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Original article

Growth and biomass partitioning of *Fagus sylvatica* L. and *Quercus robur* L. seedlings in response to shading and small changes in the R/FR-ratio of radiation

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Abstract – The effects of shading levels, comparable to the light quantity and quality below the canopy of a Norway spruce (*Picea abies* [L.] Karst.) stand on one year old European beech (*Fagus sylvatica* L.) and penduncluate oak (*Quercus robur* L.) were tested. The treatments were: shading of plants exposed to "natural shade" by using green synthetic nets (PAR reduced to 32.6%, R/FR-ratio 1.04), shading of plants exposed to "neutral shade" by using black nets (PAR reduced to 24.7%, R/FR-ratio 1.13), no shading (control, PAR 100%, R/FR-ratio 1.15). Beech seedlings showed a strong decrease in height, diameter, stem-, branch-, leaf- and root dry mass with decreasing light quantity. Neither growth rates nor total yield indicated an impact of slightly changed light quality (R/FR-ratio 1.04) on growth and biomass partitioning of beech. Relative growth rate of the main stem dry mass of oak was considerably higher for the seedlings of the shade treatment with the reduced R/FR-ratio than for the control and the other shade treatment whereas branch dry biomass exposed to changed light quantity and quality was reduced disproportional, resulting in the lowest branch-stem-ratio. The tallest oak seedlings were found under the green nets (treatment with reduced light quantity and quality), whereas the control showed the shortest seedlings.

light quality / shading / pedunculate oak / European beech

Résumé – **Répartition de la croissance et de la biomasse de plants de *Fagus sylvatica* L. et de *Quercus robur* L. soumis à ombrage et à de faibles changements du rapport R/FR de radiation.** On a testé l'effet sur des plants de un an de hêtre (*Fagus sylvatica* L.) et de chêne pédonculé (*Quercus robur* L.) de différents niveaux d'ombrage, reproduisant les conditions de lumière en quantité et qualité d'un couvert de peuplement d'épicéa (*Picea abies* Karst.). Les traitements furent les suivants : plants soumis à une « ombre naturelle » en utilisant des filets synthétiques verts (réduction du PAR à 32,6 %, rapport R/FR 1,04) ; plants soumis à une « ombre neutre », en utilisant des filets noirs (réduction de PAR à 24,6 %, rapport R/FR 1,13) ; pas d'ombrage (témoin PAR 100 %, rapport R/FR 1,15). Pour les plants de hêtre, la réduction de la quantité de lumière s'est traduite par une forte diminution de la hauteur et du diamètre, ainsi que du poids sec des tiges, branches, feuilles et racines. Un faible changement de la qualité de la lumière (rapport R/FR de 1,04) n'a pas d'effet sur la croissance et la répartition de la biomasse. En ce qui concerne les plants de chêne, la croissance en matière sèche de la tige principale est proportionnellement plus élevée pour le traitement ombrage avec rapport R/FR réduit que pour le témoin ou l'autre traitement d'ombrage. Un changement en quantité et qualité de la lumière induit donc une réduction du rapport branche/tige. On obtenait les plants de chêne les plus grands sous filet vert (traitement avec réduction en quantité et qualité de la lumière) alors que les plus petits étaient dans le témoin.

qualité de la lumière / ombrage / chêne pédonculé / hêtre

1. INTRODUCTION

As a consequence of the serious damages by biotic and abiotic factors to pure conifer stands, the conversion of those stands into mixed stands has become one of the most important tasks of silviculture in central Europe during the last decade [25]. For this purpose *Fagus sylvatica* L. or *Quercus robur* L. are often planted or sown under the canopy of conifer stands [2, 43] where the seedlings experience environmental conditions different from those in open field for a prolonged period.

It is well known, that growth and biomass partitioning of seedlings shaded by overstorey trees are strongly affected by modifications in light conditions caused by the canopy trees [4]. As a result seedlings of shaded European beech (*Fagus sylvatica* L.) and penduncluate oak (*Quercus robur* L.)

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showed different growth patterns related to seedlings grown up in open field [9, 10]. This was ascertained with seedlings under the canopy of old stands [11, 19, 21, 31] as well as in shading experiments [5, 22, 52, 55]. However, it is not known whether the modified growth patterns are caused by the reduction of radiation intensity coming through the canopy and/or by the changed spectral composition of the radiation below the canopy. In particular the ratio of the red components of radiation to those of the far red (R/FR-ratio) is altered below the crowns of the canopy trees due to the selective absorption of light by their leaves [33, 42, 48].

