TECHNISCHE UNIVERSITÄT MÜNCHEN

TUM SCHOOL OF LIFE SCIENCES

Growth potential of European oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) in unmanaged and managed stands in dependence of stand structure and site quality

Kilian Patrick Stimm

Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Forstwissenschaft (Dr. rer. silv.)

genehmigten Dissertation.

Vorsitz:	Prof. Dr. Michael Suda
Prüfer*innen der Dissertation:	1. Prof. Dr. Dr. h.c. Hans Pretzsch
	2. Prof. Dr. Thomas Knoke

Die Dissertation wurde am 13.02.2023 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 09.05.2023 angenommen.

Acknowledgements

First and foremost, I would like to kindly thank my doctoral advisor Prof. Dr. Dr. h.c. Hans Pretzsch for his continuous support and the opportunity to work and graduate at the Chair of Forest Growth and Yield Science of the Technical University of Munich.

Very special thanks go to Dr. Heinz Utschig for his valuable advices and encouragements as well as his contribution to my work. His eye for the essentials helped me throughout my doctoral thesis to view scientific results, especially in the light of practical application.

Since this dissertation was part of a cooperation project of the Technical University of Munich and the Bavarian State Institute of Forestry, I also would like to thank Stefan Tretter as former head of the department Silviculture and mountain forests and all employees of the institute who supported me in any way. Be it by providing data or by thought provoking conversations.

I would also like to thank my colleagues during the time at the Chair of Forest Growth and Yield Science. They gave me the opportunity to discuss my work and having joint leisure time activities which supported therefore also my motivation and the development of my dissertation.

Last but not least, I am particular grateful to my family for encouragement. Especially my mother for being there for me at all times and my father, to whom I owe a great deal of my passion for our forests.

Finally, and most importantly, my deepest thanks go to my wife Franziska and my sons Max and Julian for their constant and seemingly endless patience with me to finish my dissertation and their continuous support.

Content

Abstract

The two European oak species sessile (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.) are important tree species for the establishment of climate-resilient mixed stands in Central Europe with regard to their high drought tolerance. However, due to their characteristics as light-demanding tree species, they are often limited in their competitive strength compared to their admixed tree species. Therefore, the present work aims at analyzing the site-specific and structure-dependent growth potential of oak in monospecific and mixed stands. In doing so, the studies of the paper consider all stand development phases, a broad site spectrum, and a pronounced management and structural gradient.

First, oak height growth as a proxy of growth potential as a function of environmental conditions and stand structure was investigated using forest inventory data. In particular, summer temperature, water balance during the growing season, and base saturation were used as the most important site variables. Stand structure, characterized by stand density, vertical structuring, and mixture type had an additional modifying effect on tree heights. A climatically and structurally induced height growth of oaks was found. However, competitive vigor, as measured by oak height growth, seems to hardly increase even in warm-dry regions under current climatic conditions. The negative effect of the expected reduced water balance seems to eclipse the positive temperature effect and reduce the height growth of oaks also in the future. Based on the results and due to the importance of height growth for competitive performance, further silvicultural support therefore seems necessary for successful establishment and continuity of adequate oak proportions in mixed species stands (Stimm et al. 2021c).

Another aspect is represented by wood productivity, one of the most important ecosystem services provided by oak forests. Therefore, the second study examined the volume growth of oak stands and individual trees. In this study, data from 147 monospecific and mixed oak stands from long-term observations were examined. According to the results, an increase in stand productivity of up to 21% was observed for monospecific and mixed oak stands, respectively, over the past 60 years. In the investigated mixed stands, stand volume growth was on average 19% higher than in the monospecific stands. This was mainly due to higher stand densities, a vigorous secondary stand, and the admixture of beech. At the individual tree level, young and medium-aged oaks in particular showed lower growth due to interspecific competition. Tree productivity was strongly dependent on their social status within the stand. In addition, larger trees also made the largest contribution to total stand increment in young oak stands. With future mixed forests in mind, consistent promotion of dominant and vigorous oaks can produce highly productive trees while promoting the positive attributes of structured and mixed forests. A vigorous secondary stand can increase overall stand productivity at lower densities and allow silvicultural flexibility. In contrast, creating vertical stand structure to reduce competition has limited positive effects on individual tree productivity (Stimm et al. 2022a; see Chapter 3.2 and Appendix B).

Recently, long-term and small-scale regeneration methods have been increasingly used in Central Europe as part of close-to-nature forest management. Therefore, the third study of the thesis examined oak regeneration under continuous canopy cover. The observation periods of small-scale regenerated monospecific and mixed stands considered in the study ranged from 26 to 36 years. The survival probability of oaks in regeneration basically decreased during the regeneration period. Nevertheless, a considerable biomass increase was observed, especially in the case of lower standing volume. Height growth of beech is hardly slowed down by canopy closure compared to oak. The results suggest that reducing competition within the regeneration by lowering the proportion of beech greatly improves the success of oak regeneration. No significant effect of regeneration biomass on the productivity of the remaining stand was found. However, a negative trend in productivity was revealed at high regeneration biomasses. Small-scale regeneration of oak with longer regeneration periods is possible, but requires active and continuous silvicultural management adapted to specific site conditions (Stimm et al. 2022b; see Chapter 3.3 and Appendix C).

The results of this thesis deepen the knowledge about the potential of sessile and pedunculate oak as a component of structured mixed species stands. In particular, they can be used to adapt silvicultural management options and provide a valuable contribution to the establishment and long-term maintenance of an appropriate proportion of oak.

Zusammenfassung

Die beiden Baumarten Trauben- (*Quercus petraea* (Matt.) Liebl.) und Stieleiche (*Quercus robur* L.) sind aufgrund ihrer Toleranz gegenüber Trockenheitsereignissen wichtige Baumarten für den Aufbau von Mischbeständen in Mitteleuropa. Ihre Eigenschaft als Lichtbaumarten schränkt sie jedoch gegenüber anderen Baumarten in ihrer Konkurrenzfähigkeit häufig ein. Die vorliegende Arbeit zielt daher auf die Analyse der standortspezifischen Konkurrenz- und Leistungsfähigkeit der Eiche in Rein- und Mischbeständen ab. Dabei werden in den Studien der Arbeit alle Bestandsphasen, ein breites Standortspektrum sowie ein ausgeprägter Nutzungs- und Strukturgradient betrachtet.

Zuerst wurde das Höhenwachstum als Weiser der Leistungsfähigkeit von Eichen in Abhängigkeit von den Umweltbedingungen und der Bestandsstruktur anhand von Waldinventurdaten untersucht. Dabei waren insbesondere die Sommertemperatur, der Wasserhaushalt in der Vegetationsperiode und die Basensättigung die wichtigsten Standortvariablen. Die Bestandsstruktur, charakterisiert durch die Bestandesdichte, die vertikale Strukturierung und die Mischungsart hatte einen zusätzlich modifizierenden Effekt auf die Baumhöhen. Allerdings scheint die Konkurrenzkraft, gemessen an der Höhenwachstumsleistung der Eichen, selbst in den warm-trockenen Regionen unter den derzeitigen Bedingungen kaum zuzunehmen. Der negative Effekt der erwarteten verringerten Wasserverfügbarkeit scheint den positiven Temperatureffekt zu überlagern und das Höhenwachstum der Eichen auch in Zukunft zu reduzieren. Basierend auf den Ergebnissen und aufgrund der Bedeutung des Höhenwachstums für die Konkurrenzkraft, erscheint daher eine weitere waldbauliche Unterstützung für eine erfolgreiche Etablierung und Kontinuität angemessener Eichenanteile in Mischbeständen erforderlich (Stimm et al. 2021c; siehe Kapitel 3.1 und Appendix A).

Einen weiteren Aspekt der Leistungsfähigkeit stellt die Holzproduktion dar, eine der wichtigsten Ökosystemleistungen des Waldes. Zur Abschätzung des Potenzials wurde in der zweiten Studie der Bestands- und Einzelbaumzuwachs untersucht. In dieser Studie wurden die Daten von 147 langfristig beobachteten Rein- und Mischbeständen untersucht. In den letzten 60 Jahren konnte demnach eine Erhöhung der Bestandsproduktivität um bis zu 21% für Rein- und Mischbestände aus Eiche gleichermaßen beobachtet werden. In den Mischbeständen lag der Zuwachs im Durchschnitt um 19% höher als in den Reinbeständen. Dies war insbesondere durch höhere Bestandsdichten, einem wuchskräftigen Nebenbestand und die Buchenbeimischung bedingt. Auf Einzelbaumebene zeigten insbesondere junge und mittelalte

Eichen aufgrund der interspezifischen Konkurrenz geringere Zuwächse. Die Produktivität des Einzelbaums war stark von dessen sozialen Stellung innerhalb des Bestandes abhängig. Zudem leisteten größere Bäume auch den größten Beitrag zum Zuwachs des Gesamtbestands in jungen Eichenbeständen. Mit Blick auf künftige Mischwälder kann eine konsequente Förderung von vorherrschenden und vitalen Eichen hochproduktive Bäume hervorbringen und gleichzeitig die positiven Eigenschaften strukturierter und gemischter Wälder fördern. Ein vitaler Nebenbestand kann die Gesamtproduktivität des Bestandes bei niedrigeren Dichten erhöhen und waldbauliche Flexibilität ermöglichen. Dagegen hat die Schaffung einer vertikalen Bestandsstruktur zur Konkurrenzreduktion nur eine begrenzte positive Wirkung auf die Produktivität des Einzelbaums (Stimm et al. 2022a; siehe Kapitel 3.2 und Appendix B).

In der dritten Studie der Arbeit wurde die Verjüngung der Eiche unter Schirm untersucht. Im Zuge naturnaher Bewirtschaftungsmethoden werden in jüngster Zeit langfristige und kleinflächige Verjüngungsmethoden in Mitteleuropa verstärkt angewendet. Die in der Studie betrachteten Beobachtungszeiträume der kleinflächig und unter Schirm verjüngten Rein- und Mischbestände reichten von 26 bis 36 Jahren. Die Überlebenswahrscheinlichkeit von Eichen in der Verjüngung nahm im Laufe des Verjüngungszeitraums grundsätzlich ab. Trotzdem konnte ein beachtlicher Biomassezuwachs beobachtet werden, insbesondere im Falle eines geringeren Altbestandvolumens. Die Höhenentwicklung der Buche wird im Vergleich zur Eiche durch den Kronenschluss kaum gebremst. Die Ergebnisse legen nahe, dass eine Konkurrenzreduktion innerhalb der Verjüngung durch eine Senkung des Buchenanteils den Erfolg der Eichenverjüngung stark verbessert. Ein signifikanter Einfluss der Verjüngung auf den Zuwachs des Altbestands konnte nicht gefunden werden. Allerdings zeigte sich auch ein negativer Trend der Produktivität bei hohen Verjüngungsbiomassen. Eine kleinflächige und langfristige Verjüngung der Eiche ist möglich, erfordert jedoch eine aktive und kontinuierliche waldbauliche Unterstützung, die an die spezifischen Standortbedingungen angepasst werden muss (Stimm et al. 2022b; siehe Kapitel 3.3 und Appendix C).

Die Ergebnisse der vorliegenden Dissertation vertiefen die Kenntnisse über das Potenzial von Trauben- und Stieleiche als Bestandteil strukturierter Mischbestände. Insbesondere können sie dazu genutzt werden die waldbaulichen Bewirtschaftungsoptionen anzupassen, wodurch sie einen wertvollen Beitrag zur Etablierung und langfristigen Erhaltung eines angemessenen Eichenanteils leisten.

Article overview

The present thesis is submitted as a cumulative dissertation based on the three following lead authorships. For each article, the original abstract, publication status and individual author contributions are provided.

In addition, during the time span of this thesis, within a larger framework of forest ecology studies, four peer-reviewed co-authorships and eight non-peer-reviewed articles were published.

Articles – peer-reviewed

Lead authorships (Basis of the cumulative thesis)

Stimm, K., Heym, M., Uhl, E., Tretter, S., Pretzsch, H. (2021) Height-Growth related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance in mixed-species stands still required? *Forest Ecology and Management*

Stimm, K., Heym, M., Nagel, R.-V., Uhl, E., Pretzsch, H. (2022) 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. *Forests*

Stimm, K., Uhl, E., Pretzsch, H. (2022) Chances and Limitations of Mixed Oak Regeneration under Continuous Canopy Cover – Evidence from Long-Term Observations. *Forests*

Co-authorships

Heym, M., Uhl, E., Moshammer, R., Dieler, J., **Stimm, K**., Pretzsch, H. (2021) Utilising forest inventory data for biodiversity assessment. *Ecological Indicators*

Leroy, B.M.L., Lemme, H., Braumiller, P., Hilmers, T., Jacobs, M., Hochrein, S., Kienlein, S., Müller, J., Pretzsch, H., **Stimm, K**., Seibold, S., Jaworek, J., Hahn, W.A., Müller-Kroehling, S., Weisser, W.W. (2021) Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems: An experimental approach. *Ecological solutions and evidence*

del Río, M., Pretzsch, H., Bončina, A., Avdagić, A., Bielak K., Binder, F., Coll, L., Hilmers, T., Höhn, M., Kašanin-Grubin, M., Klopčič, M., Neroj, B., Pfatrisch, M., Stajić, B., **Stimm, K.**, Uhl, E. (2022) Assessment of Indicators for Climate Smart Management in Mountain Forests. In: *Tognetti, R., et al. (eds.), Climate-Smart Forestry in Mountain Regions, Managing Forest Ecosystems*

Pretzsch, H., Hilmers, T., Uhl, E., del Río, M., Avdagić, A., Bielak K., Bončina, A., Coll, L., Giammarchi, F., **Stimm, K.**, Tonon, G., Höhn, M., Kašanin-Grubin, M., Tognetti, R. (2022) Efficacy of Trans-geographic Observational Network Design for Revelation of Growth Pattern in Mountain Forests Across Europe. In: *Tognetti, R., et al. (eds.), Climate-Smart Forestry in Mountain Regions, Managing Forest Ecosystems*

Article I

Height growth-related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance still required in mixed-species stands?

Kilian Stimm, Michael Heym, Enno Uhl, Stefan Tretter, Hans Pretzsch

Published *in 2021 in Forest Ecology and Management 482 (2021) 118780*

https://doi.org/10.1016/j.foreco.2020.118780

Impact Factor (2021): 3.558

Abstract

Sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.) play an important role in increasing the resistance of central European forests to severe droughts. But outside their real niche the competitiveness of both oak species can be low in mixed-species stands. This paper examines the height growth of oaks depending on environmental conditions and inter-specific competition. Height growth of trees was analysed using data from forest inventories covering monospecific and mixed-species stands within the German federal state of Bavaria. By means of regression analyses of 23,607 height measurements, we found that site conditions and stand structure have strong effects on the height growth of oak. Summer temperature, water balance in the vegetation period and base saturation were the main explanatory site variables. The first positive effect of summer temperature had no influence at warmer sites with mean summer temperatures above 16.4 °C, while the effect of water balance was positively linear. In addition, stand density modified the height growth of oak in a mainly positive manner. Vertical structure also had a positive effect, which was found for most species compositions, except monospecific stands and oak-hornbeam mixture. In most mixtures, oaks height growth seemed to be less climate-sensitive compared to monocultures. A currently warmer and drier climate seemed to favour the height growth superiority of European beech, whereas it decreased the superiority of Scots pine. The results indicated that even if the climate changes as predicted, the growth of oak will depend upon silvicultural promotion. Our findings can be used to improve regional guidelines for oak silviculture with special regard to climate-sensitive height growth. For example, a regionally delayed introduction of admixed species can reduce silvicultural treatments by ensuring oak vitality in mixed forests at the same time.

Individual contributions

I have received the raw data from the forest inventories as well as the site data. I harmonized and merged these and prepared them for data analysis (data acquisition, 80%). I conducted the data analyses and designed and produced the figures (data analysis and figures, 95%). I wrote and revised the manuscript for the article (writing and revising, 85%). Overall, my contribution was about 90%.

Article II

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

Kilian Stimm, Michael Heym, Ralf-Volker Nagel, Enno Uhl, Hans Pretzsch

Published *in 2022 in Forests, Volume 13, Issue 5, 724*

https://doi.org/10.3390/f13050724

Impact Factor: 3.282

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.

Individual contributions

I have received the raw data of the long-term experimental plots. I ordered and homogenized the data from different sources (data acquisition, 75%). I conducted the data analyses and designed and produced the figures (data analysis and figures, 100%). I wrote and revised the manuscript for the article (writing and revising, 80%). Overall, my contribution was about 90%.

Article III

Chances and Limitations of Mixed Oak Regeneration under Continuous Canopy Cover – Evidence from Long-Term Observations

Kilian Stimm, Enno Uhl, Hans Pretzsch

Published *in 2022 in Forests, Volume 13, Issue 12, 2052*

https://doi.org/10.3390/f13122052

Impact Factor: 3.282

Abstract

Traditionally, due to its light ecology, oak is regenerated on clear cuts or areas where crown coverage is heavily reduced. Thus, regeneration phase is relatively short. Recently, selective long-term regeneration phases avoiding large gaps in the canopy but fostering mixed-species stands have been advocated as being more close-to-nature forestry in Central European forests. But examples for successful regeneration of oak in mixture following this type of regeneration are largely missing. Here, we report results of long-term experiments located in three different forest types, where oak was long-term regenerated under different mixing and canopy cover situations. Observation periods reached from 26 to 36 years. We focused on the dynamics of stem number reduction, as well as height and biomass development of oaks and their interaction with interspecific competition and canopy density. The probability of oaks occurring in the regeneration basically decreased over the duration of the regeneration period. Despite this, considerable regeneration biomass growth could be observed, especially in the case of lower standing volume of the mature stand. The development of beech as the main competitor is scarcely slowed down by the canopy cover compared to oak. Increasing canopy cover noticeably impeded oak regeneration in the considered mixed stands. Model results suggest that a reduction of competition within the regeneration by lowering the proportion of beech below 30% enhanced the success of oak regeneration in the long run even in small patches. The productivity of the remaining stand was primarily driven by standing volume. However, a negative trend of its productivity emerged with high regeneration biomasses. Study results show that small-scale oak regeneration with prolonged regeneration duration is possible in principle. However, oak regeneration requires active and continuous silvicultural assistance which has to be adjusted to the specific site conditions.

Individual contributions

I have partly received and generated the raw data of the regeneration on the long-term experimental plots. I harmonized the data from different sources (data acquisition, 75%). I conducted the data analyses and designed and produced the figures (data analysis and figures, 100%). I wrote and revised the manuscript for the article (writing and revising, 85%). Overall, my contribution was about 90%.

1. Introduction

1.1 Motivation

Changes in species composition of forests are indicated in many parts of Central Europe as an effective response to climate change (Bolte et al. 2009; Spathelf et al. 2014). Higher temperatures in combination with lower precipitation are expected, particularly during the growing season (Jacob et al. 2008). Sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.), two major oak species in Central Europe, are important in tree species portfolios and considered to be less drought-sensitive than other native tree species (Kölling and Zimmermann 2007; Manthey et al. 2007; Mette et al. 2013; Annighöfer et al. 2015). Appreciable shares of both oak species are helpful in creating mixed stands that are more climate-resilient because of their relatively broad ecological amplitude. In addition, oaks provide valuable wood (Attocchi 2015; Kenk 1993; Lüpke 1998), can positively influence the growth of admixed species (Pretzsch et al. 2013b) and show a high ecological importance for species diversity (Löf et al. 2016; Mölder et al. 2019a). Therefore, foresters increasingly rely on native oak species, when choosing suitable tree species to face changing climatic conditions (Bayerische Staatsforsten AöR 2020; Bayerisches Staatsministerium für Ernährung, Landwirtschaft und Forsten 2020). Nevertheless, oaks are also regularly affected by high pressure of insect pests, which can lead to reduced vitality or dieback (Leroy et al. 2021; Field et al. 2020). 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 (Lüpke 1998; Maleki et al. 2020). These observations are combined with long rotation periods to gain high timber quality in production oriented oak silviculture in Central Europe (Attocchi 2015; Beinhofer 2010). Weaver and Spiecker (1993) already mentioned the increasing multifunctional orientation of oak silviculture. More recently, Löf et al. (2016) 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.

However, on sites where it grows best oak has to compete with more competitive admixed species, especially European beech (*Fagus sylvatica* L.) (Ellenberg and Strutt 1988; Manthey et al. 2007). In contrast, it is able to compete naturally and find its ecological niche (Bauhus et al. 2017) in stands with distinctive and extreme site conditions, e.g. under extreme aridity, on clay soils or floodplains. Natural monospecific oak stands are rare and hardly to find where they grow best. In Germany, for example, it can be assumed that almost all monospecific oak stands have been created by human activity on sites with favourable growing conditions (Krahl-Urban 1959). Consequently, when oak is grown in mixture on the most suitable sites, silvicultural strategies are essential to maintain it as a component of the stand. Oak is traditionally artificially regenerated in many parts of Central Europe and mixed with shade-tolerant tree species introduced at later successional stages to improve its wood quality (Schütz 1993; Lüpke 1998). The admixture of European beech, in particular as a subsidiary tree species, is a widely established practice in oak management and the subject of several studies (Lüpke 1998; Bontemps et al. 2012; Mette et al. 2013; Dolos et al. 2016). On soils with a higher base saturation and clay contents, European beech will be replaced by hornbeam (*Carpinus betulus* L.) or lime species (*Tilia platyphyllos* and *Tilia cordata* L.), associated with a change from beech to oak forest communities (Ellenberg and Strutt 1988; Lüpke 1998). On the other hand, the introduction of young oak under the canopy of mature Scots pine (*Pinus sylvestris* L.) is a common silvicultural option to establish mixed stands in many parts of Central Europe. Mixed stands with aforementioned tree species occur mainly in the physiological optimum of oak.

Existing studies that address the competitiveness of oak and beech and their dependency on different climatic conditions, have investigated the occurrence of oak by using its share of basal area in mixed stands (Mette et al. 2013; Dolos et al. 2016). Dolos et al. (2016) predicted a future shift towards oak in tree species ratios by analysing basal areas derived from forest inventory data that considered the modifying effect of silvicultural interferences. Oak however, is essentially a beneficiary of the predicted climate change due to its drought resistance (Ellenberg and Strutt 1988; Kölling and Zimmermann 2007). Several studies have analyzed the height growth of trees by using the site index in monospecific stands. They focused on tree level growth and used the site index as dependent variable and surrogate for site productivity (Albert and Schmidt 2010; Nothdurft et al. 2012; Brandl et al. 2014). These studies analyzed the site index depending on different climatic conditions. Furthermore, Bontemps et al. (2012) described a shift in height growth relations between sessile oak and European beech in favour of oak in France with changing climatic conditions.

Natural mixed oak forests occur mainly in warm, dry regions (Ellenberg and Strutt 1988). In accordance with climate envelopes of oak and predicted future climate, Kölling and Zimmermann (2007) expect an increase in the distribution of these forest types. In this context, Fischer et al. (2018) predicted an increase of site conditions that favour oak-dominated forests in future as shown by the climate envelopes of both oak species and the current climate in Bavaria. Pretzsch et al. (2013b) used results from experiments with mixtures of oak and beech along an ecological gradient to predict that oak would suffer less from increased drought. Up to now, the effect of climate change on the competitiveness of oak and possible supporting silvicultural measures to ensure the continuance of oak in future compositions have only been discussed qualitatively, while hardly any such effects have been quantified in a way suitable for forest management.

Concerning the productivity analysis, a generally positive long-term growth trend was found for Central European forests in recent studies (Pretzsch et al. 2019b; Pretzsch et al. 2014b), 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 (Pretzsch et al. 2013b; Pretzsch et al. 2019a; del Río and Sterba 2009). Globally, studies have also found a positive relationship between species diversity and productivity (Liang et al. 2016). 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 (Vandermeer 1989). These interactions depend on the tree species admixture (Brockerhoff et al. 2017), prevailing site conditions (Pretzsch et al. 2013b; Pretzsch et al. 2010), stand structure (Pretzsch and Biber 2016; Condés et al. 2013; Brunner and Forrester 2020) or the development stage of the stand (Zeller and Pretzsch 2019). 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 (Zeller and Pretzsch 2019). 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 (Forrester and Pretzsch 2015; Forrester 2019). 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 (Manso et al. 2015; del Río et al. 2014b). 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 (Condés et al. 2013; Ammer 2019; del Río et al. 2016; Forrester 2014), 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 (2004). 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 (Binkley 2004; Binkley et al. 2006). The growth partitioning also provides valuable insights into tree species-specific competitive relationships (Pothier 2017; Fernández-Tschieder and Binkley 2018), which can be used to evaluate and refine silvicultural management options. Especially in view of future uncertainties, small and understory trees could contribute more to the flexibility of the stand. In this way they can mitigate the risk of substantial loss of woody biomass due to a dieback of overstory trees. Furthermore, a recent study by Pretzsch (2021) on the social drift of trees showed a great potential of initially understory beech trees.

One decisive component of an appropriate future oak participation in mature mixed stands is determined by the type of regeneration. So far, due to the comparatively high light requirements of oaks compared to those of admixed tree species, stand establishment has usually been carried out with large crown openings combined with short- to mid-term regeneration periods (Lüpke 1998; Fleder 1983). Consequently, in recent years, these large-scale shelterwood and clearcutting systems have also been increasingly criticized in the course of oak management (Jedicke and Hakes 2005; Meyer 2013).

In particular, in the course of close-to-nature silviculture clear cuts should be largely avoided (Brang et al. 2014; Puettmann et al. 2015). In addition, other core principles of close-to-nature silviculture are the promotion of site-adapted tree species, the establishment of structured mixed stands, and the promotion of natural regeneration (Spathelf et al. 2015). These principles can be implemented in practice, especially by using single-tree selection, group selection, or shelterwood systems (Brang et al. 2014). However, the utilization of natural processes, as a core element of close-to-nature silviculture in particular, puts native oaks at an additional disadvantage compared to their mostly more shade-tolerant admixed tree species (Lüpke 1998; Krahl-Urban 1959; Maleki et al. 2020; Mosandl and Abt 2016). This appears to further weaken oaks in their relative competitive strength on many sites, often resulting in a decline in vitality or loss of oaks in young and mature stands.

