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Evaluation of different approaches for modelling individual tree seedling height growth

Sven Wagner · Palle Madsen · Christian Ammer

Abstract We compared different approaches for modelling height growth of individual beech seedlings in a controlled factorial experiment as well as in field data from naturally regenerated beech seedlings under the canopy of overstorey mature beech trees. Several competition indices, a model of overstorey fine root density, relative photosynthetically active radiation (PAR) values, and soil water values were used in these approaches. In the factorial experiment *relative PAR* and soil water content were measured and used for the prediction of seedlings height growth. In the field experiment this was done by using *relative PAR* and estimated fine root biomass as a surrogate for below ground resource availability. The latter approach was compared with a model where we used various competition indices representing the impact of overstorey trees on beech seedlings. Our results suggested that (1) models which combine resource based growth functions are suitable for the prediction of individual height growth of beech seedlings. Resource based models offer the opportunity to investigate on the independent multiplicative effect of irradiance and water supply and their interactions on tree seedlings. It was (2) shown that a combined model could be used not only to predict individual height growth of beech seedlings in a controlled experiment but also in the field. The model parameters of a pure light response function for the controlled factorial experiment are comparable to those obtained in the field study. The results showed (3) that the precision of predicting beech seedlings height growth is comparable between the model types tested within this study. Approximately half of the observed variation in seedlings relative height growth rate could be explained. However, the simple competition index approach provides no information on the environmental factors constraining tree seedlings growth; whereas the multiplicative combined models can be used to get a better understanding of growth dynamics in the field.

Keywords Resource-based model · *Fagus sylvatica* (L.) · Competition index · Regeneration ecology

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Introduction

It is widely accepted that the canopy density of overstorey trees has a strong impact on survival and growth of understory seedlings and saplings (Beaudet and Messier 1998; Collet et al. 2001, 2002; Claveau et al. 2002; Kneeshaw et al. 2002). This knowledge is utilized in practical silviculture for the control of competition processes in mixtures of natural regeneration and seedling morphology (Wagner 1999; Wagner and Lundqvist 2004). The regarding silvicultural techniques are based on the fact that a mature stand determines the resource availability of other functional groups

within forest ecosystems and hence reduces growing space (sensu Oliver and Larson 1996). Growing space can therefore be seen as a surrogate to resource availability in so far, as overstorey trees affect the resource pool, e.g. of seedlings by their leaves and roots (Aussenac 2000; Collet et al. 2001). For many purposes it is sufficient to know that growing space, which can be easily expressed by competition indices, affects seedling survival and growth. For a profound understanding of regeneration dynamics and the ecologically founded further development of natural regeneration techniques however, it is essential to identify the factors influencing growth and shape of seedlings and saplings (Aussenac 2000). Moreover, examining these factors and their interactions may reveal mechanisms of both succession and managed natural regeneration processes (see Grubb et al. 1996; Battaglia et al. 2000).

One approach to study the effect of environmental factors and their interactions is to focus on the response of seedlings to limited resources (Goldberg 1990). However, this approach requires efficient measurement techniques for the evaluation of resource availability. As a consequence of the ongoing improvements in measurement technique which have been achieved, e.g. in photosynthetically active radiation (PAR)-sensors (overview in Dohrenbusch 1995) or in hemispherical photography (Chazdon and Field 1987; Rich 1990; Wagner et al. 2004), particularly the knowledge about the importance of PAR on survival and growth of seedlings has been improved very much (e.g. von Lüpke 1987; Comeau et al. 1993; Pacala et al. 1996; Collet et al. 1997; van Hees 1997; Gardiner and Hodges 1998; Welander and Ottosson 1998; Coates and Burton 1999; Williams et al. 1999; Kaelke et al. 2001; Aranda et al. 2002; Ammer 2003). In contrast to light, knowledge about the importance of belowground resources for seedling vitality and growth has been increased much less although some progress is achieved (Havranek and Benecke 1978; Reed et al. 1983; Flaig and Mohr 1990; Tognetti et al. 1994; Madsen 1995; Gerhardt 1996; Khan et al. 1996; van Hees 1997; Ammer 2002; Machado et al. 2003). In order to overcome the problem of how to get sound data of the belowground resource availability for individual seedlings, research on belowground resources has often been carried out under laboratory conditions but only rarely in the field. This is due to the fact that laboratory experiments provide the possibility to distinguish the effects of belowground resource availability on plant performance from aboveground factors like the PAR. Such a distinction is, however, much harder to achieve under natural conditions. Field research on the interactions between PAR and belowground resources and their effect on tree seedling growth are therefore a challenging and inspiring task. However, up to now the few investigations on this subject revealed contradicting results (Canham et al. 1996; Walters and Reich 1997; Finzi and

Canham 2000; Drever and Lertzman 2001; Aranda et al. 2002; Machado et al. 2003; van Hees and Clerkx 2003; Ricard et al. 2003; Sack 2004).

An elegant method to avoid laborious field measurements when assessing belowground resource availability has been reported by Kuuluvainen and Pukkala (1989). These authors calculated the amount of overstorey tree roots and used the calculated data for the evaluation of the abundance of Scots pine seedlings. The concept behind this approach is deduced from the "ecological field theory" which was developed by Wu et al. (1985). It takes the finding into account, that the amount of overstorey tree fine root biomass is related to soil moisture (Gerhardt 1996; Ammer 2002). In fact Ammer and Wagner (2002) and Lee et al. (2004) have shown that it is possible to predict the fine root biomass of mature trees by the application of tree root distribution models. Such model approaches take advantage from the fact that in contrast to radiation availability on the forest floor, belowground resources are affected more or less radialsymmetrically from the tree trunk (Wu et al. 1985), whereas light availability is influenced by a single tree heterogeneously in respect to azimuth directions on the northern hemisphere. Seedling growth may therefore be modelled using a combination of real resource information (e.g. PAR) and a surrogate for belowground resource availability of seedlings (Wagner 1999; Ammer et al. 2008).

Against this background the main objective of the present study was to test whether such a model which combines measured data of the aboveground resource PAR with data on the belowground resource availability derived by a fine root distribution model, yields better or equal results than explaining seedling growth by classic competition indices reflecting limited growing space. For this purpose we (1) derived a model for the height growth of beech seedlings in a factorial experiment which combines the resources light and soil moisture. Data from this experiment was used to find an appropriate combination of the functions describing the relationship between light and growth and soil moisture and growth. We then (2) tried to answer the question whether the derived method of a multiplicative combined factor model is also suitable to model height growth of naturally regenerated beech seedlings under the canopy of overstorey mature beech.

