

Article

Long-Term Productivity of Monospecific and Mixed Oak (*Quercus petraea* [Matt.] Liebl. and *Quercus robur* L.) Stands in Germany: Growth Dynamics and the Effect of Stand Structure

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Abstract: Wood production is one of the most important ecosystem service that forests provide to society. However, under changing climatic conditions, this appears to be subject to increasing uncertainties. In the present study we analyzed how long-term productivity of oak (*Quercus petraea* [Matt.] Liebl. and *Quercus robur* L.) stands has developed, how oak behaved on tree and stand level depending on the stand structure and which trade-offs can be observed. For the analyses, data from 147 long-term monospecific and mixed stands were investigated, which have been regularly recorded since 1898. Firstly, long-term stand productivity has increased up to 21% until 2020 as compared to 1960. This trend was observed for both, monospecific as well as mixed oak stands. Secondly, stand productivity was on average 19% higher in mixed compared to monospecific oak stands. This superiority can be explained by higher stand densities, a vigorous understory and the admixture of beech in particular. With increasing age, the observed positive effect of stand density was higher. Thirdly, individual oak productivity slowed down under interspecific competition, especially in young to mid-aged stands. In this context, the productivity of individual oaks depended strongly on their social position within the stand. Fourthly, in terms of growth partitioning larger trees contributed most in young oak stands, regardless of mixture. In order to preserve oak as a productive component of future mixed forests, the results suggest a silvicultural promotion of oak. Consistent management of dominant and vital oaks can achieve high productive trees while maintaining the positive characteristics of highly structured and mixed forests. A vigorous secondary stand can increase overall stand productivity at lower densities and allows silvicultural flexibility at the stand level. Creating vertical stand structure to reduce competition has only a limited positive effect on productivity of individual oaks that is highly related to its social status. Special attention should still be paid to beech as admixed tree species, which can continue to crowd oak even at higher stand ages.

Keywords: productivity; oak; stand structure; individual tree growth; growth dominance; long-term experiments; mixed stands; forest management

1. Introduction

In Central European forests, the uncertainties of climate change are considered as one of the important priority areas by forest managers to establish and sustain mixed species stands under rapidly changing growing conditions [1,2]. Therefore, adaptive forest management strategies are required to create structured and mixed forests that can mitigate the negative impacts of climate change by providing multiple ecosystem services on sustained basis [3]. In addition, increasing or maintaining productivity as one of the most important ecosystem services [4], appears to be highly relevant for forest managers.

For Central European forests a generally positive long-term growth trend was found in recent studies [5,6], that may contribute to the mitigation of advancing climate change. In this context, mixed stands of various tree species were regularly more productive than monospecific stands [7–9]. Globally, studies have also found a positive relationship between species diversity and productivity [10]. These observations suggest a significant mitigation potential of forests per se and a large adaptation potential of mixed forests in addition.

However, the observed mixing effects are very complex and can be an interaction of facilitation, competition and competition reduction [11]. These interactions depend on the tree species admixture [4], prevailing site conditions [7,12], stand structure [13–15] or the development stage of the stand [16]. In addition, these effects can be subject to a spatial and temporal gradient that affects the respective growth differently. For example, greater structural diversity appears to have a negative effect on productivity in young stands, whereas it may have a positive effect on stand growth in mature stands [16]. Moreover, growth response at stand level often cannot be directly inferred from growth response of the involved tree species or individual tree growth and vice versa [17,18]. At tree level, it can be decisive which social status the trees occupy in the stand. For instance, suppressed trees show different growth responses to tree species mixture than dominant trees [19,20]. Due to the complexity of influences on forest ecosystem productivity and the uncertainties caused by climate change, the analysis of structural effects on productivity had been addressed in a number of recent studies [14,21–23], but are still not fully understood.

In spatially structured mixed stands, growth partitioning within the stand is of great importance for the understanding of stand dynamics and the possibilities for adaptive forest management. One opportunity to analyze the growth partitioning within a stand is to consider the growth dominance coefficient described by Binkley [24,25]. Usually, an underlying temporal change of the coefficient over different development stages of forest stands can be observed, indicating that in older stands, smaller trees contribute more to the overall stand growth compared to young stands [24,25]. The growth partitioning also provides valuable insights into tree species-specific competitive relationships [26,27], which can be used to evaluate and refine silvicultural management options. This may also become particularly important when small and understory trees make the stand flexible for uncertainties in the future. In this way they can mitigate the risk of substantial loss of woody biomass due to a dieback of overstory trees. For example, a recent study by Pretzsch [28] on the social drift of trees showed a great potential of initially understory beech trees.

In the context of climate change, tree species with high drought resistance are increasingly important, in particular in Central Europe. Oaks (*Quercus* sp.) are considered to be tree species with a high drought resistance and a broad ecological amplitude, compared to other native tree species [7,29,30] that can contribute to the wood production during drought stress [31,32]. In addition, oaks provide valuable wood [33–35], can positively influence the growth of admixed species [7] and show a high ecological importance for species diversity [36,37]. Therefore, foresters increasingly rely on native oak species, among others, when choosing suitable tree species to face changing climatic conditions [38,39]. Nevertheless, oaks are also regularly affected by high pressure of insect pests, which can lead to reduced vitality or dieback [40,41]. This has to be considered when managing oak. Moreover, the consideration of oak in mixed species stands is not very attractive to forest managers, because of rather high silvicultural efforts to maintain oak in mixed species stands [35,42,43]. These observations are combined with long rotation periods to have high timber quality in production oriented oak silviculture in Central Europe [33,44]. Weaver and Spiecker [45] already mentioned the increasing multifunctional orientation of oak silviculture. More recently, Löf et al. [36] studied the silvicultural management of oak forest with special regard to multiple forest ecosystems. They identified suitable management options to meet multiple ecosystem services. For this purpose, knowing the growth reactions at stand and tree level as a function of stand structure is an important aspect when adjusting silvicultural management.

For the reasons mentioned above, we comparatively investigated monospecific and mixed oak stands covering a broad ecological and structural gradient as well as varying thinning practices. For this, we used a unique dataset of research plots in Germany which allows to identify the long-term growth trajectories at stand and tree level. At stand level, the observed long-term growth trends and the effect of vertical stand structure, stand density, stand age and mixing type on the productivity of oaks are analyzed, while at tree level the effect of social status was additionally investigated. For further explanation, the growth partitioning within the stands and the relevance of the tree species involved was included in the analysis. In conclusion, we formulated the following research questions:

- I. Is there a discernible long-term growth trend in oak stands over the last century?
- II. How does productivity of monospecific and mixed oak stands depend on stand structure, site conditions and stand development phase?
- III. How is productivity of individual oak trees related to their social status, vertical stand structure, mixture type and age?
- IV. What is the contribution of small tree individuals to stand growth?

2. Materials and Methods

2.1. Tree Species

In this study, stands of two oak species, sessile oak (*Quercus petraea* (Matt.) Liebl.) as well as pedunculate oak (*Quercus robur* L.) were analyzed. On the research sites the stands were partially composed of both species and likely also interspecific hybrids [46,47]. Although both oak species occupy partly diverging ecological niches, they occur equally on most of the forest area, which is particularly true for the research plots considered. Therefore, we did not distinguish between sessile and pedunculate oak and refer to "oak" from now on. In mixed stands the main additional tree species is European beech (*Fagus sylvatica* L.) followed by hornbeam (*Carpinus betulus* L.) and Scots pine (*Pinus sylvestris* L.), in the following referred to "beech", "hornbeam" and "pine", respectively. All other admixed tree species were summarized under the general term "others" (Table S1).