In this context, previous studies particularly addressed light availability and its effect on the success of oak regeneration (Lüpke 1998; Březina and Dobrovolný 2011; Ligot et al. 2013; Modrow et al. 2019). Lüpke (1998) suggested the need for at least 15% of full light for survival and 40% for the optimal height growth of oak. Furthermore, the light requirements of oaks were higher in the later development stages (Březina and Dobrovolný 2011; Annighöfer et al. 2015), which indicates continuous silvicultural interferences in the canopy cover. However, Ligot et al. (2013) demonstrated that beech outperformed oak through-out the light gradient and concluded that silvicultural control of the canopy cover is not sufficient in mixed oak and beech regenerations. Consequently, to keep survival rates high the management of mixed oak regenerations has to consider competing woody species (Kanjevac et al. 2021; Kohler et al. 2020) and ground vegetation (Kuehne et al. 2020; Löf 2000; Löf et al. 2021).

Most studies cover short- to mid-term regeneration periods. Long-term studies for oak that cover regeneration periods of up to 20 years and longer are scarcely available (Březina and Dobrovolný 2011; Kohler et al. 2020). However, prolonged regeneration after the first years of successful stand initiation is often decisive for future tree species composition and wood quality in the mature stand. This is especially true for close-to-nature silviculture and long regeneration periods of 30 years or more. In addition, the results of the studies are often limited to specific site conditions and cannot be readily applied to other stand situations or site conditions.

1.2 Research Objectives

The research objective of this cumulative thesis was to analyze the site- and structure-dependent growth potential of European oak species to deepen and develop the understanding of oak management. Firstly, the height growth of individual oak trees in monospecific and two-species mixtures was analyzed to explain their climate and site-sensitive competitiveness under consideration of the stand structure (Article I, Stimm et al. 2021). Secondly, the long-term stand and tree productivity was investigated, which is highly relevant for forest management (Article II, Stimm et al. 2022a). Last but not least, the success and constraints of the regeneration of oak established in mixtures under continuous canopy cover was assessed (Article III, Stimm et al. 2022b). The conceptual framework of this cumulative thesis with the covered stand development phases is shown in Figure 1.

In essence, the study on height growth focussed on the effect of environmental conditions and local stand structure as a proxy for competition in monospecific as well as in two-species mixtures on the height growth trajectories of oak, based on forest inventory data of the federal state of Bavaria. The article addresses following research questions: (i) what are the effects of summer temperature, water availability and nutrient supply on the height growth of oaks?; and (ii) is there a modifying effect of stand density and vertical stand structure on the height growth of oak?; and (iii) what is the effect of site conditions and structural variables on the height growth of oak in different tree species mixtures?

For the productivity study monospecific and mixed oak stands, covering a broad ecological and structural gradient as well as varying thinning practices were investigated. For this, a unique dataset of research plots in Germany was used, 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 were 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, following research questions were addressed in the article: (i) is there a discernible long-term growth trend in oak stands over the last century?; and (ii) how does productivity of monospecific and mixed oak stands depend on stand structure, site conditions and stand development phase?; and (iii) how is productivity of individual oak trees related to their social status, vertical stand structure, mixture type and age?; and (iv) what is the contribution of small tree individuals to stand growth?

The objective of the third study is to assess the success and constraints of the regeneration of oak established in mixtures under continuous canopy cover. For this, the data of monospecific pine and mixed oak stands were used, where regeneration has been monitored and measured for up to 36 years. In detail, first the survival probability of oaks over time were analyzed by hypothesizing that survival is dependent on forest site. Secondly, the course of species-specific regenerated tree density and biomass was evaluated. Here, the hypothesis that the development of density and biomass is species-specific and modified by the degree of canopy cover was tested. In the next step, the height growth rates of oaks were quantified to answer the hypothesis that the height growth of oaks is negatively influenced by canopy cover and interspecific competition. Lastly, the effect of advanced regeneration on the productivity of the remaining stand was analyzed following the hypothesis that high rates of regeneration biomass reduce the productivity of the remaining stand. From the results, silvicultural recommendations for the successful regeneration of oaks within continuous cover forestry were deduced. The article focused on four main questions. (i) What are the survival probabilities of oak in small-scale and long-term regenerated stands and do they differ between different forest types? (ii) What is the long-term development of the regenerated tree species' density and the effect of canopy cover on regeneration biomass? (iii) How does canopy cover and interspecific competition modify the heights of regenerated oaks? (iv) Is there a feedback effect of advanced regeneration on the productivity of the mature stand?

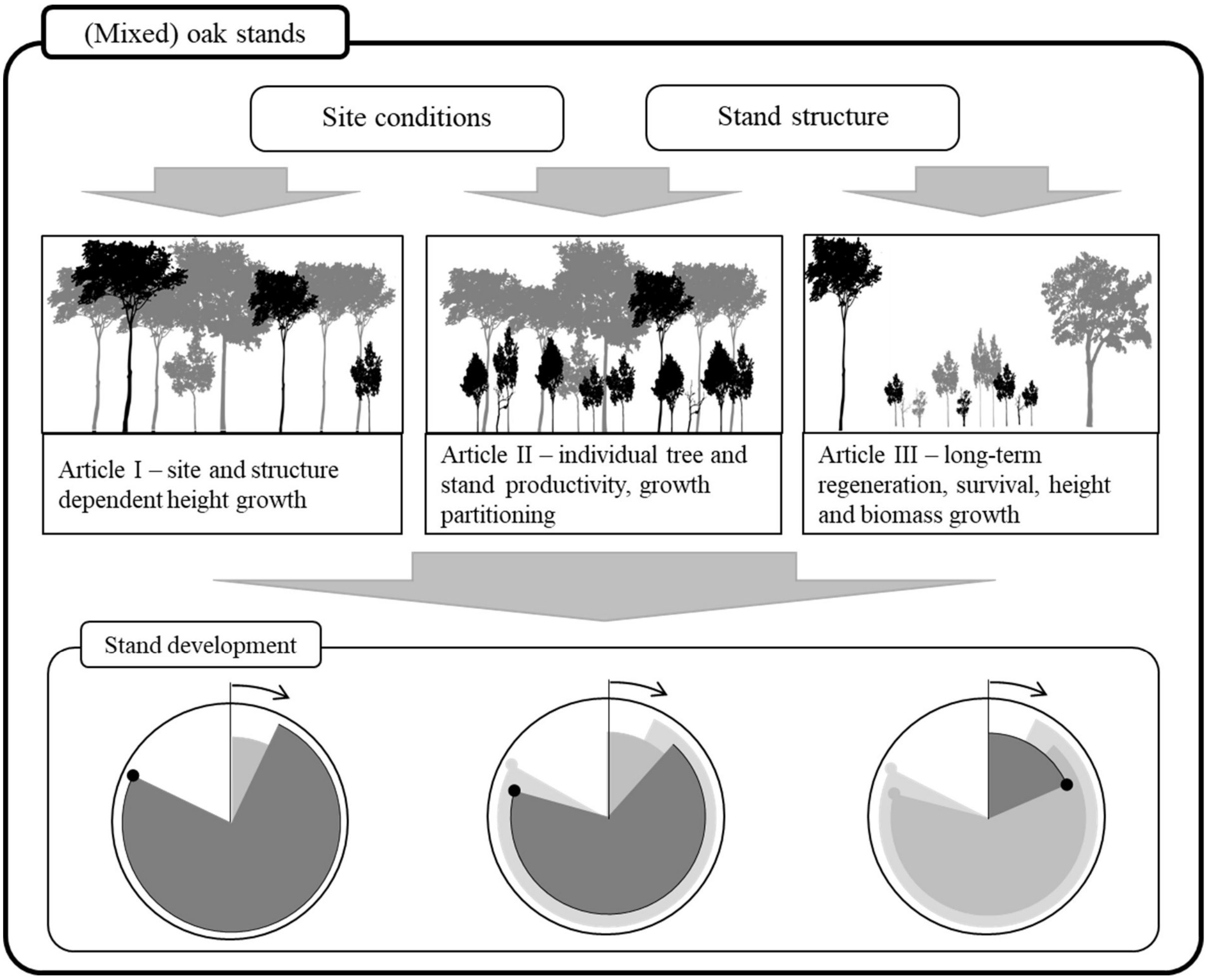

Figure 1: Conceptual framework of the cumulative thesis. Illustrated are the three articles (I – III) with the respective objectives as well as the stand development phases on which the studies are based (dark grey segments). Oaks are presented in grey and the mixed species in black.

2. Material and Methods

2.1 Research plots

Forest inventory data (Article I)

To describe the site and structure dependent height growth as one decisive component of tree and tree species competitiveness forest inventory data of the Federal State of Bavaria, located in southern Germany was used. The study is based on two sets of forest inventories, namely the National Forest Inventory of Germany (NFI) and the inventory data of the Bavarian State Forest Enterprise (BSFI). By combining both inventories, using cross-sectional and short-term longitudinal data, we obtained an adequate sample of measured tree heights, covering a broad gradient of environmental conditions across Bavaria (Figure 2).

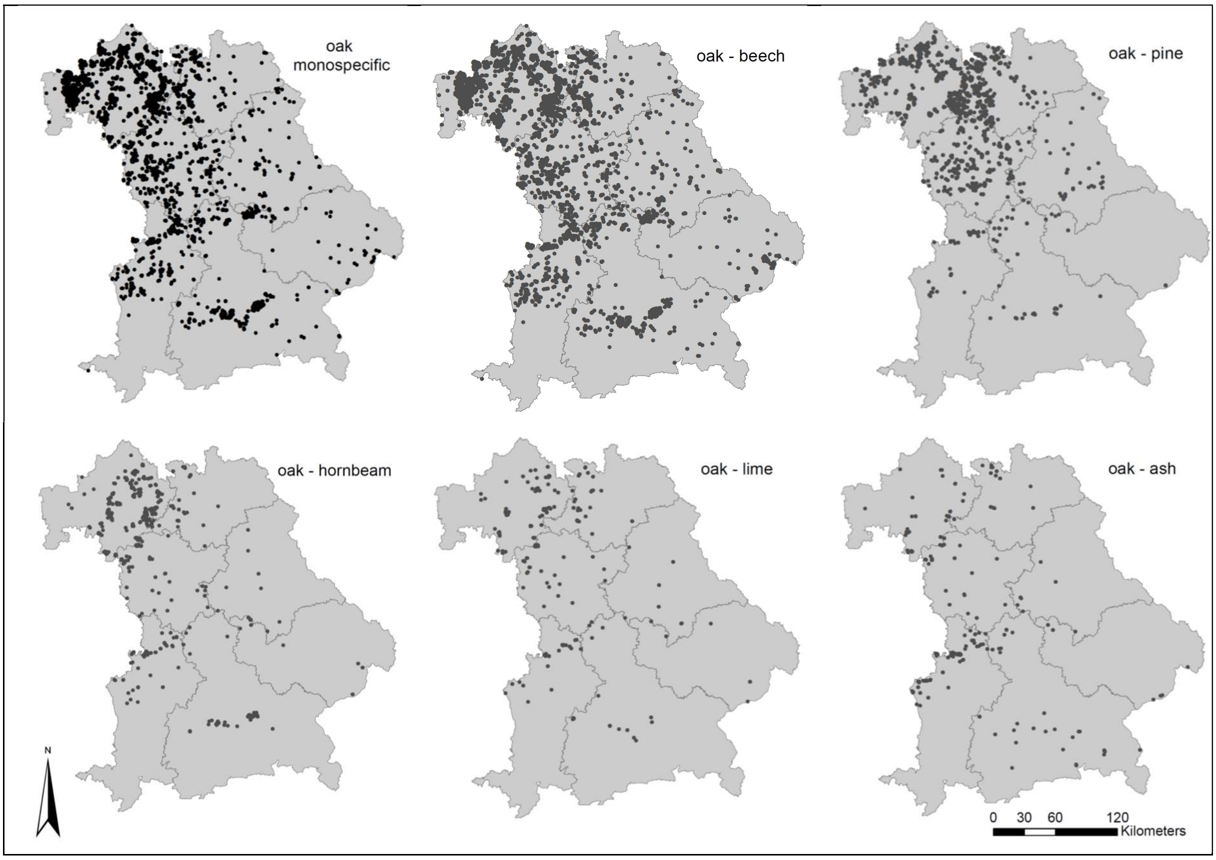

Figure 2: Spatial distribution of investigated inventory plots within the study area. (Stimm et al. 2021c)

In total, we considered the tree heights of 9,166 oaks in monospecific stands and 14,441 oaks in mixed stands. The latter were mixed with beech (n = 10,069), Scots pine (n = 2,694), hornbeam (n = 979), lime (n = 370) and ash (n = 329). The age of the investigated oaks covered a broad gradient, ranging from 7 to 394 years. Similarly, a large range is covered by the height and diameter of the considered oaks (Table 1).

Table 1: Overview of height measurement oak trees and admixed species in the inventory data; n = number of trees; mean = average value of all trees; min = minimum; max = maximum; sd = standard deviation (Stimm et al. 2021c)

Mixture	Species	Variable	Unit	n	mean	min	max	sd
monospecific	**Oak**	**Age**	year	9,166	97.8	7	394	60
		Height	m		22.5	1.4	39.5	7.8
		dbh	cm		35.6	1.5	186.5	18.8
oak-beech	**Oak**	**Age**	year	10,069	141	5	394	59
		Height	m		27.9	1.5	43.0	5.2
		dbh	cm		44.6	1.5	129.3	14.6
	European beech	**Age**	year	10,457	122	5	281	45
		Height	m		28.3	1.3	47.5	6.5
		dbh	cm		43.8	1.5	105.5	15.1
oak-pine	**Oak**	**Age**	year	2,694	106	6	263	42
		Height	m		24.3	2.0	38.0	5.3
		dbh	cm		37.6	1.5	108.5	13.6
	Scots pine	**Age**	year	2,861	104	6	281	40
		Height	m		25.8	1.5	37.8	5.2
		dbh	cm		38.6	1.5	72.5	11.1
oak-hornbeam	**Oak**	**Age**	year	979	114	8	309	56
		Height	m		23.1	1.3	36.0	6.0
		dbh	cm		40.3	1.5	112.5	17.9
	Hornbeam	**Age**	year	669	87	10	209	43
		Height	m		20.3	1.4	35.0	5.4
		dbh	cm		27.2	1.5	70.5	11.6
oak-lime	**Oak**	**Age**	year	370	107	12	259	61
		Height	m		23.3	6.3	38.5	6.9
		dbh	cm		42.3	6.5	110.5	22.1
	Lime	**Age**	year	246	78	12	200	41
		Height	m		21.7	5.3	39.0	7.0
		dbh	cm		31.4	5.5	74.5	13.8
oak-ash	**Oak**	**Age**	year	329	113	15	269	56
		Height	m		25.5	3.0	43.5	6.6
		dbh	cm		47.8	4.5	143.5	21.8
	Common ash	**Age**	year	276	91	12	189	39
		Height	m		26.5	3.5	50.5	7.6
		dbh	cm		39.9	1.5	94.5	16.6

Long-term yield trials, strict forest reserves and temporary experiments (Article II)

For productivity analyses the data from 32 long-term experiments, 25 strict forest reserves and 5 temporary experiments were used. All experiments and observations comprise 147 plots covering monospecific and mixed oak stands. The research plots were 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 (Pretzsch et al. 2019b; Pretzsch et al. 2013b).

Therefore, the data covered 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 covered 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 covered ages over 100 years the values were directly available. For plots younger than 100 years, SI was referenced from yield tables by Jüttner (1955).

Table 2: 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 [C] (1970–2000); Alt—altitude above sea level [m.a.s.l.]; mean values, min and max values in italics below. (Stimm et al. 2022a)

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

Long-term regeneration experiments (Article III)

To analyze the long-term regeneration dynamics, the data of 12 regenerated experimental plots, each located in a different stand were used; they were part of four long-term experiments in southern and central Germany (Figure 3). The size of the individual experimental plots varied between 0.1 and 1.0 ha. The investigated stands were located in three different woodland regions and sites, namely Spessart, Steigerwald, and Nuremberg, which are further referred to using their experiment codes BUS, EBR, and NUE, respectively. The stands represented mixed oak and monospecific Scots pine (*Pinus sylvestris* L.) stands. The mixed mature stands were composed of sessile oak and European beech in the case of BUS and sessile oak and European beech and Scots pine in the case of EBR. The mixed stands in BUS and EBR were mainly regenerated naturally; the planting of oaks occurred only marginally. In contrast, the monospecific pine stands in the Nuremberg region were regenerated by sowing and underplanting oak and beech, respectively. The experimental plots were established to test the different overstorey stand densities and their effect on regeneration by applying single-tree and group selection systems. The considered stands covered a broad range of small-scale canopy gaps, from approximately 0.01 to 0.25 ha, and different light situations.

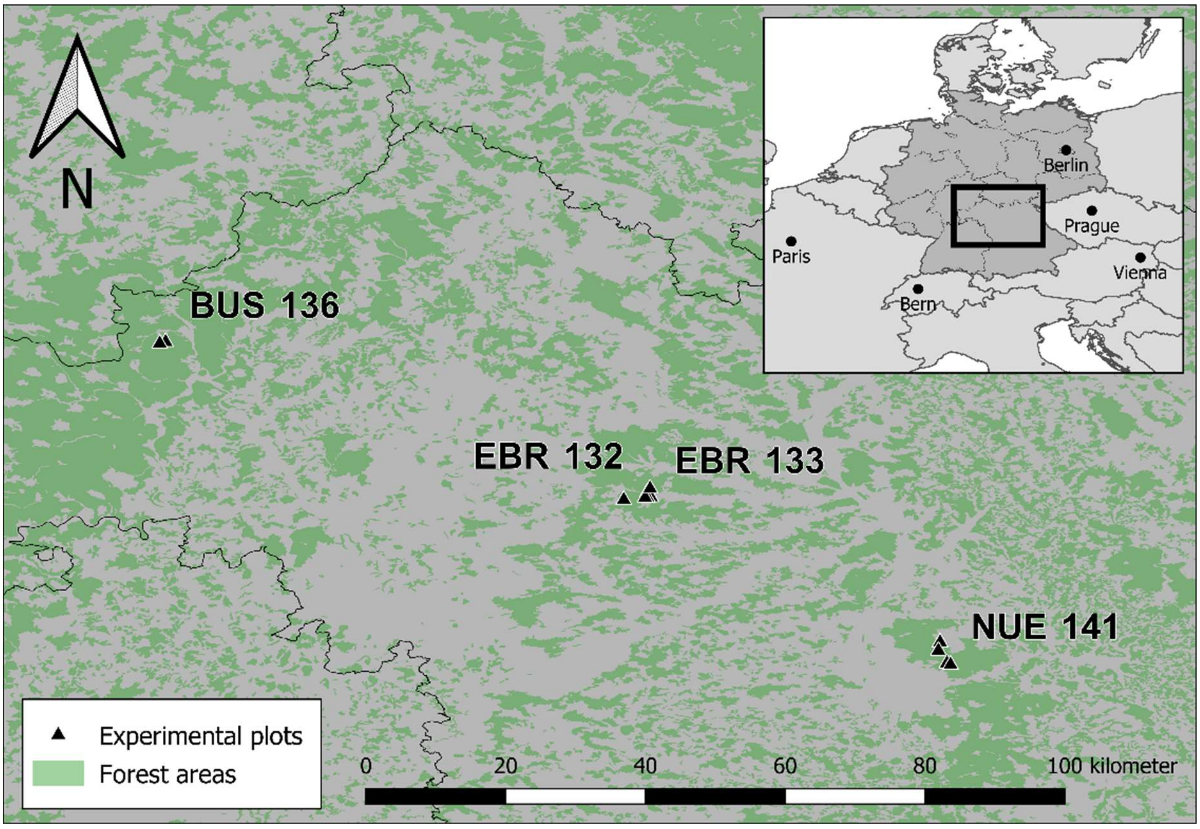

Figure 3: Geographic location of the experimental plots in southern and central Germany. Experimental plots are represented by the corresponding experimental codes; BUS 136 = Spessart, EBR 132 and 133 = Steigerwald, NUE 141 = Nuremberg (Stimm et al. 2022b)

2.2 Data

Site and structure dependent height growth (Article I)

As a consequence of different requirements for height measurements in the NFI and BSFI, the selection of the investigated trees was harmonized. Without trees with observed damages all measured heights from both inventories were selected. Based on the dominant trees (> 75% of the maximum height), the tallest trees with 90% of the maximum height at species level to better assess the ecological potential were selected. Consequently, the final data set contained only the tallest dominant trees per species. Monospecific inventory plots were identified by ≥ 90% basal area share of dominant oak. Two-species mixture plots were identified by a 10% minimum basal area share of dominant oak, one additional admixed species and a maximum of 10% of a third tree species.

All inventory plots were stratified into two groups, single-layered and multi-layered. In order to assign trees as subdominant, a threshold of 75% of the maximum height at the inventory plot level were defined. The presence of one subdominant tree at the inventory plot was determined to be indicative for a more vertically structured local stand situation in the immediate vicinity of the tree in focus. The corresponding inventory plot was then classified as multi-layered. In addition, one tree at the plot level represents a multiple of trees per hectare on the stand level. Additionally, the stand density index (SDI) of the main stand for each inventory plot, using the stem number per ha (N) of dominant trees was calculated (Reineke 1933). Differences in species-specific growing area requirements, e.g. maximum stand densities, were taken into account by applying a species-specific equivalence factor E (Pretzsch and Biber 2016).

$$SDI_i = \sum_{1}^{j} N_{ij} \times \left(\frac{25}{dq_{ij}}\right)^{-1.605} \times E_j \tag{1}$$

Here, SDI is the stand density index, N the number of trees per hectare, dq the quadratic mean diameter (cm) and E the species-specific correction as described above. Indices i and j refer to the inventory plot and tree species, respectively.

To characterize the plot-specific site conditions, interpolated climate data from the German Weather Service and regionalized environmental data from the Bavarian State Institute of Forestry were used. In accordance with the research questions, the focus was on temperature, water availability and nutrient supply as main environmental variables (Table 3).

Table 3: Descriptive data for the environmental and structural variables for regression analyses for all inventory plots (pooled data, monospecific and mixed) (Stimm et al. 2021).

Variable	Unit	mean	min	max	sd
Summer temperature (temp)	°C	16.4	13.1	18.1	0.5
Water balance vegetation period (wb)	mm	35.1	-196.1	400.0	68.3
Base saturation (bs)	%	41.4	3.3	100.0	30.0
Stand density index	n ha^{-1}	882.5	5.1	2989.7	397.7
Latitude	°		47.7	50.6	
Longitude	°		9.1	13.7	

Long-Term Productivity (Article II)

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 (Johann 1993). For productivity analyses at stand level, the mean periodic annual volume increment (PAIV) in m^3 ha^{-1} $year^{-1}$ was used.

$$PAIV = (V_2 - V_1 + V_{rem})/(t_2 - t_1) \tag{2}$$

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 the allometric relationship was parametrized for calculation of cpa values for all oak trees, according the following equation, where the oak-specific parameters were obtained from long-term experimental plots (Schwaiger et al. 2018).

$$cpa = 0.07 \times dbh^{1.70} \tag{3}$$

To evaluate the growth partitioning, the growth dominance coefficient (GDC) proposed by Binkley (2004) and formulated by West (2014) was used. 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.

$$GDC = 1 - \sum_{k=1}^{n} (v_k - v_{k-1})\,(iv_k + iv_{k-1}) \tag{4}$$

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 $v_0 = iv_0 = 0$ (West 2014). It was calculated for the overstorey on stand as well as on species level for each survey.

The description of the stand structure focused 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 SDI according to Reineke (1933). 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 (Kramer and Akça 1995) 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 (Eq. (1)).

The proportions of oak ($Prop_{oak}$) 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. 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 according to Burschel and Huss (1997). 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.

Table 4: 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. (Stimm et al. 2022a)

		PAIV	**Vol**	**Age**	**SDI**	**Prop$_{oak}$**	**SI**	**GDC**	**cvh**
[*N* = 785]		**[m³ ha⁻¹ year⁻¹]**	**[m³ 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

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 was related to the dbh of the thickest tree on the plot irrespective of the species, since measured values were available for each tree. 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. For the stands analyzed, no considerable effect of different plot sizes on the coefficient was detected.

Table 5: 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. (Stimm et al. 2022a)

		iv/cpa	**Age**	**rel_d**	**cpa**
[*N* = 67.479]		**[dm³ m⁻² year⁻¹]**	**[years]**	**[./.]**	**[m²]**
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

Long-Term Regeneration dynamics (Article III)

To quantify main stands´ yield data the DESER-standards (Johann 1993) were applied (Table 6). In addition, canopy cover CC (%) was calculated for all appropriate surveys. Based on 8 measurements per tree crown, maps were plotted with crown shape approximations by cubic splines. From this, the corresponding area covered by tree crowns could be taken for the stand and the regeneration squares (5x5 m), respectively.