Methods

Experimental designs

Controlled factorial experiment

The experiment was carried out on farmland in 1990–1991 at the Højbakkegaard agricultural experimental station

20 km west of Copenhagen, Denmark. A two-factorial split-plot design randomized in two blocks was used with light, i.e. "*relative PAR*" (see "*PAR*-measurements") as the whole-plot factor and soil moisture, i.e. "SW" as the sub-plot factor. Each of the two factors was regulated to four levels making a total of 16 different treatments. In total this experiment comprised 32 containers.

May 1st 1990 15 beech nuts were sown in each of the 20 l containers (40 cm tall and diameter 25 cm). When all seedlings had emerged they were randomly thinned to seven seedlings in each container. The growth medium of each container was 18 l of homogenized soil, which originated from a A-horizon of a 139-years old beech stand (18% clay and base saturation 37%).

Shading curtains were placed by June 2nd (3 weeks after seedling emergence) to regulate the relative light intensity to 3, 10, 30 and 65% in the four light treatments.

The experiment was located at an experimental area, which was automatically covered by a glass roof during rain. Additionally, irrigation and soil moisture measurements were carried out to control the soil moisture treatments. Madsen (1994, 1995) has described the experiment in greater detail.

Field experiment

Six gaps of 20–30 m diameter in a 110-year old 15 ha beech stand were created in March 1988 succeeding a light beech mast in October 1987. European beech (*Fagus sylvatica* L.) accounts for 88.9% of the basal area and 91% of tree number of that stand. The top height of the overstorey beech trees was 33 m. The stand is located in the forest district Göttinger Wald, Lower Saxony, Germany (51°30′N, 9°48′E; 310 m elevation). The soil is calcareous limestone bedrock topped by a fairly heterogeneous loess cover. The loess cover extents 0–40 cm in height giving pH (KCl) values of the soil from 6.5 to 4.5 depending on the thickness of the layer which is correlated to base saturation values between 90 and 50% (Meiwes and Beese 1988). The humus layer is classified as F-Mull. Precipitation reaches 680 mm a year, 340 mm falls from May to September; summer drought can be observed occasionally. The mean temperature from May to September is 14°C.

After the cuttings the entire area was fenced immediately and sample units of 0.5 m^2 were established on the gaps and in the surrounding stand to perform regeneration measurements. In each gap 20 sample units were located in the northern, eastern, western and southern part of the gap as well as in the middle of the gap. Four sample units were placed in the closed stand, southward to each corresponding gap.

Germination of beech seedlings took place in spring 1988 and the seedlings grew up without any weed control.

Thus the true radiation environment of a particular seedling changed from year to year depending on its height relationship to the surrounding vegetation (Jobidon 1994). However, it is not known to what extent the ground vegetation affected soil water availability as well. At the end of the third vegetation period the height (in millimetres) of each seedling was measured and the radiation level above each sample unit related to open field conditions was assessed by means of hemispherical photography (see "*PAR*-measurements").

Data collection

PAR-measurements

"Photosynthetically active radiation" is a wavelength range (400–700 nm). However, for ease of writing in this paper "*relative PAR*" is understood as the relative radiation intensity at 400–700 nm wavebands (μmol m^{-2} s^{-1}) measured at the forest floor in relation to the radiation intensity at 400–700 nm wavebands above canopy.

(1) Measurements in the factorial experiment

A LI-COR Quantum Sensor placed below and above the curtains determined the light levels below the shading curtains.

(2) Measurements in the field

Above every sample unit on the experimental area a hemispherical photography was taken under overcast conditions (obscured overcast sky condition—sensu Grant et al. 1996) with a Canon® AE-1 camera and a Canon 7.5 mm, f/5.6 lens on an AGFA®-ORTHO film. The zenith luminance was measured in advance within an angle of view of 5° (Wagner 1994, 1998; Clearwater et al. 1999); three stops of over-exposure were established. A photograph of an optical density wedge was taken on each film, allowing establishing film density function in the lab. With the method proposed by Wagner (1998) the photographs were analysed using the professional imaging software OPTIMAS®. The method has been proven to yield very high degree of accuracy (Wagner 1996) as, e.g. penumbra effects can be taken into account. The method allows for corrections of vignetting of the lens as well as for heterogeneous luminance distribution of an overcast sky (Wagner 2001).

"*Relative PAR*" in relation to open field was computed assuming 60% of overcast conditions and 40% of clear sky conditions (clear sky condition—sensu Grant et al. 1996) within the vegetation period (Biederbick 1992). This relative radiation value was considered to be representative to all seedlings on that particular sample unit. However, this individual seedlings radiation level cannot

be interpreted as equal for succeeding years. Thus it is not straightforward to relate the total height of the seedlings simply to the measured radiation level. Instead, individual height at the end of the fourth vegetation period was measured and the RGR of seedling height was calculated as:

$$p = (H_t + 1 - H_t)/H_t \qquad (1)$$

with "p" as the RGR, "H" the height value and "t" year.

Assessment of below ground resources and indices indicating limited growing space

Several different approaches were applied to estimate the intensity of factors important for the growth of beech seedlings besides *relative PAR*. Key variables chosen in this regard are below ground resource availability on the one hand and growing space on the other hand.

The belowground resource was directly measured in the factorial experiment, i.e. soil moisture. In the field experiment it was statistically derived by using a proxy: the modelled overstorey trees' root density. The latter approach is statistic by nature and has to be distinguished from models that are based on eco-physiological processes at the process level (e.g. Rötzer et al. 2008; Gayler et al. 2006; Zhang et al. 2006). Growing space was computed by classical position dependent competition indices algorithms.

(1) Assessment of below ground resources

Measurement of soil moisture in the factorial experiment: The target levels of soil moisture were 100, 80, 60 and 40% of field capacity in the bottom 14–28 cm of the containers, which was equivalent to 34.0, 27.2, 20.4 and 13.6 vol.% soil water content—further referred to as "SW." The soil moisture measurements were carried out by TDR technique (Topp et al. 1980; Rundell and Jarrel 1991) in 0–14 cm and 0–28 cm depth before irrigation, which was carried out weekly in the growing seasons. The soil moisture data made it possible to calculate the soil moisture in 14–28 cm depth and the amount of water necessary to reach the target moisture in 14–28 cm depth of each container.