In a number of studies the R/FR-ratio of radiation was proven to determine the status of phytochrome equilibrium, which was found to control various photomorphogenetic plant responses [36, 45]. Examples for such responses include accelerated extension growth, apical dominance and reduced branching [45]. This behaviour is typical for plants which grew in light conditions where the R/FR-ratio was reduced and can be summarized as the so called "shade avoidance syndrome" [45]. Since the future value of broad-leaf seedlings is strongly correlated with their branchiness and uprightness of the main shoot [29] these responses are of silvicultural interest.

However, only few studies investigated the effects of a modified R/FR-ratio on growth and biomass partitioning of woody plants [50]. Moreover, some of these studies are focused on how the variation in R/FR-ratio at the top of the shoots and the related growth responses are caused by neighbouring plants and not by canopy trees [20, 41], or they investigated the effect of R/FR-ratios different from those of natural environments [37, 38]. The results of other studies, in which the effects of light intensity were separated from those of light quality are not consistent [30, 39]. The ability to respond to modifications in the R/FR-ratio by changes in growth patterns seems to depend on the investigated species and its shade tolerance [26, 28]. Against this background the objective of the present study was to investigate in a shading experiment (i) how shading comparable to the light conditions below the canopy of a heavily thinned pure Norway spruce (*Picea abies* [L.] Karst.) stand affects growth and biomass partitioning of seedlings of European beech (*Fagus sylvatica* L.) and penduncalate oak (*Quercus robur* L.) and (ii) to what extent reductions of light quantity and quality, respectively, account for differences in growth and biomass partitioning between shaded and unshaded seedlings.

2. MATERIALS AND METHODS

2.1. Treatments

Following the recommendations by Smith et al. [47] the experiment was conducted with the following three treatments: (i) Plants exposed to "natural shade" [47] by using a green synthetic net (Heissner®). The amount of the photosynthetically radiation (PAR, total photon flux in µmol m^{-2} s^{-1} between 400 and 700 nm) below the green net was 32.6% of the respective amount above. The R/FR ratio (photon flux between 655 and 665 nm divided by photon flux between 725 and 735 nm), which is equal 1.15 in open field and sunsets >10° [45] was reduced by this net to 1.04 (*figure 1*). The measurements of PAR and R/FR-ratio were conducted at the GSF-research center in Munich-Neuherberg using a spectroradiometer. Reduced PAR and reduced R/FR-ratio are representative for light conditions, which were detected below the canopy of a heavily thinned pure Norway spruce (*Picea abies* [L.] Karst.) stand [1]. (ii) Plants exposed to "neutral shade" [47] by using a black net (Heissner®) which was identical to the green net regarding material and width of meshes. However, the amount of PAR was reduced to 24.7% below the net, i.e. the reduction of light intensity by the black net exceeds the respective diminution by the green net. On the contrary the R/FR ratio was nearly unaffected by the black net and amounted to 1.13. (iii) Plants without a net (control) in open field i.e. 100% light intensity and a R/FR-ratio of 1.15.

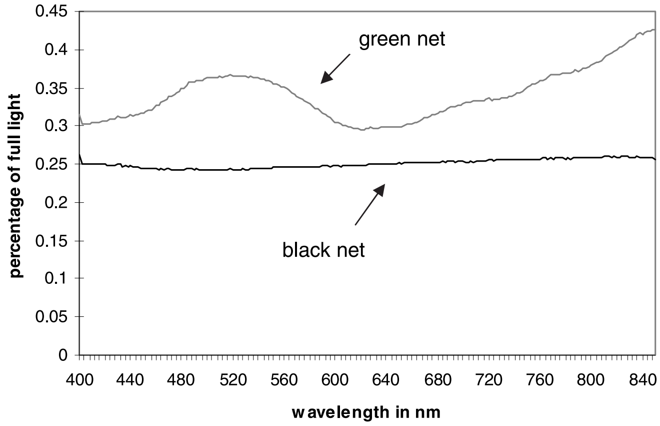

Figure 1. Spectral composition of radiation below the green and the black net.

2.2. Experimental design

The experiment was carried out in open field near Landshut (Bavaria, Germany, 11° 59' 32" E, 48° 34' 46" N). It was set up as a randomised complete block design, where the blocks represented tree species. Within each block the three treatments were replicated five times. Eight plants per species and treatment were pooled to a replication. The replications within a block were completely randomised, spaced 5 by 5 m in order to avoid interactions. The 8 seedlings of a replication were spaced 40 by 40 cm. In the case of the shading treatments the plants were arranged underneath boxes with wooden frames covered by the nets, 180 cm in length, 100 cm in width and 80 cm in height. Therefore the distance between each plant and the surrounding net was 30 cm. The experiment was conducted from April 24th to September 6th in 1999 (135 d).