Table 6: Yield data of the main stand for the first and latest survey; S—tree species; Age—stand age [yrs]; N—number of trees [n ha^{-1}]; H100—dominant height [m]; D100—dominant diameter [cm]; BA—basal area [m^2 ha^{-1}]; V—volume [m^3 ha^{-1}]; CC—canopy cover [%]; PAIBA—periodic annual basal area increment [m^2 ha^{-1} yr^{-1}]; PAIV—periodic annual volume increment [m^3 ha^{-1} yr^{-1}]; Per—observation period [yrs]. Oa—sessile oak; Be—European beech; Pi—Scots pine; Hb—hornbeam; Sp—Norway spruce. (Stimm et al. 2022b)

		First Survey								Last Survey									
Exp (Nr)	**Plot**	**S**	**Age**	**N**	**H_{100}**	**D_{100}**	**BA**	**V**	**CC**	**Age**	**N**	**H_{100}**	**D_{100}**	**BA**	**V**	**PAIBA**	**PAIV**	**CC**	**Per**
EBR (132)	**1**	Pi	147	21	30.9	53.3	4.65	66.14	37	184	12	33.27	65.01	4.15	63.15	0.05	0.76	30	36
		Be	147	42	31.34	45.12	6.66	110.2		184	21	33.05	69.6	7.93	138.81	0.1	1.76		
		Oa	147	4	31.59	46.9	0.72	12.26		184	4	32.78	67.4	1.49	26.99	0.02	0.38		
		total		67			12.03	188.61			37			13.5	228.94	0.17	2.9		
EBR (133)	**2**	Pi	143	8	27.03	51.64	1.66	20.98	60	178	2	32.07	52.2	0.39	5.79	0.01	0.11	43	36
		Be	143	77	32.44	47.15	12.24	209.08		178	53	34.78	64.37	15.4	282.88	0.19	4.09		
		Oa	143	14	29.02	46	2.33	36.71		178	13	32.65	62.1	3.94	71.18	0.05	1.05		
		total		99			16.23	266.78			68			19.7	359.84	0.24	5.24		
	4	Be	164	44	34.88	49.35	8.42	159.51	22	199	33	35.1	70.11	12.7	237.99	0.16	3.35	43	36
		Oa	164	12	33.55	46.74	2.06	37.18		199	12	33.33	61.5	3.56	65.38	0.04	0.87		
		Hb	164	1	24.38	30.7	0.07	0.92		199	1	28.44	42.5	0.14	2.11	0	0.04		
		total		57			10.55	197.61			46			16.4	305.48	0.2	4.27		
	6	Pi	162	11	27.09	53.14	2.4	30.21	62	197	9	28.68	60.38	2.44	32.49	0.02	0.18	54	36
		Be	162	44	28.72	46.56	4.92	71.82		197	34	31.29	60.43	5.64	107.13	0.07	1.51		
		Oa	162	67	28.67	43.7	9.46	145.15		197	62	30.91	54.69	14.5	241.67	0.15	3.33		
		Hb	162	10	23.53	22.54	0.24	1.81		197	10	20.37	28.98	0.49	4.73	0	0.07		
		total		132			17.02	249			115			23.9	386.03	0.24	5.08		
	7	Sp	146	1	27.55	47	0.17	2.18	22	181	16	28.5	50.85	3.25	42.9	0.03	0.55	30	36
		Pi	146	24	27.02	41.36	3.22	40.31			0	-	-	-	-	-	-		
		Be	146	25	30.12	44.64	3.91	62.53		181	19	27.76	58.43	5.09	74.79	0.06	0.72		
		Oa	146	18	25.97	40.38	2.3	32.22		181	17	26.44	57.23	4.37	64.48	0.06	1.04		
		total		68			9.61	137.25			52			12.7	182.17	0.15	2.31		
	8	Be	153	13	32.81	48.84	2.44	42.33	25	188	4	26.21	64.18	1.29	18.11	0.01	0.11	9	36
		Oa	153	19	29.34	41.73	2.6	40.89		188	15	27.67	55.3	3.6	55.22	0.05	0.85		
		Hb	153	1	21.72	18	0.03	0.26			0	-	-	-	-	-	-		
		total		33			5.06	83.48			19			4.9	73.33	0.06	0.96		
BUS (136)	**1**	Be	192	40	24.97	43.52	2.52	30.58	67	218	4	27.01	39.6	0.42	5.52	0.02	0.3	38	26
		Oa	192	66	29.31	60.12	18.74	305.77		218	52	31.34	70.58	20.3	356.57	0.19	3.82		
		total		106			21.26	336.35			56			20.7	362.09	0.21	4.11		
	2	Be	202	106	28.08	44.76	7.03	88.29	67	228	26	27.78	49.97	3.78	53.8	0.08	0.94	41	26
		Oa	202	74	28.18	61	21.63	340.19		228	48	30.92	68.54	17.7	305.72	0.16	3.24		
		total		180			28.66	428.48			74			21.4	359.52	0.24	4.17		
NUE (141)	**1**	Pi	88	400	24.1	35.76	27.07	287.45	66	116	144	26.77	39.99	16.6	203.99	0.23	3.52	35	28
	2	Pi	97	400	25.52	35.95	29.53	332.25	77	125	233	30	43.83	29.2	389.24	0.45	7.44	57	28
	3	Pi	125	189	27.57	47.56	27.62	346.41	63	153	111	30.19	52.67	23.5	327.32	0.29	4.95	42	28
	4	Pi	130	133	31.65	48.8	22.46	324.85	57	158	44	29.79	54.33	10.3	141.56	0.1	1.03	23	28

On the entire experimental plots all regenerated trees were surveyed three times. For the study the regeneration data, height and biomass was aggregated and summarized by 5x5 m squares, survey and tree species. Thus, the data of 1 916 squares were obtained per survey and 5 748 in total. Of these, 4 112, 1 200 and 432 were located in EBR, BUS and NUE, respectively. All occurring regeneration plants were recorded. Saplings smaller than 2 m were assigned to 4 height classes (0-50 cm, 51-100 cm, 101-150 cm, 151-200 cm). Plants larger than 2 m were additionally characterized by their dbh. All saplings (< 2 m and > 1.3 m) for which no measured dbh was available were assigned an estimated diameter as a function of their height using a logarithmic model. Regeneration biomass was calculated for each tree using the formula of Forrester et al. (2017).

$$ln(bm) = ln(\beta 0) + \beta 1\ ln(D) + \varepsilon \qquad (5)$$

Where the calculated biomass (bm) was the aboveground biomass of the individual tree in kg. D was the diameter in cm of the corresponding tree. β_0 and β_1 were the species-specific function parameters. A descriptive summary of the plot and species-specific regeneration data for the first and last surveys is provided in Table 7.

Table 7: Regeneration data for the first and latest survey; S—tree species; A—age of regeneration [yrs]; d—plant density [n ha⁻¹]; bm—regeneration biomass [kg ha⁻¹]; h—mean height [m]. (Stimm et al. 2022b)

			First survey				**Last survey**			
Exp (Nr)	**Plot**	**S**	**A**	**d**	**bm**	**h**	**A**	**d**	**bm**	**h**
EBR (132)	1	Pi	4	3 504	182	0.67	40	4	202	16.07
		Be		18 308	2 033	1.05		3 492	55 745	7.41
		Oa		22 104	562	1.07		271	11 015	13.45
		Hb		3 383	605	1.21		354	9 235	7.99
		Others		350	33	1.55		4	26	8.19
EBR (133)	2	Pi	6	366	22	0.89	42	0	--	--
		Be		15 464	1 767	1.11		3 709	27 696	7.1
		Oa		8 892	165	0.87		5	68	11.48
		Hb		130	16	1.74		6	716	15.48
		Others		697	118	2.85		59	3 305	12.06
	4	Pi	22	6	0	0.62	58	0	--	--
		Be		30 554	6 100	3.19		2 394	91 381	11.4
		Oa		1 140	15	1.44		6	279	13.97
		Hb		197	28	1.64		6	1 038	18
		Others		284	60	4.71		98	32 299	19.89
	6	Pi	6	100	4	0.36	42	5	125	9.27
		Be		15 791	1 056	0.65		5 280	49 307	5.72
		Oa		119 009	833	0.32		98	921	7.12
		Hb		69	9	0.87		95	2 033	9.87
		Others		153	15	1.07		77	8 714	10.21
	7	Pi	11	2 198	161	1.44	47	59	4 672	13.24
		Be		19 284	2 863	1.71		3 972	49 136	7.13
		Oa		17 402	479	1.84		613	43 182	14.41
		Hb		2 925	594	1.67		453	7 973	9.51
		Others		3 609	477	2.03		184	9 655	9.54
	8	Pi	13	70	5	1.36	49	16	2 340	16.55
		Be		7 634	891	1.53		3 203	29 103	5.72
		Oa		41 570	1 483	1.89		2 500	102 447	10.07
		Hb		3 642	897	2.14		1 553	33 505	7.81
		Others		219	27	2.37		22	6 699	14.86
BUS (136)	1	Be	5	15 878	1 052	0.67	31	11 628	12 644	2.8
		Oa		54 286	1 686	0.3		6 678	10 142	3.52
	2	Be	3	12 245	812	0.64	29	8 175	23 505	3.9
		Oa		13 302	411	0.25		5	26	7.13
NUE (141)	1	Pi	3	31 911	849	0.3	31	2 133	2 753	2.77
		Be		1 278	130	0.32		1 478	8 653	6.35
		Oa		18 889	785	0.45		2 444	6 696	3.1
		Others		544	162	0.47		356	1 714	4.67
	2	Pi	5	86 967	2 429	0.32	33	122	92	2.81
		Be		1 122	129	0.43		3 567	46 948	8.17
		Oa		42 911	1 742	0.53		822	3 120	5.09
		Others		156	47	0.38		222	950	6.14
	3	Pi	9	2 300	157	0.88	37	0	--	--
		Be		5 011	1 095	1.75		2 622	76 353	10.96
		Oa		40 211	4 230	1.56		89	3 900	14.34
		Others		7 089	3 060	1.22		322	13 313	10.41
	4	Pi	9	1 800	128	0.89	37	0	--	--
		Be		322	54	0.94		500	3 888	3.58
		Oa		23 911	2 517	1.54		1 733	100 861	11.58
		Others		1 633	670	1.22		256	6 497	6.86

2.3 Statistical Analyses

All statistical analyses were performed using the statistical software R and the additional add-on packages as needed (R Core Team 2018). The generalized additive mixed models were performed with the mgcv package (Wood 2017). For the application of linear mixed effects models the lmer function of the lme4 package was used (Bates et al. 2015).

Generalized additive mixed models (Article I)

In order to describe the environmental and structural effects on height growth of oak, the monospecific and mixed stands were considered separately. Due to the linear and non-linear behaviour of the explanatory variables to the predictor variable, a generalized additive mixed model (GAMM) was applied, which allows the consideration of both types of reaction in one model without any assumption about the underlying distribution (Zuur et al. 2009; Wood 2017). In addition, random effects were considered due to nested trees at the inventory plot level and due to temporal autocorrelation of the repeated measurements at the tree level. Summer temperature, water availability in the growing season and base saturation were used to describe individual site conditions. The individual tree dimension is considered based as a nonlinear function of the species-specific stand age. In order to describe the partial effect of stand structure on height growth, stand density and layer structure were added to the model. Geographical coordinates (lat/lon) were included in the model as a two-dimensional smoother to account for spatially structured variation in the response not explained by the available covariates. In the case of mixed stands, the GAMM was applied for each mixing type separately. Interactions between the variables were not considered because they did not improve the explanatory power of the model. All terms were kept in the model, as it was based on our hypothesis.

Linear mixed effects models (Articles II and III)

To perform productivity analysis and due to the assumed spatial and temporal dependencies, linear mixed effect models were set up to account for potential autocorrelation (Zuur et al. 2009). 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 respective models were determined by the research questions. 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 (Zuur et al. 2009, p. 537).

Also for regeneration analysis on density, height and biomass, linear mixed effects models were used, to account for potential autocorrelation due to assumed spatial and temporal dependencies, as described above (Zuur et al. 2009). All variables were set as a function of age. To describe the effect of the mature stand, canopy cover was additionally included in the model. In the case of maximum regeneration height, biomass of the admixed tree species, which was in all cases primarily constituted by beech was additionally included in the model to account for interspecific competition. The respective models with the considered interactions between covariates were determined by the research questions and applied equally for each experimental site and tree species. To describe the effect of the regeneration biomass on the productivity of the overstorey (PAIV), the periodic annual increment was estimated as a function of standing volume and total regeneration biomass on plot level.

Logistic regression model (Article III)

To describe the occurrence probability of oak, a logistic model was set up across all investigated stands. The presence of oaks was set as a function of the duration of the regeneration period and the corresponding experimental site. The predicted probability was based on the occurrence of oaks in the respective regeneration square. Each square was categorized by the binary variable as either 1 (oak occurs) or 0 (oak does not occur). With the regeneration squares lying next to each other and recorded repeatedly, the corresponding random effects were plot and square within the plot to account for spatial and temporal autocorrelation.

3. Results

3.1 Height growth-related competitiveness (Article I)

Summer temperatures showed a significant effect on the height growth of oak. The influence was strongly positive up to summer temperatures of 16.4 °C. A slight decrease and signs of stagnation at higher temperatures indicated that oak only reacts with increased height growth up to a moderate temperature rise (Figure 4a). The water balance during the vegetation period had a significant positive linear influence on height growth, which was observed for the range between -200 and 400 mm water availability (Figure 4b). The influence of base saturation on height growth was low (Figure 4c).

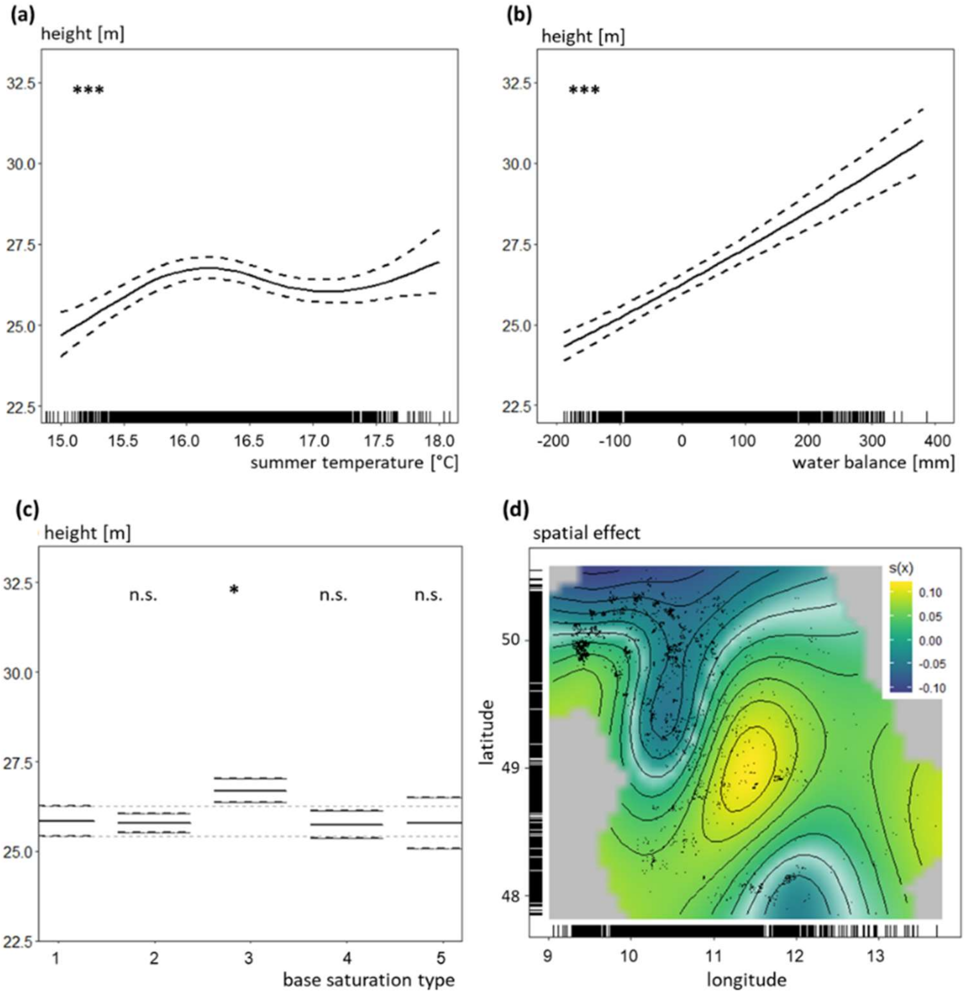

Figure 4: Partial effects of environmental variables on oak height growth in monospecific stands with summer temperature (a), water balance during vegetation period (b), base saturation type (c) and spatial distribution (d). For a graphical presentation of one-dimensional effects, the age was set to 100, while all other variables were set to their mean. The categorical variables were set to medium base saturation and multi-layered. Significance levels: p < 0.001 `***`; p < 0.05 `*`; p > 0.1 `n.s.` (Stimm et al. 2021c)

Stand density had a strong positive effect with a saturation at SDI levels of around 1,000 trees per hectare (Figure 5a). No significant partial effect of the existing stand layers was found for monospecific stands (Figure 5b).

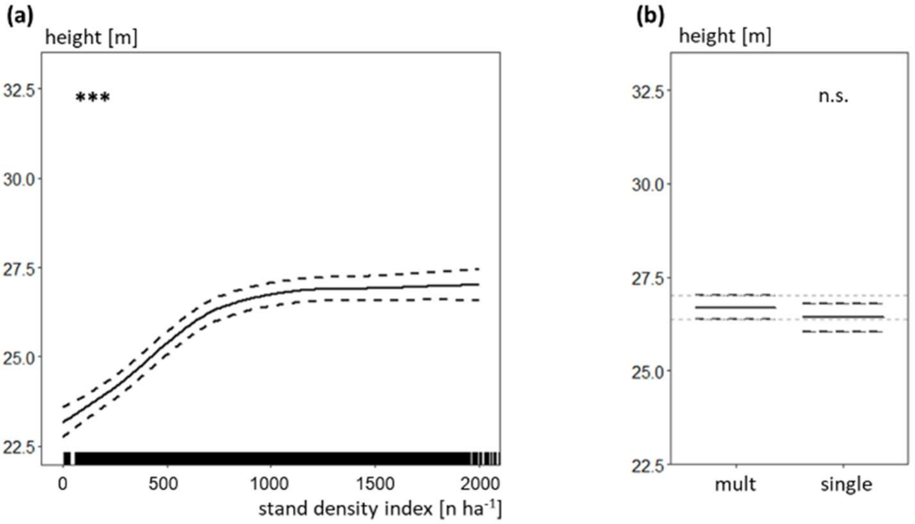

Figure 5: Partial effects of structural variables on oak height growth in monospecific stands with stand density index (a) and vertical stand structure (b). For a graphical presentation, the age was set to 100, while the other variables were set to their mean. The categorical variables were set to medium base saturation and multi-layered. Significance levels: p < 0.001 `***`; p > 0.1 `n.s.` (Stimm et al. 2021c)

The results were partly different in the considered two-species mixtures compared with monocultures of oak. In addition, a change in the significance of the partial effects could be observed. For summer temperature, the optimum of 16.4 °C that was indicated for monospecific stands did not appear to apply for mixed stands with beech (Figure 4a, Figure 6a). In mixtures with hornbeam, the results were comparable to those for monospecific oaks. In mixtures with lime, the partial effect of summer temperature on oaks' heights became positively linear. Summer temperature had no significant influence on the mixture with pine (Figure 6b) and ash. In mixture with beech, pine and lime, the water balance had a significantly positive linear effect on oak heights (Figure 6c, d). Mixed with hornbeam the positive effect was non-linear but when mixed with ash no significant effect was observed. In the case of base saturation, a significantly positive effect could be observed for the mixture with beech and hornbeam, with an optimum at medium base saturation (Figure 6e). With a well-balanced nutrient supply, low base saturation had no significant effect on height growth. A reduced growth of oak in the mixture with lime was still significant in the transition from a high base endowment to a balanced nutrient supply. The base saturation type played only a minor role for the mixtures with pine and ash (Figure 6f). Whereas the effect of temperature, water availability and base saturation was lower in the oak-beech mixture, the influence of stand density on height growth was more positive. SDI values beyond 700 had no further positive effect (Figure 7a). The positive effect, especially in less dense stands, was also observed for the oak-pine mixture (Figure 7b). When mixed with lime or ash, the effect became linear. Unlike a less climate-sensitive reaction, the structural variables became more important for oaks' height growth. Density had a significant effect on oak heights as a structural variable in all mixtures, with the exception of oak-hornbeam mixtures. Additionally, the vertical structure of the stands played a role, especially in mixture. In the mixtures with beech, pine, lime and ash, the examined oaks were significantly taller in stands with at least a second tree layer (Figure 7c, d).

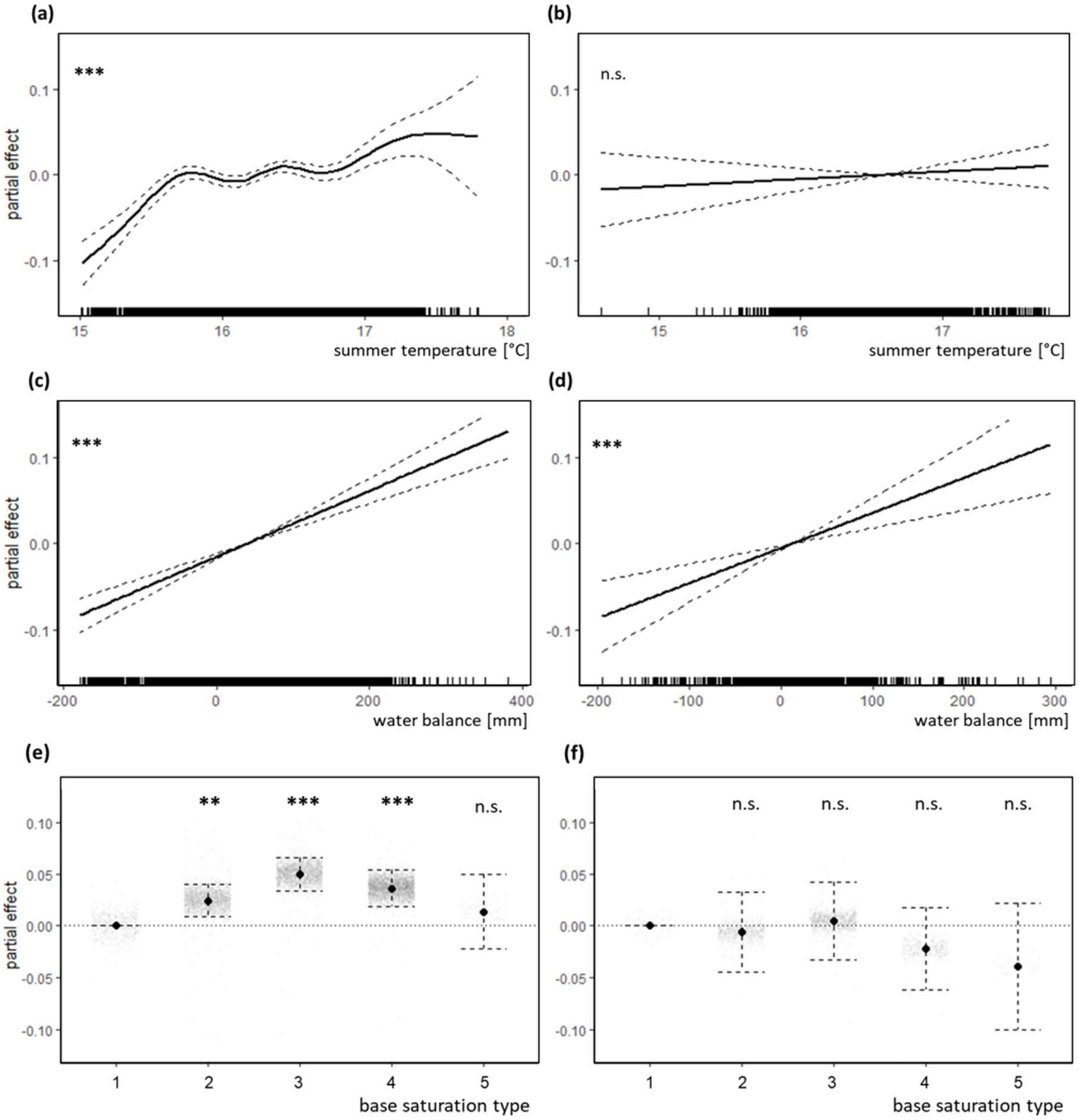

Figure 6: Partial effects of environmental variables on oak height growth in mixture with beech (left) and pine (right), with summer temperature (a, b), water balance during vegetation period (c, d) and base saturation type (e, f). Significance levels: p < 0.001 `***`; p < 0.01 `**`; p > 0.1 `n.s.` (Stimm et al. 2021c)

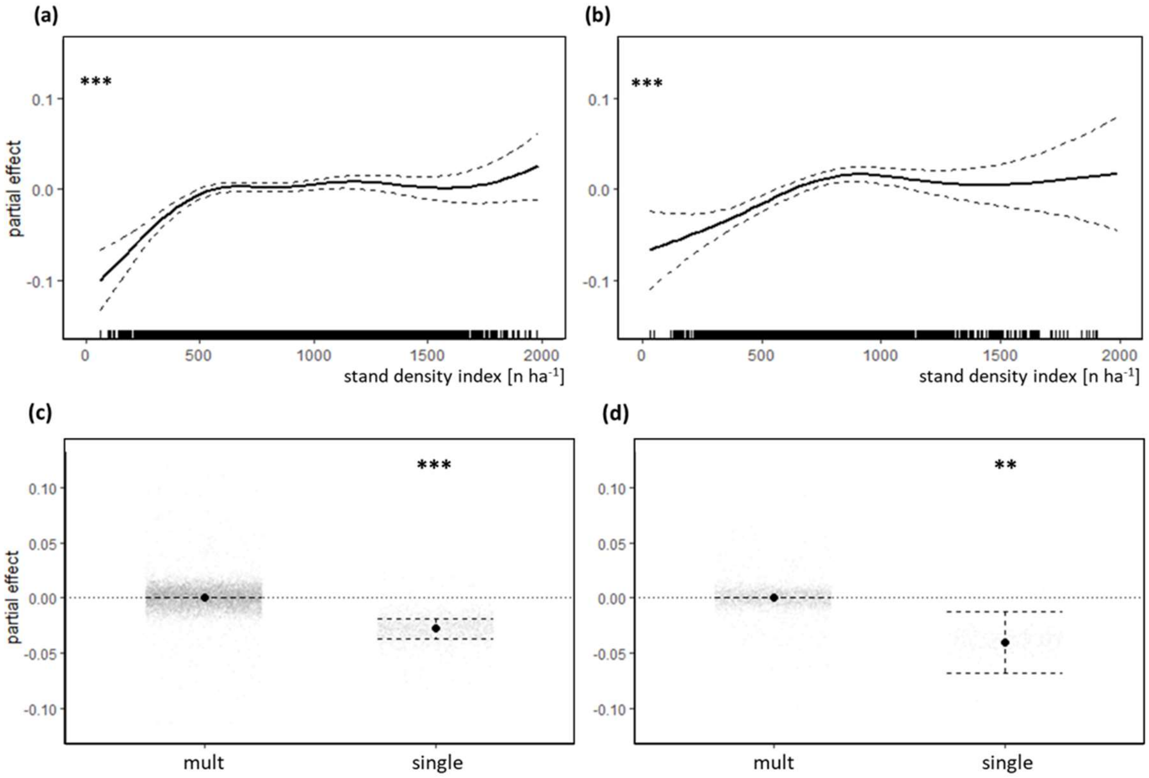

Figure 7: Partial effects of stand structure on oak height growth in mixture with beech (left) and pine (right), with stand density index (a, b) and vertical stand structure (c, d). Significance levels: p < 0.001 `***`; p < 0.01 `**` (Stimm et al. 2021c)

3.2 Long-term productivity (Article II)

The long-term positive growth trend was observed in monospecific and mixed oak stands. Stand volume and stand density had a positive effect, while stand age had a negative effect on stand productivity. 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 ha^{-1} $year^{-1}$ in monospecific and mixed stands, respectively.