Assessments in the field: Overstorey trees root density was derived from a fine root distribution model for beech. Fine root intensity of overstorey trees was estimated for each sample unit by a model developed by Nielsen and Mackenthun (1991). The model follows Wu et al. (1985) who suggested models reflecting "ecological fields" of overstorey tree roots which do not consider patchiness of root systems but which assume that tree roots are distributed simply distance dependent and radialsymmetrical to the tree trunk. This is particularly important belowground, where fine root distribution and the effects on water and nutrient resources are spatially tightly coupled while in contrast aboveground radiation effects can be measured far away from leaves. The model of Nielsen and Mackenthun (1991) predicts the amount of fine root (≤ 2 mm in diameter) in a zone of 45 cm soil depth per area soil surface (mg dry weight per cm^2 soil surface) by the following equation:

$$\text{RIS(dbh, dist)} = \left[A \left((\text{dbh}/2)^2 \pi \right)^D \right] \Big/ \left[1 + B \exp(C\text{dist}) \right] \qquad (2)$$

where "RIS" is the root intensity of a single tree, "dbh" is its diameter at breast height in decimetre, "dist" is the distance from the point of interest to the middle of the tree trunk in centimetres and A, B, C and D are parameters of the model which are taken from Wagner (1999; $A = 7.38$, $B = 0.223$, $C = 0.00825$, $D = 0.573$) for beech in a mixed stand. With these parameter values the root intensity declines monotonously with increasing distance to the trees trunk. The computed root intensity of this model depends on the diameter of the tree and is supposed to diminish further away from the trees trunk than 7 m. Based on this equation the amount of fine root biomass at a given point was computed by summing up the calculated fine root biomasses of all neighbouring trees at this point. Hence it is assumed that the total amount of fine roots at a given point results from additive contributions of the surrounding trees, located <7 m from the point of interest. No interactions between tree roots are taken into account (Nielsen and Mackenthun 1991). This results in:

$$\text{RI} = \sum_{i=1}^{n} \text{RIS}_i \qquad (3)$$

where "RI" is the total root intensity in a particular spot and "RIS$_i$" is the contribution of the i-th tree to that total. All surrounding trees which contributed to the root intensity were considered.

The value of this index is highest when the amount of overstorey fine root estimated is maximal (RI). As the scales of different indices are different, a normalisation was performed as follows:

$$\text{IRI} = 1 - \frac{\text{RI}}{\text{RI}_{(\text{max})}} \qquad (4)$$

with "RI$_{(\text{max})}$" as the maximum value of the index in that particular stand and "IRI" as the inverse root intensity. The statistically derived root density of overstorey trees is nothing else but a belowground position dependent competition index.

(2) Indices indicating limited growing space based on aboveground information

As outlined in the introduction height growth of beech seedlings was analysed by using common indices indicating growing space as independent variables (CI_1 to CI_3).

CI_1 is an adaptation of the competition index of Hegyi (1974):

$$CI_1 = \sum_{j=1}^{n} \frac{dbh_j}{dist_{ij}} \qquad (5)$$

where j represents the overstorey trees within a virtual reverse cone according to Pretzsch et al. (2002). For the determination of the overstorey trees within the cone, its vertex was assumed to be perpendicular to the position of each seedling. The angle which defines the width of the cone was 60°. The index itself is calculated by the sum of the diameters in breast height (dbh) of all selected overstorey trees divided by their distance to the subject seedling i.

CI_2 represents the competition index of Pukkala and Kolström (1987)

$$CI_2 = \sum_{j=1}^{n} \alpha_j \qquad (6)$$

where j represents the overstorey trees determined as for CI_1. The index is calculated by the sum of the angles which result by the virtual tangents from the subject tree seedling position in 1.3 m height to the each overstorey tree which laterally touch the stem in the same height.

CI_3 represents an index according to El Kateb (1991):

$$CI_3 = \frac{N^2}{ba} \qquad (7)$$

for the calculation of this index the overstorey trees are also determined as for CI_1. The index is the ratio of the square of overstorey tree number (N) and the corresponding basal area (ba).

Modifications of these indices where tested in addition. This means that we used a cone width of 90° and a radius of 15 m around the subject tree seedling for the identification of relevant overstorey trees. However, both modifications led to nearly identical results (not shown).

The values of all indices are highest when growing space is minimal. As the scales of the different indices are different, a normalisation was performed as follows:

$$ICI_i = 1 - \frac{CI_i}{CI_{i\,max}} \qquad (8)$$

with "CI_{imax}" as the maximum value of the index "i" in that particular stand and "ICI_i" as the inverse value of that competition index "i".

Data evaluation

In this study two single factor models were applied:

(1) following Drever and Lertzman (2001) and Lin et al. (2002) the Michaelis–Menten function was applied in the case of relative PAR and (2) the Mitscherlich function was applied in all other factors, i.e. SW, IRI and ICI. These models were either applied as single factor models or as combined models based on single factors each. The combination of two factors was modelled by a multiplicative approach (see, e.g. Tilman 1982; Reed et al. 1983). Thus, taking the combination of relative PAR and SW, the following equations were applied to predict the height growth of a seedling:

$$\Delta H = Hp(\text{PAR}, \text{SW}) \qquad (9)$$

where

$$
\begin{aligned}
p(\text{PAR}, \text{SW}) &= A[(\text{PAR} - B)/((A/C) + (\text{PAR} - B))] \\
&\quad \times \left[(1 - \exp(-D\text{SW}))^2 \right] \qquad (10)
\end{aligned}
$$

"ΔH" refers to height growth of a subject seedling in a given year with height "H" in the previous year, "p" is the relative growth rate (RGR) of that individual plant in the current year, depending on the specific conditions, e.g. radiation and soil water in the environment of the subject seedling represented by the availability of the resources relative PAR and SW in the previous year. Likewise we tested the effect of relative PAR and IRI instead of relative PAR and SW. The parameters were estimated by use of Eq. 9 and standard non-linear regression technique (SPSS 12.0). To test whether the height growth of the seedlings was significantly depending on both, relative PAR and additional factors, a stepwise approach was used. First, significance of bivariate correlation between relative PAR and the relative height growth value was tested. Second, the Michaelis–Menten function was parameterized with relative PAR as the only independent variable. Third, the bivariate correlation between the residuals resulting from this parameterization and the additional factor was computed and tested for significance. Finally, the two-factor function (Eq. 10) was applied if the previously mentioned correlation revealed to be significant. As independence between the two "explaining" variables is a prerequisite for application of the two-factor model we observed the correlations carefully, e.g. evaluated bivariate correlation coefficients between the two independent variables.

