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Seedling Growth and Biomass Production under Different Light Availability Levels and Competition Types

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Abstract: Light availability is a crucial resource determining seedling survival, establishment, and growth. Competition for light is asymmetric, giving the taller individuals a competitive advantage for obtaining light resources. Species-specific traits, e.g., shade tolerance, rooting depth, and leaf morphology, determine their strategical growth response under limited resource availability and different competitive interactions. We established a controlled pot experiment using European beech, Norway spruce, and Douglas fir seedlings and applying three different light availability levels—10%, 20%, and 50%. The experiment's main aim was to better understand the effects of light availability and competition type on the growth, growth allocation, and biomass production of recently planted seedlings. We planted four seedlings per pot in either monocultures or mixtures of two species. Relative height and diameter growth and aboveground woody biomass of seedlings increased with increasing light availability. All seedlings allocated more growth to height than diameter with decreasing light availability. Seedlings that reached on average greater height in the previous year allocated less growth to height in the following year. Additionally, there were general differences in growth allocation to the height between gymnosperms and angiosperms, but we did not find an effect of the competitor's identity. Our mixture effect analysis trends suggested that mixtures of functionally dissimilar species are more likely to produce higher biomass than mixtures of more similar species such as the two studied conifers. This finding points towards increased productivity through complementarity.

Keywords: shade tolerance; growth allocation; mixture effect; competition; pot experiment

1. Introduction

Light is one of the most crucial resources determining seedling survival, establishment, and growth [1,2]. Stem height and diameter determine tree size and, consequently, an individual's performance in given conditions [3]. Since competition for light resources is asymmetric, i.e., size-dependent, a taller individual has a competitive advantage over its smaller neighbors, which is particularly important during the seedling establishment and recruitment stages [4,5]. Overtopping the neighbors to seize the available light resource, thus hindering competing vegetation growth, is a typical example of a competitive growth strategy under size-asymmetric competition [6].

Seedlings growing under high light availability are generally larger and produce more biomass than seedlings receiving less light, regardless of species identity and characteristics [7,8]. However, the stress rate caused by limited light availability on seedling growth can depend on species-specific factors such as shade tolerance, plasticity, the competitive situation, and the general availability of resources [9,10].

Light-demanding species have a high competitive ability under open field conditions, where they can quickly capture light and overgrow more shade-tolerant species [11]. Light-demanding species generally react stronger to increasing light availability due to more substantial stress relief, as well as allocate large shares of the photosynthetic by-products to height growth rather than diameter growth in low light conditions to maintain contact with the light source, even if that presents a growth-survival trade-off [12–14]. On the other hand, shade-tolerant species are more adapted to low-light habitats and can use the available light more efficiently [15,16]. This is possible via higher morphological plasticity on the leaf- and crown-level, allowing trees to, e.g., capture light through horizontal expansion [17].

Aboveground allometry of height versus diameter growth determines a plant's performance and reveals a trade-off between a plant's ability to compete with neighbors (gained through height increment) and the mechanical and physiological support (attained by diameter growth) [3,18,19]. Differences between angiosperms and gymnosperms, species' shade tolerance, competition for resources, and neighbor effects can all alter seedling allometry [20,21]. Gymnosperm tree species generally have higher diameter growth per unit of stem growth than angiosperms [3,22]. Light-demanding species often risk the stability over the potential of reaching a light source, and because of this growth strategy, fewer resources get allocated to diameter growth [23]. Additionally, the neighbor effect can influence seedling allometry through reduced competition. For example, when species of different shade tolerance are growing together, and the interspecific competition for light is lower than in monospecific stands, seedlings can use light more efficiently and do not have to sacrifice their stability (i.e., diameter growth) as much [21].

The strength of intraspecific versus interspecific competition largely depends on the species niche complementarity or similarity and self-tolerance [24]. When the growing conditions in a mixed stand facilitate higher biomass production than in monospecific stands, we assume positive mixing effects, i.e., overyielding [25,26]. For example, due to its high shade tolerance and low self-tolerance, European beech (*Fagus sylvatica* L.) generally benefits from admixtures of other species [27,28]. In comparison, the more light-demanding Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) excels in mixtures with species that would not overgrow them in the early establishment stages and have high enough shade tolerance to deal with the vigorous growth after the seedlings have established [21,29,30].

The next generation of trees often has to regenerate under older generations' cover [31]. To ensure a species mixture of shade-tolerant and light-demanding species, one must provide sufficient light availability for various species to grow and develop under the canopy [32]. Light availability is influenced by the canopy characteristics and competing vegetation and will influence seedling growth in many years to come [33]. Thus, it is essential to understand the species-specific responses to resource availability in terms of growth and its allocation (for tree stability) and biomass production to make sound early management decisions. We established a controlled pot experiment to better understand the effects of light availability and competition type on growth and its allocation to height versus diameter and biomass production of young seedlings under different levels of light availability. We used three economically important tree species in Germany—European beech, Norway spruce (*Picea abies* (L.) Karst.), and Douglas fir. We propose the following hypotheses:

Hypothesis H1: *Relative height and diameter growth and total woody plant biomass increase with increasing light availability for all species. Depending on the shade tolerance of each species, these trends are more or less pronounced. According to the species shade tolerance, the impact of light availability is the highest for Douglas fir, followed by Norway spruce and European beech.*

Hypothesis H2: *Growth allocation to height increases with decreasing light availability, decreases with the increasing height achieved in the previous year, and varies depending upon the competitor's identity. According to the species shade tolerance, Douglas fir allocates more growth to height than to diameter, followed by Norway spruce and European beech.*

Hypothesis H3: *Seedlings growing under interspecific competition have higher total biomass (i.e., overyielding) than seedlings growing in monospecific neighborhoods. The positive mixture effect is particularly pronounced for Douglas fir under high light availability and beech under low light availability.*

In addition to the hypotheses, we present a novel way to analyze growth allocation to height versus diameter. The method can be used to assess the allometric relationship between height and diameter, assuming a simple cylindrical model for the stem of the seedlings. It is based on annual height and diameter increments, thus particularly suitable when short-term changes need to be captured, and legacy effect (e.g., from the nursery) should be excluded.

