Ontogenetic variation in the relative influence of light and belowground resources on European beech seedling growth

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Summary   We used height growth data from a 7-year field experiment with European beech (*Fagus sylvatica* L.) seedlings to test the hypothesis that the effects of above- and belowground resources on height growth depend on seedling size and age. Photosynthetically active radiation (PAR) was determined by hemispheric photography, and estimates of fine root biomass of the overstory trees were used as an inverse proportional surrogate for belowground resource availability. For recently germinated seedlings growing under the canopy of *Picea abies* (L.) Karst., belowground resource availability affected height growth more than light. During subsequent stages of seedling development, apart from initial seedling size, PAR increasingly determined seedling growth. Besides initial size, seedling age determined the effects of above- and belowground resources on seedling height growth. In seedlings identical in initial size but differing in age, the increase in height growth with increasing PAR was greater in older seedlings than in younger seedlings. The ranking of seedling height by year showed that small differences in size at the end of the first growing season resulted in continuously increasing differences during the following years. Mortality data indicated that the chances of a seedling surviving intraspecific competition was strongly determined by its dominance ranking within the first 5 years after establishment.

Keywords: Fagus sylvatica, initial height, intraspecific competition, ontogenesis, resource availability.

Introduction

Growth responses of tree seedlings to differences in irradiance vary from site to site (Beaudet and Messier 1998) and appear to be related to belowground resource availability (Reed et al. 1983, Madsen 1994, Drever and Lertzman 2001). However, our knowledge of the responses of tree seedlings to limited resources and varying resource combinations is based mainly on short-term studies of less than 3 years (Sack and Grubb 2001). This means that size-dependent and ontogenetic shifts in the response of tree seedlings to resource availability and resource interactions have received little study (Williams et al. 1999,

Duchesneau et al. 2001, Claveau et al. 2002). Because both seedling size and age may influence growth reponses to resource availability (Lusk 2004, Claveau et al. 2005), integrated studies on tree traits in relation to resource availability, plant size and age, and their interactions are needed (Delagrange et al. 2004).

Competition arises when adjacent plants share limited resources (Chan et al. 2003). Competition is severe for tree seedlings growing beneath the canopy of a mature stand, where survival and growth are limited by low irradiance and strong belowground competition from overstory trees for water and mineral nutrients. The common view of competition in even-aged forest stands assumes a size-dependent (symmetric) depletion of belowground resources and a greater than size-dependent (asymmetric) aboveground resource preemption (Weiner and Thomas 1986, Cannell and Grace 1993). Asymmetric competition results in increasing differentiation in plant size with increasing plant density (Newton and Jolliffe 2003). This suggests that the size rank achieved by an individual seedling early in stand development will remain roughly constant. In a differentiated Scots pine stand, Ruha et al. (1997) reported that relative height rank was well established with few trees shifting in size class. Moreover, height growth rate was determined by the height rank of the tree and it was assumed that the relative height rank was determined during the first 5 to 10 years of stand age (Ruha et al. 1997).

We present data from a 7-year regeneration experiment, in which European beech (*Fagus sylvatica* L.) seeds were sown under the canopy of a Norway spruce (*Picea abie*s (L.) Karst.) stand. We tested the hypothesis that the effects of above- and belowground resources on height growth depend on seedling size and age. We also examined whether the assumption of early differentiation of tree seedling height rank and its persistence and its importance for intraspecific competition can be confirmed in the field.

Materials and methods

Study sites and stands

The investigation was carried out in two pure Norway spruce

stands in southern Germany (Bavaria) near Freising (48°24′49″ N, 11°41′18″ E, 490 m a.s.l.) and at Landshut (48°34′46″ N, 11°59′32″ E, 465 m a.s.l.). Soils (loess) and yield classes of the stands are similar and representative of many other pure Norway spruce stands in Germany. Both stands were slightly opened in 1997. Because of a local storm in 1998 and the subsequent mortality of some trees caused by bark beetles in 1999, stand volume and basal area of the Freising stand increased much less between 1997 and 2003 than did that of the Landshut stand. For details see Ammer and Mosandl (2007).

