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The Contribution of Forest Structure to Complementarity in Mixed Stands of Norway Spruce (*Picea abies* L. KARST) and European Larch (*Larix decidua* MILL.)

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Abstract: An increasing number of investigations into mixed forest stands shows clear interactions between complementarity and stand and site characteristics. One of the least-investigated mixture types are mixed stands of Norway spruce and European larch. We investigated pure and mixed stands of these species in the northern part of the eastern intermediate Alps in Austria, at altitudes between approximately 880 and 1330 m above sea level. In these stands, 12 plots sized between 0.25 ha and 1.6 ha, with varying ages and proportions of Norway spruce, were established. All trees were measured for their coordinates, diameter at breast height, tree height, crown height, and crown projection area. The trees were cored at breast height, and from about 200 felled sample trees, equations for leaf area and for the five-year volume increment were developed. Growth efficiency (volume increment of a species per its fraction of the stand area) exhibited a clear interaction with age: in young mixed stands, spruce as well as larch grew less than the reference from the pure stands, while in the older stands especially spruce grew much better in the mixed stands. When the Clark Evans index was entered into the growth efficiency equations, it could be seen that the spatial distribution of the trees (i) explained more variance than the species proportion and (ii) showed an additional influence of stand density on the complementarity of the species.

Keywords: Clark Evans index; leaf area efficiency; growth efficiency

1. Introduction

Rising interest in the growth and yield of mixed forests is well documented by the proliferation of a large number of publications, and even new textbooks (e.g., Pretzsch et al. [1]) on mixed forests. Liang et al. [2] and Vila et al. [3] found that a positive biodiversity-productivity relationship is dominant on global and European scales. Paquette and Messier [4] also reported a strong, positive effect of biodiversity on tree productivity, however, they stressed that there is an important difference between their investigated biomes: complementarity seems less important in temperate forests growing in a more stable and productive environment, while, in the more stressful environment of boreal forests, beneficial interactions between species may be more important. For Chinese-planted forests, Guo and Ren [5] found no difference in productivity between biomes with one or two species. In natural forests, however, high diversity usually leads to higher productivity.

When studying different mixture types, more and more interactions between stand and site characteristics and complementarity were found. Pretzsch et al. [6] found an interaction effect of site productivity and admixtures in Norway spruce (*Picea abies* L. KARST) and European

beech (*Fagus sylvatica* L.); specifically, that spruce growth was accelerated by beech admixture on poor sites, while beech growth was promoted by an admixture of spruce in nutrient-rich sites. Pretzsch et al. [7] found an interaction ranging from overyielding on poor sites to underyielding on fertile sites in mixtures of sessile oak (*Quercus petraea* MATT.) and European beech (*Fagus sylvatica* L.). An investigation of Scots pine (*Pinus sylvestris* L.) and European beech in mixed versus pure stands in 32 triplets located along a productivity gradient through Europe, reaching from Sweden to Bulgaria and from Spain to the Ukraine, with climatic variables varying widely in precipitation (520–1175 mm a⁻¹), mean annual temperature (6–10.5 °C), and the drought index by de Martonne (28–61 mm °C⁻¹), indicated no dependence of overyielding on the site index and the climatic variables [8]. The authors, therefore, hypothesized that the overyielding resulted from several different types of interactions (light, water, and nutrient-related) that are all important in different circumstances. From Douglas fir (*Pseudotsuga menziesii* (MIRBEL) FRANKO)-European beech forests, Scots pine-sessile oak forests, sessile oak-European beech forests, and sessile oak-silver birch (*Betula pendula* ROTH) forests in the Netherlands, Lu et al. [9] concluded that overyielding occurs in evergreen-deciduous mixed forests, however, not in deciduous-deciduous species mixtures. Later, Lu et al. [10] concluded from the same database that the difference in leaf phenology is a main driver of overyielding and—in accordance with the stress gradient hypothesis—that overyielding is much more significant in places with poor soils than with rich soils. Mina et al. [11] investigated 6 tree species in 12 two-species mixtures and in seven three-species mixtures from individual tree data of the Swiss National Forest Inventory, and concluded that “complementarity varies strongly with stand density and stand development as well as with topographic, climatic and soil conditions”. They also stated that “careful assessments depending on the species composing the stands are required under changing resource availability as well as under different levels of stand density and development”.

Among the forest types in the Central European part of the alpine biogeographic region [12] mixed Norway spruce-European larch (*Larix decidua* MILL.) forests are the least investigated, although they are of equal importance for valuable timber as other forest types, and offer equivalent protection against avalanches and rockfall. In Austria, for example, they comprise about 10% of the commercial forests [13]. There is an old, but very detailed investigation [14,15], of about 100–120 year old, typically two-layered mixed stands of European larch and Norway spruce, showing that mixed stands generally overyield their respective pure stands by 10–12% of the growth volume. The study by Mina et al. [11], among others, also looks into this mixture based on the data of the Swiss National Forest Inventory. However, this study is based on a large sample size in terms of individual trees, but not in terms of forest stands or plots.

Studies on the effect of stand structure on complementarity are likewise limited. There are several studies showing that mixed forest stands differ in structure when compared with monospecific stands [16–18], however, only a few studies [14,15] stress the influence of structure on complementarity.

Therefore, the objective of our study was to investigate the influence of structure on the complementarity in Norway spruce-European larch forest stands.

2. Material and Methods

2.1. Site Description

The observed plots are located in the alpine biogeographic region [12] in the northern part of the eastern intermediate Alps [19] near the city of Leoben in Styria, Austria, at approximately 47°26' E and 15°05' N and at altitudes between approximately 880 and 1330 m above sea level (Figure 1).

The mean annual temperature is 5.2 °C and the mean annual precipitation is 1510 mm (the observation period was between 1971 and 2000) [20]. The maximum rainfall occurs in July. The mean Martonne index of 99 characterizes the site as very humid.

The stands in this region are usually managed according to a strip clear cut system [21], where, after clear felling, the forest regenerates naturally in three strips: in the outer strip European larch

prevails while in the inner strip Norway spruce dominates, and in the transitional zone mixed stands of both species develop.