2. Materials and Methods

2.1. Study Site and Experimental Setup

We conducted a controlled shading experiment at the University of Göttingen (51°33′21.6″ N 9°57′11.8″ E). The study site was located 174 m above sea level. According to the Köppen-Geiger climate classification, the climate in the area is temperate and oceanic. The average annual temperature is 9.2 °C, and the annual average precipitation reaches 650 mm, of which 310 mm falls between May and September (www.dwd.de, accessed on 16 March 2021).

We established the experiment using three tree species—European beech (EB), Norway spruce (NS), and Douglas fir (DF). The planting material was obtained from a local nursery (Baumschule Willenbocke GmbH, Walsrode, Germany). We used 1-year-old European beech (with an initial size of 22–56 cm), and 2-year-old Norway spruce (10–48 cm), and Douglas fir (11–30 cm) seedlings that were not undercut or transplanted.

The experiment was carried out in pots (pot dimensions: H = 0.33 m, D = 0.56 m, V = 65 l). Before planting, we filled the pots with a 5 cm layer of coarse gravel to provide better drainage and reduce the risk of anoxic conditions due to high water saturation. Nutrient-poor sand (0–2 mm) was used as a potting medium. We chose sand material to help create larger pores and protect roots from hypoxia [34]. A thin fleece material was placed between the coarse gravel and the sand to prevent the sand from leaching through the coarse gravel and the drainage holes. The pots were lined on wooden laths for additional gravity drainage. An automatic dripping irrigation system was installed, and all seedlings received the same water treatment. Precipitation was able to reach the seedlings, thereby providing additional water.

Nutrients were provided using a controlled-release fertilizer (CRF) Osmocote Exact Hi.End with 12–14 months longevity (ICL SF, Nordhorn, Germany). We planted in a total of 576 pots—6 species combinations (monocultures + mixtures) × 3 light treatments × 32 replicates (Figure 1). The pots were organized in blocks under every light treatment. There were eight blocks of 24 pots under every light treatment. The CRF released nutrients depending on the temperature but not the irrigation regime.

We planted four seedlings per pot in both monocultures (EB, NS, DF) and mixtures of two species (DF + EB, EB + NS, NS + DF) with 16 replicates per treatment (light × composition, Figure 1). The planting scheme layout was square-shaped. When planted in mixtures, seedlings of the same species were planted diagonally, opposite to one another.

During the winter, the pots were arranged in groups and close to each other. The gaps between the pots were filled with hay, and each pot cluster was wrapped in a two-layer aluminum-bubble insulation foil. The following spring, the pots were re-arranged randomly within the same light-treatment levels.
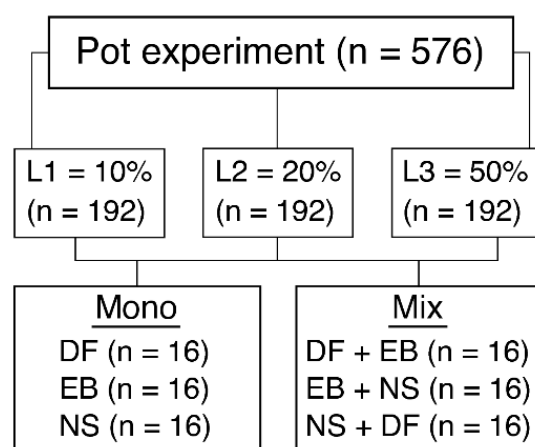
Figure 1. Experimental design. L1, L2, and L3 represent light availability levels. DF—Douglas fir, EB—European beech, NS—Norway spruce. The combinations and the number of replicates presented under the "Mono" and "Mix" categories were the same across all light levels (L1–L3).

We established three light availability levels—50%, 20%, and 10%—to assess the seedlings' response to limited light availability, and determined light availability as the proportion of irradiance available under the shading nets compared to open field conditions. Irradiance was measured with an LI-COR QUANTUM® sensor (LI-COR Biosciences, Lincoln, NE, USA). The light availability levels were chosen to mimic the light conditions in gaps of varying sizes [35].

2.2. Sampling Procedure

We examined seedling growth over two vegetation periods (April 2018–October 2019). Seedling height and diameter (5 cm above the root collar) were measured after planting and at the end of both vegetation periods—2018 and 2019.

We carried out destructive harvesting at the end of the vegetation periods 2018 and 2019. A portion of pots was harvested in 2018, and all the remaining pots, which still contained four living seedlings, were harvested in 2019. After the harvesting, we washed the seedlings and separated them by the compartments of leaves, branches, stems, and roots. These were dried at 70 °C for 72 h until a constant weight was reached. The oven-dry mass was determined to the milligram using the standard laboratory scale Sartorius MC1 LC1200S®, with an accuracy of ±0.003 g (Sartorius AG, Göttingen, Germany).

Pots with at least one dead seedling were excluded from the study since that significantly affected the growing space and the competitive situation. Mortality (see Section 4.4) and destructive harvest in 2018 reduced the final number of pots from 576 to 202 by the end of the experiment.