To investigate factors influencing successful direct seeding of European beech, experimental plots were established in 1997 under the canopy of each Norway spruce stand (see Ammer et al. 2002). On 2916 sample units of 0.5 m^2, spaced 2 × 1 m apart, on 18 plots in the two stands, 15 g of beech seeds (mean seed weight 0.228 g) were sown in May 1997 after removal of the organic soil horizons (Ammer et al. 2002). The seeds were covered with a 2-cm-thick layer of mineral soil from the same site. Both experimental stands were fenced to prevent damage by ungulates. On a subsample of 162 sample units per stand (9 sample units × 18 plots) every seedling was tagged after germination and surveyed from 1997 to 2003 (see below). However, seedlings did not germinate on every sample unit. At Freising, there were 129 sample units with seedlings and at Landshut, 145. The mean number of seedlings per sample unit decreased between 1997 and 2003 (Table 1).

Light measurements

On the total of 274 sample units with tagged seedlings at both sites, hemispheric photographs were taken in October–November 1997 and 2003 under an overcast sky, in the center of each sample unit at a height of 1.5 m, as described by Wagner (1994). The zenith luminance was measured in advance within a 5° angle of view (Wagner 1998); three stops of over-exposure were established. A photograph of an optical density wedge was taken on each film to establish the film density function in the laboratory according to the method described by Wagner (1998). The photographs were analyzed with OPTIMAS imaging software (Meyer Instruments, Houston, TX). The method is highly accurate (Wagner 1996), and takes account of penumbra effects. A photosynthetically active radiation (PAR) factor in relation to the open field was computed assuming 60% overcast skies and 40% clear skies within the vegetation period (Biederbick 1992). The resulting relative radiation value was considered representative for all seedlings in a sample unit.

Belowground resources

Because soil water and mineral nutrient content is affected by overstory tree roots (Gerhardt 1996, Ammer 2002), we used the inverse of fine root biomass of overstory trees as a surrogate for belowground resource availability (Wu et al. 1985). Overstory fine root biomass was estimated with a model for Norway spruce (Ammer and Wagner 2005) that calculates relative fine root biomass (rFRB) of an overstory tree as a function of its diameter at breast height (DBH) and its distance from a given point. In our study, rFRB at the center of each sample unit was calculated as the sum of the rFRB values of all trees contributing fine roots at that point, which were identified by the model. The sum was correlated with the fine root biomass obtained by 90 soil core samples in the Freising stand ($r = 0.85$) and 60 soil cores in the Landshut stand ($r = 0.68$; Ammer 2000). In addition, a significant negative correlation ($r = -0.74$) was detected between relative fine root biomass and soil water potential, measured at a depth of 30 cm with pressure tensiometers (T4-tensiometer, UMS GmbH, Munich, Germany) (Ammer and Wagner 2002). Because the coordinates of the sample units and those of the canopy trees of each stand belong to the same system of coordinates, it was possible to estimate the relative fine root biomass for each sample unit. Analyses indicated that seedling nutrient status was high (mean leaf nutrient concentrations were N 24.1, P 1.26, Ca 5.5, Mg 1.45 and K 5.2 mg g^{-1}) (Ammer 2000). Although interactions between soil water and nutrient availability exist (Fiedler et al. 1973, Walters and Reich 1997), we assumed that overstory fine root biomass affected the water status of the seedlings more than their nutrient status at our study sites, and in-

Table 1. Environmental and growth characteristics of European beech (*Fagus sylvatica*) seedlings grown under the canopy of two Norway spruce (*Picea abies*) stands. Abbreviations: PAR, photosynthetically active radiation; rFRB, relative fine-root biomass of overstory trees; *n*, number of sites or seedlings on all sites; and SD, standard deviation.

	Freising site					Landshut site				
	n	Mean	SD	Minimum	Maximum	*n*	Mean	SD	Minimum	Maximum
PAR (% open field)	129	15.0	12.7	3.0	52.1	145	6.1	3.1	1.6	14.1
rFRB 1997	129	1.71	0.71	0	3.38	145	1.52	0.56	0.02	2.70
rFRB 2003	129	1.98	0.81	0	3.82	145	1.90	0.61	0.21	3.25
Height (cm)										
1997	730	8.8	2.7	2.4	19.0	1310	8.9	2.3	1.9	17.5
1998	670	14.8	5.3	4.6	36.9	1229	14.7	4.4	3.1	35.1
1999	651	23.1	9.9	5.0	74.6	1163	21.6	6.9	3.7	50.0
2000	642	34.7	14.7	7.8	126.2	1155	32.2	10.6	4.7	73.6
2003	628	88.0	37.9	13.0	277.0	1148	76.0	27.8	10.0	198.5

terpreted estimated rFRB as a surrogate for soil water availability rather than nutrient supply. In theory, the effect of canopy density on soil water content is more or less independent of that of overstory fine roots, because the extent of tree lateral roots far exceeds the extent of the tree crown (Stone and Kalisz 1991). The correlation between PAR and rFRB was weak (Spearman correlation coefficient $r = -0.10$, $P = 0.23$ for the Freising stand, and $r = -0.024$, $P = 0.78$ for the Landshut stand).