Stand volume and site index showed positive effects on stand productivity. Thus, site conditions had a large effect on stand productivity that ranges on average across all stands from 5.8 m^3 ha^{-1} $year^{-1}$ on the less productive sites to 12.8 m^3 ha^{-1} $year^{-1}$ on the more productive sites. For age a positive effect on stand productivity was found for the interaction term with stand density. On average an additional understory increased total stand growth by 6%. However, in interaction with stand density, the effect on oak stand productivity was negative. At SDI values of around 300 trees per ha, the respective stand productivity dropped below the productivity of single layered stands (Figure 8b). 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.

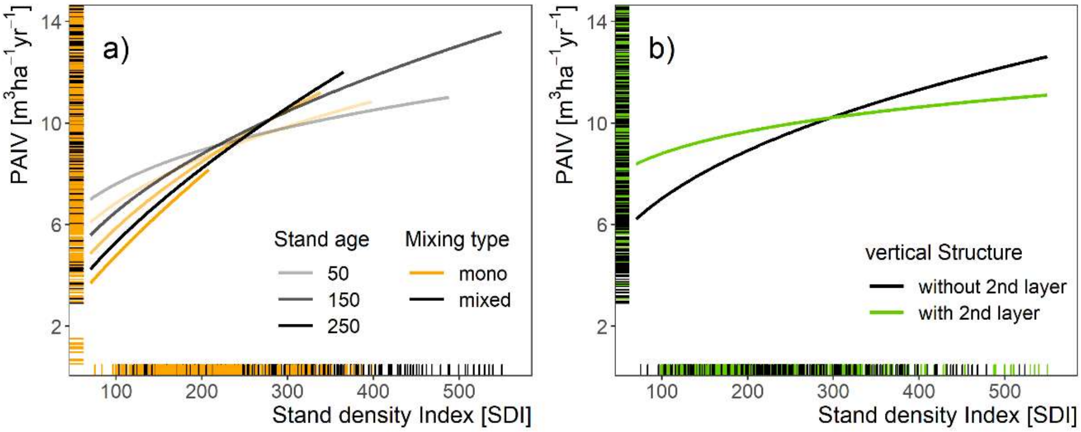

Figure 8: Stand productivity for monospecific and mixed oak stands as a function of stand density, stand age and mixing type (a) and as a function of stand density and vertical structure (b); rugs on the x-and y-axis indicate the observed values of SDI and stand productivity, respectively; all other variables were set to their mean. (Stimm et al. 2022a)

The obtained GAMM functions culminate 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 m^3 ha^{-1} $year^{-1}$ compared to the monospecific stands was observed.

Among the structural variables considered, individual social class had a strong positive effect on single tree productivity. The effect of age and stand density was additionally determined by 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 9). 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. 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. The coefficient of variation of tree height had a positive interaction effect with social class, that was particularly proved for the productivity of predominant and dominant oaks. Suppressed oaks could hardly benefit from high vertical stand structure, with scarcely detectable differences between high and low structured stands. The positive effect of the coefficient of variation of tree height decreased with age and stand density.

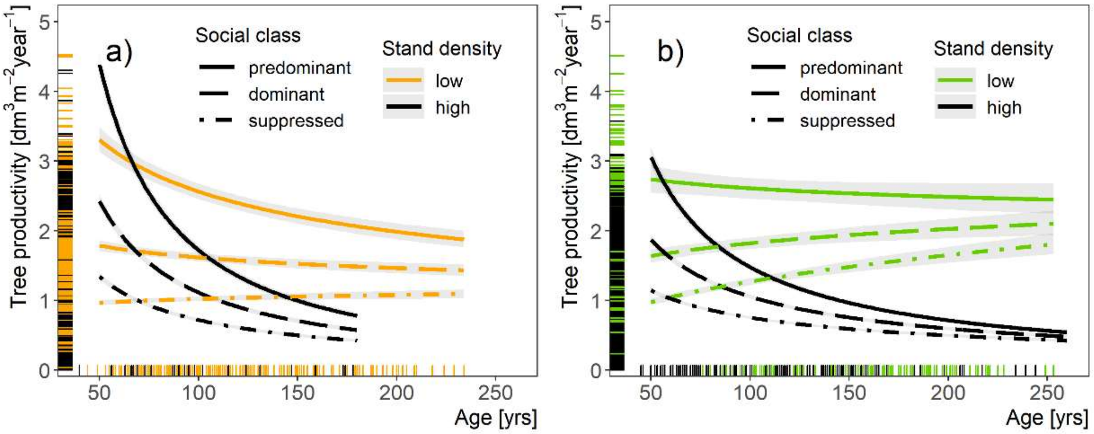

Figure 9: Productivity of oak trees growing in monospecific (a) and mixed species (b) stands as a function of Age, stand density and social class; low stand density = SDI of 100, high stand density = SDI of 350; rugs on the x-and y-axis indicate the observed values of age and tree productivity, respectively; all other variables were set to their mean. (Stimm et al. 2022a)

Overall, the distribution of growth over stand age was more balanced in the monospecific than in the mixed stands. However, growth partitioning of the investigated oak stands showed a dependence on age, stand density and mixture type. In general, the GDC reached lower values in the mixed stands and showed an increased age trend towards negative values. 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 was 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.

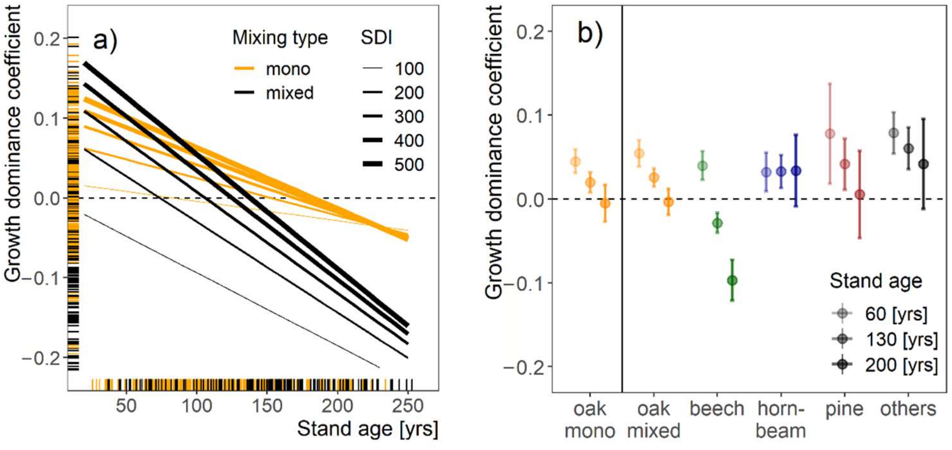

Figure 10: Growth dominance coefficient on stand level (a) in dependence of stand age and stand density for monospecific and mixed oak stands and the species-specific Growth dominance coefficient (b) for oak in monospecific and mixed stands, as well as beech, hornbeam pine and other tree species in dependence of the stand age; rugs on the x-and y-axis indicate the observed values of stand age and growth dominance coefficients, respectively. (Stimm et al. 2022a)

The GDC values of the tree species involved showed species-specific differences. 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 volume growth of the analyzed oaks corresponded increasingly to the individual tree size with increasing age. Here, the GDC values for oaks did not differ significantly for monospecific and mixed stands.

3.3 Long-term regeneration dynamics (Article III)

Regeneration period had a most significant forest site-specific negative effect on oak occurrence in the considered small-scale regenerated stands. However, in NUE, the oak presence was still high after 30 years. In contrast, for the mixed oak stands in EBR and BUS, the estimated decrease was much earlier and more pronounced.

Tree density decreased significantly with the duration of the regeneration period. The estimated trajectories were species-specific. With the exception of pine in NUE, the oak tree numbers decreased the most with age on all sites relative to all admixed tree species. In contrast, the density reduction was the lowest for beech in all investigated stands (Figure 11).

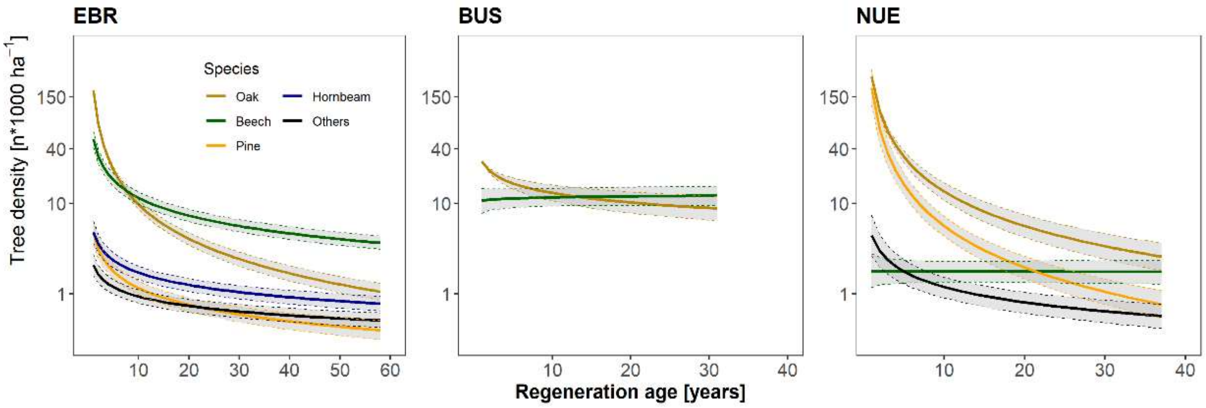

Figure 11: Estimated tree densities of the regenerated tree species; note the logarithmic scaling of the y-axis and the different scaling of the x-axes. (Stimm et al. 2022b)

Regenerated biomass was negatively affected by canopy cover. For the experimental site EBR and oak, beech, pine, and hornbeam, respectively, the effect was significant. In NUE, only oak biomass was significantly and negatively affected by canopy cover. However, in BUS, the effect was not significant for either oak or beech (Figure 12). Accordingly, oak biomass increased by 12.1 t ha^{-1}, 1.3 t ha^{-1}, and 7.3 t ha^{-1} in EBR, BUS, and NUE, respectively, at the age of 30 from non- to full-canopied stand situations.

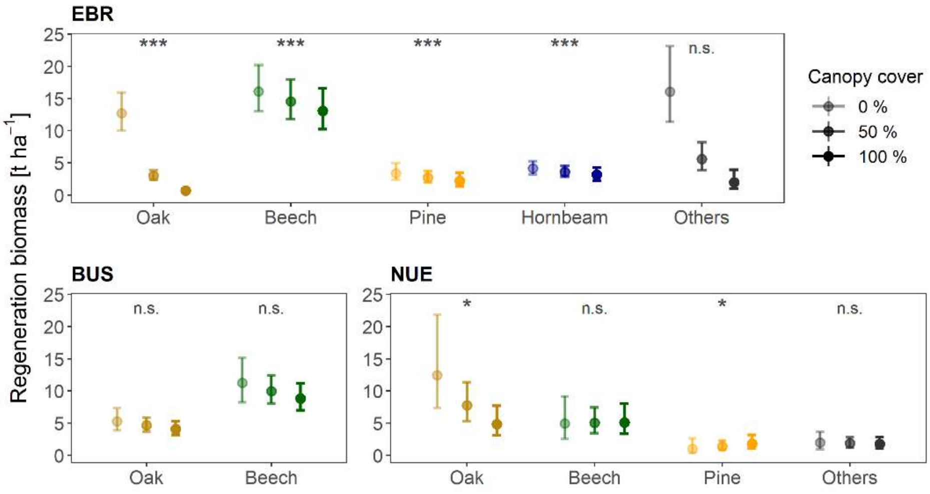

*Figure 12: Regenerated biomass of oak, beech, pine, hornbeam, and other broadleaf tree species as a function of canopy cover at the age of 30; asterisks denote the significance levels of the canopy cover effect, *** p < 0.001, * p < 0.05, n.s. not significant. (Stimm et al. 2022b)*

For the mixed stands in BUS and EBR, respectively, the effect of canopy cover on the maximum heights was evident and species-specific. The heights of the regenerated oaks were negatively affected by the canopy cover of all the investigated stands. However, in the monospecific pine stands, the effect was not significant. The strongest negative effect of the canopy cover could therefore be found for the mixed stands of EBR. There, a 50% canopy cover reduced oak heights by 33% compared to the non-canopied stand situations, which corresponds to an average reduction of 1.7 m at the regeneration age of 15 years. For BUS and NUE, regenerated oaks were 23% and 11% smaller, respectively. Consequently, the canopy cover had a stronger effect on the oak than on the beech regeneration at all the sites. Assuming a canopy cover of 50% indicates that beech trees outperform oak trees at a regeneration age of 15 years by 1.5 m and 1.4 m in the mixed oak stands in BUS and EBR, respectively. Even for the stand situations without a canopy cover, a certain advantage for beech is shown for both experimental sites.

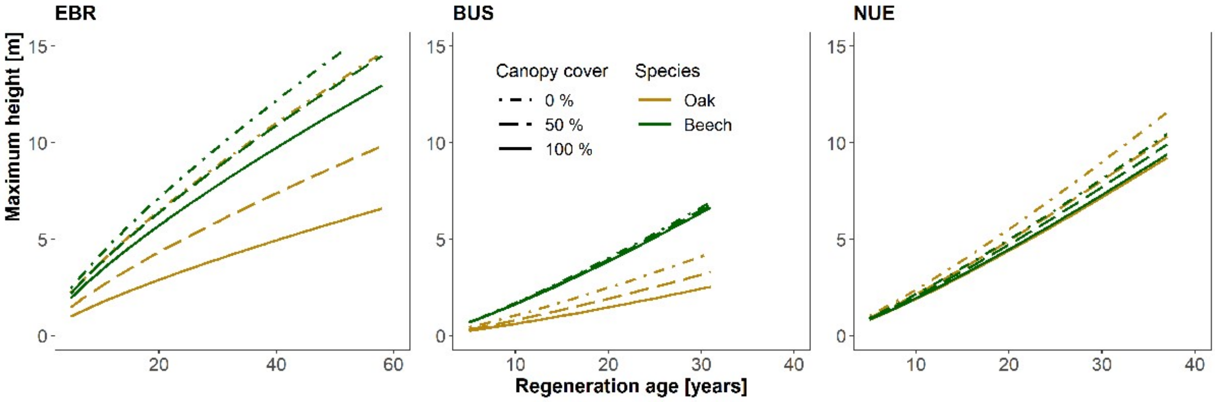

Figure 13: Estimated maximum heights of oak and beech regeneration as a function of regeneration age and canopy cover; shown are the height trajectories of oak and the most competitive beech species. Note the different scaling of the x-axes. (Stimm et al. 2022b)

In NUE, both tree species reached comparable heights, with a visible, but not significant, height advantage for oak. There, the characteristics of oak as a light-demanding tree species became more evident.

Maximum heights of the oak regeneration were additionally influenced by the interspecific competition, which was almost exclusively by the admixed beech. Increasing the beech admixture led to decreasing heights of the neighboring oaks. This effect was observed across all experimental sites.

4. Discussion

4.1 Height growth-related competitiveness (Article I)

Although the effect is not large, it is assumed that summer temperature is basically positive for oak height growth. These positive effects of temperature on oak tree growth corroborate the results of other studies, e.g. Bontemps et al. (2012), who found a significantly positive effect of temperature in the growing season by analyzing height growth trajectories of oak. Albert and Schmidt (2010) investigated the climate-sensitive site productivity and also described a positive effect of temperature. By modelling the site index, Brandl et al. (2018) found this effect on spruce and beech. Additionally, young oaks appeared also to react positively to higher temperatures (Bonfils et al. 2015). The observed positive linear effect of water balance on tree height growth correlates with several other studies dealing with the site productivity of various tree species (Albert and Schmidt 2012; Bonfils et al. 2015; Brandl et al. 2018; Zeller et al. 2018). Compared with the thresholds of water shortage risks described by Albert and Schmidt (2012), the water balance that was observed in the study, led to a moderate risk for all analyzed tree species, which explains the observed positive linear trend. Bonfils et al. (2015) found a reduced height growth in very dry site conditions for young oaks and assumed a shift in resource allocation in favour of increased root growth, which allowed oak to maintain its supply of water. The findings on the reaction of height growth of mature oaks as a function of the water balance seem to corroborate this assumption and may be an indication of better adaptability to drier site conditions during climate change. In addition, the positive temperature effect on oaks' height growth seems to be eclipsed by the negative partial effect due to lower water balance. Furthermore, areas with a negative water balance and higher temperatures were also the core region of insect pests on oak that could affect tree growth additionally (Zang et al. 2011; Fajvan et al. 2008; Rubtsov 1996). The nutrient supply, expressed through base saturation, hardly affected the height growth of oak, which assumes that water availability is more likely to be the limiting underground resource. Thus, the limiting factor for growth is the availability of water and light if sufficient nutrients are present (Forrester 2014, 2019). In essence, the potential height growth of oak will probably decrease in future due to the predicted changes in water balance.

A strong positive effect of stand density with a saturation effect beyond an SDI of 800 trees per hectare was found for monospecific stands. These results are in line with the density-height relationship described by Assmann (1970), which has also been corroborated more recently (Forrester 2019; Pretzsch 2019). This effect seems especially to be determined by the competition for light (Pretzsch and Biber 2010; Forrester 2014). Furthermore, for sessile oak, Trouvé et al. (2015) found a modifying influence of stand density on the growth allocation based on long-term experimental data. As light demanding species, oaks try to grow towards the light with increased height growth (Lüpke 1998). The partial effects of SDI on oaks growing in mixture underline the results for oaks in monospecific stands. In mixture with beech, the effect of stand density is noticeably strong. Furthermore, the visible flatter increase for oak-pine stands indicates the species-specific growth reaction and demonstrates the effect of competition for light on height growth. The interspecific competition in mixtures with beech seems to be more apparent than in mixtures with pine. In mixtures with pine, it can be assumed that oak received enough light to grow due to a higher light transmission of pine (del Río et al. 2014b; Jucker et al. 2014), and so does not require accelerated height growth. The vertical structure of stands and its effect upon oaks tree height varied between different mixture types. Mainly positive effects could be demonstrated in mixed stands. The understory seems to improve oak height growth slightly. This seems to be an additional positive interspecific effect that favours height growth and is not explained through the stand density of the main stand.

Oak showed a less climate-sensitive reaction in the two-species mixtures compared with monocultures. These findings seem to be caused by different growth allocation and complementarity effects between tree species. In mixture with beech the results are in line with previous studies analyzing the dominant height using French forest inventory data (Vallet and Perot 2016). At the same time, heights appear to be smaller in the mixture with pine. These results for both mixtures corroborate the results of former studies (Pretzsch et al. 2019a; Steckel et al. 2019). From a productivity standpoint, other studies found mixture effects due to the admixed species (Pretzsch et al. 2013b; Pretzsch et al. 2019b; Toïgo et al. 2015; Toïgo et al. 2018), even if the effect on productivity is not the same as on height growth. Consequently, the different growth allocation between stand types also effects stem taper and hence stem volume where the use of a species-specific function may be biased when ignoring these effects. Since stand structure can be influenced by forest management, the structural effect identified here provides valuable indications for forest practice on how to promote oak. Stand density regulation in particular seems to be a suitable management option to compensate for negative climatic effects. A delayed introduction of admixed species can reduce silvicultural investments while also ensuring the vitality of mixed species stands. This should also be considered when interpreting site-sensitive growth reactions that can be traced back to climatic factors.

Adaptive forest management favours stands composed of a mixture of several tree species (Lindner 2000; Lindner et al. 2010). In addition, the structure of the stands should be heterogeneous in order to increase resistance, resilience and recovery after damages caused by climate changes. In this context, oak is of special importance because it is considered to be thermophilic, drought-tolerant and wind stable (Annighöfer et al. 2015; Kölling and Zimmermann 2007). Contrary to these positive characteristics, it is competitively inferior to many tree species that grow with it in mixture (Ellenberg and Strutt 1988; Mosandl and Abt 2016). Height growth of a tree species is important for its competitiveness in terms of survival within the stands. The results show that the competitive power of oak, especially in mixture with beech, does not necessarily increase in large areas under climate change. Under current climatic conditions, oak is inferior in particular to beech, its strongest competitor, even in the warmest and driest areas. Felbermeier (1993) and Harrer (2004) analyzed the growth potential of beech in Bavaria and observed the tallest beeches in the centre of our study region. This indicates the high competitiveness of beech. A superior height growth of beech could be observed in the mixed stands under consideration in particular. It is assumed that beech seems to benefit additionally from oak in these stands due to species complementarity and facilitation, e.g. the hydraulic lift (Forrester 2014, 2019; Pretzsch et al. 2013b; Pretzsch et al. 2013a). Furthermore, improved height growth of mature beech trees after years with sufficient water availability (Mattes et al. 2013) can increase the species' superiority. Concurrent changes in temperature and precipitation regime nevertheless attest to an increase in the competitiveness and vitality of beech (Ammer et al. 2005). In contrast, oak has been found to be comparatively insensitive to climate (Pretzsch et al. 2013b; Pretzsch et al. 2019a; Steckel et al. 2020). Further studies dealing with the competitiveness of oak compared to other admixed species also show a promotion of oak under higher temperatures, especially compared to beech (Bontemps et al. 2012; Mette et al. 2013). The findings for beech and oak height growth trajectories are only partly in line with such assumptions. Shifts of height growth relations due to temperature and water regime were not in favour of oak when mixed with beech. This observation is attributed to the climatic amplitude of beech. Apparently, most of our study sites are close to the optimum for beech with regard to temperature and water balance. Mette et al. (2013) spoke of a summer temperature above 18 °C for a climatic turning point between beech and oak and Albert and Schmidt (2012) assigned an increased drought stress risk for beech as of a water deficit of -134 mm. On the basis of the results, a considerable shift in the competitive situation in favour of oak for warm and dry areas under current climatic conditions could not be identified. Nonetheless, a lower competitiveness of the admixed species, namely beech, is expected for future climatic conditions in view of a higher frequency of extreme climatic events under long-term climatic trends. This is likely to promote the interspecific competitiveness of oak.

4.2 Long-term productivity (Article II)

The present study corroborates the findings of several existing studies showing a positive tree and stand growth development in recent decades (Pretzsch et al. 2019b; Pretzsch et al. 2014b; Spiecker 1999; Bontemps et al. 2009; Pretzsch et al. 2014a). With this knowledge, this study explicitly examined trends for monospecific and mixed stands with oak, which extended the available research. No significant differences between monospecific 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 (Vannoppen et al. 2019). Regardless of the reasons for the accelerated growth, which should be associated with increased resource availability during the past century (Pretzsch et al. 2014b; Pretzsch et al. 2014a), this observation has a fundamental importance especially for silviculture with oak (Pretzsch et al. 2014a). 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 (Leroy et al. 2021; Fajvan et al. 2008). 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.

The observed positive effect of stand density is consistent with the basic relationships between density and productivity of forest stands (Forrester and Bauhus 2016; Pretzsch et al. 2019b), as well as the increased growth in oak-beech mixed stands already found (Pretzsch et al. 2013b). 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 (Pretzsch and Schütze 2016; Dieler and Pretzsch 2013). This temporal aspect of productivity of mixed stands is also mentioned by Ammer (2019) in a review on productivity and diversity relationships. Here, Zeller and Pretzsch (2019) 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. This positive age trend in structure-dependent stand productivity is attributed to the fact that complementarity effects emerge more effectively with increasing stand development and time for morphological and physiological acclimation (Zeller and Pretzsch 2019; Pretzsch 2014; Torresan et al. 2020). 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 (Forrester 2014).

The understorey and intermediate trees, in oak stands mostly required as serving secondary stands to produce high quality oaks (Attocchi 2015; Lüpke 1998), 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 overstorey. It is assumed that this in particular due to competition effects for both, under- and overstorey trees. First, the growth of the understorey was limited due to very low light availability and second, the overstorey productivity was slowed down due symmetric competition for underground resources (del Río et al. 2016).