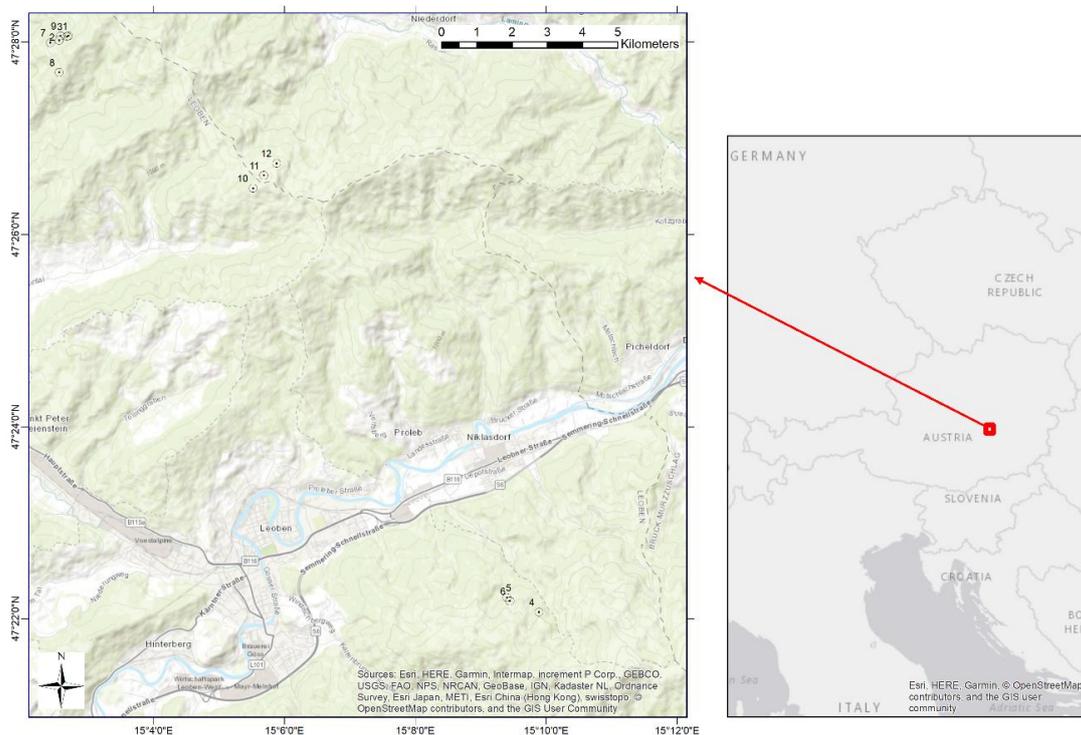


Figure 1. Location of the twelve sample plots.

2.2. Study Design

In this area we intended to establish four triplets (as in the research by Pretzsch et al. [1]) of different age, each one consisting of one mixed stand of Norway spruce and European larch, and two monospecific stands with Norway spruce and European larch, respectively. Plot size was chosen such that each plot contained at least 50 trees (minimum diameter at breast height (dbh) = 5 cm) of the respective species, resulting in plot sizes between 0.25 ha and 1.6 ha. The plot sizes and some site descriptors are given in Table 1, while further plot characteristics are given in Table 2.

Table 1. Plot size and some site descriptors: Sp indicates the spruce plots, Sp La the mixed spruce and larch plots, and La the larch plots.

| Plot Number | Mixture | Plot Size (m ²) | Number of Trees | | Slope % | Azimuth (°) | Altitude (m) |
|-------------|---------|-----------------------------|-----------------|-------|---------|-------------|--------------|
| | | | Spruce | Larch | | | |
| 1 | Sp | 2504 | 344 | 19 | 68 | 305 | 1204 |
| 2 | Sp La | 2664 | 258 | 87 | 58 | 305 | 1194 |
| 3 | La | 1379 | 234 | 88 | 65 | 305 | 1209 |
| 4 | Sp | 16,172 | 435 | 43 | 70 | 305 | 936 |
| 5 | Sp La | 11,660 | 226 | 184 | 66 | 347 | 882 |
| 6 | La | 6805 | 162 | 241 | 76 | 352 | 941 |
| 7 | Sp | 6096 | 207 | 59 | 70 | 280 | 1168 |
| 8 | Sp La | 3281 | 87 | 49 | 55 | 300 | 1177 |
| 9 | La | 11,543 | 82 | 189 | 55 | 305 | 1180 |
| 10 | Sp | 7086 | 271 | 43 | 43 | 331 | 1288 |
| 11 | Sp La | 12,886 | 218 | 136 | 50 | 333 | 1330 |
| 12 | La | 11,104 | 32 | 325 | 45 | 341 | 1281 |

Table 2. Mean plot characteristics. Sp indicates Norway spruce, La indicates European larch, hdom is the mean height of the 100 largest trees per hectare, BA is the basal area per hectare, N/ha is the tree number per hectare, and dg is the dbh (diameter at breast height) of the tree with the mean basal area. The species proportions and the stocking degree were calculated following Dinberger's and Sterba's method [22] by applying the relative density index using potential densities according to Vospernik and Sterba [23].

| Plot Number | Mixture | Age | hdom (m) | | BA (m ² /ha) | | N/ha | | dg (cm) | | Stocking | Proportion of Spruce |
|-------------|---------|-------|----------|------|-------------------------|------|------|-----|---------|------|----------|----------------------|
| | | years | Sp | La | Sp | La | Sp | La | Sp | La | | |
| 1 | Sp | 46 | 18.7 | 20.1 | 48.5 | 2.4 | 1374 | 76 | 21.2 | 20.2 | 0.81 | 0.93 |
| 2 | Sp La | 48 | 19.0 | 21.5 | 17.6 | 19.2 | 968 | 327 | 15.2 | 27.3 | 0.74 | 0.40 |
| 3 | La | 41 | 14.9 | 21.2 | 22.5 | 26.1 | 1697 | 638 | 13.0 | 22.8 | 1.01 | 0.39 |
| 4 | Sp | 98 | 40.1 | - | 47.1 | 4.1 | 270 | 26 | 47.2 | 44.7 | 0.69 | 0.87 |
| 5 | Sp La | 109 | 33.9 | 35.0 | 18.8 | 16.4 | 194 | 158 | 35.2 | 36.4 | 0.63 | 0.41 |
| 6 | La | 98 | 30.8 | 31.7 | 10.2 | 25.7 | 238 | 341 | 23.4 | 30.7 | 0.74 | 0.21 |
| 7 | Sp | 122 | 31.9 | 33.6 | 39.4 | 15.1 | 340 | 98 | 38.5 | 44.2 | 0.87 | 0.61 |
| 8 | Sp La | 127 | 32.6 | 33.5 | 34.1 | 23.2 | 265 | 149 | 40.5 | 44.5 | 0.97 | 0.47 |
| 9 | La | 147 | 34.7 | 39.3 | 11.3 | 27.2 | 71 | 164 | 44.9 | 46.0 | 0.76 | 0.19 |
| 10 | Sp | 107 | 27.2 | 27.9 | 35.6 | 8.4 | 382 | 59 | 34.4 | 42.4 | 0.68 | 0.72 |
| 11 | Sp La | 174 | 29.5 | 31.8 | 21.0 | 19.4 | 169 | 106 | 39.8 | 48.3 | 0.71 | 0.39 |
| 12 | La | 97 | - | 32.2 | 0.7 | 29.2 | 29 | 293 | 17.7 | 35.6 | 0.68 | 0.02 |

The plots were all on steep slopes mainly exposed to the northwest, and at altitudes between approximately 880 and 1330 m above sea level.