Seedling measurements

The number of established seedlings varied among sample units. Repeated measurements of various attributes were made on each seedling in October–November of 1997, 1998, 1999, 2000 and 2003. The attributes measured included: stem length (mm); stem diameter 3 cm above ground (mm); crown length (mm, length from the first living first-order branch to the top of the seedling), crown width (mm, perpendicular maximum crown width). Additionally, any damage was recorded. The total number of seedlings measured was 730 at Freising and 1310 at Landshut. The number of seedlings decreased slightly between 1997 and 2003 (Table 1). At both sites, each undamaged seedling was ranked each year by height.

Data analyses and model validation

Height growth of only those seedlings subject to the least competition from neighboring seedlings at the beginning of the growing period was analyzed. We assessed the competition status of the seedlings in each sample unit at the beginning of each growth period by a competition index. The competition index was adapted from an index for old stands (Hegyi 1974) and was calculated as:

$$CI_i = \sum_{j=1}^{n} \frac{sd_j}{sd_i} \tag{1}$$

where CI is the competition index of seedling i at the beginning of the growth period. The value is calculated as the sum of the ratio between the stem diameters (sd) 3 cm above ground of competitor j and seedling i for all n plants of a given sample unit. All seedlings per sample unit were ranked according to CI. For further analyses, only seedlings with the lowest CI values were selected (one per sample unit).

We analyzed height growth of seedlings in Year 1 (1997), i.e., seedlings with no initial height (Class 1), mean annual height growth in the three following growing seasons of seedlings with an initial height between 0 and 30 cm (Class 2), or above 30 cm (Class 3). In contrast to Classes 1 and 3, in which all plants were even-aged, the seedlings in Class 2 differed in age.

Height growth was explored by linear multiple regression analysis with PAR, rFRB, initial seedling size, age (in the case of Class 2) and their first-order interactions as independent variables. For the analysis of Class 1 seedling data, PAR measurements were made in 1997 and rFRB values were calculated from diameter at breast height (DBH) measurements of the overstory trees in 1997. The analysis of Class 3 seedlings was relative to irradiance and DBH in 2003. Values of PAR and rFRB for the analysis of Class 2 seedlings of the overstory trees were calculated by averaging the measurements of 1997 and 2003. The selection of the "best" model was made according to Quinn and Keough (2002) by using the Schwarz Bayesian Information Criterion (BIC).

The linear regression models were parameterized based only on data from the Freising stand. To test whether the resulting models are reasonable, a model validation was performed based on data from the Landshut stand. Predicted values of seedling growth at Landshut were calculated from the regression equations parameterized with the Freising data. The predicted values were then regressed against the measured data.

Results

Range of resource availability and growth responses

Compared with seedlings at Freising, seedlings at Landshut received less light (Table 1), whereas estimated rFRB varied to a much lesser extent between sites (Table 1). Seedling survival over the 7-year study was 86.0% at Freising and 87.6% at Landshut. During this period, mean annual seedling height growth was 12.6 cm year^{-1} at Freising and 10.9 cm year^{-1} at Landshut (Table 1).

Linear regression analyses

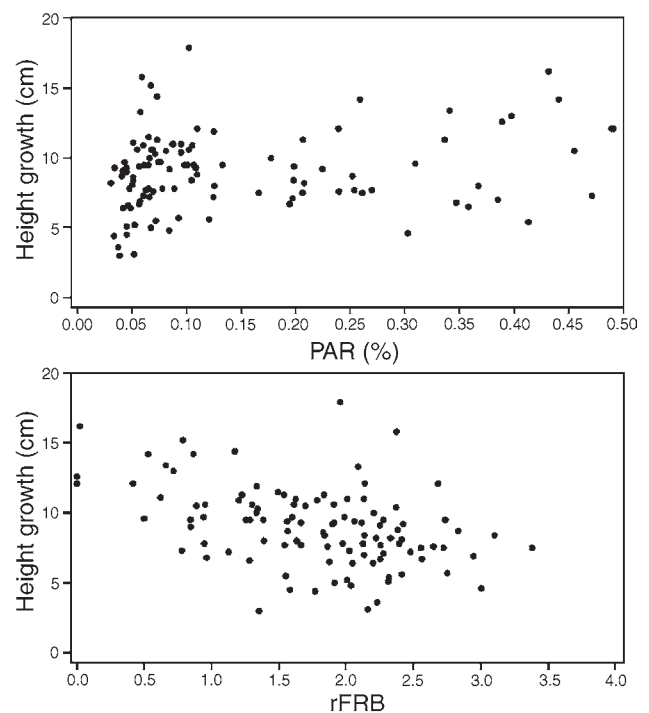Factors influencing height growth differed markedly among