2.3. Plant material, substrate, water supply and temperature

At the start of the experiment all plants were one year old. The seedlings were raised by the Bavarian Institution for Forest Seeding and Planting at Teisendorf (Bavaria, Germany) in open field. All seeds of a species originated from the same stand, which was selected according to the law on forest reproductive material. The seeds were sown into a permeable pot of 2000 cm^3 in size and the seedlings stayed there to the end of the experiment. The rooting substrate consisted of a mixture of peat and agriperl added by 7.7 g fertilizer (Osmocote plus high N 16(N)+8(P)+12(K)+12(MgO), Scotts). As the pots were not put in the soil they were watered frequently in order to avoid water stress. For this purpose up to 20.5 L per pot were poured. Despite the reduced precipitation below the nets the substrate of the shaded plants was soggier in dry periods because of the reduced evaporation. For this reason in some cases only the plants of the control were watered. However, water was never limited for any plant during the whole duration of the experiment. The temperature regime under the nets was less variable compared to the conditions in open field (control), i.e. below the nets lower maxima and higher minima were measured.

2.4. Measurements

At the beginning of the experiment as well as after 50 (first flush finished) and 135 days (end of the experiment) height (length) of the main stem (mm), diameter (tenth of a mm) of main stem collar at a permanently marked position 3 cm above the substrate surface, diameter (tenth of a mm) of the main stem at the half length of the stem, length of first order branches (mm), diameter (tenth of a mm) of first order branches at its base were measured. At the end of the experiment all plants were harvested. After the roots had been washed and dried (72 h, 65 °C) dry mass of main stem, branches, leaves and roots were measured for each plant. In addition the dry mass of every branch of a quarter of all plants was recorded. In order to obtain information on woody biomass at the start of the experiment and after 50 days, allometric equations according to Byrne and Wentworth [6] and Davis et al. [13] were derived. Based on the relationship between the volume index VS (product of stem height, collar diameter and diameter at half length (in cm respectively)) and the dry mass of the main stem (DM_{shoot}) at the end of the experiment, the dry mass of the main stem at the start of the experiment and after 50 days was estimated using the following equations:

$DM_{shoot} = 10e^{-2.9961+0.8650\cdot(\ln VS)}$ for beech
($r^2 = 0.96$, $P > 0.0001$, n = 102) and
$DM_{shoot} = 10e^{-2.877+0.8315\cdot(\ln VS)}$ for oak
($r^2 = 0.93$, $P > 0.0001$, n = 103).

Analogous the dry mass of every first order branch could be estimated based on the relationship between the volume index VB (product of branch length and the square of the diameter at branch base (in cm respectively)) and the dry mass of the branch (DM_{branch}) that was calculated using the branches of a quarter of total plant number. The respective equations are:

$DM_{branch} = 10e^{-3.5973+0.7592\cdot(\ln VB)}$ for beech
($r^2 = 0.94$, $P > 0.0001$, n = 225) and
$DM_{branch} = 10e^{-3.7010+0.8117\cdot(\ln VB)}$ for oak
($r^2 = 0.94$, $P > 0.0001$, n = 217).

Relative height growth (RHG), relative diameter growth (RDG), relative growth of the estimated dry mass of the main stem (RGDS) and relative growth of the estimated branch dry mass (RGDB) were calculated according to Evans [15] using the following equation for each variable (v): $v = (\ln(V_2) - \ln(V_1))/(t_2 - t_1)$, where V_2 is the value of the regarding variable at the end of the observed period and V_1 at the beginning respectively. In the present study the relative growth rates were calculated for the first 50 days, the following 85 days and the whole period. Thus $t_2 - t_1$ was 50, 85 and 135, respectively.

2.5. Data analyses

Simple regression analysis was used to evaluate the effect of the shading treatments on tree species. According to Draper and Smith [14] orthogonal contrasts were used to test the following hypotheses:

$H_{0.1}$: $\mu_{\text{(oak)}} = \mu_{\text{(beech)}}$
$H_{0.2}$: $\mu_{\text{(shade treatments)}} = 2\,\mu_{\text{(control)}}$
$H_{0.3}$: $\mu_{\text{(green net)}} = \mu_{\text{(black net)}}$.

For this purpose tree species and treatments were coded by dummy variables to test the following model:

$y = b_0+b_1Z_1+b_2Z_2+b_3Z_3+b_4Z_1Z_2+b_5Z_1Z_3+b_6Z_1Z_2Z_3$, where y is the dependent variable, Z_1 is 1 for oak and –1 for beech, Z_2 is –1 for the shading treatments and 2 for the control, Z_3 is –1 for the green net and 1 for the black net. Z_1Z_2, Z_1Z_3, $Z_1Z_2Z_3$ refer to interactions between tree species and treatment effects. Statistical analyses was done by using the REG procedure of SAS® (Statistical Analysis System 6.12, SAS Institute Inc., Cary, N.C.).