As can be seen from Table 2, it was impossible to find truly monospecific stands. With only two exceptions (Plots 1 and 12) the stands included a considerable admixture of other species. There were small numbers of Scots pines, white fir (*Abies alba* MILL.), sycamore maple (*Acer pseudoplatanus* L.), and European beech trees in the plots. Due to their shade tolerance the white firs were counted as Norway spruce trees, and the Scots pines were counted as European larch trees because of their shade intolerance and broadleaves resulting from their deciduous character. Please note that further on we only use the terms spruce and larch for Norway spruce and European larch, respectively.

In the mixed stands, the mean difference between the age of the larch and spruce was only 3 ± 20 years.

2.3. Data Assessment

Data were collected between August and October 2012 (plots 1–3 and 7–9) and in October 2013 (plots 4–6 and 10–12). All trees in the plots were measured for the following: diameter at breast height (dbh), tree height, and height to the crown base. The tree positions within the plot and the trees' crown perimeters were mapped using laser measuring equipment. For obtaining the crown perimeters, between six and eight points of the crown border were vertically projected to the ground surface.

All trees were cored in order to measure the radial increment of a time span of at least 20 years.

In the mixed plots 15 larch trees and 10 spruce trees were felled in order to determine their leaf area (see Dirnberger et al. [21]) and to evaluate their volume increment. In the pure plots, the same number of sample trees of the respective species were felled. The rings of the felled trees were counted at the stump to estimate stand age, depending on the stump height three to five years were added to the tree ring count. The dbh, the diameter at 3/10th of the height of the tree, the diameter at the crown base, and the height increments for at least the last 15 complete growth years were measured for each of the felled trees. To calculate the volume increments, three discs were taken from each of the sample trees: one at breast height (1.3 m), one at 3/10th of the tree's height, and one at the crown base. On these discs, the radial increments of the last 20 years were measured along 4 radii in the laboratory to the nearest 1/100th mm.

2.4. Volume Increment

The volume increments of the sample trees were calculated from the tree ring measurements of the three discs along with the height increments, using the taper equations of Eckmüller et al. [24]. In each plot the volume increments of the sample trees were modelled according to the equation $iv = \exp(a + b \cdot \ln(ig) + c \cdot \ln(dbh))$, with iv representing the five-year volume increment for 2008–2012, ig the five-year basal area increment at breast height, dbh the diameter at breast height, and a , b , and c the regression coefficients estimated species-wise by log-log-regression using the statistics software R [25]. The coefficients of determination (R^2) of these regressions, with a minimum of 0.929, a maximum of 0.992, and an average of 0.965, justified their use for calculating the volume increment of all trees in the plots with their basal area increment from the coring and their dbh .

2.5. Leaf Area

From the 194 sample trees of this study, Dirnberger et al. [21] developed a model for estimating individual tree leaf area: From the measurements of the crown radii and the crown length, the crown surface area of each tree could be calculated using Pretzsch's [26] crown shape models for spruce and larch. This crown surface area, together with the dbh , were the most important input variables for the leaf area model. Additionally, Dirnberger et al. [21] showed that the leaf area of spruce depends on the stocking of the stand and the leaf area of larch depends on the proportion of spruce in the stand. Thus, the leaf areas of all individual trees in our stand were calculated from these equations.

2.6. Variables Characterizing the Structure of the Stands

The common variables characterizing the structure of stands were the stocking and the species proportions. Dirnberger and Sterba [22] and Sterba et al. [27] showed that the species proportion, which does not take into account the different potential densities of the species involved, would lead to misinterpretations of over or underyielding of the species. Thus, we used the concept of the relative density indices (RDI) for calculating the two relevant species proportions by area as $RDI_i = \frac{N_i}{N_{max,i}}$; stocking = $\sum_i RDI_i$; proportion $_i = \frac{RDI_i}{\text{stocking}}$. In this formula N_i is the observed number of trees per hectare of the i th species, and $N_{max,i}$ is the maximum number of trees per hectare of the i th species, calculated from the maximum density line of the respective species as $N_{max} = C \cdot dg^E$ with dg representing the quadratic mean diameter of the species C and E using the coefficients estimated from the data of the Austrian National Forest Inventory by quantile regression for the 95th percentile [23].

In order to take into account the vertical structure of the species distribution in the stands, we used the ratio of the mean heights (Lorey's mean heights) of spruce and larch combined with Pretzsch's [28] species profile [18]. Pretzsch [28] distinguishes the upper layer of a stand where trees with >80% of the dominant height are located, a middle layer with between 50% and 80% of the dominant height, and a lower layer with <50% of the dominant height. This definition was also used in this study to calculate the proportion of the spruce volume, which is located in the lower and the middle layers as a further vertical structure variable.

To attribute a fraction of the stand area to each tree and to the layers, we used the circlebow-model approach [29], as programmed by Kindermann [30]. This approach divides the plot area into very small pixels, and calculates a weighted distance-number $T_i = \frac{(x-x_i)^2 + (y-y_i)^2}{weight_i}$ where x and y are the coordinates of the pixel centres, x_i and y_i are the tree coordinates, and $weight_i$ is the weight of the i th tree. A pixel is then attributed to the tree where T_i is the minimum value. In this way each tree receives a fraction of the stand area (APA = area potentially available according to Gspaltl et al. [31]), which then can be summed for the layers in which the trees are located. Since the species proportions by area are best approximated by their leaf area [22,32], the individual tree leaf area was used as the weight in this equation.

In order to characterize the spatial distribution of the species in the stands, the Clark Evans aggregation index [33]—once by species and once disregarding species—and Pielou’s segregation index [34] were calculated from the coordinates of the trees in the stands.

For the resulting statistics see Table 3. The high degree of variation of the proportion of spruce and its volume proportion in the middle and lower layer is a result of the triplet design. The variation of the Clark Evans index indicates spatial distributions between clumped (<1) and slightly regular (>1). If not distinguishing between the species, the distribution of the trees is random (CE = 1) to slightly regular. The Pielou index shows that the species are slightly associated (<0); that is, the neighbor of a reference trees has a slightly higher probability of being another species, and segregated (>0). The ratio of the mean heights of spruce and larch shows that, on average, the spruce has a lower height than the larch, and only rarely is it higher than larch ($max = 1.0325$). Considering that with two species and three layers the maximum species profile is $\ln(2 \cdot 3) = 1.79$, it varies notably from low to nearly maximum structural diversity.