Figure 1. First season height growth versus PAR and rFRB of European beech (*Fagus sylvatica*) seedlings of zero initial height in the first growing season (Class 1 seedlings).

the three seedling classes (Figures 1–4). At Freising, seedling growth during the first vegetation period (i.e., seedlings of Class 1, no initial height) was determined only by overstory fine root biomass, the inverse surrogate for belowground resource availability (Figure 1, Table 2). In seedlings of Class 2, initial seedling size, rFRB and the interaction between age and PAR influenced mean annual height growth (Figure 2, Table 2). These variables accounted for 56% of the variation in mean annual growth of the seedlings (Table 2). The growth response of 7-year-old seedlings to light differed from that of younger seedlings of the same initial height (Figure 3). In seedlings of Class 3, mean annual height growth was determined by both initial size and PAR, but not rFRB (Figure 4, Table 2). In contrast to seedlings of Classes 1 and 2, rFRB had no significant effect on height growth of seedlings of Class 3.

Growth responses of seedlings at Landshut were estimated for each of the three growing seasons, based on the equations in Table 2. Prediction of annual height growth of seedlings with the regression equations in Table 2 was best for seedlings of Class 2 (Figure 5). For this class, the regression model parameterized with the data for seedlings at Freising accounted for 43% of the variation in the data for seedlings at Landshut.

Seedling ranking from year to year

Previous-year seedling height was an important determinant of current-year height growth. The frequency distributions of changes in seedling height rank revealed that the number of seedlings showing little or no change in rank from year to year increased continuously during the first 4 years (Figure 6); meaning that rankings in consecutive years were closely correlated (Figure 7). Furthermore, this correlation increased with seedling age (Figures 6 and 7).

Discussion

Our first objective was to test whether the influence of above- and belowground resources on seedling growth depends on seedling size and age. We found that the effects of different resources changed as the seedlings grew. For small and recently
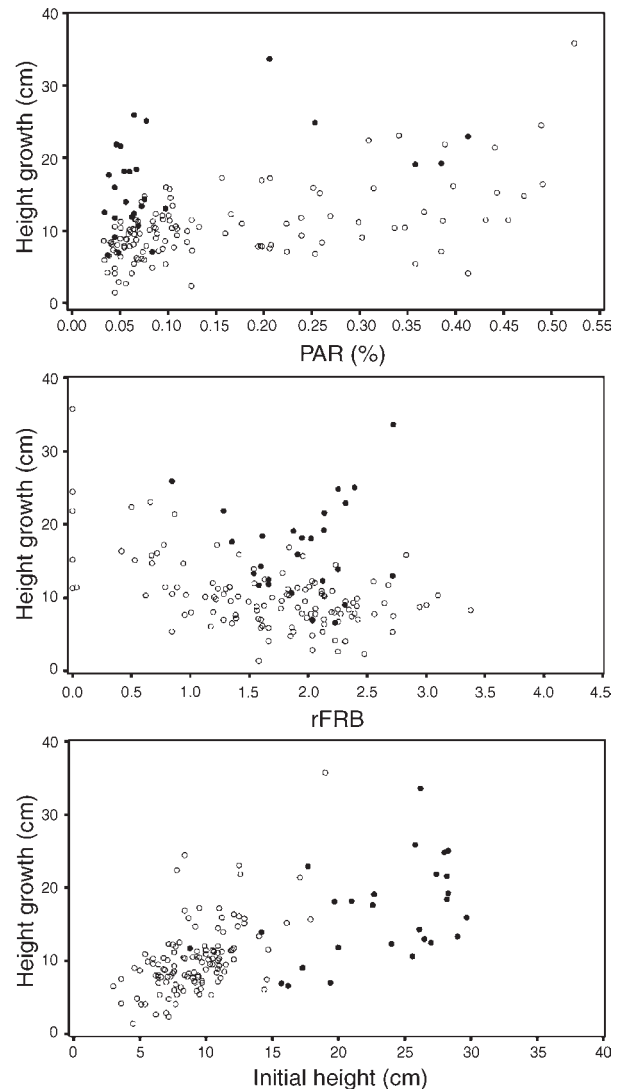