2.3. Data Processing

The significance level for all tests was $\alpha = 0.05$. All statistical analyses and tests were performed in the statistical computing software environment R, version 4.0.2 [36].

We determined the main competitor identity as the species of the two closest seedlings to the target seedling. For monospecific pots, the competitor's identity was identical to the target species. For mixed pots, where the seedlings of different species were planted diagonally, it was always the other species. For example, in European beech and Douglas fir mixtures, the competitor of European beech was always Douglas fir and vice versa.

2.3.1. Relative Height and Diameter Growth

We calculated the relative height and diameter growth to analyze the effect of light on tree growth and determine intra- and inter-specific differences along the light gradient. The relative height and diameter increment were calculated as the seasonal height or diameter increment divided by the height or diameter at the beginning of the same growing

season/the end of the previous growing season (see absolute values used in the calculation in Table S1).

2.3.2. Growth Allocation to Height

The height-to-diameter ratio often describes the allometric relationship between two size-determining parameters and an individual's competitiveness under different growing conditions [3,21]. However, we wanted to capture the short-term effects of growing conditions and exclude the legacy of the 1–2 years that the seedlings spent in the nursery [37,38]. For that purpose, we assumed a simple cylindrical model for the tree stem and computed the share of the volume growth over one growing season that attributes to height growth alone (Figure 2). We called this measure the Relative Height Volume Growth R and defined it as

$$R = \frac{\Delta V_H}{\Delta V} = \frac{\pi \cdot (D_1/2)^2 \cdot H_2 - \pi \cdot (D_1/2)^2 \cdot H_1}{\pi \cdot (D_2/2)^2 \cdot H_2 - \pi \cdot (D_1/2)^2 \cdot H_1} = \frac{D_1^2 \cdot (H_2 - H_1)}{D_2^2 \cdot H_2 - D_1^2 \cdot H_1} \tag{1}$$

where ΔV_H is the volume growth due to height growth, and ΔV is the total volume growth over one growing season. Furthermore, H_1 and H_2 are the height at the beginning and the end of the growing season, and D_1 and D_2 are the diameter at the beginning and the end of the growing season. Without measurement errors, the variable R should take values in the interval $[0, 1]$, which is why we excluded 3.5% of the data outside this interval.
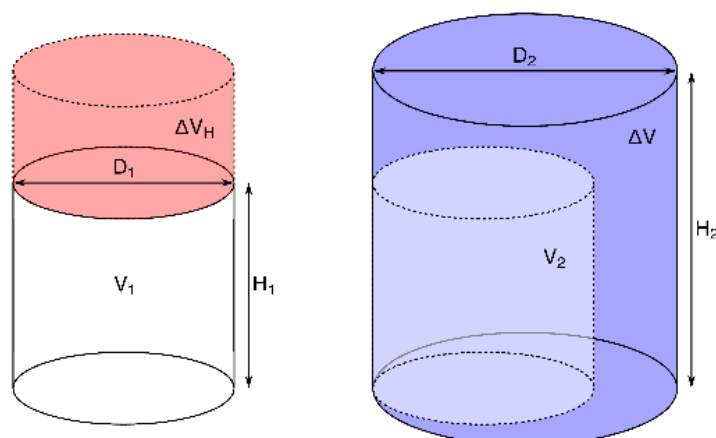

Figure 2. Visual representation of the cylindrical model for calculating the relative height volume growth (R), i.e., the share of the volume growth over one growing season attributed to height growth alone. ΔV_H is the volume growth due to height growth, ΔV is the total volume growth over one growing season, H_1 and H_2 are the height at the beginning and the end of the growing season, and D_1 and D_2 are the diameter at the beginning and the end of the growing season.

2.4. Statistical Analysis

2.4.1. Relative Height and Diameter Growth

The Shapiro–Wilk test and a visual assessment (histograms) were used to check for potential non-normality of the relative height and diameter growth and the total biomass data. Levene's test was applied to assess the assumption of variance homogeneity. Differences in relative height and diameter growth and total biomass production were assessed with the Kruskal–Wallis non-parametric test, as the data was not normally distributed, and variance homogeneity could not be assumed. The differences were tested interspecifically, intraspecifically, and across different light levels. Whenever the differences were significant, a pairwise Wilcoxon rank-sum test with Bonferroni correction was used as a post hoc test to calculate comparisons between the groups.

2.4.2. Growth Allocation to Height

To relate the relative height volume growth to explanatory variables, we used a Gaussian location-scale regression model [39], which is defined as

$$\log\left(R_{ijt}\right) = \eta_{ijt} + \varepsilon_{ijt}, \text{ where } \varepsilon_{ijt} \sim \mathcal{N}\left(0, \left(0.01 + \exp\left(\zeta_{ijt}\right)\right)^2\right). \tag{2}$$

The response variable R_{ijt} is the relative height volume growth observed for seedling j in pot i and year t. The linear predictor η_{ijt} explains the mean of the response, while the linear predictor ζ{ijt} describes the standard deviation of the error term ε_{ijt}.

We included several fixed covariate effects and random intercepts for the pots in both predictors η_{ijt} and ζ{ijt}. The explanatory variables in both predictors were the species identity, the light availability, the competitor identity, the year, and the seedling height and diameter. The height and the diameter were standardized with the species and year-specific averages. Three interactions of the species identity with the light availability, the competitor identity, and the year, were added to the mean predictor, while the predictor for the standard deviation included only one interaction between the species identity and the year.