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 (2020) 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 (Maleki et al. 2020; Hein and Dhôte 2006). These observations are due to the special ability of beech to exploit space and light conditions within the stand most efficiently (Pretzsch and Biber 2005). When mixed with oak, the more shade-tolerant beech seems to benefit especially from complementary light use and its considerable crown plasticity (Dieler and Pretzsch 2013). Furthermore, oak can additionally enhance the growth of beech in the mixed stand by acting as a hydraulic lift (Pretzsch et al. 2013b; Zapater et al. 2011). 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.

The decreasing productivity of the investigated oaks with increasing age follows the characteristic growth habit of individual trees (Pretzsch 2019). The small decrease in productivity at high ages (> 200 years) is striking. This finding of long-lasting growth performance corroborates the results found in a recent study by Pretzsch (2020) 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. (2015) and del Río et al. (2014a) for oaks mixed with beech.

The lower productivity of individual oak in mixed stands seems to be due to the high competitive power 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 (Manso et al. 2015; Hein and Dhôte 2006; del Río et al. 2014a; Vanhellemont et al. 2018). Nevertheless, the net effect of beech admixture on stand productivity in mixed oak 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. (2014a) for oak-beech mixed stands in Spain.

The decreasing and converging productivity curves (see figure 9) of oak trees in 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 (Pretzsch and Biber 2005; Pretzsch 2014; Vanhellemont et al. 2018).

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 (Pretzsch et al. 2013b; Manso et al. 2015; Vannoppen et al. 2019; Groote et al. 2018). Sometimes, increased shade tolerance of the mixed tree species also has a negative effect on the oak mixing response (Toïgo et al. 2018).

The overall lower growth dominance coefficients in mixed stands show that the growth performance of smaller trees is increased compared to monospecific stands. Beech in particular contributes to the observed reverse growth dominance (Figure 10b). This can be partly explained due to niche complementarity of the tree species involved, which is particularly evident between species of different ecological characteristics (Pretzsch and Biber 2016; Pothier 2017). 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 (Pretzsch et al. 2013b). This is especially true when oak trees are in the upper canopy layer. Observed growth dominance and its tree species-specific age trend seemed to emerge to some extent from this niche complementary effects. As a result, the admixed beech trees gain 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 (Binkley 2004; Binkley et al. 2006; Baret et al. 2017). 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.

At young stand development phases positive GDC values were observed in both, monospecific and mixed stands (see Figure 10a). 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 (Pothier 2017). The temporal decline in GDC is more pronounced in high dense stands. 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 (Fernández-Tschieder and Binkley 2018). 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.

4.3 Long-term regeneration dynamics (Article III)

A recent literature review (Kohler et al. 2020) concluded that oak regeneration is in principle possible even in small areas, but at the same time, it noted that the underlying data for this conclusion are still very limited, especially when the long-term developments of oak regeneration are considered. With the present study, the regeneration data covering a period beyond 15 years and reaching up to 36 years could be used. To our knowledge, the present study is the only study of oak regeneration that covers an observation period of more than 25 years. Furthermore, full surveys of stand regeneration in experimental stands of up to 1.0 ha in size are very rare. Here, a unique dataset encompassing half a million single data of regenerated trees could be used. In connection with the information available for the mature trees, the data cover a wide range of regeneration situations, i.e., gap sizes, species mixture, and canopy cover characteristics, as well as site conditions.

The results showed that close-to-nature silviculture with long-term (>25 years) and small-scale (0.01–0.25 ha) regeneration methods can be one option for the regeneration of oak. However, the range of regeneration development within the stands and between sites was wide, ranging from the total loss of oak to an increase in oak proportions over the entire regeneration period. High percentages of oak in the regeneration at the beginning of the regeneration period favor the success of oak regeneration, but do not necessarily lead to a corresponding percentage of oak at the beginning of the stem exclusion stage. The conclusions drawn from previous studies, namely that oak regeneration can succeed even with small-scale regeneration methods (Březina and Dobrovolný 2011; Kohler et al. 2020; Kuehne et al. 2020), could be corroborated for the long run by the present results. However, it was also revealed that at certain sites, beech is able to become dominant or even outcompete oak sooner or later (Lüpke 1998; Ligot et al. 2013; Dietz et al. 2022; Petritan et al. 2017).

This insight was also evident when considering the survival rates of oak. Accordingly, the participation of oak in a mixture with beech was not stable throughout the regeneration period and confirmed the results of some studies (Lüpke 1998; Mölder et al. 2019b; Kuehne et al. 2020; Manso et al. 2020), which can also be found in the early silvicultural principles for oak management (Fleder 1983; Vanselow 1960). Differences between experimental sites and forest stand types were clearly recognizable and should be considered in precommercial thinnings. Small-scale and long-term regeneration methods are especially promising in low-growth sites and/or monospecific pine stands. The competitive ability of oaks seemed to benefit from the higher light availability under more light-transmitting pine canopies. Lower site quality additionally reduced beech growth. The observed survival probabilities of 30% and more after 20 years of regeneration initialization also showed the remarkable potential of young oaks when small-scale regeneration methods were applied.

The observed regeneration biomass showed an enormous growth potential. Even the apparently low-growing sites in NUE showed a considerable growth potential of oak and reached maximum biomass values that were similar to those of the more vigorous sites in EBR (see Figure 12). However, without appropriate silvicultural interferences in the main stand and pre-commercial thinnings in the advanced regeneration in favor of oak, this potential remained unused. Uniformly high or increasing stand volume in the main stand counteracted this. This was also true for the development of the appreciable oak proportions.

Sessile oak reacted more strongly to the canopy cover reduction than beech at all the sites. Thus, the results match those of several studies that observed a similar trend (Modrow et al. 2019; Lüpke 1998, 2008). Interestingly, beech was still superior to oak irrespective of the canopy cover in the considered mixed stands in EBR and BUS. This observation suggested that successful oak regeneration in the mixed regenerations was apparently not possible by controlling the canopy cover alone. A similar conclusion was drawn by Modrow et al. (2019), who recommended controlling mixed tree species regardless of the regeneration gap size. At the same time, this resulted in the greatest scope for promoting oak in EBR, which may indicate that competition for light rather than soil-based resources was occurring at this site, whereas in BUS the nutrients seemed limiting. In NUE, the effect of canopy cover reduction was the lowest, which suggests that water and nutrients may be the limiting factors. Furthermore, NUE was the only experimental site where oak appeared to be superior to beech in height growth. These height relations indicated that oak's superiority compared to beech was strongly dependent on monospecific pine stands with sparse site conditions. However, it are precisely these stands that should be urgently adapted to the rapidly changing climate (Leuschner et al. 2022). Accordingly, oak requires the support of the silvicultural regulation of woody competitors for successful establishment in many sites (Lüpke 1998; Manso et al. 2020; Mölder et al. 2017).

The revealed competition of beech with the height development of oak regeneration deepens the conclusions drawn from studies considering shorter regeneration periods, which suggest a reduction in competition in favor of oak (Modrow et al. 2019; Kohler et al. 2020). For example, Hauskeller-Bullerjahn (1997) found that height growth in oak was reduced by 24% on average by competition and 30% of full light. The competition exerted by the admixture of beech was, in addition to the control of canopy cover, the most important factor for the successful establishment of oak in the considered stands. The observed competition effect by beech seemed to be influenced, on the one hand, by higher light availability and thus less by the influence of canopy cover (Skrzyszewski and Pach 2015) and, on the other hand, by increased root competition (Leuschner et al. 2001) due to lower nutrient and water availability.

Accordingly, high oak percentages at the beginning of the regeneration period and correspondingly lower beech competition showed positive effects on the development of oak regeneration. The increase in beech proportions in the regeneration resulted in a decrease in the positive competition relation of oak towards beech. This appeared to be due to the interspecific competitive pressure of beech on oak (Annighöfer et al. 2015). Therefore, the relations between oak and the admixed (competitor) species should be given special attention when creating the mixture. This is important for the success of the specific species mixture and the appropriate maintenance efforts, taking into account the natural development.

Due to the long-term regeneration periods, with regeneration ages reaching 58 years, regeneration biomasses up to more than 100 t ha^{-1} could be observed in the investigated stands. At the same time, the remaining main stand continued to produce wood increments throughout the entire regeneration period. This is particularly important for deciding on the silvicultural approach. The effect of regeneration biomass on the productivity of the main stand was not significant. However, a negative trend was visible. Accordingly, as biomass increased old-growth productivity decreased. In particular, this appeared to be due to increased belowground competition for resources between old growth and regeneration (Pretzsch et al. 2015; Knapp 1991). This conclusion is further supported by the observation that the effect was more pronounced with higher standing volumes. Conversely, this also meant that high regeneration biomasses could partially compensate for the resulting increment losses, due to the volume reduction by the harvesting of mature trees.

However, it would require further studies to assess the effect of regeneration on the overstorey conclusively. Particularly for the management of multi-layered stands, the consideration of the feedback of advanced regeneration on the remaining stand seems to be highly relevant.

4.4 Management objectives and overarching discussion

The objective of many silvicultural practices in Central Europe is to adapt forests to the rapidly changing climate (Bolte et al. 2009; Lindner et al. 2010; Puettmann and Messier 2019). Therefore, favouring oak as drought-tolerant and thermophilic species should be encouraged to improve the adaptation capacity of European mixed forests (Albert et al. 2017; Pretzsch et al. 2013b). Furthermore, societal needs regarding ecosystem services (e.g. biodiversity, recreation) are important in determining the course of forest management. Consequently, multifunctional oriented silviculture is also becoming increasingly relevant for the management of oak high forests (Löf et al. 2016; Stimm et al. 2021a; Weaver and Spiecker 1993).

In general, structured and mixed stands seem to meet the demands of the above mentioned underlying trends most effectively. However, the findings of all three studies (Articles I – III) suggest that on most sites the participation of oak in mixed stands is not stable throughout the rotation period, which is especially true when mixed with beech. It therefore appears that silvicultural assistance is needed for a successful establishment and continuity of appropriate oak proportions in mixed stands. Decreasing oak proportions and missing oak regeneration in unmanaged strict forest reserves prove this trend (Rohner et al. 2012; Stimm et al. 2021b). Conversely, traditional oak management principles rely on large-scale regeneration methods and long rotation periods to produce high valuable timber (Attocchi 2015; Fleder 1983; Vanselow 1960). While timber production per se remains the primary objective in many other Central European countries, the production of high valuable timber seems to be of minor importance (Stimm et al. 2021a).

Consequently, by adapting the silvicultural objective of oak high forests, it is also possible to extend the options for silvicultural interferences. In this regard, the results of a questionnaire conducted across 18 European countries certainly suggest large and untapped potentials in oak management. In particular, multifunctional oak silviculture appears to allow for greater flexibility, as management principles focused on timber production also appear to be mostly associated with large-scale regeneration methods (Stimm et al. 2021a).

Nevertheless, multifunctional oriented silviculture require a strong integration of ecological parameters such as site conditions, competing vegetation, and secondary tree species. Similarly, more detailed knowledge of these will be necessitated by the need to adapt forests to climate change. The thesis addresses these aspects in the individual studies (Article I – III) by examining the growth potential of oak over stand development (Figure 1).

5. Conclusion and perspectives

This thesis investigates the growth potential of oak at individual tree and stand level, considering monospecific and mixed oak stands. The evaluations are based on data from large-scale forest inventories, long-term experiments and strict forest reserves and cover a broad gradient of site conditions and stand structures. In combination with the consideration of several development phases, comprehensive silvicultural conclusions are possible.

Based on the results of this thesis, the climate sensitivity of oak trees can be lowered in mixed stands, which additionally reduce the biotic and abiotic risks. However, when considering the observed height growth reaction of oak, a fundamental change in competitive ability is apparently not to be expected. To be prepared for further climatic changes it therefore appears that further silvicultural support is needed for a successful establishment and continuity of appropriate oak proportions in mixed stands. Nevertheless, a negative reaction of beech to sharply rising temperatures and especially more frequent extreme drought periods is expected, that is also be accompanied by an improved competitiveness of oak.

For this, it is important to evaluate existing oak management concepts about their further suitability and, if necessary, adapt them. In this context, especially 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. However, to reduce growth suppression or mortality of individual oaks due to competition, a various temporal or spatial arrangement of the understory is suggested. This enables the coexistence of the species and allows the positive complementary effects to be kept while the negative competitive effects are considerably reduced. Furthermore, the findings on productivity on tree and stand level suggest, that long rotation periods, as they emerged from experiences in the middle of the 20th century, can be shortened considerably in future silvicultural guidelines.

In the overstorey, the productivity can be additionally increased by the participation of mixed tree species, due to higher maximum stand densities in mixed species stands compared to monospecific stands. As compared to traditional silvicultural guidelines, this may provide additional flexibility for management options in mixed stands. 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. However, this is also associated with high competitive strength, which can reduce the vigor of individual oaks. Reducing stand density in mixed stands at an early stage effectively reduces interspecific competition and promote the productivity of individual oaks.

The chosen regeneration method is not a static system but should change with the site and stand conditions as well as with the corresponding operational objective. The single tree and group selection systems considered in this study are one option for the establishment of oak while maintaining a balanced forest interior climate at the same time. For this to succeed, it is recommended that the standing volume of mature stands, including the serving tree layers in the area to be regenerated, should be consistently reduced. In this case, gap size or the area to be regenerated may be 0.1 ha. Depending on site conditions, the remaining stand volume should optimally be less than 250 m^3 ha^{-1} in mixed beech–oak stands and 300 m^3 ha^{-1} in monospecific pine stands, respectively. If mixed tree species are present, increased management in favor of oak must be calculated since regulation of the old stand alone is not sufficient. Mixed tree species proportions, especially those of beech, that exceed 30% significantly impair oak in early regeneration until the stem exclusion stage. Oak regeneration can be successfully practiced in small patches, assuming that the silvicultural goal is oak and that the thinnings are focused on assisting oak. The outlined results therefore show a way to maintain or establish oak in the tree species portfolio as well as the small-scale regeneration methods in the long-term.

In essence, silvicultural management is still crucial for building up and maintaining a sufficient oak proportion and foster vital, vigorous and healthy oaks within mixed stands. The silvicultural assistance mentioned here is most urgently needed on those sites where oak is grown outside its real ecological niche. Against the backdrop of rapidly advancing climate change, preparing European forests by creating mixed and structured stands is the order of the day. In particular, mixed stands with oak participation can make an important contribution to more resilient stands in the future.

6. References

Albert, Matthias; Nagel, Ralf-Volker; Nuske, Robert; Sutmöller, Johannes; Spellmann, Hermann (2017): Tree Species Selection in the Face of Drought Risk—Uncertainty in Forest Planning. In *Forests* 8 (10), p. 363. DOI: 10.3390/f8100363.

Albert, Matthias; Schmidt, Matthias (2010): Climate-sensitive modelling of site-productivity relationships for Norway spruce (Picea abies (L.) Karst.) and common beech (Fagus sylvatica L.). In *Forest Ecology and Management* 259 (4), pp. 739–749. DOI: 10.1016/j.foreco.2009.04.039.

Albert, Matthias; Schmidt, Matthias (2012): Standort-Leistungs-Modelle für die Entwicklung von waldbaulichen Anpassungsstrategien unter Klimawandel. In *Archiv f. Forstwesen u. Landsch.ökol.* 46 (2), pp. 57–71.

Ammer, Christian (2019): Diversity and forest productivity in a changing climate. In *The New phytologist* 221 (1), pp. 50–66. DOI: 10.1111/nph.15263.

Ammer, Christian; Albrecht, Ludwig; Borchert, Herbert; Brosinger, Franz; Dittmar, Ch.; Elling, W. et al. (2005): Zur Zukunft der Buche (Fagus sylvatica L.) in Mitteleuropa. Kritische Anmerkungen zu einem Beitrag von Rennenberg et al. (2004). In *Allgemeine Forst-und Jagdzeitung* 176 (4), pp. 60–67, checked on 11/7/2018.

Annighöfer, Peter; Beckschäfer, Philip; Vor, Torsten; Ammer, Christian (2015): Regeneration patterns of European oak species (Quercus petraea (Matt.) Liebl., Quercus robur L.) in dependence of environment and neighborhood. In *PLOS ONE* 10 (8), e0134935. DOI: 10.1371/journal.pone.0134935.

Assmann, Ernst (1970): The principles of Forest Yield Study. Studies in the Organic Production, Structure, Increment and Yield of Forest Stands. Oxford, New York, Toronto, Sydney, Braunschweig: Pergamon Press.

Attocchi, Giulia (2015): Silviculture of oak for high-quality wood production. Effects of thinning on crown size, volume growth and stem quality in even-aged stands of pedunculate oak (Quercus robur L.) in Northern Europe. Alnarp: Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (Acta Universitatis agriculturae Sueciae, 2015:39).

Baret, Matthieu; Pepin, Steeve; Ward, Charles; Pothier, David (2017): Long-term changes in stand growth dominance as related to resource acquisition and utilization in the boreal forest. In *Forest Ecology and Management* 400, pp. 408–416. DOI: 10.1016/j.foreco.2017.06.026.

Bates, Douglas; Mächler, Martin; Bolker, Ben; Walker, Steve (2015): Fitting Linear Mixed-Effects Models Using lme4. In *J. Stat. Soft.* 67 (1). DOI: 10.18637/jss.v067.i01.

Bauhus, Jürgen; Forrester, David I.; Pretzsch, Hans (2017): From Observations to Evidence About Effects of Mixed-Species Stands. In Hans Pretzsch, David I. Forrester, Jürgen Bauhus (Eds.): Mixed-Species Forests: Ecology and Management. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 27–71.

Bayerische Staatsforsten AöR (2020): Waldbauhandbuch Bayersiche Staatsforsten. Richtlinie zur Baumartenwahl.

Bayerisches Staatsministerium für Ernährung, Landwirtschaft und Forsten (2020): Baumarten für den Klimawald; Leitlinien der Bayerischen Forstverwaltung.

Beinhofer, Bernhard (2010): Comparing the financial performance of traditionally managed beech and oak stands with roomy established and pruned stands. In *Eur J Forest Res* 129 (2), pp. 175–187. DOI: 10.1007/s10342-009-0311-5.

Binkley, Dan (2004): A hypothesis about the interaction of tree dominance and stand production through stand development. In *Forest Ecology and Management* 190 (2-3), pp. 265–271. DOI: 10.1016/j.foreco.2003.10.018.

Binkley, Dan; Kashian, Daniel M.; Boyden, Suzanne; Kaye, Margot W.; Bradford, John B.; Arthur, Mary A. et al. (2006): Patterns of growth dominance in forests of the Rocky Mountains, USA. In *Forest Ecology and Management* 236 (2-3), pp. 193–201. DOI: 10.1016/j.foreco.2006.09.001.

Bolte, Andreas; Ammer, Christian; Löf, Magnus; Madsen, Palle; Nabuurs, Gert-Jan; Schall, Peter et al. (2009): Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. In *Scandinavian Journal of Forest Research* 24 (6), pp. 473–482. DOI: 10.1080/02827580903418224.

Bonfils, Patrick; Rigling, Andreas; Brändli, Urs-Beat; Brang, Peter; Forster, Beat; Engesser, Roland et al. (2015): Die Eiche im Klimawandel. Zukunftschancen einer Baumart. In *Merkblatt für die Praxis* 55.

Bontemps, Jean-Daniel; Herve, Jean-Christophe; Duplat, Pierre; Dhôte, Jean-François (2012): Shifts in the height-related competitiveness of tree species following recent climate warming and implications for tree community composition. The case of common beech and sessile oak as predominant broadleaved species in Europe. In *Oikos* 121 (8), pp. 1287–1299. DOI: 10.1111/j.1600-0706.2011.20080.x.

Bontemps, Jean-Daniel; Hervé, Jean-Christophe; Dhôte, Jean-François (2009): Long-Term Changes in Forest Productivity: A Consistent Assessment in Even-Aged Stands. In *for sci* 55 (6), pp. 549–564. DOI: 10.1093/forestscience/55.6.549.

Brandl, Susanne; Falk, Wolfgang; Klemmt, Hans-Joachim; Stricker, Georg; Bender, Andreas; Rötzer, Thomas; Pretzsch, Hans (2014): Possibilities and Limitations of Spatially Explicit Site Index Modelling for Spruce Based on National Forest Inventory Data and Digital Maps of Soil and Climate in Bavaria (SE Germany). In *Forests* 5 (11), pp. 2626–2646. DOI: 10.3390/f5112626.

Brandl, Susanne; Mette, Tobias; Falk, Wolfgang; Vallet, Patrick; Rötzer, Thomas; Pretzsch, Hans (2018): Static site indices from different national forest inventories. Harmonization and prediction from site conditions. In *Annals of Forest Science* 75 (2), p. 739. DOI: 10.1007/s13595-018-0737-3.

Brang, P.; Spathelf, P.; Larsen, J. B.; Bauhus, J.; Boncina, A.; Chauvin, C. et al. (2014): Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. In *Forestry* 87 (4), pp. 492–503. DOI: 10.1093/forestry/cpu018.

Březina, I.; Dobrovolný, L. (2011): Natural regeneration of sessile oak under different light conditions. In *JOURNAL OF FOREST SCIENCE* 57, pp. 359–368.

Brockerhoff, Eckehard G.; Barbaro, Luc; Castagneyrol, Bastien; Forrester, David I.; Gardiner, Barry; González-Olabarria, José Ramón et al. (2017): Forest biodiversity, ecosystem functioning and the provision of ecosystem services. In *Biodivers Conserv* 26 (13), pp. 3005–3035. DOI: 10.1007/s10531-017-1453-2.

Brunner, Andreas; Forrester, David I. (2020): Tree species mixture effects on stem growth vary with stand density – An analysis based on individual tree responses. In *Forest Ecology and Management* 473, p. 118334. DOI: 10.1016/j.foreco.2020.118334.

Burschel, Peter; Huss, Jürgen (1997): Grundriß des Waldbaus. Ein Leitfaden für Studium und Praxis. 2., neubearb. und erw. Aufl. Berlin: Parey (Pareys Studientexte, 49).

Condés, Sonia; Del Rio, Miren; Sterba, Hubert (2013): Mixing effect on volume growth of Fagus sylvatica and Pinus sylvestris is modulated by stand density. In *Forest Ecology and Management* 292, pp. 86–95. DOI: 10.1016/j.foreco.2012.12.013.

del Río, M.; Schütze, G.; Pretzsch, H. (2014a): Temporal variation of competition and facilitation in mixed species forests in Central Europe. In *Plant Biology* 16 (1), pp. 166–176. Available online at http://onlinelibrary.wiley.com/doi/10.1111/plb.12029/full.

del Río, Miren; Condés, Sonia; Pretzsch, Hans (2014b): Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (Fagus sylvatica L.) mixed stands. In *Forest Ecology and Management* 325, pp. 90–98. DOI: 10.1016/j.foreco.2014.03.047.

del Río, Miren; Pretzsch, Hans; Alberdi, Iciar; Bielak, Kamil; Bravo, Felipe; Brunner, Andreas et al. (2016): Characterization of the structure, dynamics, and productivity of mixed-species stands. Review and perspectives. In *Eur J Forest Res* 135 (1), pp. 23–49. DOI: 10.1007/s10342-015-0927-6.

del Río, Miren; Sterba, Hubert (2009): Comparing volume growth in pure and mixed stands of Pinus sylvestris and Quercus pyrenaica. In *Ann. For. Sci.* 66 (5), p. 502. DOI: 10.1051/forest/2009035.

Dieler, Jochen; Pretzsch, Hans (2013): Morphological plasticity of European beech (Fagus sylvatica L.) in pure and mixed-species stands. In *Forest Ecology and Management* 295, pp. 97–108. DOI: 10.1016/j.foreco.2012.12.049.

Dietz, Lucie; Gégout, Jean-Claude; Dupouey, Jean-Luc; Lacombe, Eric; Laurent, Lisa; Collet, Catherine (2022): Beech and hornbeam dominate oak 20 years after the creation of storm-induced gaps. In *Forest Ecology and Management* 503, p. 119758. DOI: 10.1016/j.foreco.2021.119758.

Dolos, Klara; Mette, Tobias; Wellstein, Camilla (2016): Silvicultural climatic turning point for European beech and sessile oak in Western Europe derived from national forest inventories. In *Forest Ecology and Management* 373, pp. 128–137. DOI: 10.1016/j.foreco.2016.04.018.

Ellenberg, H. H.; Strutt, G. K. (1988): Vegetation Ecology of Central Europe: Cambridge University Press. Available online at https://books.google.de/books?id=LQNxbuyPxawC.

Fajvan, Mary Ann; Rentch, Jim; Gottschalk, Kurt (2008): The effects of thinning and gypsy moth defoliation on wood volume growth in oaks. In *Trees* 22 (2), pp. 257–268. DOI: 10.1007/s00468-007-0183-6.

Felbermeier, Bernd (1993): Der Einfluß von Klimaänderungen auf die Areale von Baumarten. Methodenstudie und regionale Abschätzung für die Rotbuche (Fagus sylvatica L.) in Bayern. In *Forstlicher Forschungsbericht*.

Fernández-Tschieder, Ezequiel; Binkley, Dan (2018): Linking competition with Growth Dominance and production ecology. In *Forest Ecology and Management* 414, pp. 99–107. DOI: 10.1016/j.foreco.2018.01.052.

Field, Elsa; Castagneyrol, Bastien; Gibbs, Melanie; Jactel, Hervé; Barsoum, Nadia; Schönrogge, Karsten; Hector, Andrew (2020): Associational resistance to both insect and pathogen damage in mixed forests is modulated by tree neighbour identity and drought. In *J Ecol* 108 (4), pp. 1511–1522. DOI: 10.1111/1365-2745.13397.

Fischer, Hagen S.; Michler, Barbara; Fischer, Anton (2018): Die zukünftige pnV Bayerns. Wie man sich Vorstellungen über die Standortsituation der Zukunft erarbeiten kann. In *LWF Aktuell* (4), pp. 46–49.