(2) Models using indices of growing space availability
We took the general relation

$$\Delta H = Hp(ICI_i) \tag{11}$$

and

$$P(ICI_i) = A\left[(1 - \exp(-DICI_i))^2\right] \tag{12}$$

using the Mitscherlich function where "A" represents the asymptotic RGR and "D" is a scaling factor for the index in regard.

Results

Controlled factorial experiment

The relevance of *relative PAR* to the relative height growth rate ("p") is obvious as is the relevance of soil moisture (SW) to the residuals of the pure *relative PAR* model (Table 1). There was no significant correlation between *relative PAR* and SW (Table 1).

The application of the combined resource use model (Eq. 10) to the measured growth rates of the single trees yielded the parameter estimates given in Table 2 for the factorial experiment. From this an asymptote value for the 2-year-old beeches of more than 200% relative height growth rate can be taken ($A = 2.31$). This means that 1-year-old beech seedlings might triple height in the second growth season if the conditions, i.e. resource availability are optimal. In addition the goodness of fit is shown in Fig. 1 and in Table 2 (seventh column). Thus 54% of the observed variation in individual tree height growth could be explained by a model which combines information on light and soil moisture and integrate these resources within a multiplicative growth function. Figure 1 provides information on the residuals of the height growth model with respect to the two independent variables *relative PAR* and SW. *Relative PAR* and SW were not correlated to the

residuals of the combined resource model of Eq. 10 (Table 1). Merely the residuals of the model with respect to seedlings height of the previous year were not as evenly distributed as for the two resources (Fig. 1).

Field experiment

As the model used in "Controlled factorial experiment" revealed reasonable results we tested the combined resource model for the prediction of beech seedling in the field. The analysis of the field data showed a significant relationship between *relative PAR* and the relative height growth rate ("p") of the seedlings (Table 1) which is comparable to the controlled factorial experiment. Moreover, applying the one-resource use model based on *relative PAR*, IRI showed significant correlations to the residuals (Table 1). This means that IRI provides additional information which could be used modeling combined resources as shown in Eqs. 9 and 10. In contrast to the factorial experiment however, there is an albeit weak but significant correlation between *relative PAR* and IRI (Table 1). Parameter estimates of the field experiment using *relative PAR* and IRI in a model of two combined resources are shown in Table 2. The asymptote value for 4-year-old beeches amounted to 48% relative height growth rate. This means that a 3-year-old beech would add nearly 50% of its actual height in the fourth growing season at maximum if conditions are optimal under the given conditions, i.e. if best resource availability in the field experiment is given. The goodness of fit, when using the full combined resource use model (Eq. 9), can be seen from Fig. 2 and Table 2 (seventh column). Nearly 50% of the variation in individual seedling height growth could be explained by the model (Table 2, column 7). Residual plots of the combined resource use model with respect to the three independent variables *relative PAR*, IRI and *h* are presented in Fig. 2. It is evident from this figure and Table 1 that there is no significant correlation between the residuals and the three independent variables.

Table 1 Bivariate correlation coefficients for the two models based on one and two combined resources

Factorial experiment		Field experiment	
One resource			
Relative PAR ⇔ *p*	0.222 $P = 0.003$	*Relative PAR* ⇔ *p*	0.175 $P = 0.000$
SW ⇔ resid	0.551 $P = 0.000$	*IRI* ⇔ resid	0.121 $P = 0.008$
Relative PAR ⇔ *SW*	−0.073 $P = 0.287$	*Relative PAR* ⇔ IRI	−0.129 $P = 0.005$
Two resources			
Relative PAR ⇔ resid	0.033 $P = 0.667$	*Relative PAR* ⇔ resid	−0.021 $P = 0.652$
SW ⇔ resid	−0.114 $P = 0.134$	*IRI* ⇔ resid	−0.087 $P = 0.056$
h ⇔ resid	−0.276 $P = 0.000$	*h* ⇔ resid	−0.046 $P = 0.311$
N	174		482

Table 2 Parameter estimates and asymptotic standard error values for the combined resource use model (Eq. 12)

	A	B	C	D	N	r^2
Factorial experiment	2.31 ± 0.23	338.4 ± 98.2	0.02	5.93 ± 0.67	174	0.54
Field experiment	0.48 ± 0.03	87.9 ± 30.8	0.02	3.52 ± 0.55	482	0.49