Figure 2. Mean annual height growth of European beech (*Fagus sylvatica*) Class 2 seedlings (with initial heights between 0 and 30 cm) during the last 3 years of 4-year-old (filled symbols) and 7-year-old (open symbols) seedlings versus PAR, rFRB and initial height.

Table 2. Results of linear regression analyses on annual height growth (h_g) of European beech (*Fagus sylvatica*) Class 1 seedlings with an initial height (h_i) of zero, i.e., newly germinated seedlings ($h_g = 12.34 - 1.89 \text{rFRB}$), Class 2 seedlings with h_i between 0 and 30 cm ($h_g = 4.09 + 0.30 h_i + 2.52(\text{age}(\text{PAR}^{0.25}) - 1.83 \text{rFRB})$) and Class 3 seedlings with h_i above 30 cm ($h_g = 15.95 + 0.17 h_i + 11.29(\text{PAR}^{0.25})$).

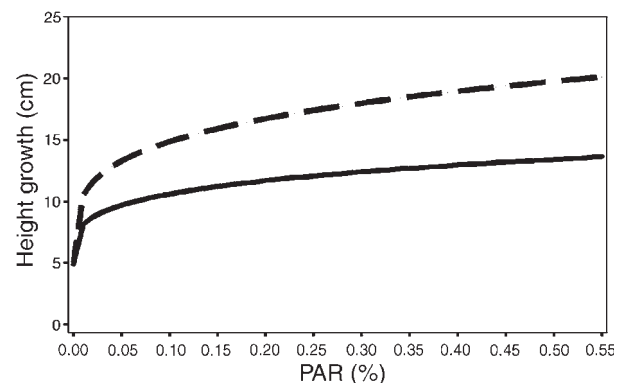| MSE	F	P	r^2	n
Class 1				
4.63	39.46	< 0.0001	0.27	103
Class 2				
10.33	62.14	< 0.0001	0.56	143
Class 3				
26.52	19.92	< 0.0001	0.30	88