Fleder, W. (1983): Vom unterfränkischen Verjüngungsbetrieb. In *Allgemeine Forstzeitschrift* 38, pp. 1013–1014.

Forrester, David I. (2014): The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. In *Forest Ecology and Management* 312, pp. 282–292. DOI: 10.1016/j.foreco.2013.10.003.

Forrester, David I. (2019): Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. In *Forest Ecology and Management* 447, pp. 139–157. DOI: 10.1016/j.foreco.2019.05.053.

Forrester, David I.; Bauhus, Jürgen (2016): A Review of Processes Behind Diversity—Productivity Relationships in Forests. In *Curr Forestry Rep* 2 (1), pp. 45–61. DOI: 10.1007/s40725-016-0031-2.

Forrester, David I.; Pretzsch, Hans (2015): Tamm Review: On the strength of evidence when comparing ecosystem functions of mixtures with monocultures. In *Forest Ecology and Management* 356, pp. 41–53. DOI: 10.1016/j.foreco.2015.08.016.

Forrester, David I.; Tachauer, I.H.H.; Annighoefer, Peter; Barbeito, Ignacio; Pretzsch, Hans; Ruiz-Peinado, Ricardo et al. (2017): Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. In *Forest Ecology and Management* 396, pp. 160–175. DOI: 10.1016/j.foreco.2017.04.011.

Groote, Stefanie R.E. de; Vanhellemont, Margot; Baeten, Lander; van den Bulcke, Jan; Martel, An; Bonte, Dries et al. (2018): Competition, tree age and size drive the productivity of mixed forests of pedunculate oak, beech and red oak. In *Forest Ecology and Management* 430, pp. 609–617. DOI: 10.1016/j.foreco.2018.08.050.

Harrer, E. (2004): Wachstumstrends der Buche in Bayern. Untersuchungen zur Auswirkung der Bestandesbehandlung auf das Wachstum der Buche. unpublished final report.

Hauskeller-Bullerjahn, Karen (1997): Wachstum junger Eichen unter Schirm. Dissertation. Universität, Göttingen.

Hein, Sebastian; Dhôte, Jean-François (2006): Effect of species composition, stand density and site index on the basal area increment of oak trees (***Quercus*** sp.) in mixed stands with beech (***Fagus sylvatica*** L.) in northern France. In *Annals of Forest Science* 63 (5), pp. 457–467. DOI: 10.1051/forest:2006026.

Jacob, D.; Goettel, H.; Kotlarski, S.; Lorenz, P.; Sieck, K. (2008): Klimaauswirkungen und Anpassung in Deutschland - Phase 1: Erstellung regionaler Klimaszenarien für Deutschland. In *Fachbibliothek Umwelt*.

Jedicke, Eckhard; Hakes, Wilfried (2005): Management von Eichenwäldern im Rahmen der FFH-Richtlinie. In *Naturschutz und Landschaftsplanung* 37 (2), pp. 37–45.

Johann, K. (1993): DESER-Norm 1993. Normen der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten zur Aufbereitung von waldwirtschaftlichen Dauerversuchen. In *Berichte der Jahrestagung des Deutschen Verbandes Forstlicher Sektion Ertragskunde*, pp. 96–104.

Jucker, Tommaso; Bouriaud, Olivier; Avacaritei, Daniel; Dănilă, Iulian; Duduman, Gabriel; Valladares, Fernando; Coomes, David A. (2014): Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. In *J Ecol* 102 (5), pp. 1202–1213. DOI: 10.1111/1365-2745.12276.

Jüttner, O. (1955): Eichenertragstafeln. In Schober (Ed.): Ertragstafeln der wichtigsten Baumarten. Frankfurt a. Main: (1971) JD Sauerländer´s Verlag, 12-25, 134-138.

Kanjevac, Branko; Krstić, Milun; Babić, Violeta; Govedar, Zoran (2021): Regeneration Dynamics and Development of Seedlings in Sessile Oak Forests in Relation to the Light Availability and Competing Vegetation. In *Forests* 12 (4), p. 384. DOI: 10.3390/f12040384.

Kenk, G. K. (1993): New perspectives in German oak silviculture. In *Ann. For. Sci.* 50 (6), pp. 563–570. DOI: 10.1051/forest:19930605.

Knapp, E. (1991): Zur Wuchsleistung der Unterbaubuche im ungleichaltrigen Kiefern-Buchen-Mischbestand vor und nach ihrer Übernahme als Hauptbestand auf …

Kohler, Martin; Pyttel, Patrick; Kuehne, Christian; Modrow, Tobias; Bauhus, Jürgen (2020): On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests—a literature review. In *Annals of Forest Science* 77 (4). DOI: 10.1007/s13595-020-00998-2.

Kölling, Christian; Zimmermann, Lothar (2007): Die Anfälligkeit der Wälder Deutschlands gegenüber dem Klimawandel. In *Gefahrstoffe-Reinhaltung der Luft* 67 (6), pp. 259–268.

Krahl-Urban, J. (1959): Die Eichen: forstliche Monographie der Traubeneiche und der Stieleiche: P. Parey. Available online at https://books.google.de/books?id=54ROAAAAMAAJ.

Kramer, Horst; Akça, Alparslan (1995): Leitfaden zur Waldmesslehre. 3 rd Edition. Frankfurt am Main: Sauerländer.

Kuehne, Christian; Pyttel, Patrick; Modrow, Tobias; Kohnle, Ulrich; Bauhus, Jürgen (2020): Seedling development and regeneration success after 10 years following group selection harvesting in a sessile oak (*Quercus petraea* [Mattuschka] Liebl.) stand. In *Annals of Forest Science* 77 (3). DOI: 10.1007/s13595-020-00972-y.

Leroy, Benjamin M. L.; Lemme, Hannes; Braumiller, Philipp; Hilmers, Torben; Jacobs, Martin; Hochrein, Sophia et al. (2021): Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems: An experimental approach. In *Ecological Solutions and Evidence* 2 (1), e12045. DOI: 10.1002/2688-8319.12045.

Leuschner, Christoph; Förster, Agnes; Diers, Marco; Culmsee, Heike (2022): Are northern German Scots pine plantations climate smart? The impact of large-scale conifer planting on climate, soil and the water cycle. In *Forest Ecology and Management* 507, p. 120013. DOI: 10.1016/j.foreco.2022.120013.

Leuschner, Christoph; Hertel, Dietrich; Coners, Heinz; Büttner, Volker (2001): Root competition between beech and oak: a hypothesis. In *Oecologia* 126 (2), pp. 276–284. DOI: 10.1007/s004420000507.

Liang, Jingjing; Crowther, Thomas W.; Picard, Nicolas; Wiser, Susan; Zhou, Mo; Alberti, Giorgio et al. (2016): Positive biodiversity-productivity relationship predominant in global forests. In *Science (New York, N.Y.)* 354 (6309). DOI: 10.1126/science.aaf8957.

Ligot, Gauthier; Balandier, Philippe; Fayolle, Adeline; Lejeune, Philippe; Claessens, Hugues (2013): Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. In *Forest Ecology and Management* 304, pp. 391–398. DOI: 10.1016/j.foreco.2013.05.050.

Lindner, Marcus (2000): Developing adaptive forest management strategies to cope with climate change. In *Tree physiology* 20 (5_6), pp. 299–307. DOI: 10.1093/treephys/20.5-6.299.

Lindner, Marcus; Maroschek, Michael; Netherer, Sigrid; Kremer, Antoine; Barbati, Anna; Garcia-Gonzalo, Jordi et al. (2010): Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. In *Forest Ecology and Management* 259 (4), pp. 698–709. DOI: 10.1016/j.foreco.2009.09.023.

Löf, M. (2000): Establishment and growth in seedlings of Fagus sylvatica and *Quercus robur*: influence of interference from herbaceous vegetation. In *Can. J. For. Res.* 30 (6), pp. 855–864. DOI: 10.1139/x99-257.

Löf, Magnus; Barrere, Julien; Engman, Mattias; Petersson, Linda K.; Villalobos, Adrian (2021): The influence of fencing on seedling establishment during reforestation of oak stands: a comparison of artificial and natural regeneration techniques including costs. In *Eur J Forest Res*. DOI: 10.1007/s10342-021-01369-w.

Löf, Magnus; Brunet, Jörg; Filyushkina, Anna; Lindbladh, Matts; Skovsgaard, Jens Peter; Felton, Adam (2016): Management of oak forests: striking a balance between timber production, biodiversity and cultural services. In *International Journal of Biodiversity Science, Ecosystem Services & Management* 12 (1-2), pp. 59–73. DOI: 10.1080/21513732.2015.1120780.

Lüpke, Burghard von (1998): Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. In *Forest Ecology and Management* 106 (1), pp. 19–26. DOI: 10.1016/S0378-1127(97)00235-1.

Lüpke, Burghard von (2008): Einfluss unterschiedlicher Hiebsformen auf die Naturverjüngung eines Traubeneichen-Buchen-Mischbestandes. In *Forstarchiv* 79, pp. 4–15, checked on 1/15/2019.

Maleki, K.; Zeller, L.; Pretzsch, H. (2020): Oak often needs to be promoted in mixed beech-oak stands - the structural processes behind competition and silvicultural management in mixed stands of European beech and sessile oak. In *iForest* 13 (2), Article 3172, pp. 80–88. DOI: 10.3832/ifor3172-013.

Manso, Rubén; Ligot, Gauthier; Fortin, Mathieu (2020): A recruitment model for beech–oak pure and mixed stands in Belgium. In *Forestry: An International Journal of Forest Research* 93 (1), pp. 124–132. DOI: 10.1093/foresj/cpz056.

Manso, Rubén; Morneau, François; Ningre, François; Fortin, Mathieu (2015): Effect of climate and intra- and inter-specific competition on diameter increment in beech and oak stands. In *Forestry* 88 (5), pp. 540–551. DOI: 10.1093/forestry/cpv020.

Manthey, Michael; Leuschner, Christoph; Härdtle, Werner (2007): Buchenwälder und Klimawandel.

Mattes, Arno; Kahle, Hans-Peter; Spiecker, Heinrich (2013): Höhenwachstumsveränderungen nach Trockenstress. Reagieren Buchen und Traubeneichen unterschiedlich? In *DVFFA, Sektion Ertragskunde: Beiträge zur Jahrestagung*, pp. 95–106.

Mette, Tobias; Dolos, Klara; Meinardus, Cathrin; Bräuning, Achim; Reineking, Björn; Blaschke, Markus et al. (2013): Climatic turning point for beech and oak under climate change in Central Europe. In *Ecosphere* 4 (12), pp. 1–19.

Meyer, Peter (2013): Forstwirtschaft und Naturschutz - Konfliktpotenzial und Synergien am Beispiel von Natura 2000. In Lehrke S., Ellwanger G., Buschmann A., Frederking W., Paulsch C., Schröder E., Ssymank A. (Ed.): Natura 2000 im Wald - Lebensraumtypen, Erhaltungszustand, Management, Naturschutz und Biologische Vielfalt, vol. 131 (131), pp. 177–197.

Modrow, Tobias; Kuehne, Christian; Saha, Somidh; Bauhus, Jürgen; Pyttel, Patrick L. (2019): Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes. In *Eur J Forest Res* 116, p. 346. DOI: 10.1007/s10342-019-01238-7.

Mölder, Andreas; Meyer, Peter; Nagel, Ralf-Volker (2019a): Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. In *Forest Ecology and Management* 437, pp. 324–339. DOI: 10.1016/j.foreco.2019.01.006.

Mölder, Andreas; Nagel, Ralf-Volker; Meyer, Peter; Schmidt, Marcus; Rumpf, Hendrik; Spellmann, Hermann (2017): Historischer Rückblick auf die Verjüngung von Eichen im Spessart des 19. Jahrhunderts– Bedeutung der angewandten Verfahren für die heutige Eichenwirtschaft. In *Forstarchiv* 88 (Heft 3), pp. 67–78.

Mölder, Andreas; Sennhenn-Reulen, Holger; Fischer, Christoph; Rumpf, Hendrik; Schönfelder, Egbert; Stockmann, Johannes; Nagel, Ralf-Volker (2019b): Success factors for high-quality oak forest (*Quercus robur*, *Q. petraea*) regeneration. In *For. Ecosyst.* 6 (1), p. 262. DOI: 10.1186/s40663-019-0206-y.

Mosandl, Reinhard; Abt, Alexander (2016): Waldbauverfahren in Eichenwäldern gestern und heute. In *AFZ - Der Wald* (20), pp. 28–32, checked on 12/5/2017.

Nothdurft, Arne; Wolf, Thilo; Ringeler, Andre; Böhner, Jürgen; Saborowski, Joachim (2012): Spatio-temporal prediction of site index based on forest inventories and climate change scenarios. In *Forest Ecology and Management* 279, pp. 97–111. DOI: 10.1016/j.foreco.2012.05.018.

Petritan, Any Mary; Bouriaud, Olivier; Frank, David C.; Petritan, Ion Catalin (2017): Dendroecological reconstruction of disturbance history of an old-growth mixed sessile oak-beech forest. In *J Veg Sci* 28 (1), pp. 117–127. DOI: 10.1111/jvs.12460.

Pothier, David (2017): Relationships between patterns of stand growth dominance and tree competition mode for species of various shade tolerances. In *Forest Ecology and Management* 406, pp. 155–162. DOI: 10.1016/j.foreco.2017.09.066.

Pretzsch, H.; Schütze, G.; Uhl, E. (2013a): Resistance of European tree species to drought stress in mixed *versus* pure forests. Evidence of stress release by inter-specific facilitation: Drought stress release by inter-specific facilitation. In *Plant Biology* 15 (3), pp. 483–495. DOI: 10.1111/j.1438-8677.2012.00670.x.

Pretzsch, H.; Steckel, M.; Heym, M.; Biber, P.; Ammer, C.; Ehbrecht, M. et al. (2019a): Stand growth and structure of mixed-species and monospecific stands of Scots pine (Pinus sylvestris L.) and oak (Q. robur L., Quercus petraea (Matt.) Liebl.) analysed along a productivity gradient through Europe. In *European Journal of Forest Research*. DOI: 10.1007/s10342-019-01233-y.

Pretzsch, Hans (2014): Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. In *Forest Ecology and Management* 327, pp. 251–264. DOI: 10.1016/j.foreco.2014.04.027.

Pretzsch, Hans (2019): Grundlagen der Waldwachstumsforschung. Berlin, Heidelberg: Springer Berlin Heidelberg, checked on 3/26/2019.

Pretzsch, Hans (2020): The course of tree growth. Theory and reality. In *Forest Ecology and Management* 478, p. 118508. DOI: 10.1016/j.foreco.2020.118508.

Pretzsch, Hans (2021): The social drift of trees. Consequence for growth trend detection, stand dynamics, and silviculture. In *Eur J Forest Res* 140 (3), pp. 703–719. DOI: 10.1007/s10342-020-01351-y.

Pretzsch, Hans; Biber, Peter (2005): A re-evaluation of Reineke's rule and stand density index. In *Forest science* 51 (4), pp. 304–320. Available online at http://www.ingentaconnect.com/content/saf/fs/2005/00000051/00000004/art00004.

Pretzsch, Hans; Biber, Peter (2010): Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. In *Canadian Journal of Forest Research* 40 (2), pp. 370–384.

Pretzsch, Hans; Biber, Peter (2016): Tree species mixing can increase maximum stand density. In *Can. J. For. Res.* 46 (10), pp. 1179–1193. DOI: 10.1139/cjfr-2015-0413.

Pretzsch, Hans; Biber, Peter; Schütze, Gerhard; Bielak, Kamil (2014a): Changes of forest stand dynamics in Europe. Facts from long-term observational plots and their relevance for forest ecology and management. In *Forest Ecology and Management* 316, pp. 65–77. DOI: 10.1016/j.foreco.2013.07.050.

Pretzsch, Hans; Biber, Peter; Schütze, Gerhard; Uhl, Enno; Rötzer, Thomas (2014b): Forest stand growth dynamics in Central Europe have accelerated since 1870. In *Nature communications* 5, p. 4967. DOI: 10.1038/ncomms5967.

Pretzsch, Hans; Biber, Peter; Uhl, Enno; Dauber, Erhard (2015): Long-term stand dynamics of managed spruce–fir–beech mountain forests in Central Europe: structure, productivity and regeneration success. In *Forestry* 88 (4), pp. 407–428. DOI: 10.1093/forestry/cpv013.

Pretzsch, Hans; Bielak, Kamil; Block, Joachim; Bruchwald, Arkadiusz; Dieler, Jochen; Ehrhart, Hans-Peter et al. (2013b): Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. In *European Journal of Forest Research* 132 (2), pp. 263–280. DOI: 10.1007/s10342-012-0673-y.

Pretzsch, Hans; Block, Joachim; Dieler, Jochen; Dong, Phan Hoang; Kohnle, Ulrich; Nagel, Jürgen et al. (2010): Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. In *Annals of Forest Science* 67 (7), p. 712. DOI: 10.1051/forest/2010037.

Pretzsch, Hans; del Río, Miren; Biber, Peter; Arcangeli, Catia; Bielak, Kamil; Brang, Peter et al. (2019b): Maintenance of long-term experiments for unique insights into forest growth dynamics and trends: review and perspectives. In *Eur J Forest Res* 138 (1), pp. 165–185. DOI: 10.1007/s10342-018-1151-y.

Pretzsch, Hans; Schütze, Gerhard (2016): Effect of tree species mixing on the size structure, density, and yield of forest stands. In *Eur J Forest Res* 135 (1), pp. 1–22. DOI: 10.1007/s10342-015-0913-z.

Puettmann, Klaus J.; Messier, Christian (2019): Simple Guidelines to Prepare Forests for Global Change: The Dog and the Frisbee. In *nwsc* 93 (3-4), p. 209. DOI: 10.3955/046.093.0305.

Puettmann, Klaus J.; Wilson, Scott McG; Baker, Susan C.; Donoso, Pablo J.; Drössler, Lars; Amente, Girma et al. (2015): Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? In *For. Ecosyst.* 2 (1), pp. 1–16. DOI: 10.1186/s40663-015-0031-x.

R Core Team (2018): R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Reineke, L. H. (1933): Perfecting a stand-density index for even-aged forests. In *Journal of Agricultural Research* 46 (7), pp. 627–638.

Rohner, Brigitte; Bigler, Christof; Wunder, Jan; Brang, Peter; Bugmann, Harald (2012): Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. In *J Veg Sci* 23 (5), pp. 892–905. DOI: 10.1111/j.1654-1103.2012.01408.x.

Rubtsov, V. V. (1996): Influence of repeated defoliations by insects on wood increment in common oak (Quercus robur L). In *Ann. For. Sci.* 53 (2-3), pp. 407–412. DOI: 10.1051/forest:19960223.

Schütz, Jean-Philippe (1993): High-quality oak silviculture in Switzerland: concepts of education and production in the marginal range of European oak. In *Ann. For. Sci.* 50, pp. 553–562, checked on 4/26/2019.

Schwaiger, Fabian; Poschenrieder, Werner; Biber, Peter; Pretzsch, Hans (2018): Species Mixing Regulation with Respect to Forest Ecosystem Service Provision. In *Forests* 9 (10), p. 632. DOI: 10.3390/f9100632.

Skrzyszewski, Jerzy; Pach, Maciej (2015): Crookedness of pedunculate oak (*Quercus robur* L.) growing under a canopy of Scots pine (*Pinus sylvestris* L.). In *Scandinavian Journal of Forest Research* 30 (8), pp. 688–698. DOI: 10.1080/02827581.2015.1048713.

Spathelf, Peter; Bolte, Andreas; van der Maaten, Ernst C. D. (2015): Is Close-to-Nature Silviculture (CNS) an adequate concept to adapt forests to climate change? In *Landbauforschung - applied agricultural and forestry research* (3-4/2015), pp. 161–170. DOI: 10.3220/LBF1452526188000.

Spathelf, Peter; van der Maaten, Ernst; van der Maaten-Theunissen, Marieke; Campioli, Matteo; Dobrowolska, Dorota (2014): Climate change impacts in European forests: the expert views of local observers. In *Annals of Forest Science* 71 (2), pp. 131–137. DOI: 10.1007/s13595-013-0280-1.

Spiecker, Heinrich (1999): Overview of Recent Growth Trends in European Forests. In Lucy J. Sheppard, J. Neil Cape (Eds.): Forest Growth Responses to the Pollution Climate of the 21st Century. Dordrecht, s.l.: Springer Netherlands, pp. 33–46.

Steckel, M.; del Río, M.; Heym, M.; Aldea, J.; Bielak, K.; Brazaitis, G.; et al (2020): Species mixing reduces drought susceptibility of Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. In *Forest Ecology and Management*.

Steckel, M.; Heym, M.; Wolff, B.; Reventlow, D.O.J.; Pretzsch, H. (2019): Transgressive overyielding in mixed compared with monospecific Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) stands – Productivity gains increase with annual water supply. In *Forest Ecology and Management* 439, pp. 81–96. DOI: 10.1016/j.foreco.2019.02.038.

Stimm, Kilian; Ambs, Dominik; Uhl, Enno; Pretzsch, Hans (2021a): Ziele und Wege der Eichenbewirtschaftung in Europa. In Kilian Stimm (Ed.): Die Eiche. Facetten zu Ökologie, Naturschutz, Wachstum und waldbaulichen Perspektiven. Freising (Forstliche Forschungsberichte München, 221), pp. 31–46.

Stimm, Kilian; Heym, Michael; Blaschke, Markus; Uhl, Enno; Tretter, Stefan; Pretzsch, Hans (2021b): Zur Bestandsdynamik und Verjüngungssituation in Naturwaldreservaten mit Eichenbeteiligung. In Kilian Stimm (Ed.): Die Eiche. Facetten zu Ökologie, Naturschutz, Wachstum und waldbaulichen Perspektiven, vol. 221. Freising (Forstliche Forschungsberichte München, 221), pp. 183–201.

Stimm, Kilian; Heym, Michael; Nagel, Ralf-Volker; Uhl, Enno; Pretzsch, Hans (2022a): 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. In *Forests* 13 (5), p. 724. DOI: 10.3390/f13050724.

Stimm, Kilian; Heym, Michael; Uhl, Enno; Tretter, Stefan; Pretzsch, Hans (2021c): Height growth-related competitiveness of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) under climate change in Central Europe. Is silvicultural assistance still required in mixed-species stands? In *Forest Ecology and Management* 482, p. 118780. DOI: 10.1016/j.foreco.2020.118780.

Stimm, Kilian; Uhl, Enno; Pretzsch, Hans (2022b): Chances and Limitations of Mixed Oak Regeneration under Continuous Canopy Cover—Evidence from Long-Term Observations. In *Forests* 13 (12), p. 2052. DOI: 10.3390/f13122052.

Toïgo, Maude; Perot, Thomas; Courbaud, Benoit; Castagneyrol, Bastien; Gégout, Jean-Claude; Longuetaud, Fleur et al. (2018): Difference in shade tolerance drives the mixture effect on oak productivity. In *J Ecol* 106 (3), pp. 1073–1082. DOI: 10.1111/1365-2745.12811.

Toïgo, Maude; Vallet, Patrick; Perot, Thomas; Bontemps, Jean-Daniel; Piedallu, Christian; Courbaud, Benoit (2015): Overyielding in mixed forests decreases with site productivity. In *J Ecol* 103 (2), pp. 502–512. DOI: 10.1111/1365-2745.12353.

Torresan, Chiara; del Río, Miren; Hilmers, Torben; Notarangelo, Monica; Bielak, Kamil; Binder, Franz et al. (2020): Importance of tree species size dominance and heterogeneity on the productivity of spruce-fir-beech mountain forest stands in Europe. In *Forest Ecology and Management* 457, p. 117716. DOI: 10.1016/j.foreco.2019.117716.

Trouvé, Raphaël; Bontemps, Jean-Daniel; Seynave, Ingrid; Collet, Catherine; Lebourgeois, François (2015): Stand density, tree social status and water stress influence allocation in height and diameter growth of Quercus petraea (Liebl.). In *Tree physiology* 35 (10), pp. 1035–1046. DOI: 10.1093/treephys/tpv067.

Vallet, Patrick; Perot, Thomas (2016): Tree diversity effect on dominant height in temperate forest. In *Forest Ecology and Management* 381, pp. 106–114. DOI: 10.1016/j.foreco.2016.09.024.

Vandermeer, John H. (1989): The ecology of intercropping. Cambridge: Cambridge University Press.

Vanhellemont, Margot; Bijlsma, Rienk-Jan; Keersmaeker, Luc de; Vandekerkhove, Kris; Verheyen, Kris (2018): Species and structural diversity affect growth of oak, but not pine, in uneven-aged mature forests. In *Basic and Applied Ecology* 27, pp. 41–50. DOI: 10.1016/j.baae.2018.01.003.

Vannoppen, Astrid; Kint, Vincent; Ponette, Quentin; Verheyen, Kris; Muys, Bart (2019): Tree species diversity impacts average radial growth of beech and oak trees in Belgium, not their long-term growth trend. In *For. Ecosyst.* 6 (1), p. 252. DOI: 10.1186/s40663-019-0169-z.

Vanselow, K. (1960): Die Waldbautechnik der Eiche im bayerischen Spessart in geschichtlicher Betrachtung. In *Forstwissenschaftliches Centralblatt* 79 (9), pp. 270–286.

Weaver, G. T.; Spiecker, Heinrich (1993): Silviculture of high-quality oaks: questions and future research needs. In *Ann Sci For.*

West, P. W. (2014): Calculation of a Growth Dominance Statistic for Forest Stands. In *Forest science* 60 (6), pp. 1021–1023. DOI: 10.5849/forsci.13-186.

Wood, S. N. (2017): Generalized Additive Models: An Introduction with R (2nd edition).: Chapman and Hall/CRC.