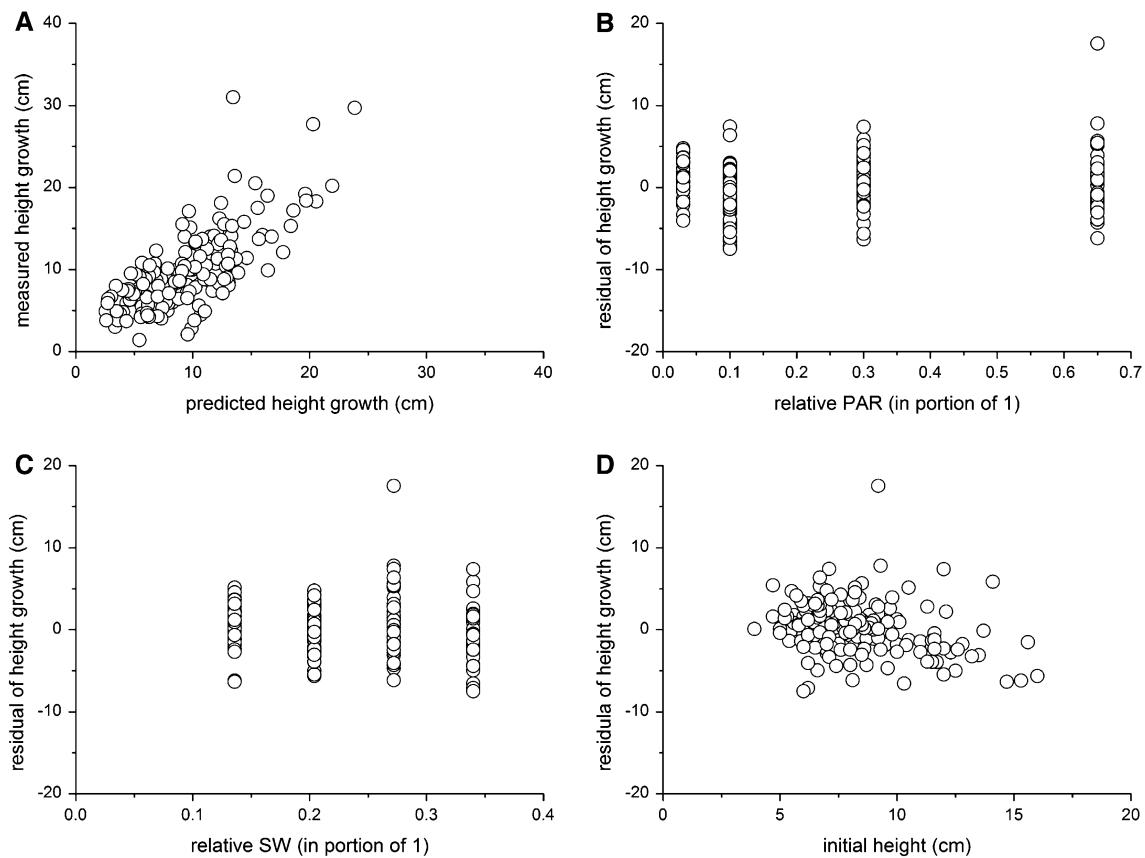The value of C was determined in advance

Fig. 1 Factorial experiment; goodness of fit of the combined resource use model and bisector (**a**) and the corresponding residuals in relation to *relative PAR* (**b**), soil moisture (*SW*) (**c**) and initial height (**d**)

In addition to the resource based prediction of beech seedling growth a simple model using growing space availability expressed by several indices (CI_1 to CI_3) was comparatively tested. This approach (Eq. 11) yielded the parameter estimates given in Table 3. It is evident that the differences between the indices in explaining beech seedling height growth are small. The best prediction of relative height growth showed index CI_2 (Table 3; Fig. 3). Although the goodness of fit is satisfying (Fig. 3a) it seems that a slight bias is to be observed in so far, that neither the highest measured values are predicted very well nor are the lowest. Residuals of the growing space model (Eq. 12) taking index CI_2 into account were neither significantly correlated to ICI_2 nor to initial height (Fig. 3). However, residuals were correlated to *relative PAR* ($r = 0.117$, $P = 0.010$). A look at the estimates of this index reveals an

asymptote value for the investigated 4-year-old beech seedlings of approximately 42% relative height growth rate (Table 3). This means that a 3-year old beech would add around 40% of its actual height in the fourth growing season at maximum if the conditions are optimal.

Discussion

Is a model combining resource based growth functions suitable for the prediction of individual height growth of beech seedlings?

To answer the first question outlined in the introduction, we used existing data from the controlled factorial experiment. It is evident that both *relative PAR* and *SW*
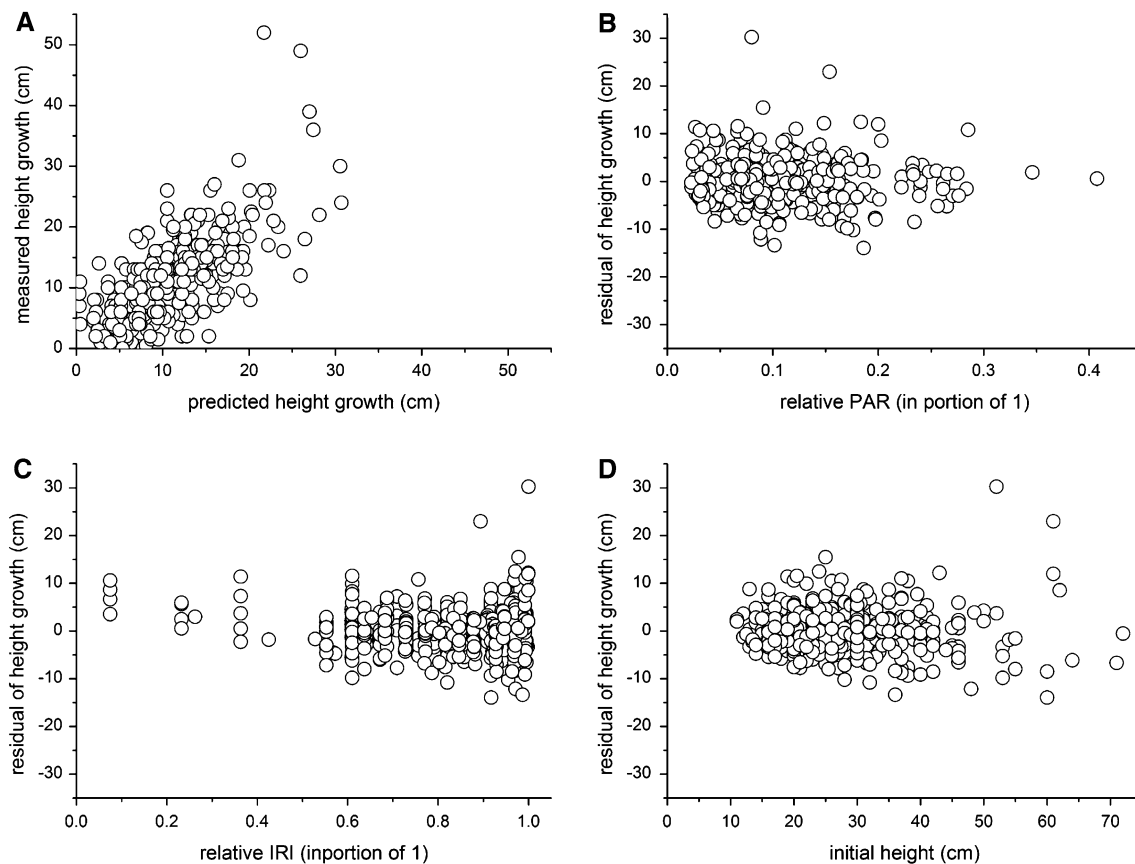
Fig. 2 Field experiment; goodness of fit of the combined resource use model and bisector (**a**) and the corresponding residuals in relation to *relative PAR* (**b**), *IRI* (**c**) and initial height (**d**)

are relevant resources for the height growth of beech seedlings (Tables 1, 2; Fig. 1). This finding is well known from previous studies (Burschel and Schmaltz 1965a; Tognetti et al. 1994; Madsen 1994, 1995; van Hees 1997; Collet et al. 2001, 2002; Ammer 2002). However, to our knowledge there exists no investigation where the appropriateness of a multiplicative approach of modelling *relative PAR* and soil water effect on height growth of beech seedlings has been tested. Such an approach has so far merely been presented for a combination of growth functions for tree seedlings response to light and nitrogen supply by Reed et al. (1983). In general, as stated by Coomes and Grubb (2000) "little is known from experiments about the combined effects of water shortage and shade". It is therefore noticeable that the factorial experiment revealed not only the result that the availability of soil moisture strongly influences seedling growth under different radiation regimes, but also the suitability of a multiplicative approach for the reasonable combination of growth functions. However, applying the multiplicative approach to our data resulted in a systematic weakness of the model in predicting height growth if high radiation availability was combined with poor water