The model was estimated with the gam (Generalized Additive Model) function and the gaulss family from the mgcv package for R [40]. We also computed the model's estimated marginal means (also known as least-square means) to compare selected covariate constellations using the emmeans package [41].

2.4.3. Mixing Effect

Using a quadratic linear regression model, we assessed the mixing effect on species productivity in terms of total aboveground biomass. The total aboveground biomass of the target species in mixed pots was compared to the expected productivity for a neutral mixing effect, i.e., the mean productivity of the species in monospecific pots. The mean aboveground biomass of the two compared species in pure pots was used as the fixed points of the regression curve, and the curvature was estimated through the modeling process as

$$p_{1,2} - p_2 - (p_1 - p_2) \times m = \beta_2\left(m^2 - m\right), \tag{3}$$

where: $p_{1,2}$—productivity of a mixture; p_1, p_2—species-specific productivity; m—mixture proportion of species 1; β_2—quadratic term.

For more detailed information, please consult Pretzsch et al. (2017) and Pretzsch et al. (2013) [42,43].

3. Results

3.1. Relative Height and Diameter Growth and Biomass Production

Relative height and diameter increment increased with increasing light availability for all species (Figure 3). The only exception was European beech, for which there were no significant differences between the relative height increment under 10% and 20% light availability levels.

Relative height and diameter increment also increased with decreasing species shade tolerance across the light availability levels, i.e., European beech < Norway spruce < Douglas fir, (Figure 3). Relative height growth increased from $35 \pm 25\%$ under 10% light availability to $72 \pm 40\%$ under 50% light availability for European beech, from $32 \pm 14\%$ to $87 \pm 38\%$ for Norway spruce, and from $105 \pm 43\%$ to $200 \pm 70\%$ for Douglas fir. Relative diameter growth increased from $29 \pm 18\%$ under 10% light availability to $53 \pm 22\%$ under 50% light availability for European beech, from $64 \pm 35\%$ to $134 \pm 41\%$ for Norway spruce, and from $89 \pm 33\%$ to $209 \pm 53\%$ for Douglas fir.

The total aboveground woody biomass increased with increasing light availability for all the species (Figure 3). On average, the aboveground woody biomass was 2.4 times higher under 50% light availability than under 10% light availability for European beech, 4.8 times

higher for Norway spruce, 8.8 times higher for Douglas fir. Pronounced interspecific differences were not observed under the 10% light availability level. European beech's woody aboveground biomass was 9.4 ± 5.5 g, on average, and did not significantly differ from Norway spruce's (8.4 ± 5.3 g) and Douglas fir's (9.9 ± 4.6 g) biomass. However, the interspecific differences became more pronounced with increasing light availability. Namely, the most light-demanding species, Douglas fir, had a significantly higher woody aboveground biomass than Norway spruce and European beech under 20% and 50% light availability levels.
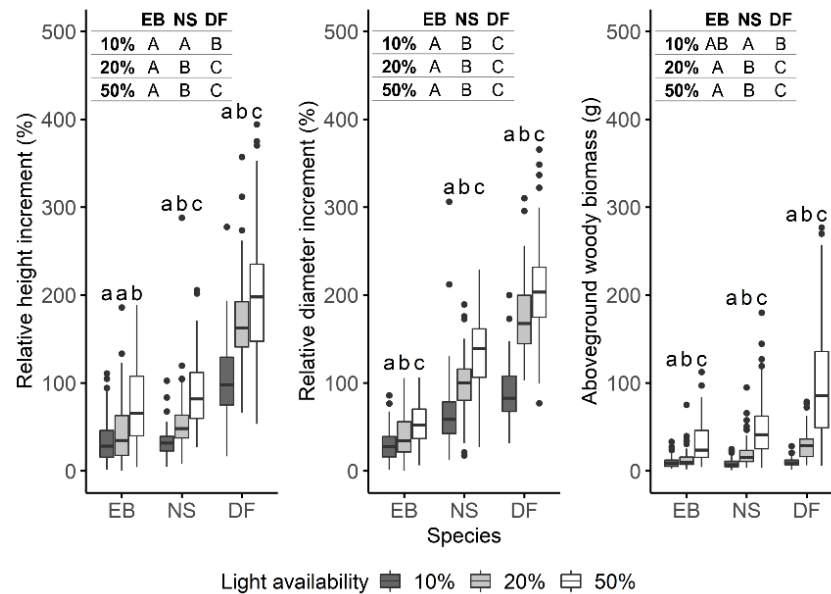
Figure 3. Relative height and diameter growth (%) and aboveground woody biomass (g) production along the light gradient. The letters above the boxplots indicate intraspecific differences across light levels. The tables above every figure show interspecific differences between three species under different light levels. Different letters indicate significant differences ($p < 0.05$). Light availability levels range from 10–50%. Species are arranged from most to least shade-tolerant [44,45]. Species: EB—European beech, NS—Norway spruce, DF—Douglas fir.

3.2. Growth Allocation to Height

All species allocated relatively more growth to height than diameter with decreasing light availability, with the strongest effect of light observed for Douglas fir (Figure 4). The predicted probability distributions of the relative height volume growth shifted to the right with decreasing light availability, indicating a negative relationship between the expected value of the relative height volume growth and light availability. The most apparent "gap" between the probability distributions for 50% and 20% light availability was observed for Douglas fir. Another effect of decreasing light availability was the higher relative height volume growth variance, meaning that individual differences in resource allocation were more pronounced under a lower light availability.