Table 3. The distribution of the structural variables in the 12 plots. Stocking and the proportion of spruce are defined above. $h_{Lspruce}/h_{Llarch}$ is the ratio between Lorey’s mean height of spruce and larch. CE is the Clark Evans index. Please note that when there are only two species in a stand, the Pielou index for both species is the same.

| Variable | Minimum | Maximum | Mean | Standard Deviation | CV (%) |
|--|---------|---------|--------|--------------------|--------|
| Stocking | 0.6314 | 1.0057 | 0.7736 | 0.1190 | 15 |
| Prop. of spruce (by area) | 0.0170 | 0.9290 | 0.4650 | 0.2743 | 59 |
| $h_{Lspruce}/h_{Llarch}$ | 0.5624 | 1.0325 | 0.8306 | 0.1478 | 18 |
| Species profile | 0.6689 | 1.6626 | 1.2016 | 0.2765 | 23 |
| Prop. of spruce volume in the lower and middle layer | 0.0154 | 0.1491 | 0.0891 | 0.0442 | 50 |
| CE spruce | 0.8700 | 1.3900 | 1.1550 | 0.1448 | 13 |
| CE larch | 0.6500 | 1.3200 | 1.1125 | 0.1888 | 17 |
| CE all species | 1.0700 | 1.3900 | 1.2325 | 0.0977 | 8 |
| Pielou index | −0.1600 | 0.2460 | 0.0804 | 0.1494 | 186 |

2.7. Definitions

The leaf area index of a stand is defined as the leaf area of the stand divided by the stand’s area. In order to define the leaf area index of a species in a mixed stand, the leaf area of all trees of the i th species has to be related to species proportion by area, as in:

$$LAI_i [m^2 m^{-2}] = \frac{LA_i \left[\frac{m^2}{ha} \right]}{prop_i} \quad (1)$$

The leaf area efficiency relates the volume increment to the leaf area, thus:

$$LAEff_i \left[m^3 a^{-1} ha^{-1} \right] = \frac{iv_i \left[m^3 a^{-1} ha^{-1} \right]}{LA_i \left[ha \cdot ha^{-1} \right]} \quad (2)$$

where LA_i is the total leaf area of the i th species in the plot.

In order to compare the growth per hectare of the species, as it depends on the mixture of species and other variables, we defined the species growth efficiency as its growth divided by its proportion by area. This is the growth of a species in a stand, related to the area which it occupies:

$$GrowthEff_i \left[m^3 a^{-1} ha^{-1} \right] = \frac{iv_i \left[m^3 a^{-1} ha^{-1} \right]}{prop_i} \quad (3)$$

Following Mina et al. [11], who stated that it may be difficult to differentiate between the three fundamental diversity effects (competition, facilitation, and competitive reduction [7,35]), we described them collectively as complementarity [36], defining:

$$\text{Complementarity} = \frac{\text{GrowthEff}_{\text{species}}}{\text{Growth}_{\text{species, reference}}} \quad (4)$$

where the reference for a species is its growth in a comparable monospecific stand. For the complementarity of the total stand growth (the two species together) the reference is the growth of the respective monospecific stands, weighted by their proportions by area:

$$\text{Growth}_{\text{total, reference}} \left[\text{m}^3 \text{a}^{-1} \text{ha}^{-1} \right] = \sum_{\text{species}=1}^2 iv_{\text{species, pure}} \left[\text{m}^3 \text{a}^{-1} \text{ha}^{-1} \right] \cdot \text{prop}_{\text{species}} \quad (5)$$

where $iv_{\text{species, pure}}$ can be calculated from the equations for the growth efficiency of the species by inserting 1 for the species proportion.

Complementarities > 1 are called overyielding, meaning that the growth is higher than in the comparable monospecific stand, while complementarity < 1 means underyielding, or that the growth is lower than in the comparable monospecific stand.

In order to define the fraction of stand area potentially available for the species in the layers, we calculated Voronoi diagrams weighted by the individual trees' leaf areas [31].

2.8. Statistical Methods

The statistical analyses were performed in R [25]. For modelling growth efficiency, leaf area at its available fraction of the stand area (LA/APA) and leaf area efficiency, we used linear regression models. Model selection was based on the minimum Akaike information criterion (AIC). The model with all available independent variables and all possible interaction effects was used as starting point for the stepwise selection procedure using the R library MASS [37]. Strata with less than 12 trees were disregarded in the analysis. Levels of significance are indicated by * for $\alpha = 0.05$, ** for $\alpha = 0.01$ and *** for $\alpha = 0.001$.

3. Results

3.1. Leaf Area and Growth

From the calculations described above, the leaf area and the volume increments of the plots are given in Table 4. From these figures and the species proportions by area given in Table 2, the leaf area index of the species according to Equation (1), the leaf area efficiency (Equation (2)), and the growth efficiency (Equation (3)) were derived (see Table 5, Figure 2).

All three figures differ highly significantly by species ($p < 0.01$).

Although the leaf area efficiency of larch is about 35% higher than that of spruce, the growth efficiency of spruce is more than twice that of larch. The reason for this is the much higher leaf area index of spruce (+192%).

It can be seen that the leaf area indices—by species as well as in total—are independent of the stocking degree ($R^2_{\text{spruce}} = 0.238$; $R^2_{\text{larch}} = 0.056$; $R^2_{\text{total}} = 0.008$). The LAI of spruce is also independent of the spruce proportion, while the LAI of larch increases significantly with its proportion, and the total LAI decreases highly significantly with an increasing proportion of larch; that is, it increases with an increasing proportion of spruce (Figure 1).

Table 4. Leaf area and annual volume increment of the plots by species. Volume increment is the average increment of the years 2008–2012. SD is the standard deviation.

| Plot ID | Leaf Area (m ² /m ²) | | | Volume Increment (m ³ a ⁻¹ ha ⁻¹) | | |
|---------|---|-------|-------|---|-------|-------|
| | Spruce | Larch | Total | Spruce | Larch | Total |
| Min | 0.15 | 0.16 | 3.57 | 0.4 | 0.8 | 7.1 |
| Max | 8.94 | 3.66 | 9.10 | 29.9 | 11.7 | 30.7 |
| Mean | 4.50 | 2.12 | 6.44 | 9.65 | 4.90 | 14.55 |
| SD | 2.66 | 1.34 | 1.62 | 7.81 | 3.70 | 7.54 |

Table 5. Leaf area indices (LAI) and efficiencies (LA eff is the leaf area efficiency, i.e., increment per leaf area, and Growth eff is growth efficiency, i.e., growth per available stand area of the species). SD is the standard deviation.