Table 3 Parameter estimates and asymptotic standard error values for the growing space model

Index	A	D	N	r^2
CI_1	0.405 ± 0.012	7.570 ± 2.620	482	0.474
CI_2	0.416 ± 0.015	5.152 ± 1.146	482	0.478
CI_3	0.419 ± 0.012	6.157 ± 1.220	482	0.476

supply (Fig. 4). These conditions led to an extreme low increment which is contradicted by the idea of stable asymptotic *relative PAR* reaction of the plants over the whole range of soil moisture (Sack 2004). Nevertheless, the combined resource use model approach presented here offers the opportunity to investigate the independent multiplicative effect of irradiance and water supply combinations on woody species as suggested by Sack and Grubb (2002). Thus, the applicability of a combined resource use model was proven successfully in height growth modelling of beech (Table 1; Fig. 1).

While the growth of the seedlings in this experiment was not restricted by nutrient availability (Madsen 1994) the only belowground factor modified within the experiment
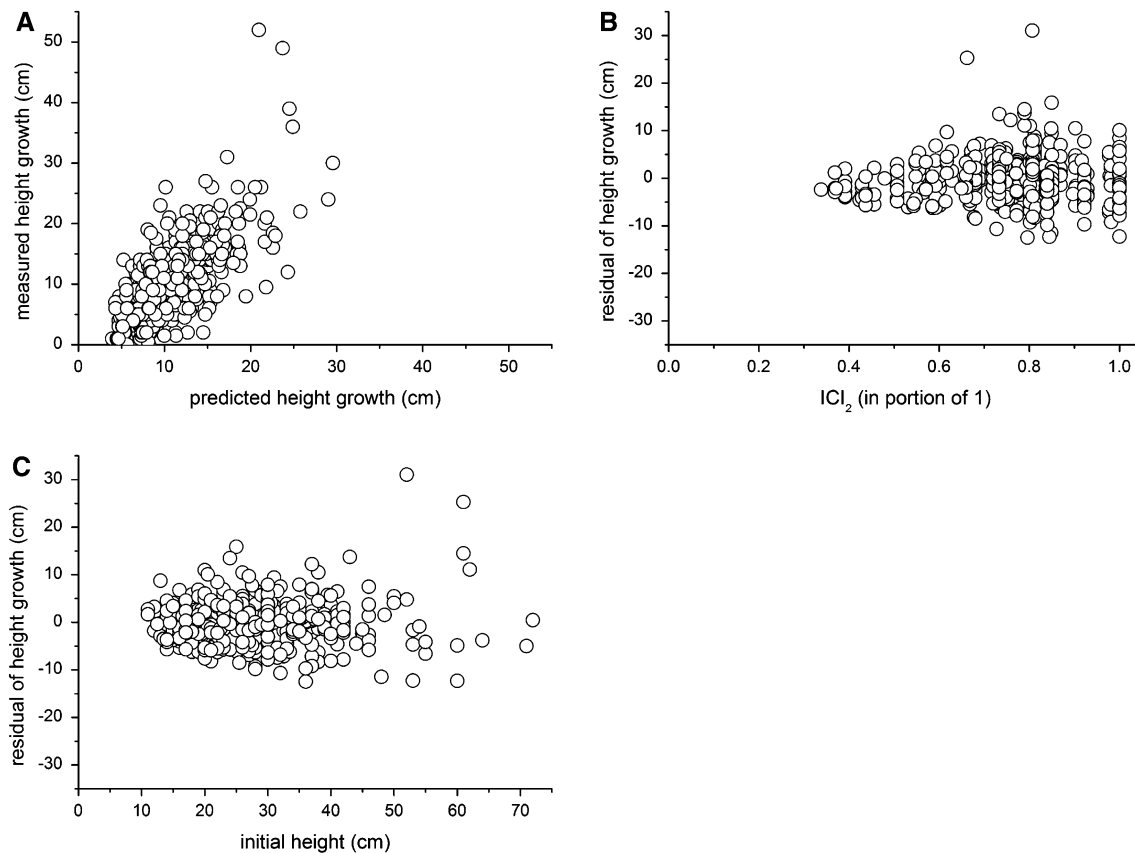
Fig. 3 Field experiment; goodness of fit of the index based model and bisector (**a**) and the corresponding residuals in relation to ICI$_2$ (**b**) and initial height (**c**)

was water supply. As a consequence the parameterisation of the combined resource use model should yield parameter values of the Michaelis–Menten portion ("B" and "C") for true *relative PAR* response. This means that without belowground resource constraints this parameterisation should hold true and should therefore be considered "pure *relative PAR* dependent" (Shainsky and Radosevich 1991; Mou and Fahey 1993).

Is it possible to predict individual height growth of beech seedlings in the field by a model which combines measured (light) and estimated (belowground resources) resource availability?

Against the background of the results of the factorial experiment and the physiological plausibility of combined resource use models (Smith and Huston 1989; Holmgren et al. 1997; Battaglia et al. 2000) it was expected that the chosen approach is also suitable to parameterise field data. As in the factorial experiment, water and not nutrients was likely to be the limiting belowground resource in the field experiment. This assumption is based on site characteristics like the pH (KCl) values of the soil, which range from 6.5

to 4.5 and the fact that the humus layer was classified as F-Mull. Ignoring the fact that there was a weak correlation between *relative PAR* and *IRI* (Table 1, fourth column) which will be discussed in the following, the multiplicative approach yielded satisfying results also for the field data (Table 2; Fig. 2).