On average, European beech invested twice as much growth to height than Douglas fir or Norway spruce (Figure 4). This pattern was true across the light levels. Under 10% and 20% light availability levels, Douglas fir's relative height volume growth was only slightly yet significantly higher than that of Norway spruce (by 2–3.5%, on average), whereas, under 50% light availability, Norway spruce's and Douglas fir's relative higher volume growth decreased to $10 \pm 6\%$.
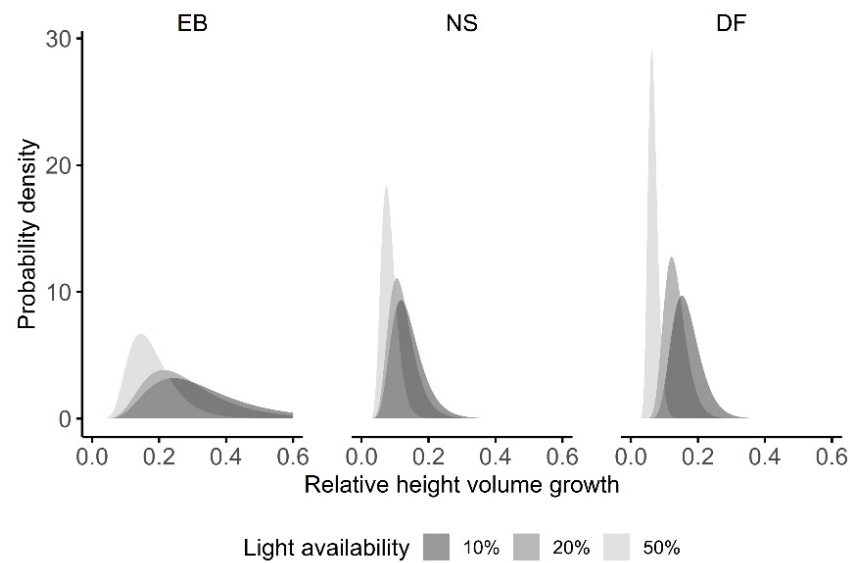
Figure 4. Predicted probability distributions of the relative height volume growth (R) for European beech (EB), Norway spruce (NS), and Douglas fir (DF) under 10%, 20%, and 50% light availability levels. The predictions were based on the location-scale regression model (Equation (2)). All other covariates were fixed to a representative value.

The identity of the competing species did not have a significant effect on relative height volume growth.

The seedlings that were taller than the species average in the previous year invested less in height growth in the following year (Figure 5). In contrast, the seedlings with a greater diameter than the species average in the last year had a significantly higher relative height volume growth in the following year. This is indicated by the decrease of the predicted expected value and the predicted quantiles of the relative height volume growth (y-axis) as the height (as a difference to the species average, x-axis) increases, meaning that taller seedlings prioritized diameter growth over height growth.
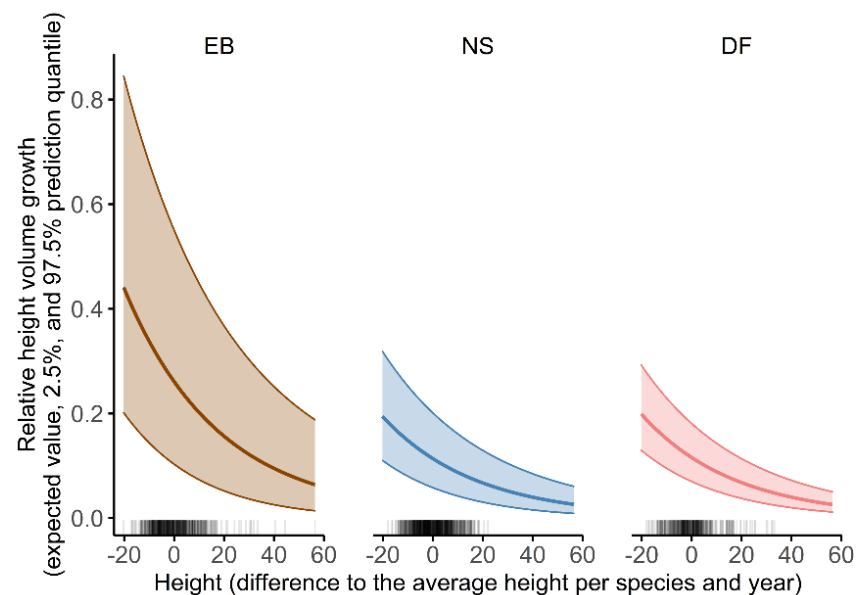

Figure 5. Predicted probability distributions (expected value, 2.5%, and 97.5% quantile) of the relative height volume growth (R) of European beech (EB), Norway spruce (NS), and Douglas fir (DF) with different heights. The predictions were based on the location-scale regression model (Equation (2)). All other covariates were fixed to a representative value.

3.3. Mixing Effect

We observed overall trends of positive mixing effect in mixtures of European beech with either of the conifers and the conifer mixture under 50% light availability (Figure 6). The strongest overyielding was predicted for European beech and Douglas fir mixture under 50% light availability level, with both species predicted to have significantly higher biomass production when mixed, resulting in a significantly positive mixture effect (Figure 6A3). Decreasing light availability negatively affected Douglas fir's total aboveground biomass production, and under 10% light availability, the species were predicted to produce significantly lower biomass in mixtures than in pure pots, i.e., to underyield (Figure 6A1).

A similar pattern was observed in mixtures of Douglas fir and Norway spruce. Douglas fir was predicted to produce significantly higher biomass under 50% light availability (Figure 6C3) and underyield under 10% light availability (Figure 6C1). However, the mixture effect on Douglas fir's biomass production did not significantly affect the overall biomass production of the mixture. Moreover, the predicted trends (not statistically significant) for the most part showed a neutral mixture effect across the light levels (Figure 6C1,C2), with a slightly positive trend under 50% light availability—primarily a result of the predicted overyielding of Douglas fir (Figure 6C3).