3. RESULTS

3.1. Total yield after 135 days

The effect of the shade treatments on seedling height at the end of the growing period was different between tree species (*table I, figure 2a*). This is indicated by the significant interaction between variable Z_1 (coding tree species) and variable Z_2 (testing differences between shade treatments and control). Oak seedlings were taller under shade than in controls, while beech was taller in control. In both cases a significant difference in height was also detected between the seedlings of the two shade treatments (*table I*). The seedlings under the green nets were taller than those under the black coverage (*table I, figure 2a*). In contrast to almost all other variables, stem diameter did not differ among species, but was clearly affected by shade (*table I, figure 2b*). In both species diameter was larger in seedlings of the unshaded control. Similarly the dry mass of the main stem was larger in control than in shade. However, the difference in stem dry mass between control and shade treatments was more pronounced for beech than for oak (see interaction Z_1 and Z_2). Thus oak seedlings under the green net showed the same stem dry mass than in controls (*table I, figure 2c*). In contrast no difference in branch dry mass and leaf dry mass was detected between the two shade treatments (*table I, figure 2d* and *2e*). However, both variables differed between tree species (variable Z_1) and between the control and the two shade treatments (variable Z_2) (*table I*). Branch dry mass of beech was higher than that of oak (negative value of variable Z_1), whereas leaf dry mass of oak exceeded that of beech (positive value of variable Z_1) (*table I*). The same result was found for root dry mass (*table I, figure 2f*) and total dry mass (*table I*). For both traits the mass of the seedlings of the control was considerably larger than the corresponding values of the shade treatments. However, the shade treatments yielded significantly different root and total dry masses (*table I*). As the positive value of the significant interaction of variable Z_1 and variable Z_2 revealed, the difference in the root-shoot ratio between the control and the shade treatments was much more pronounced for oak than for beech (*table I, figure 2g*). A different result was found analysing the ratio of branch and stem dry mass. Whereas that ratio was reduced for the shaded seedlings of both species, a significant low branch biomass per unit main stem under the green net was found only for the oak seedlings, but not for beech (*table I, figure 2h*). The degree of determination of the regression models ranged between 0.63 (stem dry mass) and 0.91 (root dry mass) (*table I*).

Table I. Results of regression analyses after 135 days.

Attribute	Regression equation	MS model	MS Error	Pr > F	R^2
height (cm)	$y = 35.19 + 3.57\ Z_1 - 1.86\ Z_3 - 2.75\ Z_1Z_2$ Z_1: ***; Z_3: *; Z_1Z_2 : ***	301.56	14.07	< 0.0001	0.71
diameter (mm)	$y = 6.78 + 0.50\ Z_2 - 0.36\ Z_3$ Z_2: ***; Z_3: *	8.85	0.38	< 0.0001	0.64
stem dry mass (mg)	$y = 364.91 + 45.42\ Z_2 - 36.47\ Z_3 - 27.52\ Z_1Z_2$ Z_2: ***; Z_3: *; Z_1Z_2 : **	65273	4453.26	< 0.0001	0.63
branch dry mass (mg)	$y = 117.00 - 12.00\ Z_1 + 31.48\ Z_2$ Z_1: *; Z_2: ***	31882	711.39	< 0.0001	0.77
root dry mass (mg)	$y = 884.03 + 129.87\ Z_1 + 233.98\ Z_2 - 86.36\ Z_3$ Z_1: ***; Z_2: ***; Z_3: **	1313336	14705	< 0.0001	0.91
leaf dry mass (mg)	$y = 388.53 + 121.46\ Z_1 + 84.92\ Z_2$ Z_1: ***; Z_2: ***	437643	6909.33	< 0.0001	0.82
total dry mass (mg)	$y = 1754.47 + 253.90\ Z_1 + 395.80\ Z_2 - 156.05\ Z_3$ Z_1: ***; Z_2: ***; Z_3: **	3940098	55627	< 0.0001	0.89
root-shoot-ratio	$y = 1.81 + 0.26\ Z_1 + 0.21\ Z_2 + 0.13\ Z_1Z_2$ Z_1: ***; Z_2: ***; Z_1Z_2 : **	1.88	0.10	< 0.0001	0.69
branch-stem-ratio	$y = 0.32 - 0.04\ Z_1 + 0.04\ Z_2 + 0.02\ Z_1Z_2 - 0.03\ Z_1Z_2Z_3$ Z_1: ***; Z_2: ***; Z_1Z_2 : **; $Z_1Z_2Z_3$: *	0.045	0.002	< 0.0001	0.73

* significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$; Z_1: oak vs. beech; Z_2: shade treatments vs. control; Z_3: green vs. black net; Z_1Z_2, $Z_1Z_2Z_3$: interactions.