Figure 3. Mean annual height growth of the last 3 years of 4-year-old (solid line) and 7-year-old (dashed line) European beech (*Fagus sylvatica*) Class 2 seedlings (with an initial height of 15 cm and an rFRB of 2.5) in response to PAR according to the regression equation in Table 2.
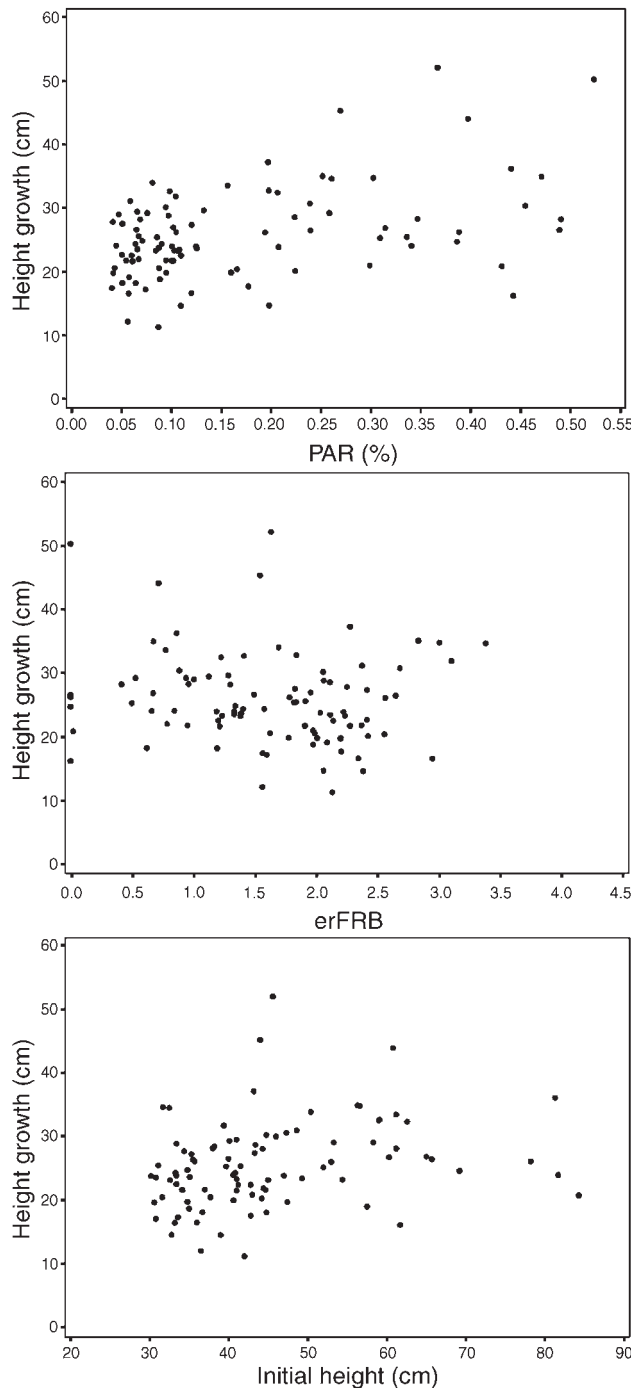
Figure 4. Mean annual height growth of the last 3 years versus PAR, rFRB and initial height of European beech (*Fagus sylvatica*) Class 3 seedlings with initial heights above 30 cm in the first growing season.
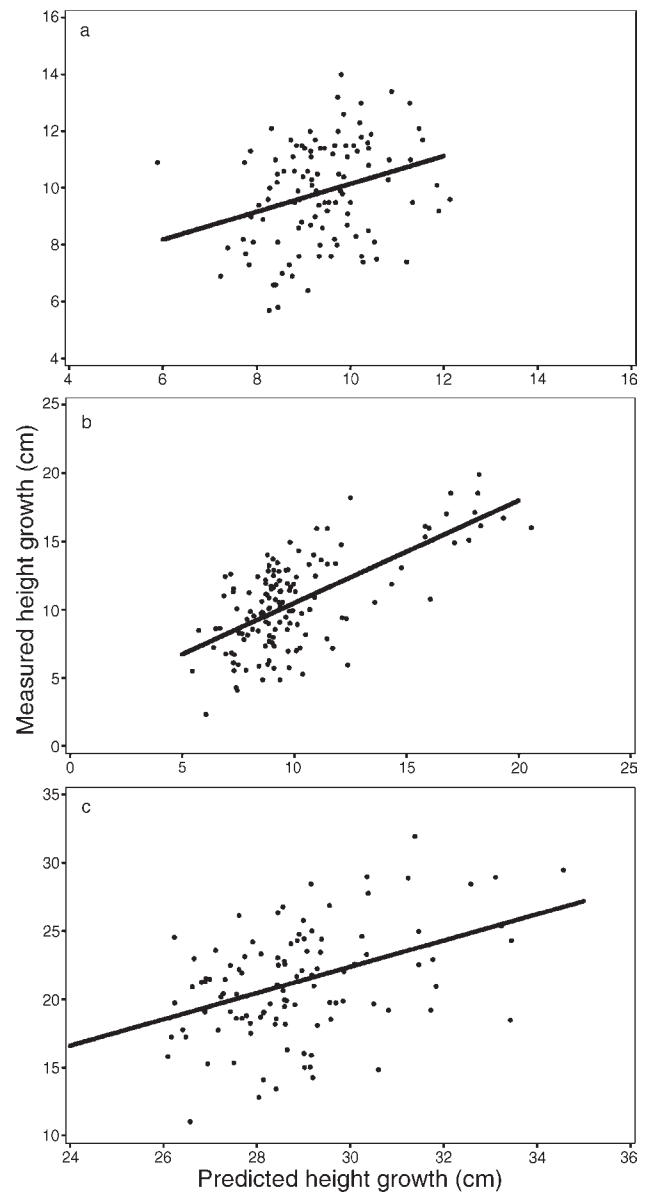
Figure 5. Relationship between measured and predicted mean annual seedling height growth of European beech (*Fagus sylvatica*) seedlings of Classes (a) 1, (b) 2 and (c) 3 at Landshut. Predicted values were calculated based on the regression equations shown in Table 2 which were derived by analyzing data for seedlings at Freising.