Significant overyielding was predicted for European beech and Norway spruce mixtures under 20% and 50% light availability levels (Figure 6B2,B3). Predicted overyielding under 20% light availability was mainly due to significantly higher biomass production of Norway spruce in the mixtures with European beech, whereas the overyielding under 50% light availability level could be attributed to the positive mixture effect on the biomass production of European beech when mixed with Norway spruce.
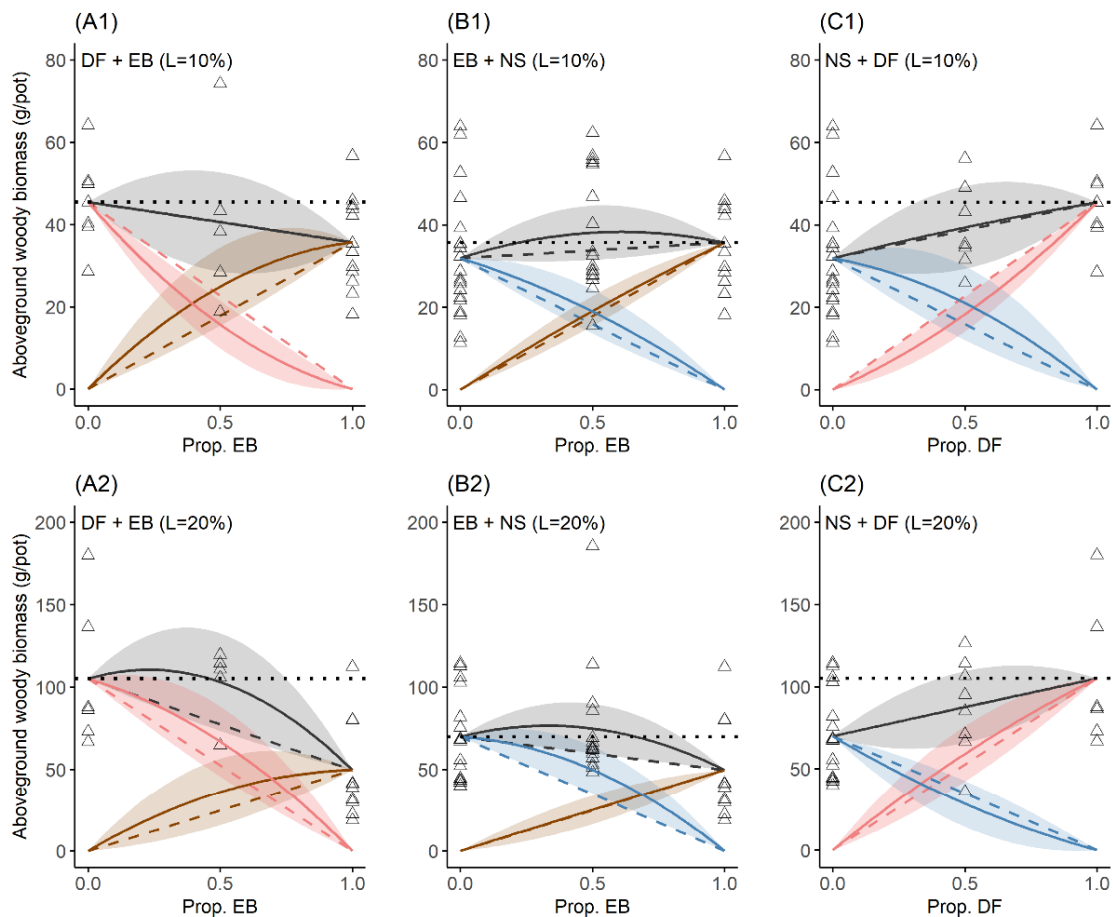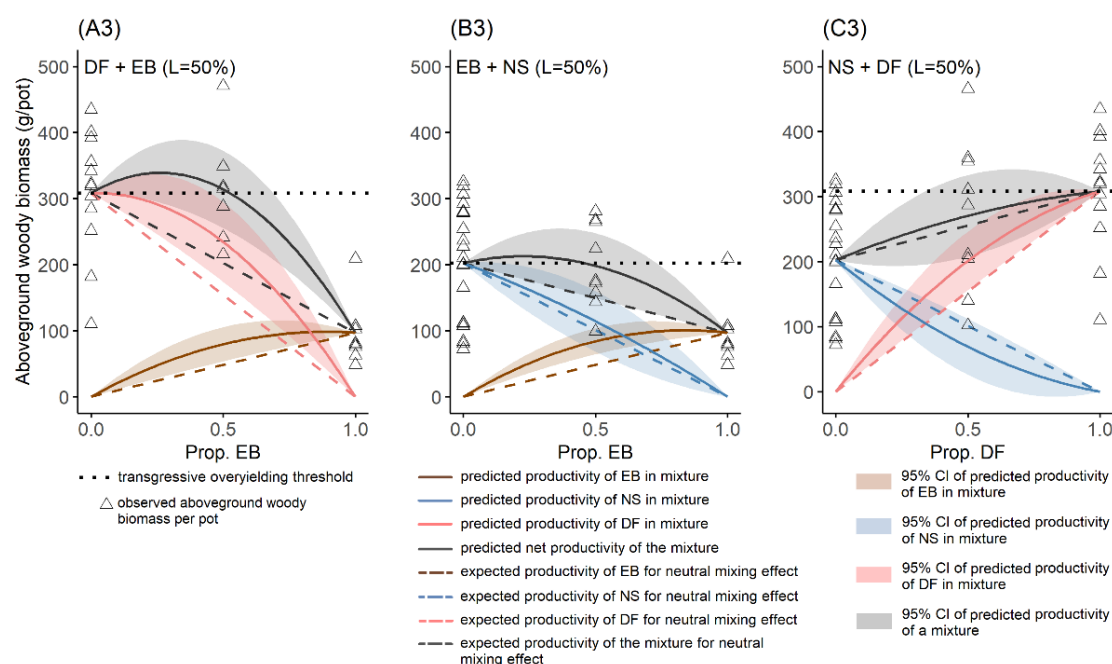