3.2. Relative growth rates

The relative growth rates were less affected by the shading treatments during the first part of the growing period than during the second (*table II, figure 3a–d*). For example, relative height growth (RHG) was clearly affected by the shade treatments not before the second part of the growing period (*table II, figure 3a*). The differences in the relative growth rates between the two parts of the growing season and the effects of the shade treatments were particularly pronounced for oak (*figure 3a–c*). In contrast to oak, beech showed significant differences between shaded and unshaded seedlings already in the first part of the growing period, e.g. RDG and RGDS were reduced by the nets even in the first part of the growing period (*table II, figure 3b* and *3c*).

The significant interaction between the variables Z_1 and Z_2 for RHG and RGDS in the second part of the growing period as well as in the total period indicates that the difference between the control and the shade treatments in height growth and stem dry mass increment was related to tree species (*table II*). RHG and RGDS in particular of the seedlings under the green nets were higher than those of the control for oak, whereas they were lower for beech (*table II, figure 3a* and *3c*). In contrast to height and stem dry mass, RDG of both tree species was affect in the second part of the growing period as well as in the total period by the shade treatments in the same way (*table II*, *figure 3b*). For both tree species RDG was significantly higher for the seedlings of the control (positive value of variable Z_2) (*table II*). In addition a significant difference between the two shade treatments was found, revealing a higher RDG of the seedlings under the green nets (negative value of variable Z_3) (*table II*). In contrast to all other attributes RGDB was much lower in the second part of the growing period than in the first part (*figure 3d*). Moreover, the fit of the regression model was much lower for RGDB than for the relative growth rates of the other attributes (*table II*).

4. DISCUSSION

Shading affected significantly growth and biomass partitioning of oak and beech seedlings. Because previous year growth has after effects on initial twig and leaf expansion of oak and beech, early growth is influenced to some extent by the light conditions of the previous year [11, 51, 52]. Presumably this is the reason why the growth responses of beech and oak were particularly noticeable in the second part of the growing season (*figure 3a–d*). For beech a strong decrease in height, diameter, stem-, branch-, leaf- and root dry mass with decreasing light quantity was found (*figure 2a–f*). These results are in accordance with many other investigations [5, 9, 17, 35, 49]. As shading reduced root biomass more then the aboveground biomass and branch biomass more than the biomass of the main stem, root-shoot-ratio and branch-stem-ratio of the beech seedlings under the nets were lower then the related values of the control (*figure 2g* and *2h*). Whereas a reduced root-shoot-ratio due to shading is confirmed by most of the above mentioned studies on beech as well as on other tree species [8, 27, 40, 44, 54], the ratio of branch biomass to main stem biomass has not been calculated very often. Thus comparisons with the results of other studies are difficult. However, an increasing percentage of second or third order branch biomass with increasing light intensity was found by Cornelissen [12] for *Castanopsis fargesii* and by Wiebel et al. [53] for *Garcinia mangostana*. In addition, an increasing number of branches of young *Quercus petraea* and an increasing length growth of these branches with increasing