Separating the effect of light and belowground resources in the field requires a broad range of values of both variables. To distinguish between the effects of *relative PAR* and a radial symmetric belowground resource within one experiment it is necessary to minimize the correlation between these two resources. This can experimentally be achieved by gap creation. In higher latitude on the northern hemisphere a high *relative PAR*-intensity on the northern edge of a gap and a low *relative PAR*-intensity on the southern part of a gap can be found (Canham et al. 1990). In contrast to *relative PAR*, assuming a distance dependency of fine root density distribution (Ammer and Wagner 2005; Zerihun et al. 2007), root density is constant in a particular distance to the gap edge (Brockway and Outcalt 1998; Ammer and Wagner 2002; Müller and Wagner 2003). However, while in the controlled factorial experiment no significant correlation between *relative PAR* and
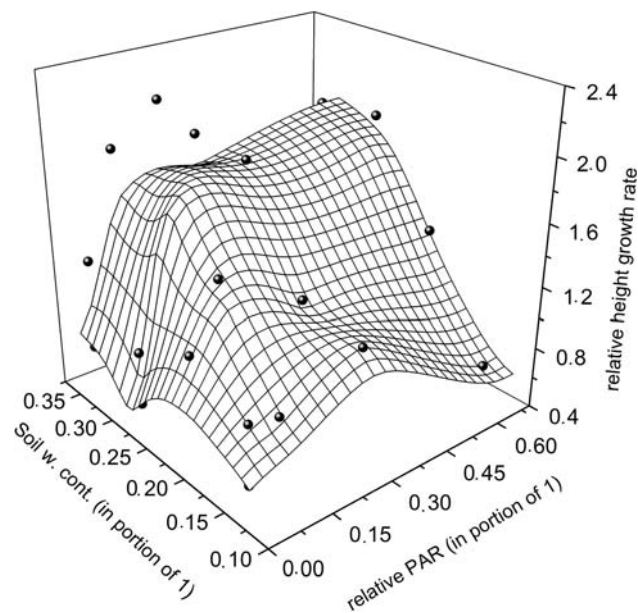
Fig. 4 Three-dimensional surface plot of radiation (relative PAR in portion of 1) and water (soil water content in portion of 1) impact on relative length growth rate of beech seedlings in the factorial experiment. *Open* and *solid* dots show values of the relative growth rate of each of the two plots per factor combination. The surface is computed by local linear regression. The low rlgr-value at relative PAR = 0.6 and SW = 0.15 is commented in the discussion

Fig. 5 Model function graphs of predicted relative height growth rate in relation to relative PAR (Michaelis–Menten portion for true *relative PAR* response of combined resource use model, Eq. 10) for the factorial experiment (*dashed line*) and the field experiment (*solid line*)

SW values was observed, a weak but significant correlation was given in the field experiment between *relative PAR* and IRI although we carried out the investigation using gaps.

Beside the independency of above- and belowground resources, the detection of resource effects on seedling growth is facilitated by a high variation of the resource in regard. This means that for example investigations which failed to identify a significant impact of soil moisture status on seedling growth (Burschel and Schmaltz 1965b; Pacala et al. 1994) presumably did not provide a resource variation which was high enough to do so. The stand investigated here matches the requirement of high water resource variability in so far that steep gradients of soil moisture availability were likely to occur in stands with large gaps and shallow soils. In such stands the variety of stand densities ranges from gaps to closed stand sections. The assumption that a high variation of soil moisture can be found in heterogeneously stocked mature stands was recently confirmed by Ammer and Wagner (2002). Like *relative PAR* which is attenuated by overstorey trees to very low light levels [in beech forests down to 2% compared to open field conditions (Larcher 1994; Mayer et al. 2002)] overstories can also drastically reduce soil moisture available for seedlings (Aranda et al. 2002). The idea of stand density as being a steering feature to soil water supply for seedlings is supported by work of Riegel et al.
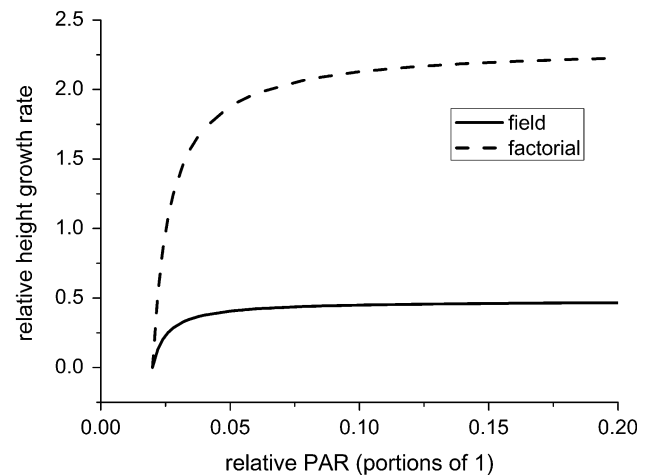
(1995), Walters and Reich (1997) and Coomes and Grubb (2000) who pointed out the distinct relationship between fine root mass and soil moisture and nutrient availability. Belowground resource availability is therefore supposed to be inversely related to the fine root intensity of overstorey trees. Based on this idea, which was promoted by Wu et al. (1985), we used IRI as a rough estimator for soil moisture availability. In fact Ammer and Wagner (2002) could show that fine root biomass predicted by models which integrate information about tree dimension and spatial distribution is correlated to soil moisture. Moreover, Ammer et al. (2008) recently showed that modelled fine root biomass of overstorey trees could partly explain variation in early seedling growth. Indeed the goodness of fit of the combined resource use model was fairly satisfying and the residuals were well balanced (Fig. 2).

Because IRI is radial symmetric, the parameterisation of the combined resource use model should yield parameter values of the Michaelis–Menten portion ("B" and "C") for true *relative PAR* response. The parameterisation should therefore hold true without belowground resource constraints. As hypothesised in the introduction it should be considered "pure *relative PAR* dependent" and parameters should be comparable to those of the factorial experiment.

Looking at the pure *relative PAR* response of the relative height growth of beech seedlings of both experiments in Fig. 5, two features are obvious: the two beech cohorts differ markedly in the value of the asymptotic RGR given unlimited *relative PAR* supply (2.3 versus 0.45) and the curves both pass through their steepest portions when *relative PAR* supply is <10%. Both features lead to almost identical curves when the ratio of the two asymptote values is taken as a factor for the conversion of one curve into the

other. In other words: if the Michaelis–Menten function parameterised for the 4-year-old beeches of the field experiment is multiplied with a value of 4.8 (ratio 2.31 to 0.48, the values of the parameter "A" in Table 2) a function results which is fairly the same than the one resulting from the parameterisation for the 2-year-old beeches of the factorial experiment. Thus, the Michaelis–Menten function of one experiment can simply be converted to the Michaelis–Menten function of the other experiment by multiplication with a constant. This finding is important in regard to parameterisation techniques for regeneration models in so far that a complete parameterised light response curve from controlled conditions (e.g. in the lab) might be taken to field data. Thus, parameter estimates will be more confident allowing for reduction of parameters to be estimated from field data, i.e. instead of three parameters of Michaelis–Menten function only one is necessary (asymptote).