germinated seedlings (Class 1), belowground resource availability seemed more important than PAR during the first growing season. In the following stages, however, PAR increasingly determined seedling growth (Table 2). Whereas the variation in mean annual height growth of Class 2 seedlings could be explained by the estimated belowground resource availability and PAR, PAR alone predicted height growth of Class 3 seedlings (Table 2). These findings indicate the increasing importance of PAR as a determinant of growth with increasing seedling size. The effects of above- and belowground resources on seedlings height growth were dependent not only on seedlings size but also on seedling age, as demonstrated by the significant interaction between PAR and age in Class 2 seedlings, the only class to include seedlings of different ages but similar initial heights (Table 2, Figure 3).

Our results confirm the results of other studies indicating the importance of above- and belowground resources such as light and soil water content for seedling growth (e.g., Madsen
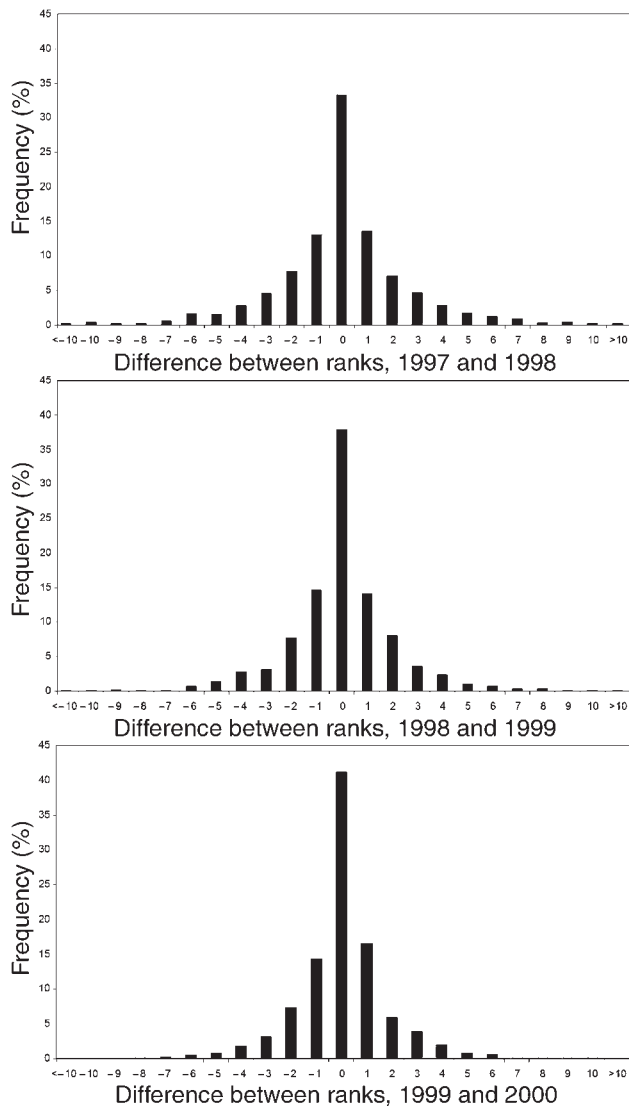
Figure 6. Frequency distribution of the magnitudes of year-to-year height rank changes in European beech (*Fagus sylvatica*) seedlings. Observations for all seedling classes at both sites have been combined. Positive and negative values indicate an increase or a decrease, respectively, in height rank of a given sample unit.
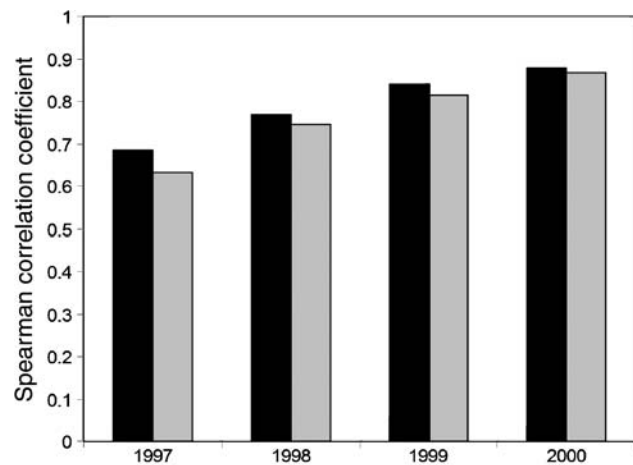

Figure 7. Spearman correlation coefficients between the seedling height rank of European beech (*Fagus sylvatica*) seedlings at Freising (black bars) and Landshut (gray bars) in 2003 and their rank in the preceding years.