Zang, Christian; Rothe, Andreas; Weis, Wendelin; Pretzsch, Hans (2011): Zur Baumarteneignung bei Klimawandel: Ableitung der Trockenstress-Anfälligkeit wichtiger Waldbaumarten aus Jahrringbreiten. In *Allgemeine Forst-und Jagdzeitung* 182 (5/6), pp. 98–112, checked on 11/7/2018.

Zapater, Marion; Hossann, Christian; Bréda, Nathalie; Bréchet, Claude; Bonal, Damien; Granier, André (2011): Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. In *Trees* 25 (5), pp. 885–894. DOI: 10.1007/s00468-011-0563-9.

Zeller, Laura; Liang, Jingjing; Pretzsch, Hans (2018): Tree species richness enhances stand productivity while stand structure can have opposite effects, based on forest inventory data from Germany and the United States of America. In *For. Ecosyst.* 5 (1), p. 3. DOI: 10.1186/s40663-017-0127-6.

Zeller, Laura; Pretzsch, Hans (2019): Effect of forest structure on stand productivity in Central European forests depends on developmental stage and tree species diversity. In *Forest Ecology and Management* 434, pp. 193–204. DOI: 10.1016/j.foreco.2018.12.024.

Zuur, Alain F.; Ieno, Elena N.; Walker, Neil; Saveliev, Anatoly A.; Smith, Graham M. (Eds.) (2009): Mixed effects models and extensions in ecology with R. New York: Springer (Statistics for Biology and Health).

Appendix

A - Article I

Title:

Height growth-related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance still required in mixed-species stands?

Authors:

Kilian Stimm, Michael Heym, Enno Uhl, Stefan Tretter, Hans Pretzsch

Journal:

Forest Ecology and Management 482 (2021) 118780

Impact Factor (2021):

3.558

Forest Ecology and Management 482 (2021) 118780

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Height growth-related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance still required in mixed-species stands?

Kilian Stimm[a,*], Michael Heym[a], Enno Uhl[a], Stefan Tretter[b], Hans Pretzsch[a]

[a] *Chair of Forest Growth and Yield Science, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, Freising 85354, Germany*
[b] *Department of Silviculture and Mountain Forests, Bavarian State Institute of Forestry, Hans-Carl-von-Carlowitz-Platz 1, Freising 85354, Germany*

ABSTRACT

Sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.) play an important role in increasing the resistance of central European forests to severe droughts. But outside their real niche the competitiveness of both oak species can be low in mixed-species stands. This paper examines the height growth of oaks depending on environmental conditions and inter-specific competition. Height growth of trees was analysed using data from forest inventories covering monospecific and mixed-species stands within the German federal state of Bavaria. By means of regression analyses of 23,607 height measurements, we found that site conditions and stand structure have strong effects on the height growth of oak. Summer temperature, water balance in the vegetation period and base saturation were the main explanatory site variables. The first positive effect of summer temperature had no influence at warmer sites with mean summer temperatures above 16.4 °C, while the effect of water balance was positively linear. In addition, stand density modified the height growth of oak in a mainly positive manner. Vertical structure also had a positive effect, which was found for most species compositions, except monospecific stands and oak-hornbeam mixture. In most mixtures, oaks height growth seemed to be less climate-sensitive compared to monocultures. A currently warmer and drier climate seemed to favour the height growth superiority of European beech, whereas it decreased the superiority of Scots pine. The results indicated that even if the climate changes as predicted, the growth of oak will depend upon silvicultural promotion. Our findings can be used to improve regional guidelines for oak silviculture with special regard to climate-sensitive height growth. For example, a regionally delayed introduction of admixed species can reduce silvicultural treatments by ensuring oak vitality in mixed forests at the same time.

1. Introduction

Changes in species composition of forests are indicated in many parts of Central Europe as a response to climate change (Bolte et al., 2009; Spathelf et al., 2014). Higher temperatures in combination with lower precipitation are expected, particularly during the growing season (Jacob et al., 2008). Sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.), two major oak species in Central Europe, are important in tree species portfolios and considered to be less drought-sensitive than other native tree species (Annighöfer et al., 2015; Kölling and Zimmermann, 2007; Manthey et al., 2007; Mette et al., 2013). Appreciable shares of both oak species are helpful in creating mixed stands that are more climate-resilient because of their relatively broad ecological amplitude.

However, oak has to compete with more competitive admixed species on sites where it grows best, especially European beech (*Fagus sylvatica* L.) (Ellenberg and Strutt, 1988; Manthey et al., 2007). In contrast, it is able to compete naturally and find its ecological niche (Bauhus et al., 2017) in stands with distinctive and extreme site conditions, e.g. under extreme aridity, on clay soils or floodplains. These natural monospecific oak stands are rare and hardly to find in their optimum growth. In Germany, for example, it can be assumed that almost all monospecific oak stands have been created by human activity on sites with favourable growing conditions (Krahl-Urban, 1959). Consequently, when oak is grown in mixture on the most suitable sites for the species, silvicultural strategies are essential to maintain it as a component of the stand. Oak is traditionally artificially regenerated in many parts of Central Europe and mixed with shade-tolerant tree species introduced at later successional stages to improve its wood quality (Lüpke, 1998; Schütz, 1993). The admixture of European beech, in particular as a subsidiary tree species, is a widely established practice in oak management and the subject of several studies (Bontemps et al., 2012; Dolos et al., 2016; Lüpke, 1998; Mette et al., 2013). On soils with a higher base saturation and clay contents, European beech will be replaced by hornbeam (*Carpinus betulus* L.) or lime species (*Tilia platyphyllos* and *Tilia cordata* L.), associated with a change from beech to oak forest communities (Ellenberg and Strutt, 1988; Lüpke, 1998). On the other hand, the introduction of young oak under the canopy of mature Scots pine (*Pinus*

---

* Corresponding author.
E-mail address: kilian.stimm@tum.de (K. Stimm).

https://doi.org/10.1016/j.foreco.2020.118780
Received 31 July 2020; Received in revised form 1 November 2020; Accepted 5 November 2020

sylvestris L.) is a common silvicultural option to establish mixed stands in many parts of Central Europe. Mixed stands with aforementioned tree species occur mainly in the physiological optimum of oak.

Existing studies that address the competitiveness of oak and beech and their dependency on different climatic conditions, have investigated the occurrence of oak by using its share of basal area in mixed stands (Dolos et al., 2016; Mette et al., 2013). Dolos et al. (2016) predicted a future shift towards oak in tree species ratios by analysing basal areas derived from forest inventory data that considered the modifying effect of silvicultural interferences. Oak however, is essentially a beneficiary of the predicted climate change due to its drought resistance (Ellenberg and Strutt, 1988; Kölling and Zimmermann, 2007). Several studies have analysed the height growth of trees by using the site index in monospecific stands. They focused on tree level growth and used the site index as dependent variable and surrogate for site productivity (Albert and Schmidt, 2010; Brandl et al., 2014; Nothdurft et al., 2012). These studies analysed the site index depending on different climatic conditions. Furthermore, Bontemps et al. (2012) described a shift in height growth relations between sessile oak and European beech in favour of oak in France with changing climatic conditions.

Natural mixed oak forests occur mainly in warm, dry regions (Ellenberg and Strutt, 1988). In accordance with climate envelopes of oak and predicted future climate, Kölling and Zimmermann (2007) expect an increase in the distribution of these forest types. In this context, Fischer et al. (2018) predicted an increase of site conditions that favour oak-dominated forests in future as shown by the climate envelopes of both oak species and the current climate in Bavaria (Fig. 1). Pretzsch et al. (2013a) used results from experiments with mixtures of oak and beech along an ecological gradient to predict that oak would suffer less from increased drought. Up to now, the effect of climate change on the competitiveness of oak and possible supporting silvicultural measures to ensure the continuance of oak in future compositions have only been discussed qualitatively, while hardly any such effects have been quantified in a way suitable for forest management.

Going beyond the aforementioned studies, we analysed the height growth of individual oak trees to explain their climate and site-sensitive competitiveness. Height growth is used as an indicator for silvicultural decisions (Klemmt and Bachmann, 2012) and is highly relevant for forest management. However, mixtures of trees may follow slightly different principles than monospecific stands. Vospernik (2017) highlighted the lack of knowledge about mixed and uneven-aged stands which limits the predictions of forest growth models. The prognosis of a warmer and drier future climate, which should facilitate the competitiveness of oak in relation to its admixed tree species, is widely reported (Bonfils et al., 2015; Bontemps et al., 2012; Pretzsch et al., 2013a). In this study, we explained the effects of climatic conditions on height growth of individual trees in monospecific stands as well as two species mixtures.

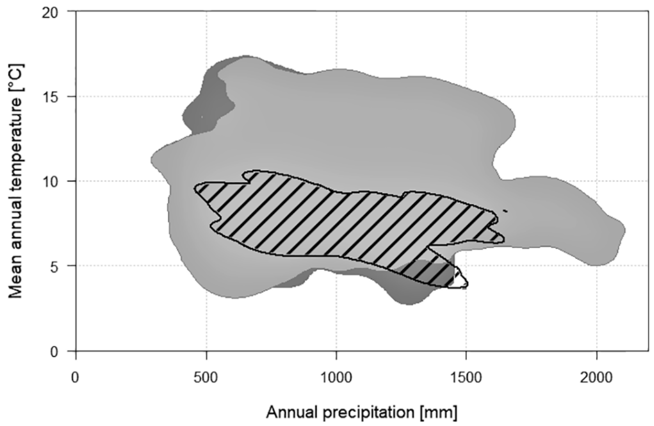

Fig. 1. Climate envelopes of sessile oak, *Quercus petraea* (Matt.) Liebl., (light + dark grey area) and pedunculate oak, *Quercus robur* L., (light grey area)(Strona et al., 2016); current climate in Bavaria (1971–2000; hatched lines).

Apart from site conditions, local competition may also influence tree growth (Gadow, 2003; Hertel, 1999; Leuschner et al., 2001; Pretzsch et al., 2013a; Pretzsch, 2019). We therefore investigated structural effects that are mainly controllable by silvicultural management, using stand density and mixture type as explanatory variables.

In essence, our research therefore focussed on the effect of (i) environmental conditions and (ii) local stand structure as a proxy for competition in (iii) monospecific as well as in two-species mixtures on the height growth trajectories of oak, based on inventory data. We formulated the following research questions:

(i) What are the effects of summer temperature, water availability and nutrient supply on the height growth of oaks?
(ii) Is there a modifying effect of stand density and vertical stand structure on the height growth of oak?
(iii) What is the effect of site conditions and structural variables on the height growth of oak in different tree species mixtures?

2. Materials and methods

2.1. Forest inventory data sets

Our study area is the Federal State of Bavaria, located in southern Germany. The study is based on two sets of forest inventories, namely the National Forest Inventory of Germany (NFI) and the inventory data of the Bavarian State Forest Enterprise (BSFI). By combining both inventories, using cross-sectional and short-term longitudinal data, we obtained an adequate sample of measured tree heights, covering a broad gradient of environmental conditions across Bavaria.

NFI - The NFI is generally based on a 4 km × 4 km grid, although in some areas a 2.83 km × 2.83 km grid is used. On each intersection of the grid, a square with an edge length of 150 m is located (Polley, 2011). Each corner of a square marks the centre of an inventory plot. From the centre of each inventory plot, angle count sampling was conducted with a counting factor, ACF of 4 in order to identify sample trees. The species of all sample trees was determined and the respective diameter at breast height (dbh) measured. The minimum dbh was 7 cm. In addition, height measurements were carried out for a subsample of each tree species, covering the middle and upper diameter range. A unique tree number verified that the same trees have been measured. Up to three repeated measurements were available for the NFI, carried out in 1986, 2002 and 2012 (Thuenen-Institut, 2017).

BSFI - The average grid width of the BSFI is 200 m × 200 m. Thus it is much more compact than the NFI grid and covers the state owned forests. We used up to three repeated measurements from the BSFI, most of which were surveyed at intervals of 10 years. Repeatedly measured trees could be identified by a tree number generated from local stem coordinates. Unlike the NFI, the BSFI assesses the inventory data in concentric circles up to an area of 500 m^2. Trees were recorded depending on their individual tree size and distance to the centre (Neufanger, 2011). The minimum dbh that was measured was 1 cm. Height measurements were taken from a subsample of each tree species covering the upper diameter range of all species present at the plot.

2.2. Inventory data and data preparation

Tree species - As the inventory data provided no reliable species information and covered areas where both oak species hybridise (Aas, 2000; Aas, 2002), we pooled the data of sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.), referred to as oak in the following. According to Grundmann and Roloff (2009), both oak species are suitable for all site conditions except wet sites. However, both species react almost identically with regard to height growth relations and competitiveness, especially in relation to the admixed species (Pretzsch et al., 2013a).

We treated small-leaved lime (*Tilia cordata* Mill.) and large-leaved lime (*Tilia platyphyllos* Scop.) in the same way and consolidated both species (lime in the following).

For the analysis, individual tree data was extracted for oak in monospecific stands as well as in two-species mixtures with European beech (*Fagus sylvatica* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.), lime (*Tilia spec.*) and common ash (*Fraxinus excelsior* L.). The classification monospecific or mixed stand is described in detail in the next section.

Tree heights - As a consequence of different requirements for height measurements in the NFI and BSFI, we harmonised the selection of the investigated trees. We selected the measured heights from both inventories and removed all trees with observed damages. We tried to reduce the influence of silvicultural treatments on height growth by considering only the taller trees (Assmann, 1970; Pretzsch, 2019). To this end, we classified each tree as dominant or subdominant and related each tree height measurement to the maximum height of the respective species in a given plot. Dominant trees reached at least 75% of this maximum height, subdominant trees were smaller. Based on the selected dominant trees, we repeated the procedure with 90% of the maximum at species level to better assess the ecological potential of height growth. Consequently, the final data set contained only the tallest dominant trees per species.

Tree age - The age used was determined in the inventories by means of whorl and annual ring counts, estimates of species specific stand age or, in the case of repeated surveys, by age updates from previous surveys (Neufanger, 2011; Polley, 2011).

Tree species composition - Monospecific inventory plots were identified by ≥ 90% basal area share of dominant oak. Two-species mixture plots were identified by a 10% minimum basal area share of dominant oak, one additional admixed species and a maximum of 10% of a third tree species.

Inventory data - In total, we considered the tree heights of 9,166 oaks in monospecific stands 14,441 oaks in mixed stands (Table 1). The latter were mixed with beech (n = 10,069), Scots pine (n = 2,694), hornbeam (n = 979), lime (n = 370) and ash (n = 329). The age of the investigated oaks covered a broad gradient, ranging from 7 to 394 years. Similarly, a large range is covered by the height and diameter of the considered oaks. An overview of the investigated inventory data for oak and its admixed tree species is provided in Table 1.

The spatial distribution of all investigated inventory plots (n = 10,171) is shown in Fig. 2. Monospecific as well as mixed inventory plots are similar distributed and cover the entire study area.

2.3. Environmental data

We used interpolated climate data from the German Weather Service and derived regionalised environmental data from the Bavarian State Institute of Forestry for all surveyed inventory plots. In accordance with our research questions, we focused on temperature, water availability and nutrient supply as main environmental variables. Tree growth is particularly influenced by climatic conditions during growing season, therefore summer temperature and water availability during the growing season were used. In addition, both variables are subject to an apparently high dynamic in the course of climate change.

We took the summer temperature (*temp*) as one explanatory variable to explain part of the environmental effect. It was derived as the mean for the meteorological summer months of June, July and August from regionalised, long-term mean values for the years 1971 to 2000. It thus covered a substantial part of the growth period of the investigated trees. For monospecific oak plots, the observed summer temperatures range from 14.8 °C up to 18.1 °C, with an average of 16.4 °C. Mixed stands of oak and beech are located on sites with a mean temperature of 16.2 °C.

Table 1
Overview of height measurement oak trees and admixed species in the inventory data; n = number of trees; Mean = average value of all trees; min/max = minimum and maximum; sd = standard deviation.

Mixture	Species	Variable	Unit	n	Mean	min	max	sd
monospecific	Oak	Age	year	9,166	97.8	7	394	60
		Height	m		22.5	1.4	39.5	7.8
		dbh	cm		35.6	1.5	186.5	18.8
oak-beech	Oak	Age	year	10,069	141	5	394	59
		Height	m		27.9	1.5	43.0	5.2
		dbh	cm		44.6	1.5	129.3	14.6
	European beech	Age	year	10,457	122	5	281	45
		Height	m		28.3	1.3	47.5	6.5
		dbh	cm		43.8	1.5	105.5	15.1
oak-pine	Oak	Age	year	2,694	106	6	263	42
		Height	m		24.3	2.0	38.0	5.3
		dbh	cm		37.6	1.5	108.5	13.6
	Scots pine	Age	year	2,861	104	6	281	40
		Height	m		25.8	1.5	37.8	5.2
		dbh	cm		38.6	1.5	72.5	11.1
oak-hornbeam	Oak	Age	year	979	114	8	309	56
		Height	m		23.1	1.3	36.0	6.0
		dbh	cm		40.3	1.5	112.5	17.9
	Hornbeam	Age	year	669	87	10	209	43
		Height	m		20.3	1.4	35.0	5.4
		dbh	cm		27.2	1.5	70.5	11.6
oak-lime	Oak	Age	year	370	107	12	259	61
		Height	m		23.3	6.3	38.5	6.9
		dbh	cm		42.3	6.5	110.5	22.1
	Lime	Age	year	246	78	12	200	41
		Height	m		21.7	5.3	39.0	7.0
		dbh	cm		31.4	5.5	74.5	13.8
oak-ash	Oak	Age	year	329	113	15	269	56
		Height	m		25.5	3.0	43.5	6.6
		dbh	cm		47.8	4.5	143.5	21.8
	Common ash	Age	year	276	91	12	189	39
		Height	m		26.5	3.5	50.5	7.6
		dbh	cm		39.9	1.5	94.5	16.6

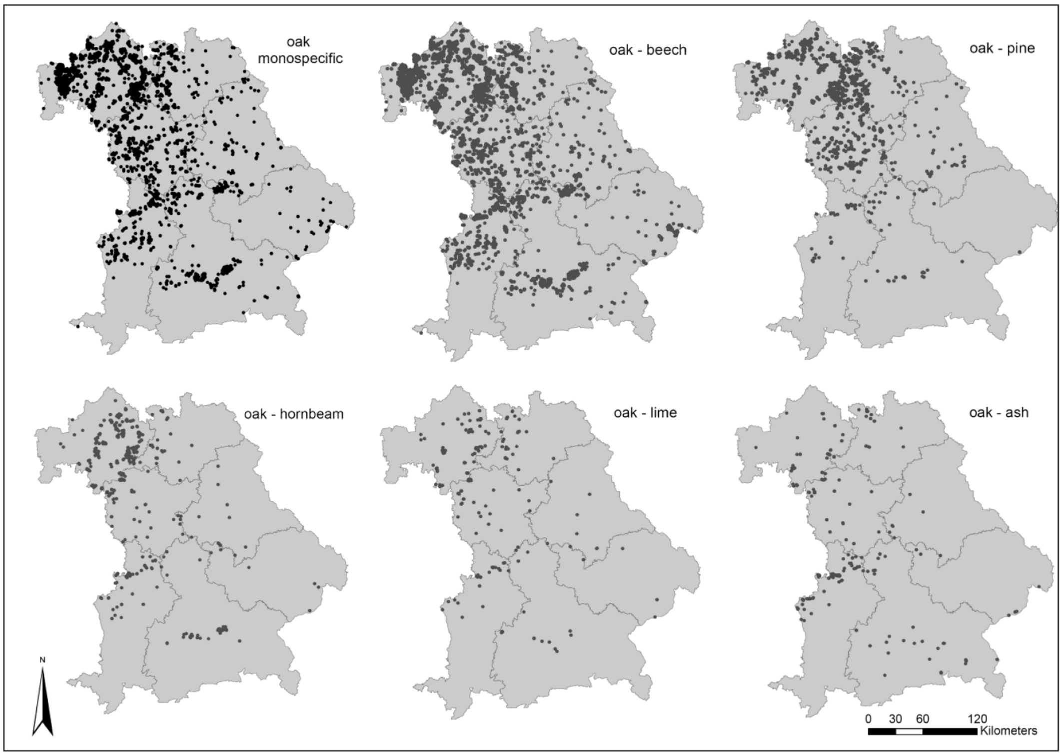

Fig. 2. Spatial distribution of investigated inventory plots within the study area.

Mixtures with pine and lime as well as hornbeam and ash occupied sites with mean summer temperatures of 16.6 °C and 16.7 °C, respectively. Accordingly, all stands, monospecific and mixed, comprise comparable average summer temperatures (Table 2, Supplement Table A1).

In addition, we investigated the influence of water availability in the vegetation period. We therefore calculated the mean water balance (*wb*) for the vegetation period from May until September. It was defined as the sum of the climatic water balance (*cwb*) and the available water capacity of the soil (*awc*). The *cwb* was calculated as the difference of the precipitation sum and the potential evapotranspiration that was calculated according the equation of Turc L. (1961). The mean water balance ranged from −188.3 mm at dry sites up to very moist conditions with values of 387.6 mm in monospecific oak stands. The average was 39.6 mm. Mixed stands covered the same range, with a minimum of −196.1 mm and a maximum of 399.8 mm. The mean value was 32.2 mm. For descriptive and schematic visualisation, we used negative values (<0 mm) as low and positive values (>0 mm) as high water balances (Table 2, Supplement Table A1).

We used the base saturation types (*bs_type*) described by Kölling (2010) for the nutrient supply. Type 1 classifies soils with high base saturation throughout the entire soil profile and can be found for all mixture types. Types 2 and 3 provide more or less ideal nutrient conditions for tree growth. Both types also account for the majority of all stand types studied. Type 4 is characterised by an increasing acidification of the soil. Type 5 describes the highest acidification level and was only observed for a few stands (Table 3).

Table 2

Descriptive data for the environmental and structural variables for regression analyses for all inventory plots (pooled data, monospecific and mixed).

Variable	Unit	Mean	min	max	sd
Summer temperature (temp)	°C	16.4	13.1	18.1	0.5
Water balance vegetation period (wb)	mm	35.1	−196.1	400.0	68.3
Base saturation (bs)	%	41.4	3.3	100.0	30.0
Stand density index	n ha^{-1}	882.5	5.1	2989.7	397.7
latitude	°		47.7	50.6	
longitude	°		9.1	13.7	

All environmental variables were available for each inventory plot.

2.4. Stand structure variables

We stratified all inventory plots into two groups, single-layered and multi-layered. In order to assign trees as subdominant, we defined a threshold of 75% of the maximum height at the inventory plot level. We determined the presence of one subdominant tree at the inventory plot was indicative for a more vertically structured local stand situation in the immediate vicinity of the tree in focus. The corresponding inventory plot was then classified as multi-layered. In addition, one tree at the plot level represents a multiple of trees per hectare on the stand level.

Additionally, we calculated the stand density index (*SDI*) of the main stand for each inventory plot, using the stem number per ha (*N*) of dominant trees (Reineke, 1933). Differences in species-specific growing area requirements, e.g. maximum stand densities, were taken into account by applying a species-specific equivalence factor *E* (Pretzsch and Biber, 2016).

$$SDI_i = \sum_{1}^{j} N_{ij} \times \left(\frac{25}{dq_{ij}}\right)^{-1.605} \times E_j \tag{1}$$

Table 3

Frequency of occurrence of base saturation types.

	Oak monospecific	Oak-beech	Oak-pine	Oak-hornbeam	Oak-lime	Oak-ash
bs_type1	516	690	119	174	32	107
bs_type2	3,027	2,546	841	593	238	162
bs_type3	2,392	2,685	1,200	158	88	47
bs_type4	3,118	4,050	480	54	12	11
bs_type5	113	98	54	–	–	2

Here, *SDI* is the stand density index, *N* the number of trees per hectare, *dq* the quadratic mean diameter (cm) and *E* the species-specific correction as described above. Indices *i* and *j* refer to the inventory plot and tree species, respectively.

Height growth trajectories for a descriptive and schematic representation of the observed heights were visualised for oak, beech and pine and the corresponding mixture types (monospecific, oak-beech and oak-pine) by incorporating a Chapman-Richards function (Richards, 1959).

$$h = a \times \left(1 - e^{-bt}\right)^{c} \tag{2}$$

Here, *h* is the tree height, *t* the stand age and *a, b* and *c* are function parameters.

2.5. General additive mixed model (GAMM)

In order to characterise the environmental and structural effects on height growth of oak, we considered the monospecific and mixed stands separately. Due to the linear and non-linear behaviour of the explanatory variables to the predictor variable, we applied a general additive mixed model (GAMM), which allows the consideration of both types of reaction in one model without any assumption about the underlying distribution. In addition, we considered random effects due to nested trees at the inventory plot level and due to temporal autocorrelation of the repeated measurements at the tree level. We used summer temperature, water availability in the growing season and types of base saturation to describe individual site conditions. The individual tree dimension is considered based as a nonlinear function of the species-specific stand age. In order to describe the partial effect of spatial stand structure on height growth, we added stand density and layer structure to the model. In the case of mixed stands, we applied the GAMM for each mixing type separately. Interactions between the variables were not considered because they did not improve the explanatory power of the model. All terms were kept in the model, as it was based on our hypothesis.

$$\ln\left(h_{ijk}\right) = \alpha + \beta_1{*}layer_i + \beta_2{*}bs\_type_i + f_1\left(age_{ijk}\right) + f_2(temp_i) + f_3(wb_i) + f_4(sdi_{ik}) + f_5(lat_i, lon_i) + b_i + b_{ij} + \varepsilon_{ijk} \tag{3}$$

$$\varepsilon_{ijk}\ N\left(0, \sigma^2\right)$$

Here, *h* refers to the tree height, α defines the intercept and β_1 and β_2 the coefficients of stand layer structure *(layer)* and base saturation types (*bs_type)*. We considered one-dimensional smoother functions such as f_1 for tree species age *(age)*, f_2 for summer temperature *(temp)*, f_3 for water balance in the growing season ***(wb)*** and f_4 for the stand density index ***(sdi),*** as well as the two-dimensional smoother f_5 for geographical coordinates *(lat/lon)*. The smoother f_5 was included in the model to account for spatially structured variation in the response not explained by the available covariates. The spatial and temporal autocorrelation was taken into account by the random effects b_i and b_{ij}. The indices *i* and *j* refer to the inventory plot and tree number within each plot, respectively.