2.2. Research Plots

We used data from 32 long-term experiments, 25 strict forest reserves and 5 temporary experiments (Table 1). In total, the experiments and observations comprise 147 plots covering monospecific and mixed oak stands. The research plots are located in Germany, embedded in a unique network of long-term research plots first recorded in 1898 and measured repeatedly up to 23-times on single plots e.g., [5,7]. Therefore, the data cover different stages of stand development per plot. The size of the individual research plots varied between 0.03 and 1.8 hectares. The plots studied cover high productive as well as low productive sites, expressed by the site index (*SI*) of oak. *SI* was defined as the quadratic mean tree height at age of 100 years. As most of the research plots cover ages over 100 years the values were directly available. For plots younger than 100 years, *SI* was referenced from yield tables by Jüttner [48].

Table 1. Main characteristics of the investigated research plots; *N*—number of experiments/research sites; *n*—number of research plots/stands; *S*—plot size [ha]; Per—observation period [calendar year]; Int—inventory intervals [yrs]; hq 100—quadratic mean height at the age of 100 years; Prec—average annual precipitation [mm] (1970–2000); Temp—mean annual temperature [$^{\circ}$ C] (1970–2000); Alt—altitude above sea level [m.a.s.l.]; mean values, min and max values in italics below.

	<i>N</i>	<i>n</i>	<i>S</i> [ha]	Per	Int [yrs]	hq 100 [m]	Prec [mm]	Temp [$^{\circ}$ C]	Alt [m a.s.l.]
Long-term Experiments	32	112	0.37 0.03–1.0	1898–2020	7 3–22	26.1 16.9–34.5	772 570–1019	8.2 7.4–9.5	364 37–534
Strict Forest Reserves (SFR)	25	25	0.9 0.1–1.8	1977–2017	14 3–29	25.7 15.6–33.6	774 643–1174	8.1 7.7–8.9	429 286–579
Temporary Experiments	5	10	0.16 0.06–0.28	2007–2017	5 5–5	24.7 19.6–30.8	728 715–734	9.2 8.8–9.6	391 320–479

2.3. Productivity and Growth Dominance

On all considered plots the diameter at breast height (*dbh*) and tree height (*h*) was measured periodically. From these measurement data the yield data were derived for every survey according the DESER standard [49].

For productivity analyses at stand level, we used the mean periodic annual volume increment (*PAIV*) in $m^3 \text{ ha}^{-1} \text{ year}^{-1}$.

$$PAIV = (V_2 - V_1 + V_{rem}) / (t_2 - t_1) \quad (1)$$

V_1 is the remaining stand volume before the measurement period at time t_1 and V_2 at the end of the period at time t_2 . V_{rem} denotes the removed or dead volume.

The single tree productivity was calculated by the stem volume growth (*iv*) of each tree per crown projection area (*cpa*). Based on repeated samples of crown measurements we parametrized the allometric relationship for calculation of *cpa* values for all oak trees, according the following equation.

$$cpa = 0.07 \times dbh^{1.70} \quad (2)$$

where the oak-specific parameters were obtained from long-term experimental plots [50].

To evaluate the growth partitioning, we used the growth dominance coefficient (*GDC*) proposed by Binkley [24,25] and formulated by West [51]. The *GDC* describes the volume growth of an individual tree (*iv*) relative to its stem volume (*v*) and can thus provide an explanation of the growth dominance within forest stands. For the calculation of the *GDC*, the following statistic was used (Equation (3)).

$$GDC = 1 - \sum_{k=1}^n (v_k - v_{k-1})(iv_k + iv_{k-1}) \quad (3)$$

where *n* is the number of trees, *k* is the relative position (rank) of a tree in an ascending order of tree volumes, v_k and iv_k denote the cumulative proportion of trees ranked 1 to *k* in the total stand volume and in the total stand volume increment, respectively, and $v_0 = iv_0 = 0$ [51]. It was calculated for the overstory on total stand as well as on species level for each survey.

If the coefficient value is 0, all trees contribute proportionally to the total growth relative to their stem size. If the value is negative (<0), the smaller trees contribute disproportionately high to the total stand growth. Positive values (>0) indicate that the growth is concentrated on the largest trees in the stand.

2.4. Individual Tree and Stand Characteristics

The description of the stand structure focuses on stand density, mixture type, the presence of a lower stand layer, social tree status and vertical heterogeneity. All structural variables were calculated for each survey on plot and tree level, respectively.

Stand density was quantified using the stand density index (*SDI*) according to Reineke [52]. For the calculation of the *SDI*, only trees of heights > 2/3 of dominant stand height, defined as the height corresponding to the quadratic mean diameters of the 20% largest trees [53] were used. The understory was considered separately. In mixed stands, *SDI* values were calculated for each tree species separately and then summed over species for entire stands (Equation (4)). We considered the different growing space requirements of oak and the admixed species by applying the species-specific correction factor [13].

$$SDI = \sum_1^m n_m \times \left(\frac{25}{d_{qm}} \right)^{-1.605} \times E_m \quad (4)$$

where *SDI* is the density of the stand, *n* is the number of trees per ha, *dq* denotes the quadratic mean diameter in cm and *E_m* is a species-specific correction factor. The index *m* refers to the tree species.

The proportions of oak (*Prop_{oak}*, Equation (5)) in the overstory were calculated for each plot by using the species-specific *SDI* of oak (*SDI_{oak}*) in relation to total *SDI*. Thus, by using the *SDI* as a density measure, stand densities and proportions were comparable across different developmental stages.

$$Prop_{oak} = \frac{SDI_{oak}}{SDI} \quad (5)$$

The proportions obtained were the basis for the classification of the mixture type (*MT*). In this context, the threshold for monospecific stands was an oak proportion of 90%. Stands with a lower proportion of oak were assigned to mixed stands.

To describe the vertical structure on stand level, all stands were divided into two classes, in mono-layered stands without and two-layered stands with understory trees, respectively. The classification was based on the definition of the understory in Burschel and Huss [54]. All trees smaller than 2/3 of the dominant stand height were assigned to the understory. To avoid an over-representation of single trees, the basal area of trees of the understory had to reach a minimum of 5% of the total stand basal area.

For the tree level analysis, the social status for each tree of interest within the stand (*rel_d*) was considered. Here, the *dbh* of the tree in focus (*dbh_f*) was related to the *dbh* of the thickest tree (*dbh_{max}*) on the plot irrespective of the species, since measured values were available for each tree (Equation (6)).

$$rel_d_f = \frac{dbh_f}{dbh_{max}} \quad (6)$$

Index *f* refers to the tree in focus. We applied equation 6 to each plot likewise. If the tree of interest had a relative *dbh* of at least 0.9 or 0.7, it was classified as predominant or dominant, respectively. All others were considered as suppressed trees.

To characterize vertical heterogeneity, the coefficient of variation of tree heights (*cvh*) was calculated for the stand and each survey (Equation (7)).

$$cvh = \frac{sd_h}{\bar{h}} \quad (7)$$

where *sd_h* and \bar{h} are the standard deviation and mean tree height of the respective plot, respectively. For the stands analyzed, no considerable effect of different plot sizes on the coefficient was detected.

Tables 2 and 3 summarizes the stand and single tree attributes.