However, the different value of the asymptote ("A") cannot fully be explained by the availability of *relative PAR*. Keeping in mind that the RGR is supposed to be (1) determined by endogen plant properties (e.g. age: Wenk et al. 1990; Ammer et al. 2004) and (2) by environmental properties (e.g. availability of resources: Thomas and Weiner 1989) and that soil moisture availability or belowground competition by overstorey tree roots was implemented in the models, only endogen plant properties remain as explaining variables for the different asymptotic values of the two growth functions.

In growth and yield research several functions have been developed to describe the age effect on RGR assuming no resource limitations, e.g. open field conditions (see Wenk et al. 1990; Weiner and Thomas 2001). These functions follow the assumption of a more or less steep decline of the RGR within the first years. Thus, the difference in the RGR level (value of the asymptote) between the two experiments might simply be explained by differences in age or initial height of the beeches. While a 1-year old 8 cm tall beech seedling in the factorial experiment yielded 9.6 cm height increment in the second year at average and a 1-year-old 11 cm tall beech seedling in the field experiment yielded 8.4 cm in the second year—both more than 0.7 RGR—a 3-year old 27 cm tall beech seedling of the field experiment yielded only 10.7 cm height increment in the fourth year. This corresponds to a RGR of approximately 0.4 (Table 4). To yield the same RGR as the 1-year-old 11 cm tall seedling 3-year old 27 cm seedling would have had to

grow 20 cm in the following year. In this phase of seedling development RGR values of the asymptote are thus not probable to stay constant over subsequent years (see second and third year in Table 4). This is in accordance to the findings of Brand (1986), Kneeshaw et al. (1998) and Ammer et al. (2004). In contrast to these authors Collet et al. (2002) could not find any effect of beech seedling age on any parameter of seedling growth. Another explanation for the differences in the true *relative PAR*-response of the two cohorts may be differing carry-over effects. As Löf and Welander (2000) pointed out biomass production of beech seedlings is influenced by previous year drought. In contrast to the seedlings of the factorial experiment the saplings of the field study could have been affected thereof.

Is a model based on a traditional index for growing space availability more suitable for the prediction of beech seedling's height growth than a resource based model?

A easy way to determine the effect of overstorey trees on seedlings is to use competition indices (Herling 2005). Such indices integrate the limitation of above- and belowground resource availability to a dimensionless value which increases which decreasing growing space. Many of these indices are distance dependent and radial symmetric (Bachmann 1998).

The results of the present study show that the variation of beech seedling's height growth which could be explained by either a model where the initial height and a competition index served as independent variables or by a model where initial height and above- and belowground resources were used as independent variables was more or less comparable (Table 3). Thus with both approaches approximately half of the observed variation in seedlings RGR could be explained. Note that the differences between the two approaches regarding the zone affected by an overstorey tree (radial symmetric in the case of the growing space indices, but radial symmetric (belowground resource availability) and radial asymmetric (*relative PAR* considering direct radiation) in the case of the combined resource use model) obviously did not influence the predictive ability of a model. However, qualitatively there is a big difference between the two concepts. While the growing space-index approach provides no information on the environmental factors constraining tree seedlings growth, the multiplicative combined resource model can be used to

Table 4 Mean height (MH) and mean height increment (MHI) in cm; RGR in brackets

	MH, year 1	MHI, year 2	MH, year 2	MHI, year 3	MH, year 3	MHI, year 4	N
Factorial experiment	8.28	9.60 (1.16)	17.88				174
Field experiment	11.05	8.37 (0.76)	19.42	7.72 (0.40)	27.14	10.68 (0.39)	482

get a better understanding of growth dynamics in the field. In fact there is for example an ontogenetic variation in the relative influence of light and belowground resources in beech seedling growth (Ammer et al. 2008). In addition, we observed a slight bias in the simple competition index model (see Fig. 3a) which might be due to the lack of any *relative PAR*-information in this model. Taking the radial symmetrical character of the competition index into account it is possible that the beeches received less *relative PAR* on the southern part of the gaps compared to western or eastern parts. This is not indicated by the any of the tested competition indices. This interpretation is in fairly good concordance with the less obvious bias in Fig. 2a, where *relative PAR*-information and the radial symmetrical root competition index are combined. However, only in the factorial experiment the model is free of any bias (Fig. 1a) indicating a problem of the field experiment which cannot be fully explained.

Comparing the different competition indices tested in our study it can be stated, that the type of the index and the underlying approach of selecting overstorey trees affecting growing space seem not to be very important for the amount of explained variation (Table 3).

Conclusions

The present study attempted to model the height growth of single beech seedlings in the field. According to Goldberg (1990) seedling growth is the response on resource availability determined by the presence and dimension of overstorey trees. Given a maximum RGR development over age, a stable RGR, i.e. a stable form of the response curve of a species to resource limitation within the years of seedling stage might be expected. This assumption is confirmed by the results of our study. Based on various physiological responses Aranda et al. (2002) demonstrated the high importance of the light/water interactions for beech under canopies of different closure. Taking the findings of Aranda et al. (2002) and the results of the present study into account, it can be concluded that the combined resource use model approach is appropriate for modelling height growth of beech seedlings in the field by using an indirect method of estimating belowground resource availability. From a silvicultural point of view the application of such models is of great interest in order to get rough estimations of the growth potential of seedlings under given conditions. For this purpose however, models using competition indices which require only easy to measure data, are suitable as well. However, it might be helpful to develop competition indices which include belowground factors, especially when predicting seedling growth. Realistic predictions of height growth are for example important for controlling inter (tree) specific competition and weed interference and for planning partial-cutting treatments and predicting their long-term consequences (Drever and Lertzman 2001). Nevertheless, only the combined resource use model approach provides an improved ecophysiological understanding of seedling growth in the field. The implementation of the underlying functions into generalised models of forest productivity (e.g. Landsberg and Waring 1997) may be an option.

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