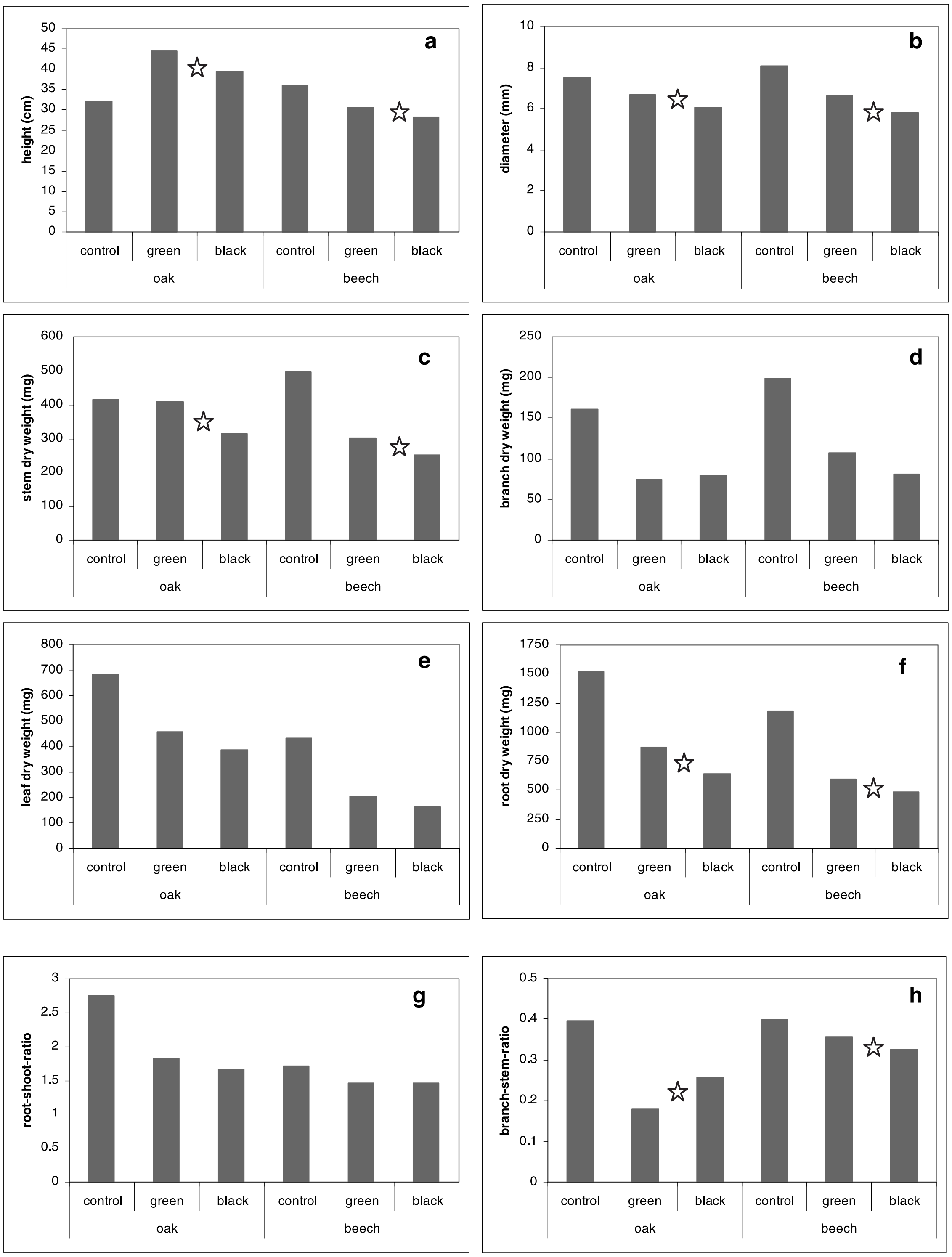

Figure 2. Growth components measured on seedlings of oak and beech exposed to full sun (control), neutral shade (black net) or a modified R/FR regime (green net) during one growing season. Mean values. Stars indicate significant differences between the shade treatments.