Table 2. Stand data; *PAIV*—periodic annual increment; *Vol*—standing volume; *Age*—stand age; *SDI*—stand density index; *Prop_{oak}*—proportions of oak; *SI*—site index; *GDC*—growth dominance coefficient; *cvh*—variation coefficient of tree heights; shown are mean, min, max and *sd* values for monospecific and mixed oak stands; *N* and *n*—number of observations.

		<i>PAIV</i>	<i>Vol</i>	<i>Age</i>	<i>SDI</i>	<i>Prop_{oak}</i>	<i>SI</i>	<i>GDC</i>	<i>cvh</i>
[N = 785]		[m ³ ha ⁻¹ year ⁻¹]	[m ³ ha ⁻¹]	[years]	[n ha ⁻¹]	[%]	[m]	[.]	[.]
mono-specific [n = 390]	mean	9.15	278.37	96	200	99	24.46	0.02	0.13
	min	2.92	42.03	17	75	90	16.91	-0.20	0.00
	max	20.91	729.62	229	399	100	32.17	0.19	0.44
	sd	3.43	124.60	45	63	2	3.74	0.06	0.08
mixed [n = 395]	mean	10.94	428.02	117	266	63	26.86	-0.03	0.24
	min	2.90	73.66	27	102	2	15.63	-0.53	0.03
	max	26.90	1139.87	360	549	90	34.53	0.20	0.58
	sd	3.32	175.79	51	94	23	3.19	0.10	0.10

Table 3. Tree data; *iv/cpa*—single tree productivity; *Age*—age (oak); *rel_d*—relative *dbh* (social class); *cpa*—crown projection area; shown are mean, min, max and *sd* values for monospecific and mixed oak stands; *N* and *n*—number of observations.

		<i>iv/cpa</i>	<i>Age</i>	<i>rel_d</i>	<i>cpa</i>
[N = 67.479]		[dm ³ m ⁻² year ⁻¹]	[years]	[.]	[m ²]
mono-specific [n = 40.827]	mean	0.92	79	0.62	17.21
	min	0.00	22	0.15	1.91
	max	4.52	234	1.00	232.97
	sd	0.52	38	0.16	17.04
mixed [n = 26.652]	mean	0.95	106	0.62	31.46
	min	0.00	28	0.09	2.01
	max	5.70	371	1.00	252.07
	sd	0.45	48	0.16	26.94

2.5. Statistical Analyses

To perform the statistical analyses and due to the assumed spatial and temporal dependencies, linear mixed effect models were set up to account for potential autocorrelation [55]. To avoid potential multicollinearity among predictor variables caused by the consideration of interaction terms, numerical predictors were centered by subtracting the mean. Thus, the interpretation of the coefficients did not change, but multicollinearity was eliminated effectively. The respectively calculated variance inflation factors (*VIF*) are listed in the supplementary material (Table S2).

The respective models were determined by the research questions (Equations (8)–(11)). Thus, all 2-way interactions between covariates considered were predefined supported by its significance. Here, covariates with non-significant main effects were left in the model if interactions were significant [55] (p. 537).

To answer the first research question regarding the long-term growth trend (I), we set up the final model in the following form.

$$\ln(PAIV_{ijt}) = a_0 + a_1 \times \ln(V_{ijt}) + a_2 \times \ln(SDI_{ijt}) + a_3 \times A_{ijt} + a_4 \times MT_{ijt} + a_5 \times Y_{ijt} + a_6 \times (MT_{ijt} \times Y_{ijt}) + b_i + b_{ij} + \varepsilon_{ijt} \quad (8)$$

where *PAIV* is the stand productivity in m³ ha⁻¹ year⁻¹. *V* is the standing volume in m³ ha⁻¹, *A* is the stand age, *SDI* the stand density index and *Y* the calendar year (year of survey). We used calendar year as a surrogate variable reflecting a possible gradual change of climatic conditions. The mixing type *MT* is included as a binary dummy variable with

0 = mixed and 1 = monospecific stands. a_0 – a_6 are the parameter estimates, b_i and b_{ij} are the random effects on experiment or research site to account for site specific random effects not covered by the model variables and on plot level to account for temporal autocorrelation in case of repeated inventories. The indices i , j and t denote the experiment or research site, the plot and the calendar year, respectively. ε_{ijt} are i.i.d. errors ($\varepsilon_{ijt} \sim N(0; \sigma_3^2)$).

For stand productivity estimation (II) we set up the following model (Equation (9)).

$$\ln(PAIV_{ijt}) = a_0 + a_1 \times \ln(V_{ijt}) + a_2 \times \ln(SI_{ij}) + a_3 \times A_{ijt} + a_4 \times \ln(SDI_{ijt}) + a_5 \times MT_{ijt} + a_6 \times Lay_{ijt} + a_7 \times (A_{ij} * \ln(SDI_{ijt})) + a_8 \times (\ln(SDI_{ijt}) \times MT_{ijt}) + a_9 \times (\ln(SDI_{ijt}) \times Lay_{ijt}) + b_j + b_{jt} + \varepsilon_{ijt} \quad (9)$$

In addition to the previous model (Equation (8)), the site index, SI in m is included in the model. Lay as a binary dummy variable (0 = mono-layered and 1 = two-layered) describes the vertical structure. a_0 – a_9 are the parameter estimates and b_j and b_{jt} the random effects on research plot and calendar year to account for autocorrelation. ε_{ijt} are i.i.d. errors ($\varepsilon_{ijt} \sim N(0; \sigma_3^2)$).

On tree level (III), the productivity-structure relationship was estimated using the following model.

$$\ln\left(\frac{iv}{cpa}_{ijft}\right) = a_0 + a_1 \times \ln(A_{ijft}) + a_2 \times \ln(SDI_{ijt}) + a_3 \times rel_d_{ijft} + a_4 \times MT_{ijt} + a_5 \times cvh_{ijt} + a_6 \times (\ln(A_{ijft}) \times \ln(SDI_{ijt})) + a_7 \times (\ln(A_{ijft}) \times rel_d_{ijft}) + a_8 \times (\ln(A_{ijft}) \times MT_{ijt}) + a_9 \times (\ln(A_{ijft}) \times cvh_{ijt}) + a_{10} \times (rel_d_{ijft} \times MT_{ijt}) + a_{11} \times (rel_d_{ijft} \times \ln(SDI_{ijt})) + a_{12} \times (rel_d_{ijft} \times cvh_{ijt}) + a_{13} \times (cvh_{ijt} \times \ln(SDI_{ijt})) + a_{14} \times (MT_{ijt} \times \ln(SDI_{ijt})) + a_{15} \times (MT_{ijt} \times cvh_{ijt}) + b_j + b_{jf} + b_{jft} + \varepsilon_{ijft} \quad (10)$$

where iv/cpa is the single tree productivity in $\text{dm}^3 \text{ m}^{-2} \text{ year}^{-1}$. rel_d is the relative dbh as a surrogate for social class and cvh the vertical heterogeneity of the stand. a_0 – a_{15} are the parameter estimates, b_j , b_{jf} and b_{jft} the random effects for plot, tree number and calendar year to account for autocorrelation. The indices i , j , f and t denote the experiment or research site, the plot, the tree and the calendar year, respectively. ε_{ijft} are i.i.d. errors ($\varepsilon_{ijft} \sim N(0; \sigma_4^2)$).

