growth reduction was not large enough to give a competitive advantage to spruce and beech. Therefore, within the size range of our study, fir and beech regeneration had growth rates similar to those of the mid-tolerant spruce.

When no advanced regeneration is present, opening the canopy would give a competitive advantage to spruce, being better adapted to regenerate in open space (Haralamb 1967; Stanescu et al. 1997). However, in this case, openings should be large enough to permit not only installation of patches of spruce regeneration, but also vigorous growth of the seedlings at rates comparable to those of the other two species. If openings are not large enough further growth is impeded as canopies reclose. This is especially true when the overstory surrounding the gap contains beech trees because this species is able to expand rapidly and close adjacent openings (Assmann 1970; Padraic et al. 1998).

Current management guidelines in Romania suggest that conifer regeneration should be established up to 10 years before regenerating beech, as this species is considered to have a much faster growth during the first decade (Negulescu and Ciumac 1959; Florescu and Nicolescu 1998). Therefore establishment at the same time of all three species followed by canopy removal would give a clear advantage to beech to outcompete both

**Table 6** Estimates and differences between estimates of empirical (direct) and prediction (indirect) models for growth as a function of basal area

Regression model	Species	Range of estimates		Differences range (absolute values)
		Empirical	Predicted	
Height versus basal area	Silver fir	(0.089–0.154)	(0.086–0.172)	(0.003–0.018)
	Norway spruce	(0.033–0.179)	(0.032–0.179)	(3.4e-5–0.001)
	European beech	(0.081–0.147)	(0.083–0.143)	(0.002–0.004)
Volume versus basal Area	Silver fir	(0.168–0.269)	(0.172–0.296)	(0.001–0.028)
	Norway spruce	(0.035–0.307)	(0.059–0.304)	(1.7e-4–0.023)
	European beech	(0.166–0.273)	(0.170–0.275)	(4.5e-5–0.005)

Absolute values of differences are presented here; real values of differences, positive or negative, are presented in Fig. 6

conifers. However, our results show that for previously established mixed regeneration, overstory removal promotes vigorous growth at similar rates for all three species. Furthermore, although growth rates seem to be similar, beech tends to grow less in open space compared to both fir and spruce.

Our regeneration trees were measured in relatively uniform growth conditions for the last 3–5 years or more. Therefore, possible differences in growth of the subject species as a response to a sudden release were not included here. In such a case, the beech may have some competitive advantages. Being deciduous, it is able to adapt its entire foliage to the new environment over a single year. Due to its decurrent growth (the largest crown diameter is usually in the upper third), it is adding much more new foliage in a more productive part of the crown compared to the conic-shaped crowns of conifers. It also has polycyclic growth which means, if environmental conditions are favorable, the bud set in place after shoot elongation ended could flush again and produce an additional estival (summer) shoot during the same growing season (Collet et al. 2002). This would probably permit greater growth for beech (compared to the preformed growth of conifers) for a sequence of successive years with favorable growing conditions (especially if they persist late in the growing season when conifer growth has ceased). Furthermore, it has a particular capacity of forming short shoots to exploit the growing space and long shoots to explore the available growing space (Thiebaut 1986; Thiebaut et al. 1985; Dupré et al. 1986). Such morphological plasticity helps this species not only explore new environments but also overtop the neighboring trees through lateral crown spread. Although adapting to the new light environment is slower for conifers, the spruce may have a slight advantage over the fir. This advantage may be due to a shorter period for needle retention (Stanescu et al. 1997) and to higher photosynthetic efficiency in high light environments where fir seems to be inhibited or at least less efficient (Grassi and Bagnaresi 2001).

Management to maintain more than one cohort (or canopy strata) on a site makes uneven-aged silviculture a challenging task. Furthermore, structural and functional complexity increases considerably when mixtures of different species are sought in the future stand.

Managers should try to match the light transmission through the canopy with light requirements for growth of desired species in the understory (Lieffers 1999). Even though seedlings of shade tolerant species can survive underneath closed canopies, their response to change in canopy cover is enhanced by vigorous growth before release (Helms and Standiford 1985). Therefore, our results could help managers decide when and how to release regeneration of these forests in order to avoid loss of growth vigor and also to favor different species in the future stand.

**Acknowledgements** The National Forest Administration and Retezat National Park granted access to field sites and inventory data. Access to laboratory supplies and technology was provided by Faculty of Biology and Geology (“Babes-Bolyai” University, Cluj, Romania) and by Traian Cadariu (Orastie, Romania). Assistance provided by Daniel Vasiu with field and laboratory work is greatly appreciated.

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