Figure 6. *Cont.*

Figure 6. Cross diagrams showing the mixing effect of European beech (EB), Norway spruce (NS), and Douglas fir (DF) seedlings growing in monospecific and mixed pots under 10%, 20%, and 50% light availability levels. The points present the observed aboveground woody biomass per pot (g). The overyielding or underyielding effect is significant when the prediction curve's confidence bands do not overlap with the reference line. Mixed Douglas fir and European beech pots under 10% light availability level: DF+EB (L=10%) (**A1**), mixed Douglas fir and European beech pots under 20% light availability level: DF+EB (L=20%) (**A2**), mixed Douglas fir and European beech pots under 50% light availability level: DF+EB (L=50%) (**A3**), mixed European beech and Norway spruce pots under 10% light availability level: EB+NS (L=10%) (**B1**), mixed European beech and Norway spruce pots under 20% light availability level: EB+NS (L=20%) (**B2**), mixed European beech and Norway spruce pots under 50% light availability level: EB+NS (L=50%) (**B3**), mixed Norway spruce and Douglas fir pots under 10% light availability level: NS+DF (L=10%) (**C1**), mixed Norway spruce and Douglas fir pots under 20% light availability level: NS+DF (L=20%) (**C2**), mixed Norway spruce and Douglas fir pots under 50% light availability level: NS+DF (L=50%) (**C3**).

4. Discussion

4.1. Relative Height and Diameter Growth and Biomass Production

The positive effect of light availability was reflected through increased growth and total biomass production of all species along the light gradient, as reported in other studies [8,46–50]. The light-demanding Douglas fir seedlings had higher relative height and diameter growth than the moderately shade-tolerant Norway spruce and the shade-tolerant European beech seedlings, thus corroborating previous results that reported higher growth rates for light-demanding tree species both under high and low light availability levels [7,13,51]. Additionally, the impact of light availability decreased with increasing species' shade tolerance. The strong reaction to light by increased relative height and diameter growth of light-demanding Douglas fir indicates that the seedlings were more stressed under lower light availability levels, and that increased light availability reduced light-stress in seedlings [52].

Plants respond plastically to limited light availability by employing shade avoidance or shade tolerance strategies [17,53,54]. A prominent expression of the shade avoidance strategy is enhanced vertical growth to escape shade and maintain contact with the light source [50,54]. This growth strategy is associated with that of light-demanding species [55]. Shade-tolerant species generally suppress shade avoidance traits and have lower growth rates than light-demanding species in high and low resource environments [53,56].

Light-demanding species use primarily height and diameter growth, at the expense of other compartments such as branches and roots, to keep a minimum growth performance in low-resource environments [7]. This competitive strategy could explain the high competitiveness of Douglas fir seedlings in terms of relative height and diameter growth, yet lower total biomass under 10% light availability. Namely, the growth of below-ground organs is likely to be hampered, and the resources are allocated primarily to the above-ground light-capturing organs.

4.2. Growth Allocation to Height

All tree species increased the growth allocation to height, i.e., relative height volume growth, with decreasing light availability. Interestingly, species' identity had a more significant impact on growth allocation to height than species' shade tolerance. Specifically, European beech seedlings allocated more growth to height than the seedlings of the two conifer species, regardless of the light availability. It is likely because of the general differences in height-diameter allometry of gymnosperms and angiosperms, with gymnosperms, especially conifers, investing more in diameter growth per unit of height growth than angiosperms [3,57].

We also expected that, depending on the species composition in pots, the main competitor would alter the light availability to the extent that it impacts the growth strategy of the target species, i.e., with seedlings trying to maximize the exposure to light by investing more growth to height [23]. However, we found no effect of competitors' identity on the relative height volume growth across different light availability levels. The lack of competition effect could result from a too-short time spent under the competitive situation [49], or competition occurring in the plant organs not covered in this study—branches, roots, and leaves [58].

The relationship between growth allocation to height versus diameter determines the seedlings' position and social rank [59]. Our study shows that all species' relative height volume growth decreased with increasing height gained in the previous year. This growth strategy indicates that the dominant seedlings could invest more in diameter growth (also to support the expanding crown), whereas the stressed seedlings continued to invest in height growth [37,59].

4.3. Mixing Effect

Overyielding is a highly desirable property of mixed forests and has served as an important economic incentive for establishing mixed forests. We investigated the mixing effect across light availability levels and between competition types (monospecific vs. mixed) to determine if a positive mixture effect could be observed in the early seedling establishment phases. However, the results from the controlled experimental conditions should not necessarily be transferred to open field conditions without further considerations.