| | Spruce | | | | Larch | | | |
|---|--------|-------|-------|------|-------|-------|------|------|
| | Min | Max | Mean | SD | Min | Max | Mean | SD |
| LAI _i (m ² m ⁻²) | 7.67 | 12.32 | 9.57 | 1.16 | 1.50 | 6.04 | 3.27 | 1.35 |
| LAEff _i (m ³ a ⁻¹ ha ⁻¹) | 1.25 | 4.88 | 2.13 | 0.80 | 1.04 | 4.88 | 2.88 | 1.17 |
| GrowthEff _i (m ³ a ⁻¹ ha ⁻¹) | 12.45 | 36.82 | 20.49 | 8.38 | 3.79 | 19.30 | 8.98 | 4.74 |

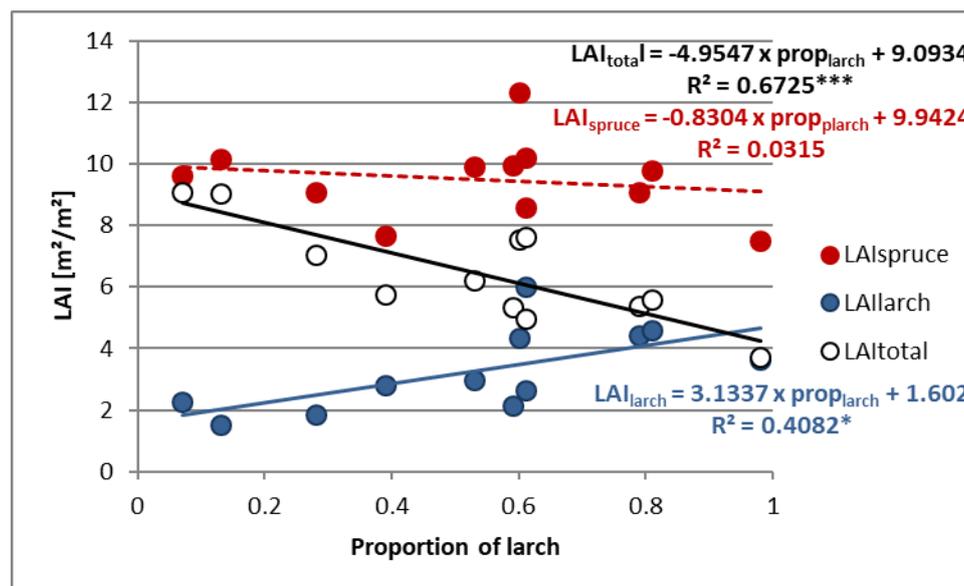


Figure 2. Leaf area index (LAI) by species and in total, depending on the proportion of larch (prop La). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

When comparing the leaf area at its available fraction of the stand area (APA) the two species differ significantly ($p = 0.020$), while there is no significant difference regarding the leaf area efficiency and growth efficiency. For larch there is a decline of leaf area per APA, leaf area efficiency, and growth efficiency from the upper layer to the middle layer; however, these declines are not significant (Figure 3).

The lower layer exists only for spruce (there is no larch in the lower layer with the exception of three trees in the whole study area). Leaf area per APA is highest for this layer and differs significantly ($p = 0.043$) from the two other layers. The leaf area efficiency is also highest in this layer, however, the differences are not significant. Consequently, growth efficiency in the lower layer is also highest ($p = 0.017$) (Figure 3).

3.2. Modelling Growth Efficiency

Del Rio and Sterba [38] and Condés et al. [39] used data of forest inventories where stand age was not known for depicting growth efficiency as a function of dominant height, quadratic mean diameter, stocking, and species proportion. They used the dominant height at a given mean diameter as a proxy for site quality, and mean diameter at a given dominant height as a proxy for age.

In our data age was known and, thus, we first investigated growth efficiency, as it may depend on age, dominant height, quadratic mean diameter, stocking, and species proportion using linear regression.

The resulting best equation was:

$$\ln(GrowthEff_{spec}) = a + prop_{spec} \cdot (b + c \cdot \ln(age)) \quad (6)$$

with coefficients and statistics given in Table 6.

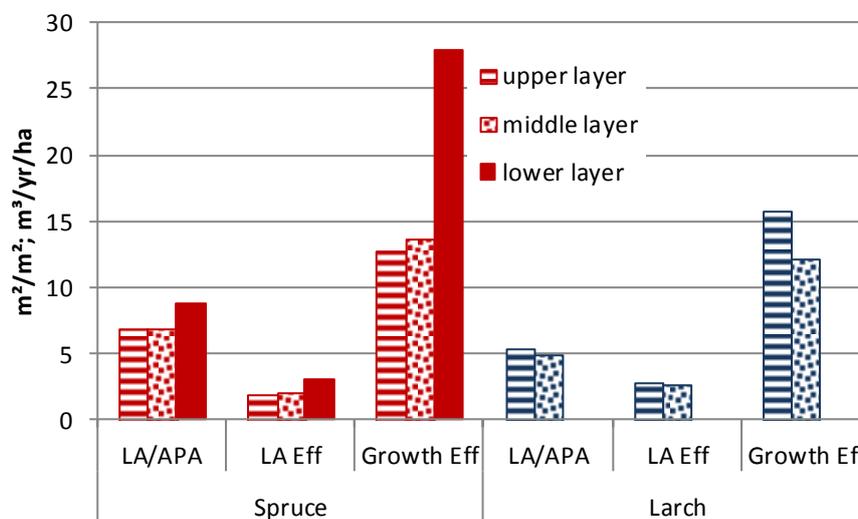


Figure 3. Leaf area per available area (LA/APA in m^2/m^2), leaf area efficiency (LA Eff in $m^3/year$ and ha), and growth efficiency (Growth Eff in $m^3/year$ and ha) by species and layer. Cells with $n < 15$ have been omitted.

Table 6. Estimates for the coefficients and statistics of Equation (6).

| | a | b | c | R^2_{adj} |
|--------|-----------|-----------|------------|-------------|
| Spruce | 3.088 *** | 5.292 ** | −1.249 ** | 0.524 * |
| Larch | 2.022 *** | 7.380 *** | −1.528 *** | 0.695 ** |

*: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

The interaction between age and species proportion was always highly significant, although the main effect of age was not significant at all. None of the other variables—dominant height, quadratic mean diameter, and stocking—contributed significantly to this equation, probably because, in addition to the limited sample size, the variation of site quality was small.

As an example, Figure 4 shows the annual growth per ha as it results from Equation (6), with the coefficients of Table 6 for a spruce proportion of 40% compared with the growth in the pure stands. Their growth is calculated with the same equation and coefficients, however, with a proportion of 1 for the respective species. Starting with an age of 75 years, the mixed stand clearly overyields the pure larch stand, and starting at an age of about 110 years the mixed stand overyields the pure spruce stand. The reference stand's growth is overyields by the total growth of the mixed stands starting at an age of 90 years.