To answer the fourth question regarding the growth dominance within the stands (IV), the final model was set up in the following form.

$$GDC_{ijt} = a_0 + a_1 \times A_{ijt} + a_2 \times MT_{ijt} + a_3 \times \ln(SDI_{ijt}) + a_4 \times (A_{ijt} \times MT_{ijt}) + a_5 \times (A_{ijt} \times \ln(SDI_{ijt})) + a_6 \times (MT_{ijt} \times \ln(SDI_{ijt})) + b_j + b_{jt} + \varepsilon_{ijt} \quad (11)$$

GDC , the growth dominance coefficient of the stand was the dependent variable explained by stand age (A), mixing type (MT) and stand density (SDI). a_0 – a_6 are the parameter estimates, b_j and b_{jt} the random effects plot and calendar year to account for autocorrelation. ε_{ijt} are i.i.d. errors ($\varepsilon_{ijt} \sim N(0; \sigma_3^2)$). In addition, the species-specific GDC was predicted for monospecific and mixed stands as a dependent of age and SDI (Table S3).

For the mixed stands a non-linear relationship between oak proportion and stand productivity was assumed [7]. For this reason, a generalized additive mixed model (GAMM) was fitted to the mixed stands data (Table S4). Since the investigated mixed stands are not only a mixture of two tree species, but rather several tree species, the species-specific combination may affect stand productivity. Therefore, and due to the importance of beech as an admixed tree species, total stand productivity was estimated using the interaction term of oak proportions and the proportion of beech in the admixture. Volume and age were used in the model as additional state variables of the stands. To account for potential autocorrelation random effects were considered at research site and plot level.

All statistical evaluations were conducted with the statistical software R [56]. For the application of linear mixed effects models the `lmer` function of the `lme4` package

was used [57]. The generalized additive mixed models were performed with the mgcv package [58]. All figures were produced using the package ggplot2 [59].

3. Results

3.1. Long-Term Growth Trends of Oak Stands

The long-term positive growth trend was observed in both monospecific and mixed oak stands (Table 4, Figure 1a). Due to the non-significant interaction term between mixture type and year ($p = 0.933$) no difference between monospecific and mixed oak stands in terms of long-term growth trend was apparent. Stand volume, stand density and stand age relationships underlying stand productivity were most significant ($p < 0.001$). Thus, the variables stand volume and stand density had a positive effect on productivity, while stand age had a negative effect. Monospecific stands were somewhat less productive (Table 4).

Table 4. Results of the linear mixed effects model on long-term stand productivity (Equation (8)); est—model estimates, se—standard errors, p -values and significance levels *** <0.001 , * <0.05 , ns for the fixed effects; sd—standard deviations are shown for the random effects and residuals; n obs—number of observations; pseudo- R^2 m—marginal/c—conditional; RMSE—root mean square error.

Parameters	Variables	est	se	p-Value	sig.	Random Effects	sd
a ₀		2.244	0.029	<0.001	***	b_i	0.14
a ₁	ln (V)	0.382	0.031	<0.001	***	b_{ij}	0.00
a ₂	ln (SDI)	0.285	0.040	<0.001	***	ε_{ijt}	0.26
a ₃	Age	-0.004	0.000	<0.001	***		
a ₄	MT [mono]	-0.073	0.033	0.025	*	n obs	728
a ₅	Year	0.003	0.000	<0.001	***	pseudo- R^2 (m/c)	0.62/0.71
a ₆	MT [mono] * Year	0.000	0.001	0.933	n.s.	RMSE	0.25

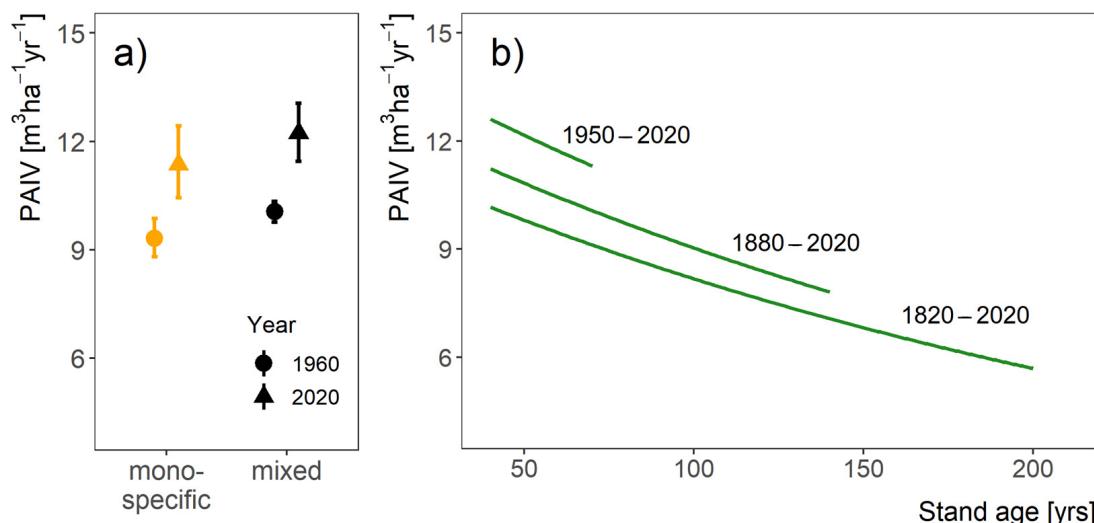


Figure 1. Stand productivity for monospecific and mixed oak stands at the age of 100 for different Calendar years (a); stand productivity for monospecific oak stands as a function of stand age after culmination (not shown) for different growing periods (b); all other variables were set to their mean.

For example, stand productivity of 100-year old oak stands increased over the last 60 years by 21.9% and 21.6% to 11.4 and 12.2 $m^3 \text{ ha}^{-1} \text{ year}^{-1}$ in monospecific and mixed stands, respectively (Figure 1a). The temporal decrease in stand productivity with higher stand ages was observed for all stands on different levels (Figure 1b). Regardless of calendar year the observed productivity decreased by 30% for stands at 50 to 150 years of age, even when the growth level was generally higher in recent years.

3.2. Stand Productivity as Modulated by Stand Characteristics

Stand productivity was dependent on stand age together with stand structure (Table 5). Stand volume ($p = 0.003$) and site index ($p < 0.001$) showed positive effects on stand productivity. Both variables were not significant in interactions and therefore only included as main effect. Age had no significant influence in the main effect. In contrast, a positive influence on stand productivity was found for the interaction term with stand density ($p < 0.001$). An additional understory generally increased stand growth significantly. However, in interaction with stand density, the effect on oak stand productivity was negative. The effect of stand density on productivity was significantly higher in monospecific stands.

Table 5. Results of the linear mixed effects model on stand productivity (Equation (9)); est—estimates, se—standard errors, p -values and significance levels *** <0.001 , ** <0.01 , * <0.05 , ns for the fixed effects; sd—standard deviations are shown for the random effects; n obs—number of observations; pseudo- R^2 m—marginal/c—conditional; RMSE—root mean square error.

Parameters	Variables	est	se	p-Value	sig.	Random Effects	sd
a ₀		2.175	0.094	<0.001	***	b_j	0.14
a ₁	ln (V)	0.108	0.036	0.003	**	b_{jt}	0.22
a ₂	ln (SI)	1.047	0.114	<0.001	***	ε_{ijt}	0.12
a ₃	Age	−0.000	0.000	0.250	ns		
a ₄	ln (SDI)	0.355	0.051	<0.001	***	n obs	785
a ₅	MT [mono]	−0.027	0.023	0.258	ns	pseudo- R^2 (m/c)	0.42/0.92
a ₆	lay [2nd]	0.059	0.018	0.001	***	RMSE	0.07
a ₇	Age * ln (SDI)	0.002	0.001	<0.001	***		
a ₈	ln (SDI) * MT [mono]	0.110	0.051	0.014	*		
a ₉	ln (SDI) * lay [2nd]	−0.209	0.038	<0.001	***		

Site conditions had a large effect on stand productivity that ranges on average across all stands from $5.8 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ on the less productive sites to $12.8 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ on the more productive sites.