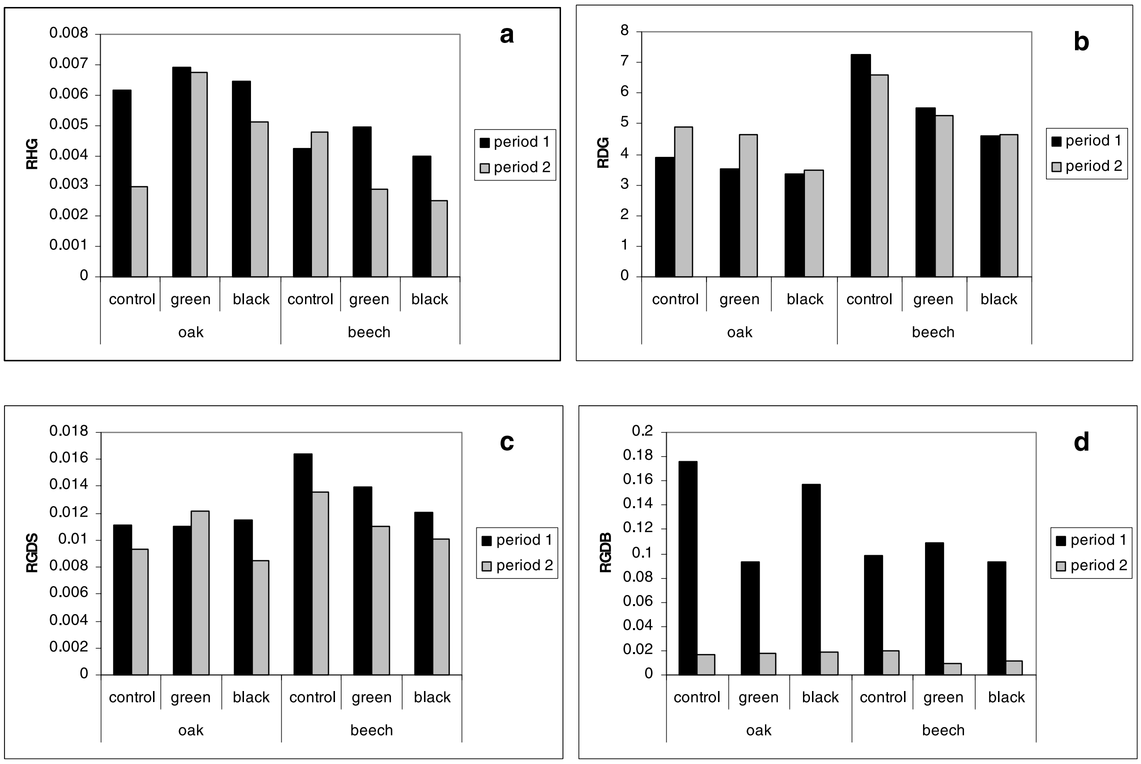

Figure 3. Relative height growth (RHG), relative diameter growth (RDG), relative growth of estimated stem dry mass (RGDS) and relative growth of estimated branch dry mass (RGDB) for the first 50 days (period 1) and the following 85 days (period 2). Mean values.

light availability was reported by Collet et al. [9]. However, from an ecological point of view the observed patterns of biomass partitioning is ingenious. Considering limited resources height growth should have highest priority. Otherwise a subject tree will be overtopped by competitors. Thus branch extension is intensified only if the amount of carbon gain allows additional investments.

Neither growth rates nor total yield indicates an impact of the slightly changed light quality under the green nets on growth and biomass partitioning of beech. This interpretation seems to be valid in spite of the fact that an exact distinction between the effects of reduced light quantity and modified light quality on shaded seedlings based on the nets used in the present study is not possible. For that purpose experiments are required where the shading variants are characterized by an identical amount of PAR but different R/FR-ratios. However, such preconditions are only given in phytotrons, but the limited numbers of phytotrons where specific light conditions can be set up often do not allow replications [24]. In the present case phytotrons were not available. However, for ecological interpretations a satisfying solution can be attained also by using nets (Smith, per. communication). Admittedly nets do not only modify the light environment but also other factors such as soil moisture, temperature and the wind regime around the plants, potentially influencing plant growth. Although soil water availability should not have differed between the three variants due to repeated watering, slight differences are possible anyway. Unfortunately neither soil moisture nor plant water status were measured for financial and technical reasons. However, more likely than water effects are differences in plant growth due to the modified temperature regime under the nets. Nevertheless, although the more balanced temperature conditions below the nets may have enhanced growth, temperature is not supposed to be a key factor in the present experiment. As the high degrees of determination show, the regression model comprised the main factors regarding growth and biomass allocation (*table I*). However, the most important draw-back of the experimental design is, that it was not possible to obtain different R/FR-ratios coincident with identical reductions in PAR with the nets used in the present study as can be seen from the data given in the methodical section and from *figure 1*. Thus the differences between shaded and unshaded seedlings could not unequivocally be assigned to the reduction in light intensity or to the effect of light quality. Nevertheless it is likely that some growth responses ascertained in the experiment can be attributed to changes in light quality. This applies for all cases like e.g. total biomass, where the normal non-linear trend of decreasing biomass production with decreasing light intensity was modified. As the results show such modifications could not be observed for beech but for oak. RGDS of oak was considerably higher under the green nets than for the control and for the seedlings under the black nets (*figure 3c*). In contrast to stem dry mass, branch dry mass of oak was reduced disproportional under the green nets, resulting in the lowest branch-stem-ratio (*figure 2h*). These growth patterns, enhanced apical dominance and reduced branching, are characteristic responses of shade avoiding species to a reduced

Table II. Results of regression analyses of relative height growth (RHG), relative diameter growth (RDG), relative growth of estimated stem dry mass (RGDS) and relative growth of estimated branch dry mass (RGDB) for the first 50 days (I), the following 85 days (II) and the total growing period (135 days).