The Kelty diagrams (“replacement series” according to Kelty [40]) show the interaction between age and species proportion: Young stands clearly exhibit underyielding of both species and, thus, the total, while in old stands the total overyielding is mainly a result of the overyielding of spruce. Both the total overyielding and the total underyielding are transgressive for these cases (Figure 5).

The complementarity, according to Equation (4), shows that larch is underyielding (complementarity < 1) as long as the stands are younger than 110 years, whereas spruce is already clearly overyielding at that age. The complementarity, both in under and overyielding, is highest at a spruce proportion between 40% and 50% (Figure 6).

3.3. Growth Efficiency and Stand Structure

When investigating the effect of the stand structure on growth efficiency, we found a clear dependency of the species specific Clark Evans index (Figure 7) in that the growth efficiency increased with increasing regularity of the spatial distribution of the trees in the stand. The Clark Evans index was the only structural characteristic which showed such a clear and significant dependency.

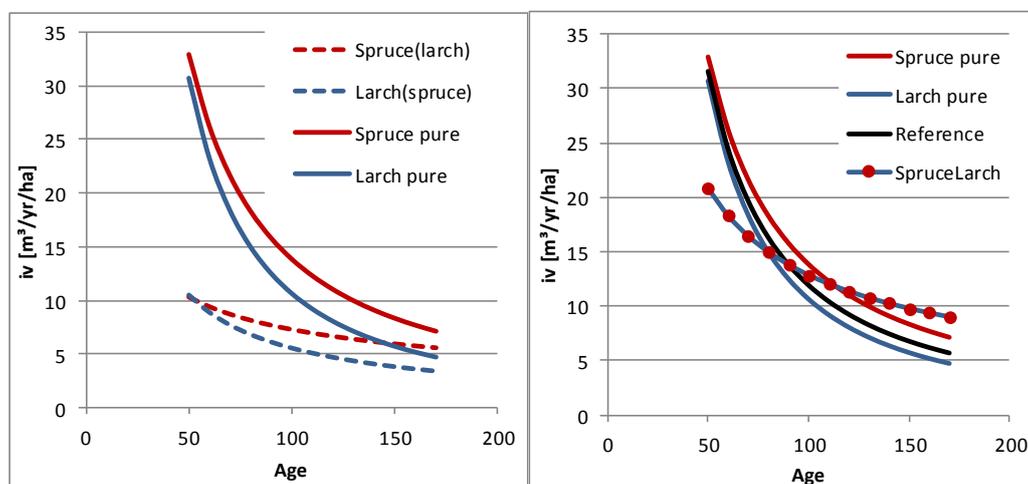


Figure 4. Volume growth of spruce and larch at a spruce proportion of 40%, depending on the stand age (**left template**). Spruce (larch) indicates the growth of spruce when admixed with larch, and Larch (spruce) indicates the growth of larch when admixed with spruce. SpruceLarch (**right template**) indicates the total growth of spruce and larch in the mixed stand, while the reference is the growth in the hypothetical mixed stand if there were no mixing effects.

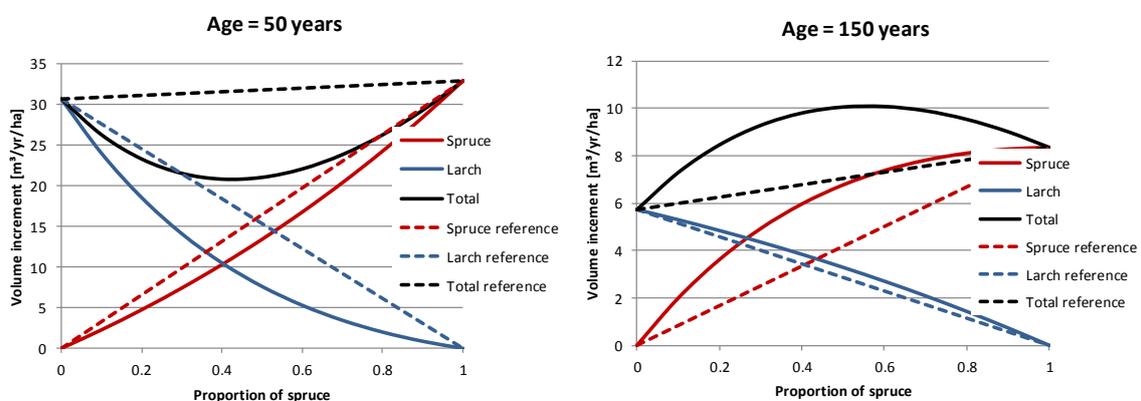


Figure 5. The Kelty diagrams as they result from Equation (6), with coefficients from Table 6.

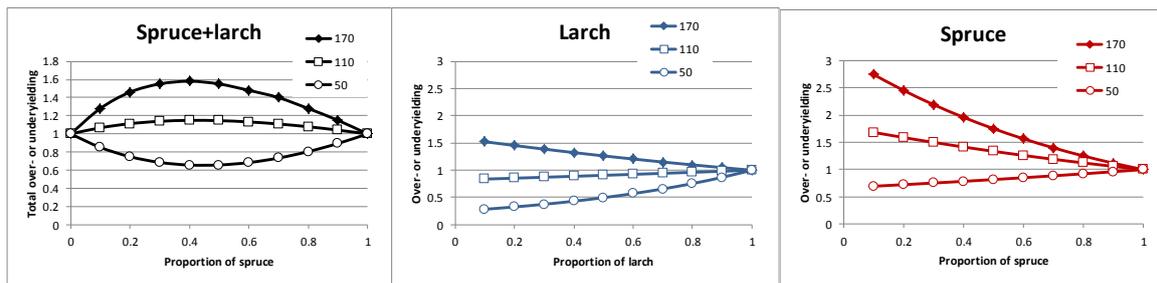


Figure 6. Relative complementarity at stand ages of 50, 110, and 170 years, depending on the species proportion.

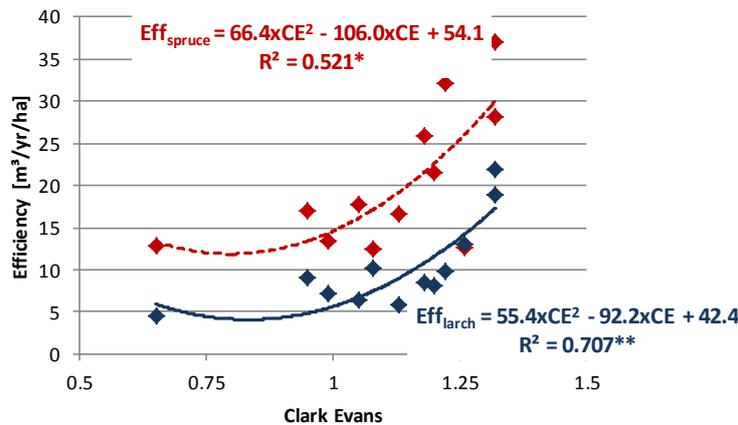


Figure 7. Growth efficiency and spatial distribution. * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

A more detailed investigation of this relationship showed that it was modified for spruce and larch by age and stocking degree respectively, resulting in the following equation:

$$\ln(GrowthEff_{spec}) = a + b \cdot \ln(CE_{spec}) + c \cdot \ln(age) \cdot \ln(CE_{spec}) + d \cdot stocking \cdot \ln(CE_{spec}) \quad (7)$$

The estimated coefficients and statistics are given in Table 7.