In monospecific stands, the negative effect of low densities on stand productivity was more apparent compared to mixed stands. Here, the observed stand productivity was particularly controlled by stand density. At higher densities (>300 trees per ha) young monospecific stands are more productive than mixed stands. However, the observed maximum stand densities of the investigated research plots are consistently lower in the monospecific stands. On average, young (<100 years) and old mixed stands (>200 years) were 18% and 43% more dense, respectively.

The presence of an understory can thus increase the productivity of the total stand by 6% on average. In stands with low density the effect was even stronger and led to an increase of total stand productivity up to 14% compared to stands without an understory. However, as densities of the overstory trees increased, the positive effect of the understory is progressively reduced. At SDI values of around 300 trees per ha, the respective stand productivity dropped below the productivity of single layered stands (Figure 2b).

The GAMM functions show that stand productivity increases with decreasing oak proportions (Figure 3). Thus, productivity culminates at oak proportions of about 40% and is highest in a two species mixture with beech. For the mixed stands studied, an average increase in growth of 19% or $1.6 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ compared to the monospecific stands was observed. If the mixed stands consist of three or more tree species, the positive effect of the beech admixture was also evident as can be seen from the nonlinear functions for a beech component in the admixture of 60% and 20%, respectively.

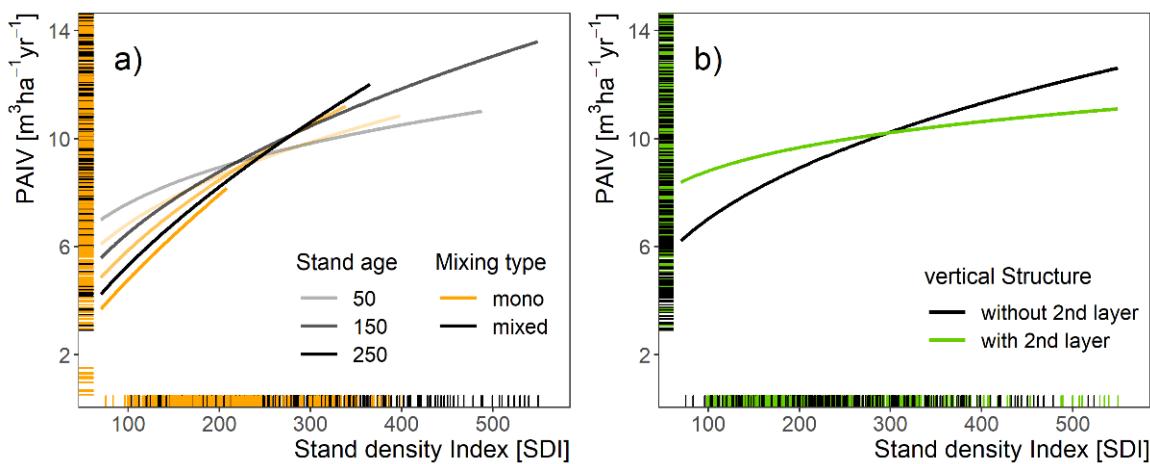


Figure 2. Stand productivity for monospecific and mixed oak stands as a function of stand density, stand age and mixing type (**a**) and as a function of stand density and vertical structure (**b**); rugs on the x-and y-axis indicate the observed values of SDI and stand productivity, respectively; all other variables were set to their mean.

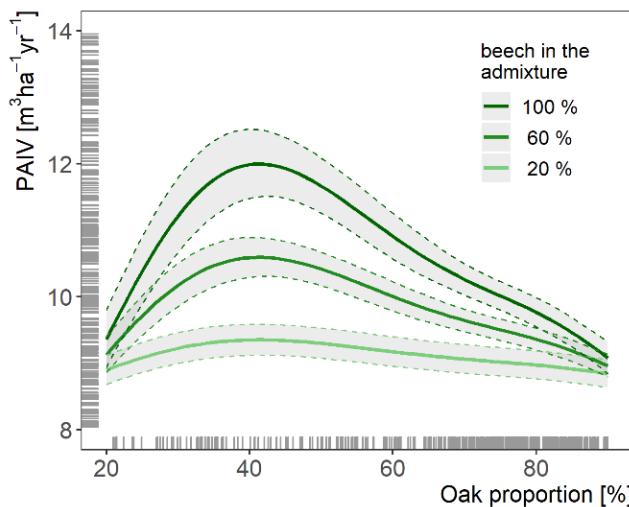


Figure 3. Non-linear smooth functions (GAMM) of stand productivity for mixed oak stands as a function of oak proportions and proportion of beech in the admixture; rugs on the x-and y-axis indicate the observed values of oak proportions and stand productivity, respectively; for the underlying model statistics we refer to the supplementary material (Table S4).

3.3. Individual Tree Productivity of Oaks Depending on Tree and Stand Characteristics

For all structural variables considerable effects on the productivity of individual oak trees were found (Table 6, Equation (10)). Among the structural variables considered, individual social class had a strong positive effect ($p < 0.001$). However, for age and stand density, the main effect was additionally determined by the predominantly negative interactions. In particular, the interaction between age and social class reveals a clear negative competition effect on the age-productivity trajectory. Simultaneously, predominant oaks were more productive at younger ages, but declined more in productivity with age, relatively speaking, than dominant or suppressed oaks (Figure 4).

Table 6. Results of the linear mixed effects model on individual tree productivity (Equation (10)); mixed stands (reference); est—estimates, se—standard errors, *p*-values and significance levels *** <0.001, ** <0.01, * <0.05, ns for the fixed effects; sd—standard deviations are shown for the random effects; *n* obs—number of observations; pseudo-*R*² m—marginal/c—conditional; RMSE—root mean square error.

Parameters	Variables	est	se	<i>p</i> -Value	sig.	Random Effects	sd
a ₀		−0.122	0.040	0.002	**	b_j	0.21
a ₁	ln (Age)	−0.209	0.019	<0.001	***	b_{jf}	0.29
a ₂	ln (SDI)	−0.234	0.025	<0.001	***	b_{jft}	0.31
a ₃	<i>rel_d</i>	2.636	0.037	<0.001	***	ε_{ijft}	0.46
a ₄	MT [mono]	−0.061	0.011	<0.001	***		
a ₅	<i>cvh</i>	0.260	0.061	<0.001	***	<i>n</i> obs	67.479
a ₆	ln (Age) * ln (SDI)	−0.782	0.027	<0.001	***	pseudo- <i>R</i> ² (m/c)	0.38/0.70
a ₇	ln (Age) * <i>rel_d</i>	−1.493	0.041	<0.001	***	RMSE	0.42
a ₈	ln (Age) * MT [mono]	−0.298	0.024	<0.001	***		
a ₉	ln (Age) * <i>cvh</i>	−0.231	0.093	0.013	*		
a ₁₀	<i>rel_d</i> * MT [mono]	0.669	0.048	<0.001	***		
a ₁₁	<i>rel_d</i> * ln (SDI)	−0.126	0.058	0.030	*		
a ₁₂	<i>rel_d</i> * <i>cvh</i>	2.953	0.197	<0.001	***		
a ₁₃	<i>cvh</i> * ln (SDI)	−0.341	0.109	0.002	**		
a ₁₄	MT [mono] * ln (SDI)	0.136	0.027	<0.001	***		
a ₁₅	MT [mono] * <i>cvh</i>	0.273	0.085	0.001	**		