Our results on mixing effects were mainly statistically insignificant. The observed trends in aboveground biomass production depending on light availability and mixture type were in line with numerous findings from forest stands [24,25,60]. These findings emphasize the importance of species' functional dissimilarity and complementarity as the main drivers of overyielding in mixed stands. Namely, we found trends of positive mixing effect, i.e., higher biomass production in mixed than in monospecific pots, for European beech's mixtures with either of the conifers. Contrariwise, biomass production trends in mixed Douglas fir and Norway spruce pots indicated a more neutral mixing effect. On the species level, light availability positively affected the predicted biomass production of European beech and Douglas fir in mixed pots. Both species were also predicted to overyield under 50% light availability levels regardless of the mixture type. By contrast, the limited light availability (10%) resulted in the underyielding of Douglas fir both in mixtures with European beech and Norway spruce.

Species complementarity can be expressed through growth facilitation and competitive reduction (interspecific competition < intraspecific competition) [27,61]. Therefore,

functionally dissimilar species, i.e., species with different phyletic affiliation, shade tolerance, rooting depth, and leaf phenology, are likely to use resources more complementary, resulting in a positive mixture effect and higher biomass production [25,62]. However, competition reduction and facilitation lead to higher biomass production and growth only if the resource uptake is improved; otherwise, the positive effect can be masked by the increased use of the resource by the species that benefited from the competition reduction the most [60,63].

4.4. The Experimental Design

The experimental design of the current study was created to analyze the effects of light and nutrient availability, species identity, competition type, and interactions of these factors on selected tree growth parameters and biomass production of planted seedlings. However, similar to many other pot experiments, our research suffers from several limitations such as (i) short duration of the experiment (two vegetation periods), (ii) limited above- and belowground growing space in the later stages of the experiment, and (iii) the potential effect of shading nets on light quality [11,34,64,65]. Additionally, our experiment was negatively impacted by the high mortality of seedlings and failed nutrient treatment.

Seedling mortality: Factors such as planting shock and aphid infestation influenced the survival and vitality of the studied species. Many Douglas fir seedlings were lost shortly after planting, which significantly reduced the number of replicates for pure Douglas fir pots and pots where Douglas fir was mixed with European beech and Norway spruce. Douglas fir seedlings have been previously reported to be prone to transplanting shock [66]. Growing seedlings from seeds or cuttings can significantly increase the survival rates and yield seedlings that are better adapted to the experimental conditions than seedlings from a nursery [65].

A severe woolen aphid (*Phyllaphis fagi* L.) infestation impacted European beech seedlings' health and vigor. In the first year of the study, the infestation was contained. However, in the second year of the experiment, many beach seedlings experienced rapid dieback in the late spring, which was presumably caused by the same aphids' infestation. The infestation significantly reduced the number of usable replicates. Norway spruce seedlings experienced a brown spruce shoot aphid (*Cinara pilicornis* Hartig) infestation, but most seedlings recovered after insecticide Spruzit AF Schädlingsfrei (Neudorff GmbH, Emmerthal, Germany) applications. Aphid infestations are widespread in conditions where constant air exchange is limited, such as in nursery greenhouses or our experiment where the shading nets blocked some of the airflow [67].

Fertilizer treatment: Initially, the experiment was established with two levels of fertilizer treatment. Half of the pots received light treatment (2 g CRF per liter of the substrate) and the other half received heavy treatment (5 g CRF per liter of the substrate). Temperature is one of the main factors affecting CRF's nutrient release [68], and the first summer of the experiment (2018) was extremely hot, with 20 days above 30 °C (http://www.wetterstation-goettingen.de/, accessed on 16 March 2021). The heat caused the fertilizer to break down uncontrollably and significantly impact the nutrient treatment quality. The fertilizer leached into the pots and had to be washed out since the trees could not take up water. After the CRF's breakdown, we did not see an effect of the different fertilizer treatment levels in the preliminary analysis; thus, it was excluded from further analysis. At the same time, seedlings did not show any significant signs of lack of nutrients, like discolored or curled leaves, burnt leaf tips, terminal bud die-off [69]. Therefore, repeated fertilizer application was not carried the second time, but seedlings were closely monitored for the signs of nutrient deficiency. It has to be considered that the given fertilizer treatment might have benefited some species more than others and changed the competitive ability for some species, for example, if comparing the studied species, the growth of Norway spruce has been reported to be impacted by the nutrient availability more than European beech or Douglas fir [21,48].

Against this background, we suggest considering the discussed limitations when interpreting and generalizing the results.

5. Conclusions

Understanding the growth strategy of seedlings grown under different light availability levels and competition types can be crucial for early forest regeneration and management decisions. Our study confirmed that more light-demanding seedlings react stronger to increased light availability while retaining high growth rates in lower light availability levels as a shade avoidance strategy.

We devised a new solution to analyze relative growth allocation to height versus diameter by assuming a tree stem's simple cylindric model. We confirmed general differences in growth allocation strategies between angiosperms and gymnosperms, with angiosperms investing more in height growth and gymnosperms—in diameter growth. We also found that trees allocated relatively more growth to height with decreasing light availability and that the height from the previous year determined growth allocation in the following year. As a result, if the seedlings have enough growth resources available to expand their crowns, they can begin investing more growth to diameter to gain mechanical support.

Higher species functional dissimilarity (gymnosperms vs. angiosperms) and sufficient light availability were the main drivers of positive mixture effect trends, i.e., higher biomass production in mixed than monospecific pots.

Our study emphasized the importance of light availability for growth and biomass production of economically desirable European beech, Norway spruce, and Douglas fir species under controlled experimental conditions (ex situ). Further research on how the desired state is achieved in situ by managing mixed-species regenerations with controlling canopy density is critical for areas where close-to-nature forestry and a strong preference for mixed-species forests (at the stand-level) prevail.

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