Table 7. Estimates for the coefficients and statistics of Equation (7).

| | a | b | c | d | R ² _{adj} |
|--------|------------|-----------|------------|-----------|-------------------------------|
| Spruce | 2.9085 *** | - | -1.8827 ** | 11.129 ** | 0.604 ** |
| Larch | 1.9876 *** | 11.978 ** | -2.3005 * | - | 0.733 ** |

*: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

The effect of the species proportion in Equation (5) is replaced by the effect of the Clark Evans index, leading to even higher coefficients of determination (R^2_{adj}).

In young stands, growth efficiency of larch increases dramatically with increasing regularity of the spatial distribution of the larch trees, while in older stands the increase is negligible (Figure 8).

At high stocking degrees the efficiency of spruce generally increases with the regularity of the spatial distribution of the spruce trees. At lower stocking degrees the efficiency of spruce increases only slightly with increasing regularity in young stands. In older stands with lower stocking degrees, the efficiency is even higher when the spatial distribution is clumped (aggregated). In stands where the spruce trees are regularly distributed, the efficiency clearly increases with increasing stocking, while in stands where the spatial distribution of spruce trees is clumped, the efficiency decreases with increasing stocking (Figure 9).

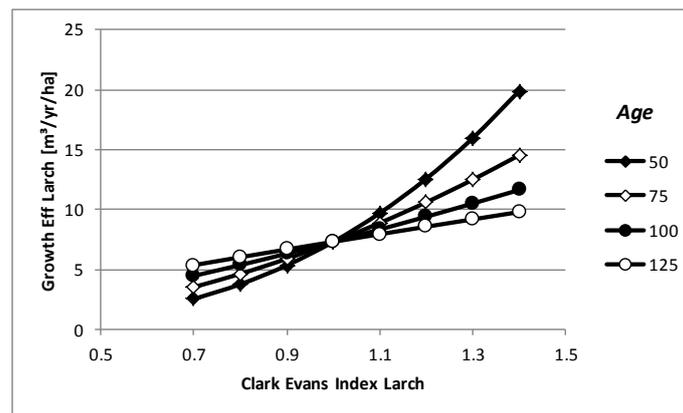


Figure 8. Growth efficiency of larch depending on its spatial distribution and age.



Figure 9. Growth efficiency of spruce depending on its spatial distribution, age, and stocking.

The significant positive correlation between the stand age and the Pielou index indicates a tendency of older stands to segregate the species ($R^2 = 0.347^*$). The higher the proportion of spruce, the more similar the mean heights of larch and spruce are ($R^2 = 0.529^{**}$) and the more regular the spatial distribution of spruce is ($R^2 = 0.560^{**}$). As expected, Pretzsch’s species profile is positively correlated with the proportion of spruce in the middle and lower stand layer ($R^2 = 0.389^*$).

Since the only structural characteristic that influenced the growth efficiencies were the respective Clark Evans indices, their relationships were investigated in more detail. The Clark Evans index of spruce only depended on the proportion of spruce:

$$\ln(CE_{spruce}) = 0.2443^{***} + 0.1006^{***} \cdot \ln(prop_{spruce}) \tag{8}$$

with $R^2_{adj} = 0.691^{***}$, thus indicating that the higher the proportion of spruce, the more regular the spatial distribution of the spruce. The Clark Evans index of larch—interestingly, nearly uncorrelated with the Clark Evans index of spruce ($r = 0.028$)—depended on the stand age and the proportion of larch (Equation (9), Figure 9):

$$\ln(CE_{larch}) = 0.346^* - 0.00523^{**} \cdot age + 0.00488^* \cdot age \cdot prop_{larch} \tag{9}$$

with $R^2_{adj} = 0.485^*$.

With increasing age, the spatial distribution of larch becomes more clumped ($CE < 1$) and this tendency is strongest when the proportion of larch is small. At a given age the spatial distribution becomes more regular ($CE > 1$) if its proportion increases. This tendency is strongest in old stands, and less pronounced in young stands (Figure 10).

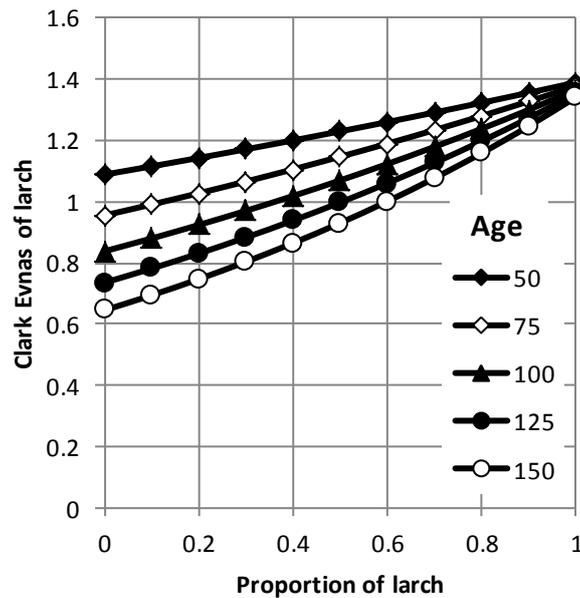


Figure 10. The Clark Evans index of larch, depending on stand age and the proportion of larch.

Building the ratio between the proportion of growth of a species on the total growth and the proportion by area also results in an indication for under or overyielding. If the proportion by growth is smaller than the proportion by area, the species uses its available space less efficiently. Table 8 clearly shows that spruce uses its available area significantly more efficiently than larch. The proportion of larch growth is always smaller than its proportion by area, while the proportion of spruce by growth is nearly 3.6 times as high as its proportion by stand area.

Table 8. The ratios between the proportions by growth and the proportions by area.

| | Spruce | Larch |
|------------------------|------------------|--------------|
| min | 1.049 | 0.359 |
| max | 3.561 | 0.986 |
| <i>mean</i> | 1.567 | 0.642 |
| SD | 0.725 | 0.223 |
| <i>Mean difference</i> | 0.925 *** | |

*: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

While there is no clear relationship between this ratio of larch and any structural characteristic, there is a strong relationship between (i) this ratio of spruce and its Clark Evans index, and (ii) the proportion of spruce growth in the middle and lower layer of spruce and the Clark's Evans index (Figure 11).