1994, van Hees 1997, Chan et al. 2003). There is, however, no widely accepted theory on the relative importance of these resources. The existence of interactions between soil water content and light in deep shade is controversial (Sack and Grubb 2002, Machado et al. 2003, Sack 2004). Moreover, species differ in their growth responses to covariation in PAR and belowground resource availability (Walters and Reich 2000, Chan et al. 2003). Our finding that the importance of PAR and belowground resources varied with seedling size and age might explain the contradictory findings of others concerning the responsiveness of seedlings to belowground competition (Coomes and Grubb 2000, Ricard et al. 2003). Studies that showed no effect of belowground resource availability on pa-

rameters such as seedling height or diameter may have ignored the earliest stages of seedling establishment. It is reasonable to suppose that water is a crucial factor for seedling growth and survival in the first growing season when root establishment occurs (cf. Niinemets 1998). In older plants, however, soil nutrient and water availability accounts for much less variation in growth of juvenile trees than does light. Gratzer et al. (2004) argued that the spatial heterogeneity of belowground resources at the stand level is lower than that of light. However, our results indicate that heterogeneity in belowground resource availability within a stand can have significant effects on tree seedling growth in the earliest stages, as demonstrated by the significant inverse relationship between overstory fine root biomass and first season seedling growth.

Several studies have shown that effects of irradiance vary with tree size (Williams et al. 1999, Delagrange et al. 2004, Claveau et al. 2002, 2005). To our knowledge none of these investigations differentiated between effects of seedling size and age, probably because seedling size and age are usually well correlated, and their effects difficult to distinguish. Our analysis of Class 2 seedlings, however, suggests that both size and age influence the responses of *Fagus sylvatica* seedlings (Table 2, Figure 3).

Our results are consistent with work on ontogenetic variation in biomass allocation in shade-grown juvenile trees. In evergreen forests, seedlings of shade-tolerant species develop a large root mass fraction during their first year (Kitajima 1994, Paz 2003, Lusk 2004), which corresponds with our finding that belowground resources are most influential during this stage. The increase in aboveground biomass fraction during the following years (Lusk 2004, Lusk and Piper 2007) suggests the increasing importance of light.

Our second objective was to test whether the assumption of early differentiation of tree seedling rank, its persistence and

importance for intraspecific competition, could be confirmed in the field. We found that the statement of Ruha et al. (1997) that height rankings within seedling populations are largely determined during the first 5 to 10 years of growth can be extended. Within only 5 years of germination, we observed substantial differentiation in seedling height. Even small differences in height at the end of the first growing season resulted in larger differences during the following years. The process of asymmetric competition is therefore responsible for the increase in constancy of height ranking within cohorts (Figures 6 and 7). Thus, the pattern of asymmetric competition found among older trees (*Fagus sylvatica* between 35 and 85 years; Nord-Larsen et al. 2006) is similar in seedling populations. In addition to genetic and microsite factors, there are two possible reasons for the large early differences in heights of seedlings at the end of the first growing season. First, early germination may have given some seedlings a substantial advantage in growth duration. Second, differences in seed size probably affected the speed with which seedlings developed a resource-gathering system (Hewitt 1998). Seed mass accounts for much of the variation in initial seedling height when comparing different species (Moles and Westoby 2004, Green and Juniper 2004). Seed size also has a marked effect on seedling growth within species (Tripathi and Kahn 1990, Bonfil 1998). As a consequence of differences in initial seedlings height, the growth rate of each seedling is determined to an increasing extent by its previous-year relative height, as shown in Figures 6 and 7 (Ruha et al. 1997). For this reason, the regression models for Class 2 and 3 seedlings included initial height.

Growth responses of an individual seedling are difficult to predict because many factors are involved (Drever and Lertzman 2001). For example, substantial differences between provenances of *Fagus sylvatica* in response to differences in soil water contents have been recorded (Nielsen and Jørgensen 2003). In other studies, the coefficients of determination of regression for models describing the effects of resources on tree growth ranged between 0.1 and 0.7. The values in our study are within this range (Table 2). Direct comparisons of model predictions and measured data using an independent dataset are rare. Our results show that the models led to reliable predictions of seedling growth for the independent data but tended to overestimate measured growth.

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