Attribute	Regression equation	MS model	MS Error	Pr > F	R^2
RHG I (d^{-1})	$y = 0.054 + 0.011\ Z_1$ Z_1: ***	0.00033	0.000011	< 0.0001	0.53
RHG II (d^{-1})	$y = 0.042 + 0.008\ Z_1 - 0.008\ Z_1Z_2$ Z_1: **; Z_1Z_2: ***	0.00030	0.000014	< 0.0001	0.61
RHG (d^{-1})	$y = 0.048 + 0.009\ Z_1 - 0.005\ Z_3 - 0.006\ Z_1Z_2$ Z_1: ***; Z_2: ***; Z_1Z_2: **	0.00016	0.000007	< 0.0001	0.73
RDG I (d^{-1})	$y = 4.69 - 1.09\ Z_1 + 0.445\ Z_2 - 0.292\ Z_1Z_2$ Z_1: ***; Z_2: **; Z_1Z_2: *	0.00018	0.000010	< 0.0001	0.67
RDG II (d^{-1})	$y = 4.92 - 0.573\ Z_1 + 0.407\ Z_2 - 0.452\ Z_3$ Z_1: **; Z_2: **; Z_3: *	0.00795	0.000744	< 0.0001	0.55
RDG (d^{-1})	$y = 4.84 - 0.766\ Z_1 + 0.421\ Z_2 - 0.388\ Z_3$ Z_1: ***; Z_2: ***; Z_3: *	0.01041	0.000581	< 0.0001	0.67
RGDS I (d^{-1})	$y = 0.014 - 0.002\ Z_1 - 0.001\ Z_1Z_2$ Z_1: ***; $Z_1 \cdot Z_2$: *	0.00004	0.000005	< 0.0001	0.40
RGDS II (d^{-1})	$y = 0.012 - 0.001\ Z_1 - 0.001\ Z_3 - 0.007\ Z_1Z_2$ Z_1: *; Z_3: *; Z_1Z_2: *	0.00002	0.000004	< 0.0001	0.39
RGDS (d^{-1})	$y = 0.012 - 0.001\ Z_1 - 0.001\ Z_3 - 0.001\ Z_1Z_2$ Z_1: **; Z_3: *; Z_1Z_2: **	0.00002	0.000003	< 0.0001	0.49
RGDB I (d^{-1})	not significant	-	-	-	-
RGDB II (d^{-1})	$y = 0.016 - 0.002\ Z_1Z_2$ Z_1Z_2: *	0.00024	0.000043	0.0242	0.17
RGDB (d^{-1})	$y = 0.055 + 0.009\ Z_1$ Z_1: *	0.00247	0.00057	0.0467	0.13

* significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$; Z_1: oak vs. beech; Z_2: shade treatments vs. control; Z_3: green vs. black net; Z_1Z_2, $Z_1Z_2Z_3$: interactions.

R/FR-ratio [45, 46]. Thus, it is likely that the growth responses in branching of oak where caused by the slight changes in the R/FR-ratio under the green nets. The question whether the reduction of the R/FR-ratio under the green nets was not high enough to cause changed growth pattern also for beech or whether beech as other shade tolerant species, does not respond to reductions in R/FR-ratio at all [26] cannot be answered within the scope of the study.

At the end of the experiment RHG as well as total height of oak were found to be highest under the green nets. However, it is not clear whether this result was caused by the reduced R/FR-ratio or by the reduced light quantity. On the one hand accelerated height growth is the most frequent response of light demanding species to a reduced R/FR-ratio [23, 45]. On the other hand, in contrast to beech, height growth of oak seedlings in the first years is known to be highest in moderate shade [18, 55]. As even the oak seedlings under the black nets were taller than the seedlings of the control at the end of the experiment, the reduction of the light quantity seems to be of primary importance (*figure 2a* and *3a*). However, the reduced R/FR-ratio under the green nets could have intensified the growth response of the shaded seedlings. As in other studies the relative growth rates were not constant through the study period, which is supposed to be a consequence of changing net assimilation rates [3].

5. CONCLUDING REMARKS

As former studies showed [16] not only red, but also blue light reductions, which are supposed to occur in all shade treatments, are inducing morphogenetic responses of tree seedlings. Subsequently further investigations studying the effect of modified light environments on tree seedling growth are of great interest. However, even in the context of the present study many questions remained open. Thus it is not clear whether beech will respond to R/FR-ratios lower than the ratio tested in the present study. Therefore further investigations with substantially lowered R/FR-ratios considering interactions between light quantity and light quality are needed [23, 34]. In addition, further studies should be focused on the question how the distinct growth responses of oak to changes in light quantity and slightly changed light quality will be change over time. Evidence exists that for oak maximum growth and optimum light conditions change with age [55] and that biomass allocation patterns in general are a function of tree age [7, 12, 32]. However, if the results of the present study can be verified for other R/RF-ratios occurring under overstorey canopies and other tree species, the further development of growth models will benefit from integrating the effect of light quality on growth, at least for light demanding species [20, 41]. In addition silviculture in general will benefit from an improved understanding of the interactions between microclimate including light quality on tree ecophysiology as it "makes it possible to produce viable applications which are useful for silviculture during stand formation, and for applying silvicultural treatments" [4].

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