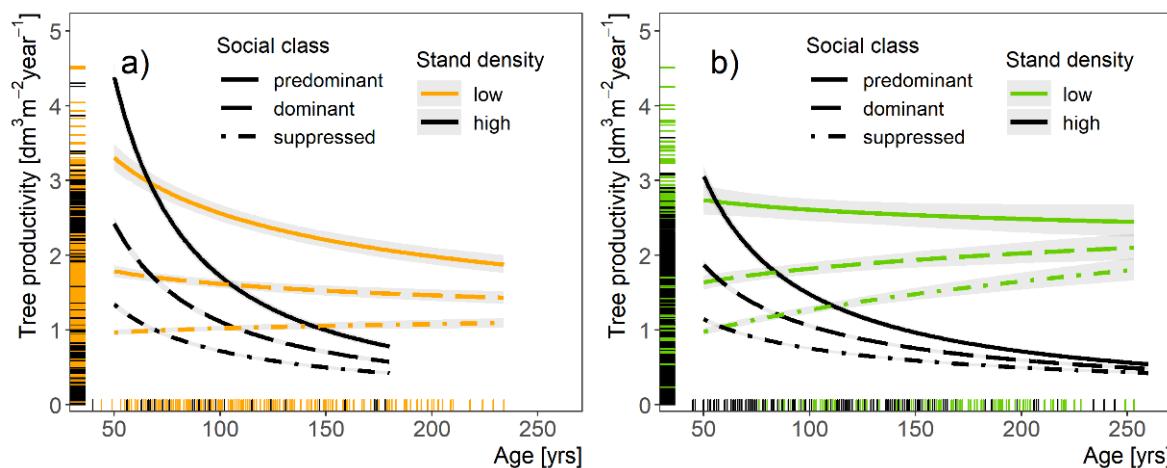


Figure 4. Productivity of oak trees growing in monospecific (a) and mixed species (b) stands as a function of Age, stand density and social class; low stand density = SDI of 100, high stand density = SDI of 350; rugs on the x-and y-axis indicate the observed values of age and tree productivity, respectively; all other variables were set to their mean.

On average, tree productivity decreased up to a tree age of 150 years for predominant oaks by 63% and for suppressed oaks by 39%, compared to the age of 50. In absolute terms, however, the productivity of large, predominant trees continued to outpace smaller tree individuals even at older ages up to 200 years, which was particularly true for trees growing in stands with low density. Similarly, the negative age trend is lower in stands with low stand density. For the suppressed oaks, there is even some indication of a positive trend. Increasing stand densities interact with higher age to a negative effect on productivity of individual oaks ($p < 0.001$). Oak productivity was negatively affected, especially in mixed species stands, at high densities. In contrast, at low densities, oak productivity was slightly higher at higher ages in the mixed stands (Table 6, Figure 4).

The coefficient of variation of tree height had a positive interaction effect with social class ($p \leq 0.001$). This effect was particularly proved for the productivity of predominant and dominant oaks. Suppressed oaks can hardly benefit from high vertical stand structure, with scarcely detectable differences between high and low structured stands (Figure 5). The positive effect of the coefficient of variation of tree height decreases with age and stand density (Table 6).

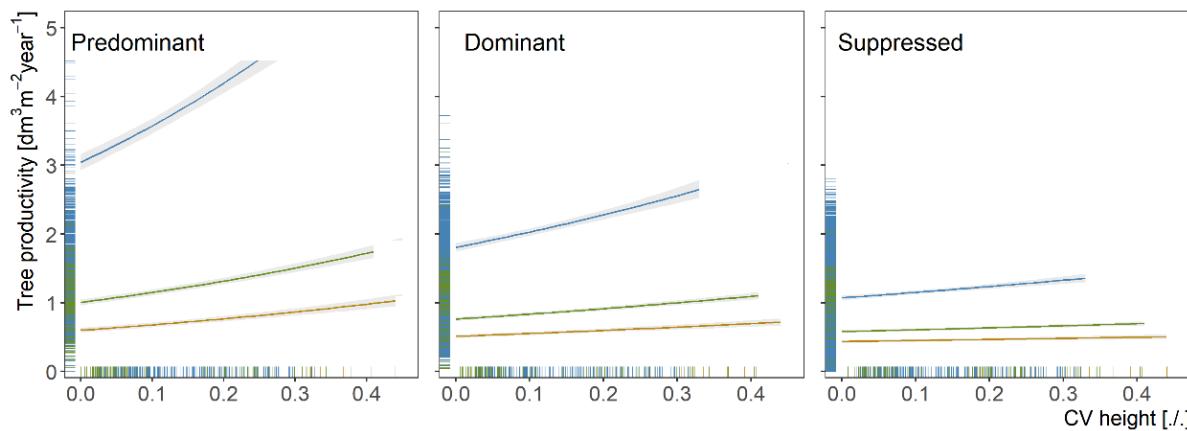


Figure 5. Productivity of oak trees as a function of coefficient of variation of tree heights and age for predominant ($rel_d > 0.9$), dominant ($rel_d < 0.9$ and > 0.7) and suppressed ($rel_d < 0.7$) oaks in monospecific stands; rugs on the x-and y-axis indicate the observed values of cvh and tree productivity, respectively; all other variables were set to their mean.

3.4. Stand Growth Partitioning between Trees of Different Sizes

The model (Equation (11)) for the growth partitioning within the overstory of the investigated oak stands showed a dependence on age, stand density and mixture type. If the Growth Dominance Coefficient (*GDC*) is 0, all trees contribute equally to the total growth relative to their size. If the value is negative (<0), the smaller trees contribute disproportionately more to the total stand growth than tall trees. Positive values (>0) indicate that the growth is concentrated on the largest trees in the stand.

In general, the *GDC* reached lower values in the mixed stands (Table 2). Especially the mixed stands showed an increased age trend towards negative *GDC* values (Table 7, Figure 6a). At low stand densities, the small stand individuals in the mixed stands contributed more to the total stand growth at an earlier stand development stage. At medium to high densities, the contribution to the total growth in young stands is more pronounced for the larger trees. This was true for both, monospecific and mixed stands. In monospecific stands, this effect worked up to an age of 170 years. In the mixed stands, the growth for medium densities was disproportionately carried by non-dominant tree individuals already from an age of 120 years. Overall, the distribution of growth over stand age is more balanced in the monospecific than in the mixed stands.

The *GDC* values of the tree species involved showed species-specific differences (Figure 6b, Table S3). With increasing age, especially the smaller beech trees contributed disproportionately to the total growth of beech. In general, at young stand ages, growth for all tree species was disproportionately in the predominant trees. The negative temporal trend in the *GDC* value was evident for all analyzed tree species except hornbeam. Accordingly, the volume growth of the analyzed oaks corresponded increasingly to the individual tree size with increasing age. Here, the *GDC* values for oaks does not differ significantly for monospecific and mixed stands (Figure 6b).

Table 7. Results of the linear mixed effects model on the Growth dominance coefficient (Equation (11)); est—estimates, se—standard errors, *p*-values and significance levels *** < 0.001, ** < 0.01, * < 0.05, ns for the fixed effects; sd—standard deviations are shown for the random effects; *n* obs—number of observations; pseudo-*R*² m—marginal/c—conditional; RMSE—root mean square error.