The ratio between the proportion of spruce growth and total growth is always larger than its proportion by stand area (ratio > 1), however, it decreases with the regularity of its spatial distribution. The proportion of spruce growth in the middle and lower layer also decreases with the regularity of its spatial distribution, with nearly 100% of its growth occurring in the middle and lower layer when its distribution is clumped, while only 10–15% of its growth occurs in this area when its spatial distribution is regular.

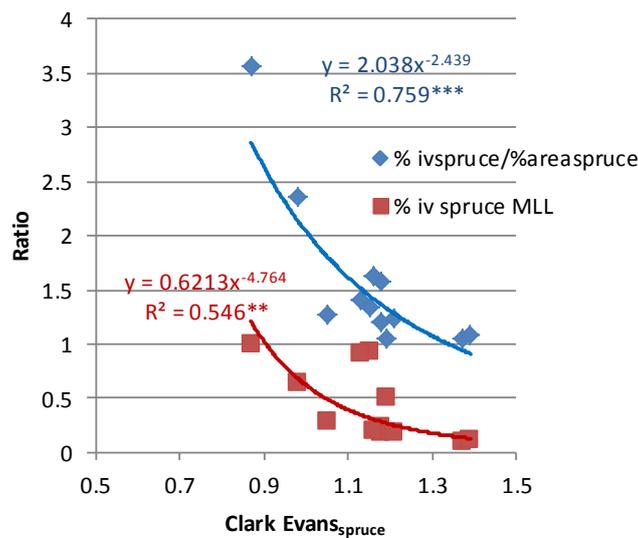


Figure 11. The ratios “growth of spruce by total growth divided by its proportion by area” (%iv spruce/%area spruce) and “growth of spruce in the middle and lower layer (MLL) by total growth of spruce” (%iv spruce MLL), depending on the spatial distribution (Clark Evans index) of spruce. * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

4. Discussion

We first found a clear and significant interaction between age and species proportion for the estimation of the growth efficiency of Norway spruce and European larch. The result of this interaction is that, in young stands, both species grow worse in mixtures than in their respective pure stands. In older stands, however, Norway spruce especially benefits from mixture with larch.

Mina et al. [11] stressed the fact that multiple factors modulate tree growth complementarity, based on a large sample of individual trees in the Swiss national forest inventory. Many stand and site characteristics were considered, however, no interactions with age were considered in that research. The same is true with most studies based on national forest inventories (e.g., see the research by del Rio and Sterba [38] and Condés et al. [39]), because, frequently, data on age is not provided. In several of these investigations the mean diameter was used as a proxy for age if the respective equations contained stand density, and another proxy (e.g., dominant height) was used for site quality. These variables frequently play a significant role in the respective equations for growth or growth efficiency, however, not in the interaction with the species proportion, and thus in complementarity. This does not mean that there is no complementarity, but only that its magnitude does not depend on other stand or site characteristics. In the study by Mina et al. [11] the equations for basal area growth contained many site and stand characteristics. The mixture effect was described by the dummy-variable CATMIX, indicating whether the plot belonged to a certain mixture type or was characterized as a monospecific stand. In this way, interactions of the complementarity with site or stand variables were considered as long as the influence of CATMIX was significant. Interestingly, neither for spruce nor for larch was the contribution of CATMIX significant (see Table S2 in Mina et al., 2017), indicating no complementarity effects in the larch-spruce mixture at an individual tree level.

On the other hand, Zöhrer [14] found clear—and even transgressive—overyielding in his spruce-larch mixtures. That he did not find our interactions with the age of his stands may be due to the fact that his investigations only contained stands where the larch was older than 100 years. The overyielding he found was clearly greater than what we found in our mixed stands. This may be due to two facts:

1. His stands were located in the eastern part of the subcontinental inner Alps [19] with a Martonne index of about 55, which is distinctly drier than our site. The yield class of his stands is

about 8 m³/yr/ha according to the yield table [41], while in our stand the yield class is about 10 m³/year/ha. The higher overyielding in this site would, thus, be in line with the stress-gradient hypothesis.

2. His stands have been clearly two layered with spruce in the lower layer [14]. While the ratio between the mean heights of spruce and larch in our stands lay between 0.56 and 1.03, with an average of 0.83 (Table 3), in his stands it was between 0.21 and 0.69 with an average of 0.455 [15]. He therefore presumes that “the optimum mixture probably is at a spruce proportion (by basal area) of 0.3 and 0.4. At higher proportions of spruce the layered structure, favorable for growth, may be lost”.

This is quantified in the significant increase of the ratio between the mean heights of spruce and larch and the Clark Evans index, along with the increasing spruce proportions. Additionally, we find Zöhrer’s presumption confirmed by the decreasing Clark Evans index; that is, with increasing clumpiness of the spatial distribution of spruce, the proportion of the spruce growth in the lower layer increases (Figure 11). This, in turn, is illustrated by the facts that in the lower layer the available stand area is best equipped with leaf area, and that the leaf area efficiency is highest in the lower layer. Thus, the growth efficiency of the lower layer is highest compared to the other layers (Figure 3). This behavior is different from the findings of Pretzsch et al. [42] in mixed stands of Norway spruce and European beech, where the annual net primary productivity was 37% higher when Norway spruce and European beech were mixed tree-wise, while there was no difference compared to the pure stands when the species were mixed group-wise. A possible explanation for this deviation from our study may be that in the study by Pretzsch et al. [42], in terms of the tree-wise mixture, the difference in mean height between the spruce and beech was 4.4 m and the ratio of the two mean heights was about 0.79, while in the group-wise mixture the difference was only 1.7 m with a respective ratio of 0.94. Thus, the tree-wise mixture may be more similar to the vertical structure of our stands (see Table 3).

5. Conclusions

At the investigated sites, complementarity in European larch-Norway spruce stands depends on age, stand density (stocking degree), and the spatial distribution of the trees. European larch grows somewhat worse in mixture with Norway spruce. Norway spruce underyields in young one-layered stands, while it overyields clearly in older stands, where its spatial distribution is clumped. This is mainly due to the leaf area equipment and the high growth efficiency of spruce in the lower layer.

Generally, the role of stand structure, spatially and by layers, should be considered more frequently in investigations of complementarity in mixed species forest stands.

Author Contributions: H.S. designed the experiment and wrote the first draft of the manuscript. G.D. supervised the fieldwork and calculated the increments and leaf areas. T.R. performed the statistical analyses and communicated the manuscript. All authors contributed to the final version of the manuscript.

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