Parameters	Variables	est	se	<i>p</i> -Value	sig.	Random Effects	sd
a ₀		0.021	0.007	0.005	**	b_i	0.01
a ₁	Age	−0.003	0.000	<0.001	***	b_{ij}	0.04
a ₂	MT [mixed]	−0.060	0.008	<0.001	***	ε_{ijk}	0.06
a ₃	ln (SDI)	0.037	0.015	0.012	*		
a ₄	Age * MT [mixed]	−0.001	0.000	<0.001	***	<i>n</i> obs	740
a ₅	Age * ln (SDI)	−0.001	0.000	0.093	ns	pseudo- <i>R</i> ² (m/c)	0.45/0.60
a ₆	MT [mixed] * ln (SDI)	0.051	0.019	0.007	**	RMSE	0.06

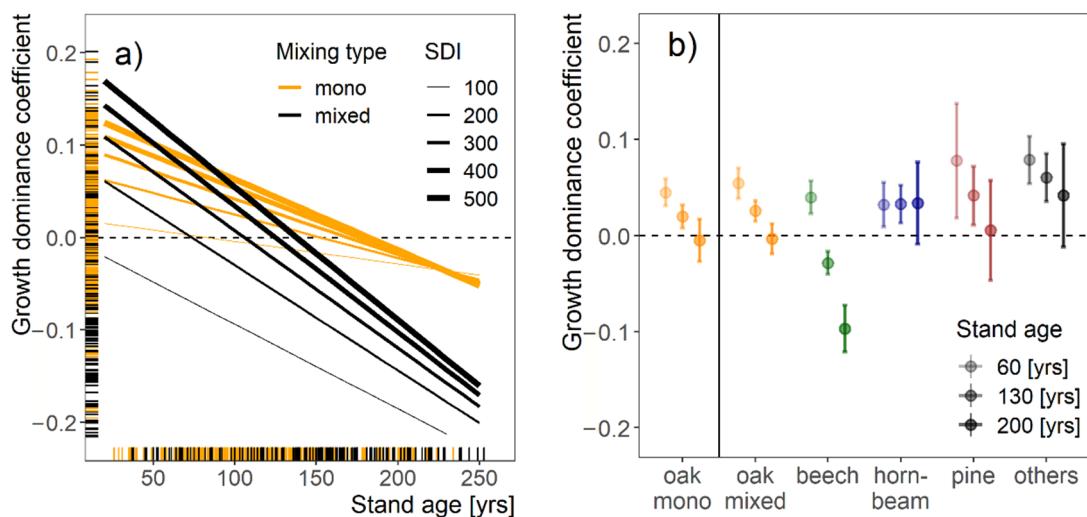


Figure 6. Growth dominance coefficient on stand level (a) in dependence of stand age and stand density for monospecific and mixed oak stands and the species-specific Growth dominance coefficient (b) for oak in monospecific and mixed stands, as well as beech, hornbeam pine and other tree species in dependence of the stand age; rugs on the x-and y-axis indicate the observed values of stand age and growth dominance coefficients, respectively; for the underlying model statistics see Table S3.

4. Discussion

4.1. Long-Term Growth Trends

The present study corroborates the finding of several existing studies showing a positive tree and stand growth development in recent decades [5,6,60,61]. For example, the growth increased from 1960 to 2000 over 10% and 30% for monospecific Norway spruce and European beech, respectively [6]. The same was partly true for other important tree species [5,62]. Based on 14 long-term experiments, Pretzsch et al. [63] were able to find an increased stand volume increment of 18% for monospecific oak stands compared to the reference period. With this knowledge, this study explicitly examined trends for monospecific and mixed stands with oak, which extended the available research. Our results, in particular the 21% increase in productivity, are in line with this trend. Considering the species-specific growth trends, the growth trend of mixed species stands can follow different directions. This was particularly evident in spruce-beech-fir stands, which did not show a stand-specific growth trend, but had species-specific differences in their growth behavior [64]. No significant differences between pure and mixed oak stands suggest that the tree species involved followed a similar growth trend compared to oak. This observation is consistent with the results on the long-term radial growth trend from beech-oak stands in Belgium [65]. Regardless of the reasons for the accelerated growth, which

should be associated with increased resource availability during the past century [6,63], this observation has a fundamental importance especially for silviculture with oak [63]. In addition, higher productivity is also associated with higher carbon sequestration in oak stands. Thus, these oak stands can positively contribute to climate change mitigation with an increase in captured carbon.

The growth improvement observed in the analysis shows a general trend. The long-term research plots were largely unaffected by biotic and abiotic disturbances. This is particularly important against the background of mass reproduction of insects, which can lead to growth reductions and even dieback processes in oak at the regional level [40,66]. Despite this, whether and how oak stand productivity will evolve with a rapidly changing climate in the near and distant future will remain to be observed.

4.2. Stand Productivity

The positive effect of stand density on the productivity of oak stands is consistent with the basic relationships between density and productivity of forest stands [5,67], as well as the increased growth in oak-beech mixed stands already found [7]. However, the driving factors of stand productivity seem to change over stand age. For example, in young stands, interspecific competition for light appears to drive productivity, whereas at advanced ages, stand density per se and higher maximum densities in mixed stands in particular have a positive effect on productivity [68,69]. This temporal aspect of productivity of mixed stands is also mentioned by Ammer [21] in a review on productivity and diversity relationships. Here, Zeller and Pretzsch [16] described a negative structural effect on the productivity of young stands based on long-term experimental plots, which turned positive in later stages of the stand's development. We attribute this positive age trend in structure-dependent stand productivity to the fact that complementarity effects emerge more effectively with increasing stand development and time for morphological and physiological acclimation [16,70,71]. The effect of higher densities in mixed species stands becomes particularly more apparent in later development phases. Stand growth may depend more on higher densities or greater structural diversity than from species mixing per se [23].

The understory and intermediate stand, in oak stands mostly required as serving secondary stands to produce high quality oaks [33,35], can buffer the negative effect on stand increment at low stand densities and keep productivity at comparatively high levels. However, a secondary stand can also have a negative effect on the productivity of the oak stand. This was especially the case when high densities were observed in the overstory. We attribute this in particular to competition effects for both, under- and overstory trees. First, the growth of the understory was limited due to very low light availability and second, the overstory productivity was slowed down due symmetric competition for underground resources [22].

The observed correlation between productivity and tree species proportions was particularly interesting for the admixture of beech. Our results showed that high growth performance of beech significantly promoted the productivity of the investigated stands. Stand growth is not driven solely by the regulation of the proportion of oak. However, the main driver of stand productivity in the mixed oak stands seems to be beech. Brunner and Forrester [15] found on long-term spruce-fir-beech experimental plots that mainly beech contributes to the overyielding of the mixed stands, which increased with stand density. This increase proves the high growth and thus competitive power of beech [42,72]. We attribute the observations to the special ability of beech to exploit space and light conditions within the stand most efficiently [73]. When mixed with oak, the more shade-tolerant beech seems to benefit especially from complementary light use and its considerable crown plasticity [74]. Furthermore, oak can additionally enhance the growth of beech in the mixed stand by acting as a hydraulic lift [7,75]. Thus, the overyielding in mixed oak stands increases mainly due to higher stand densities. The higher holding capacity of mixed stands especially benefits the admixed beech.

4.3. Tree Productivity

The decreasing productivity of the investigated oaks with increasing age follows the characteristic growth habit of individual trees [76]. The small decrease in productivity at high ages (>200 years) is striking. This long-lasting growth performance of oak is consistent with a recent study by Pretzsch [77] in which growth trajectories of native tree species were considered. The temporal trend, which is hardly observable in suppressed oaks, seems to be due to the effect of competition from more dominant trees overriding the structural effects that have a positive effect, especially at young ages. The social position of oaks in the stand is crucial for their productivity, that can more than double it. The positive effect of social position in the stand has also been found by Manso et al. [19] or del Río et al. [78] for oaks mixed with beech.

The lower productivity of individual oak in mixed stands seems to be due to the high competitive strength of the admixed species, especially beech. These observations are consistent with results from several studies on single-tree growth of oak in mixed stands with beech [19,72,78,79]. Nevertheless, the net effect of beech admixture on stand productivity in mixed stands is positive.

Only older oak trees can benefit somewhat from the mixture. The age-related decrease in competitive vigor or the removal of mature mixed tree species seems to support this trend. Although at lower levels, the productivity of suppressed oaks in mixed stands is increased relative to that in monospecific stands. However, this inverse trend suggests increased intraspecific asymmetric competition. Similar growth responses were found by del Río et al. [78] for oak-beech mixed stands in Spain.

The decreasing and converging productivity curves (see Figure 4) of monospecific and mixed stands with age seem to reflect the changing competitive situation. On the one hand, oak as a light demanding tree species benefits from an early culmination of increments compared to its admixed tree species, and on the other hand, the dominant individuals in the experimental plots in particular belong to the partially promoted tree collective. This silvicultural promotion to regulate competition is particularly important in mixed stands on vigorous sites. The creation of structured stands can further support the competitive ability of oak over beech. Free canopy space can be increasingly used by oak if it is in the dominant layer, especially in younger stands. The barely observed positive effect of vertical structure in suppressed oaks apparently results from increased crown competition in the understory [70,79,80].

The results show that mixing effects and structural effects are also subject to a temporal trend at the individual tree level. This is also supported by various studies that identify increased competition, in addition to promotion, as a cause of the corresponding growth responses [7,19,65,81]. Sometimes, increased shade tolerance of the mixed tree species also has a negative effect on the oak mixing response [82].

4.4. Growth Partitioning

The overall lower growth dominance coefficients in mixed stands show that the growth performance of smaller trees is increased compared to monospecific stands (Table 2). Beech in particular contributes to the observed reverse growth dominance (Figure 6b). This can be partly explained due to niche complementarity of the tree species involved, which is particularly evident between species of different ecological characteristics [13,26]. For example, oaks, as light-demanding tree species, appear to be highly productive in the uppermost canopy layer. Beech, on the other hand, still seems to be very light efficient in the lower canopy layers [7]. This is especially true when oak trees are in the upper canopy layer. We assume that the observed growth dominance and its tree species-specific age trend emerges to some extent from this niche complementary effects. As a result, the admixed beech gains a competitive advantage over oaks over time. In addition to growth improvement of the non-dominant trees, a decline in growth of the dominant trees can equally lead to a negative age trend of growth dominance in the stands [24,25,83]. In any case, the decreasing productivity of dominant oaks with age suggests that this

assumption is also relevant in monospecific and mixed stands analyzed in the present study (see Figure 4).

At young stand development phases positive GDC values were observed in both, monospecific and mixed stands (see Figure 6a). This proves that stand growth is disproportionately dominated by the large trees, regardless of the mixing ratios. Maintenance and thinning interventions particularly promote large individual trees, especially in high dense stands [26]. The temporal decline in GDC is more pronounced in high dense stands (Table 7, Figure 6a). The effect enhanced in the mixed stands, indicates that stand growth is increasingly supported by the admixed tree species, especially beech at high densities. Thinning from above increasingly benefit the non-dominant mixed trees in the stand [27]. Lower densities seem to mitigate this trend, as well as in monospecific stands. Thus, the growth performance of oaks seems to depend on the treatment especially at young and middle age stages.

4.5. Implications for Silvicultural Management Strategies

Climate change, with its effects on forest ecosystems and ecosystem services represents a major challenge for forestry and its silvicultural concepts [2]. In principle, the establishment of mixed and structurally rich stands is one of the most important management guideline to mitigate the consequences of climate change and to increase the stability of forest ecosystems [1,31,84–86]. In this respect, the selection of tree species is one of most important management options in forestry. Furthermore, the participation of oaks as deep rooting and drought-tolerant tree species can additionally enhance the mechanical stability and reduce the vulnerability of forest stands to disturbances [29]. Together with their typical species richness [37,87], the genus oak, characterized by a large genetic species diversity [88], can contribute to the promotion of natural biodiversity, which has recently become an increasingly important management goal [4,36,89,90].

For these reasons, the maintenance and establishment of mixed oak stands and individual oaks in mixed stands can be fundamentally beneficial for the principal goal of creating climate-resilient forest stands. Even though this could be associated with reduced productivity in certain stand situations (see Figures 2 and 4).

Against this background, it is important to evaluate existing oak management concepts about their further suitability and, if necessary, adapt them. In this context, despite the coppice management [37] traditional oak silviculture is mostly focused on the production of high-value timber [33–35]. Many management options include a secondary stand of shade-tolerant tree species to ensure high quality oaks in particular [35]. In terms of stand productivity, a vigorous understory can have an additional positive effect on growth in low to moderate stand densities and should remain as a key component of oak management. Furthermore, potential growth losses that may occur because of silvicultural interventions or natural disturbances can be buffered (see Figure 2). However, to reduce growth suppression or mortality of individual oaks due to competition, we suggest a various temporal or spatial arrangement of the understory. This enables the coexistence of the species and allows the positive complementary effects to be kept while the negative competitive effects are considerably reduced [81,91,92].

In the overstory, the productivity can be additionally increased by the participation of mixed tree species [7]. This is due to higher maximum stand densities in mixed species stands compared to monospecific stands [13,93]. As compared to traditional silvicultural guidelines of monospecific stands, this may provide additional flexibility for management options in mixed stands [92]. In particular, consideration should be given to adjust the number and tree species of future crop trees and the intensity of thinning interventions [93,94]. If these higher maximum stand densities are not considered by managers, possible growth reductions or loss of additional carbon sequestration may result. In this context and due to the high plasticity and efficiency, stand productivity can be optimized by admixture of beech (see Figure 3) [74]. However, this is also associated with high competitive strength, which can reduce the vigor of individual oaks [42,72,81,95]. We suggest reducing stand

density in mixed stands at an early stage to reduce interspecific competition and effectively promote the productivity of individual oaks. At the same time, predominant and dominant oak trees are obtained, which can decisively increase their productivity compared to suppressed oaks (see Figure 3) [19,78].

Long rotation periods, as they emerged from experiences in the middle of the 20th century, were incorporated into silvicultural guidelines [33,96,97]. On stand level the observed long-term trend in productivity indicates that currently young oak stands can produce as much in 130 years as stands harvested 30 years ago at the age of 180 (see Figure 1). At the tree level, the findings suggest that early crown thinning can have a strong positive influence on the growth of future crop trees. Thus, the promoted oaks can reach their target diameter much earlier and minimize the rotation period additionally.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13050724/s1>, Table S1: List of tree species, summarized under the general term “others”; Table S2: Variance inflation factors (VIF) for the linear mixed effects models (Equations (8)–(11)); Table S3: Results of the linear mixed effects model for species-specific Growth Dominance Coefficients. Table S4: Results of the generalized additive mixed model (GAMM) to represent stand productivity as a function of tree species proportions of oak and beech

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