In order to visualise the different partial effects of the explanatory variables, the age was set to 100 and all other variables were set to their mean. The categorical variables were set to medium base saturation (bs_type3) and multi-layered.

We partly compare the results of separately fitted models for different stand types, so that there is no statistical test behind the comparison. Due to the large data sets and the required high computational capacity a model including the variable mixture did not converge. The effects on height growth revealed by the models result from the statistical output each.

All statistical analysis was performed with the statistical software R (R Core Team, 2018). The R-package mgcv was used specifically to apply the GAMM (Wood, 2017).

3. Results

3.1. Height growth trajectories

A visual comparison of the descriptive height growth trajectories obtained from fitted Chapman-Richards functions reveals a tendency towards superior height growth of oaks in oak-beech mixtures, when compared with monospecific stands. Oaks growing in mixtures with pine tend to slightly lower their height growth, according the height growth trajectories (Fig. 3).

By analysing the shift in height growth relations, we were able to plot age-height curves (Richards, 1959) for both dry and moist site conditions in combination with high temperatures (>16.5 °C). According to the standard errors of the model parameters the height differences between monospecific and mixed stands in dependence on the water availability and temperatures were low (Fig. 3, Supplement Table A2). The tree height of mono-specifically growing oak hardly differed from the height of oak in mixture on sites with ample water supply. However, the differences were higher for middle-aged oaks growing in monospecific stands on sites with a lower water availability (Fig. 3a). This noticeable positive effect of an admixed species on height growth seemed partly compensating any lower water availability.

3.2. Height growth of oaks in monospecific stands

3.2.1. Summer temperature and spatial distribution

We found that summer temperatures had a significant effect on the height growth of oak. The influence was strongly positive up to summer temperatures of 16.4 °C. A slight decrease and signs of stagnation at higher temperatures indicated that oak only reacts with increased height growth up to a moderate temperature rise (Fig. 4a). However, the trend towards taller trees at higher summer temperatures (>17.4 °C) was not statistically confirmed.

A slight increase in tree heights could be observed from North to South, with distinctive differences between regions, by considering the effect of spatial distribution (Fig. 4d). A reduced height growth could be detected for large parts of the northwest of Bavaria. The data showed a growth optimum for oak further towards the southeast.

3.2.2. Water balance and base saturation

The water balance during the vegetation period had a significant positive linear influence on height growth, which was observed for the range between −200 and 200 mm water availability (Fig. 4b).

The influence of base saturation on height growth was low (Fig. 4c). A significantly positive effect on oak heights compared to the reference (bs_type1) could only be identified for a balanced base saturation (bs_type3). However, we detected no significant difference across all other base saturation types.

3.2.3. Stand structure

In addition to the environmental variables, we also found that the stand structure variables had a significant effect on the height growth of oak (Table 4). Stand density had a strong positive effect with a saturation at SDI levels of around 1,000 trees per hectare. An increase in stand density beyond this level did not modify the heights of oak (Fig. 5a).

We found no significant influence of the partial effect of the existing stand layers for monospecific stands (Fig. 5b).

3.3. Height growth reaction in mixture

We discovered that the effect of the most decisive site variables and selected structural variables on height growth was partly different in two-species mixtures with beech, pine, hornbeam, lime and ash compared with monocultures of oak. In addition, a change in the significance of the partial effects could be observed. Partial effects of oaks in mixture with beech or pine are shown in this section, the statistical

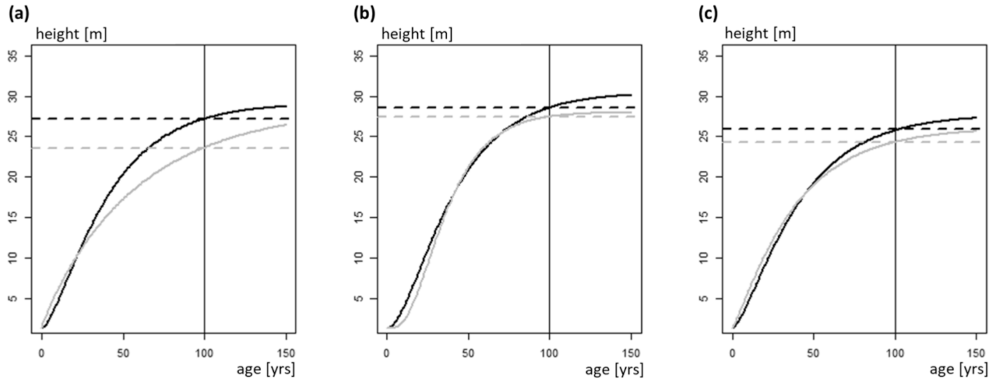

Fig. 3. Chapman-Richards height growth trajectories for oaks in monospecific stands (a), oak in mixture with beech (b), oak in mixture with pine (c). The height [m] is shown across a range of stand age [years] on the x-axis. Black solid lines represent a high water balance (>0 mm) and solid grey lines a low water balance (<0 mm).

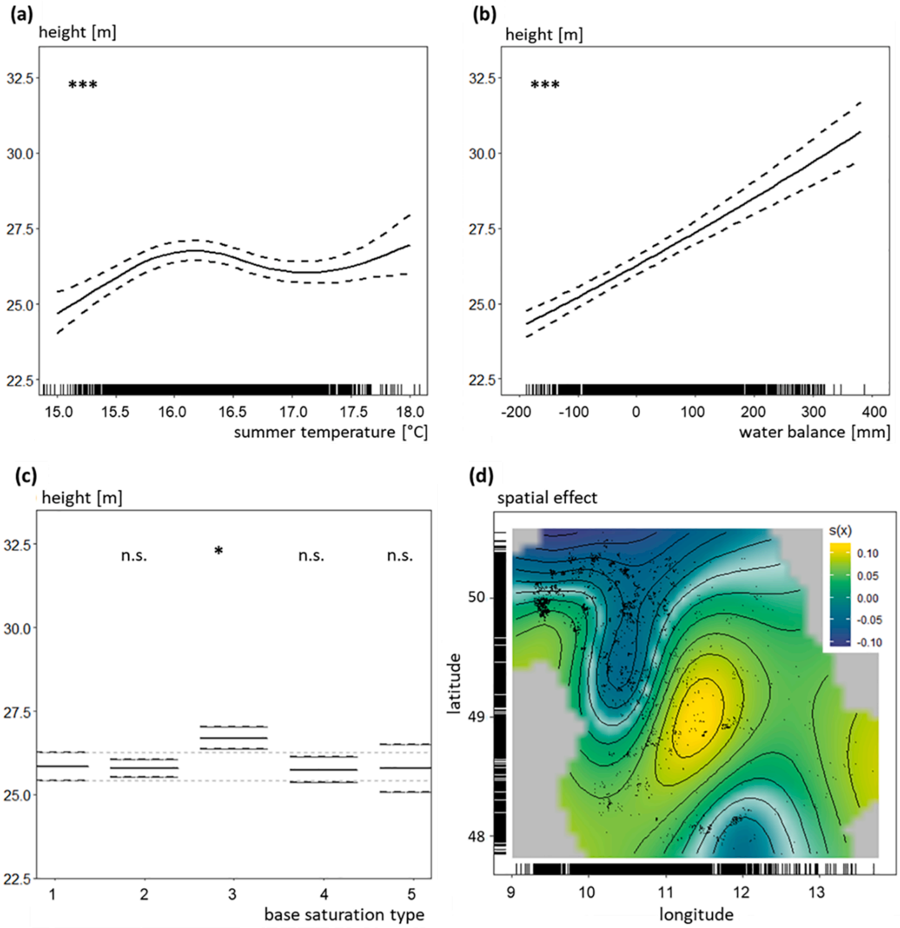

Fig. 4. Partial effects of environmental variables on oak height growth in monospecific stands with summer temperature (a), water balance during vegetation period (b), base saturation type (c) and spatial distribution (d). For a graphical presentation of one-dimensional effects, the age was set to 100, while all other variables were set to their mean. The categorical variables were set to medium base saturation and multi-layered. Significance levels: $p < 0.0001$ '***'; $p < 0.001$ '**'; $p < 0.01$ '*'; $p < 0.05$ '.'; 'n.s.'.

results for mixtures with hornbeam, lime and ash appear in Table 4 and supplementary material (Figures A1-A2).

3.3.1. *Summer temperature*

An improved height growth was observed for oak mixed with beech with rising temperatures. However, the optimum temperature 16.4 °C that was indicated for monospecific stands did not appear to apply for mixed stands (Fig. 4a, Fig. 6a). In mixtures with hornbeam, the results were comparable to those for monospecific oaks. In mixtures with lime, the partial effect of summer temperature on oaks' heights became positively linear. Summer temperature had no significant influence on the mixture with pine (Fig. 6b) and ash (Table 4).

3.3.2. *Water balance and base saturation*

In mixture with beech, pine and lime, the water balance had a significantly positive linear effect on oak heights (Fig. 6c, d, Table 4). Mixed with hornbeam the positive effect was non-linear but when mixed with ash no significant effect was observed (Table 4).

In the case of base saturation, a significantly positive effect could be observed for the mixture with beech and hornbeam, with an optimum at medium base saturation (Fig. 6e, Table 4). With a well-balanced nutrient supply, low base saturation had no significant effect on height growth. A reduced growth of oak in the mixture with lime was still significant in the transition from a high base endowment to a balanced nutrient supply. The base saturation type played only a minor role for the mixtures

Table 4
Statistical GAMM output for oak in monospecific and mixed stands.

Variable	Oak monospecific *Est ± SE* *(Sig.)*	Oak (beech) *Est ± SE* *(Sig.)*	Oak (pine) *Est ± SE* *(Sig.)*	Oak (hornbeam) *Est ± SE* *(Sig.)*	Oak (lime) *Est ± SE* *(Sig.)*	Oak (ash) *Est ± SE* *(Sig.)*
Intercept	**3.033 ± 0.012** (***)	**3.278 ± 0.007** (***)	**3.168 ± 0.018** (***)	**3.087 ± 0.019** (***)	**3.120 ± 0.032** (***)	**3.196 ± 0.021** (***)
layer_single	−0.010 ± 0.008 (n.s.)	**−0.028 ± 0.005** (***)	**−0.040 ± 0.014** (**)	0.019 ± 0.024 (n.s.)	**−0.075 ± 0.030** (*)	**−0.123 ± 0.037** (**)
bs_type2	−0.001 ± 0.013 (n.s.)	**0.024 ± 0.008** (**)	−0.006 ± 0.020 (n.s.)	−0.009 ± 0.022 (n.s.)	−0.044 ± 0.034 (n.s.)	0.009 ± 0.029 (n.s.)
bs_type3	**0.032 ± 0.013** (*)	**0.050 ± 0.008** (***)	0.004 ± 0.019 (n.s.)	**0.058 ± 0.026** (*)	**0.074 ± 0.040** (.)	**0.069 ± 0.040** (.)
bs_type4	−0.003 ± 0.014 (n.s.)	**0.036 ± 0.009** (***)	−0.022 ± 0.020 (n.s.)	**0.069 ± 0.035** (*)	−0.069 ± 0.059 (n.s.)	−0.043 ± 0.069 (n.s.)
bs_type5	−0.002 ± 0.028 (n.s.)	0.013 ± 0.018 (n.s.)	−0.038 ± 0.031 (n.s.)	–	–	0.063 ± 0.149 (n.s.)
	Edf *(Sig.)*	*Edf* *(Sig.)*	*Edf* *(Sig.)*	*Edf* *(Sig.)*	*Edf* *(Sig.)*	*Edf* *(Sig.)*
f_1(age)	**8.915** (***)	**8.979** (***)	**8.856** (***)	**8.875** (***)	**7.488** (***)	**8.352** (***)
f_2(temp)	**3.949** (***)	**7.276** (***)	1.000 (n.s.)	**3.820** (**)	**1.000** (.)	1.000 (n.s.)
f_3(wb)	**1.000** (***)	**1.000** (***)	**1.000** (***)	**2.485** (***)	**1.000** (.)	1.000 (n.s.)
f_4(sdi)	**4.727** (***)	**5.458** (***)	**3.328** (***)	**2.308** (.)	**1.000** (**)	**1.000** (***)
f_5(lon, lat)	**10.574** (***)	**10.699** (***)	**7.187** (***)	7.828 (n.s.)	**2.000** (*)	**7.311** (***)
R-sq. (adj.)	0.82	0.74	0.73	0.77	0.86	0.80

Est = estimated parameter value, SE = standard error, Edf = effective degrees of freedom, Sig. = Significance levels: $p < 0.0001$ '***'; $p < 0.001$ '**'; $p < 0.01$ '*'; $p < 0.05$ '.'; 'n.s.'; layer_single = partial effect (p.e.) of single-layered stand situation (ref. multi-layered stand situation), bs_type2-bs_type5 = p.e. of base saturation types (ref. bs_type1), f(age) = p.e. of age, f(temp) = p.e. of summer temperature, f(wb) = p.e. water balance, f(sdi) = p.e. stand density index, f(lon, lat) = p.e. of lon / lat; R-sq. (adj.) = adjusted R-squared; significant coefficients are written in bold.

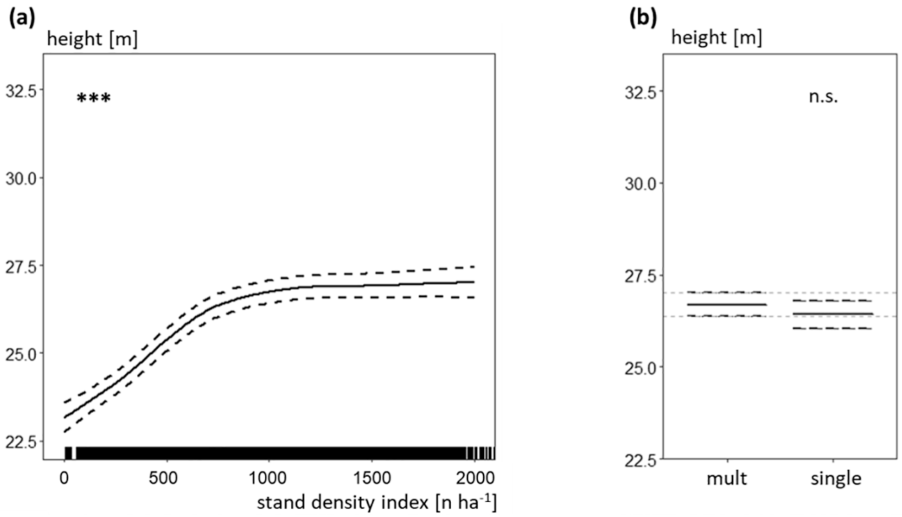

Fig. 5. Partial effects of structural variables on oak height growth in monospecific stands with stand density index (a) and vertical stand structure (b). For a graphical presentation, the age was set to 100, while the other variables were set to their mean. The categorical variables were set to medium base saturation and multi-layered. Significance levels: $p < 0.0001$ '***'; $p < 0.001$ '**'; $p < 0.01$ '*'; $p < 0.05$ '.'; 'n.s.'.

with pine and ash (Fig. 6f, Table 4).

3.3.3. Stand structure

Whereas the effect of temperature, water availability and base saturation was weaker in the oak-beech mixture, the influence of stand density on height growth was more positive. SDI values beyond 700 had no further positive effect (Fig. 7a). The positive effect, especially in less dense stands, was also observed for the oak-pine mixture (Fig. 7b). When mixed with lime or ash, the effect became linear. Unlike a less climate-sensitive reaction, the structural variables became more important for oaks' height growth. Density had a significant effect on oak heights as a structural variable in all mixtures, with the exception of oak-hornbeam mixtures (Table 4).

Additionally, the vertical structure of the stands played a role, especially in mixture. In the mixtures with beech, pine, lime and ash, the examined oaks were significantly taller in stands with at least a second tree layer (Fig. 7c, d, Table 4).

Depending on the mixture type, we found that both environmental

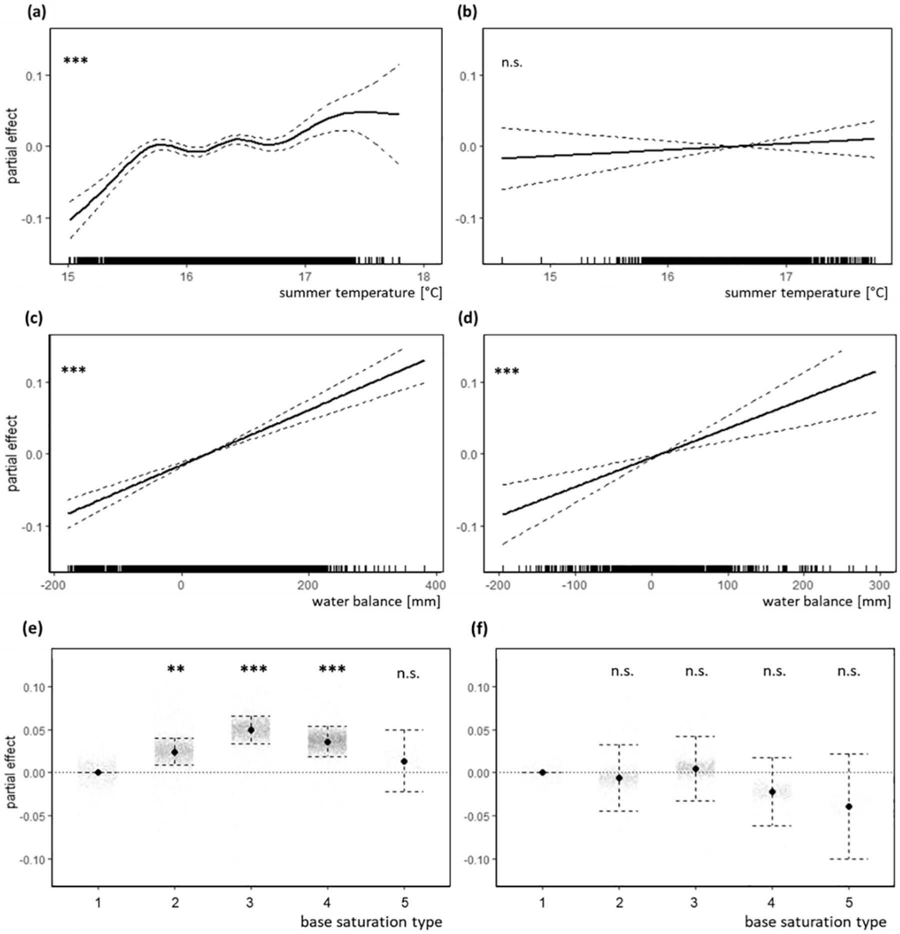

Fig. 6. Partial effects of environmental variables on oak height growth in mixture with beech (left) and pine (right), with summer temperature (a, b), water balance during vegetation period (c, d) and base saturation type (e, f). Significance levels: $p < 0.0001$ '***'; $p < 0.001$ '**'; $p < 0.01$ '*'; $p < 0.05$ '.'; 'n.s.'.

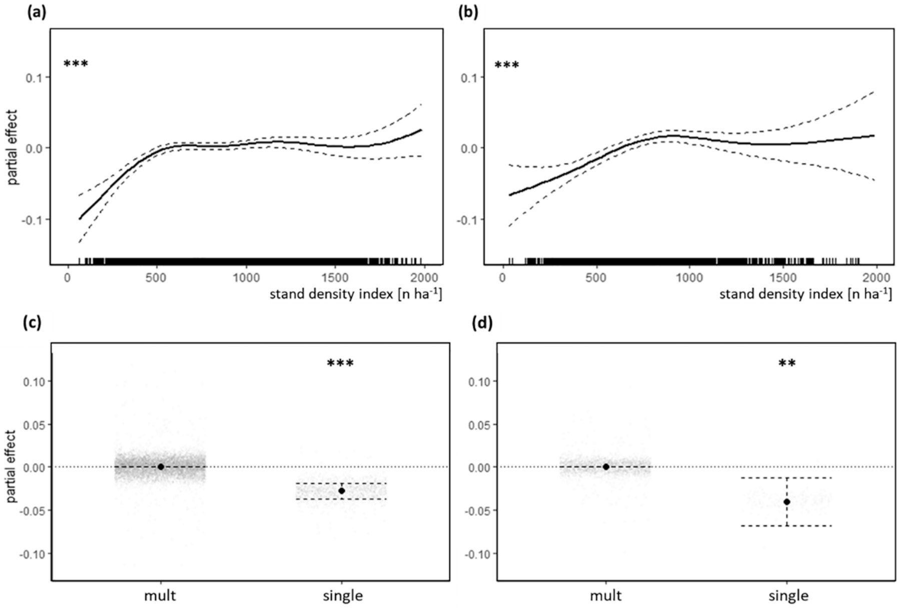

Fig. 7. Partial effects of stand structure on oak height growth in mixture with beech (left) and pine (right), with stand density index (a, b) and vertical stand structure (c, d). Significance levels: $p < 0.0001$ '***'; $p < 0.001$ '**'; $p < 0.01$ '*'; $p < 0.05$ '.'; 'n.s.'.

and structural variables had noticeably different partial effects on the tree height development of oaks.

With the exception of the oak-hornbeam mixture, the addition of the coordinates to the model revealed a significant spatial trend (Table 4).

4. Discussion

4.1. Methodological approach

By examining inventory data from two different sources, we were able to achieve a high spatial resolution with a broad gradient of site conditions and a high number of observations, including repeated measurements. Our data covered a wide range of forest practices, although the effect of forest management was not specifically considered in the model, but was indirectly covered by the use of structural effects such as stand density and layer structure.

The fact that we considered chronosequences as well as short-term longitudinal data may be a disadvantage for analysing height growth trajectories since young stands grew under slightly different climatic conditions than old stands (Klemmt, 2007). However, we argue that these affected both monospecific and mixed stands equally.

Forrester et al. (2013), for example, scrutinised the utilization of site indices for evaluating tree growth in mixture. Our approach characterised the height growth potential without a site index. We considered dominant tree heights, climatic and soil parameters with a high resolution which have been derived from a regionalised environmental database.

4.2. Effects on height growth of oaks

4.2.1. The effects of summer temperature, water availability and nutrient supply

We were able to show that the height growth of oak was modified by site-specific climatic conditions, such as summer temperature. Based on our results we assume that summer temperature is basically positive for oak height growth, although the effect is not large. These positive effects of temperature on tree growth have been reported in other studies, e.g. Bontemps et al. (2012), who found a significantly positive effect of temperature in the growing season by analysing height growth trajectories of oak over the last century. Albert and Schmidt (2010) investigated the climate-sensitive site productivity of five main tree species in Germany and also described a positive effect of temperature. By modelling the site index, Brandl et al. (2018) found this effect on spruce and beech. Additionally, young oaks appeared also to react positively to higher temperatures (Bonfils et al., 2015).

Water balance also has a significant effect on tree height growth (Fig. 4b). The positively linear effect we observed correlates with several other studies dealing with the site productivity of various tree species (Albert and Schmidt, 2012; Bonfils et al., 2015; Brandl et al., 2018; Zeller et al., 2018). Albert and Schmidt (2012) described thresholds for the seasonal water balance and the corresponding water shortage risks for the main tree species. According to this, oak and pine had a high risk with a water balance $<$ -500 mm and beech $<$ -400 mm. Compared with the water balance we observed in our study, we concluded that the risk for all analysed tree species is moderate, which explains the observed positive linear trend. Bonfils et al. (2015) found a reduced height growth in very dry site conditions for young oaks. The reason seemed to be a shift in resource allocation in favour of increased root growth, which allowed oak to maintain its supply of water. We assume that our findings on the reaction of height growth of mature oaks as a function of the water balance follow similar physiological rules and may be an indication of better adaptability to drier site conditions during climate change. In addition, the positive temperature effect on oaks' height growth seems to be eclipsed by the negative partial effect due to an expected lower water balance.

Furthermore, areas with a negative water balance and higher temperatures are also the core region of insect pests (e.g. green oak moth, gypsy moth) on oak that could affect tree growth (Zang et al., 2011). A negative effect on radial growth has been described in several studies (Fajvan et al., 2008; Rubtsov, 1996). In addition, oak powdery mildew can also have an increasing influence on oaks with changing climate (Marçais and Desprez-Loustau, 2014). The present study is unable to say whether there has been an effect of biotic or abiotic pests on height growth. However, regions with reduced growth appear to be emerging in the north and south.

The nutrient supply, expressed through base saturation, hardly affected the height growth of oak (Fig. 4c). We assume that water availability is more likely to be the limiting underground resource. Thus, the limiting factor for growth is the availability of water and light if sufficient nutrients are present (Forrester, 2014; Forrester, 2019).

We conclude that the potential height growth of oak will fall in future due to the predicted changes in water balance. Without knowing the effect of changing climate on the potential height growth of other species, we cannot predict whether this will result in any improvement in the height growth-related competitiveness of oaks.

4.2.2. The modifying effect of stand density and vertical stand structure

The structural variables of stand density and mixture affected the height growth of oak. We found a highly positive effect of stand density with a saturation effect beyond an SDI of 800 trees per hectare for monospecific stands (Fig. 5a). These results are in line with the density-height relationship described by Assmann (1970). He identified a positive effect of stand density on the tree height up to a certain level, which has also been corroborated more recently (Forrester, 2019; Pretzsch, 2019). Pretzsch and Biber (2010) described an increased competition for light if soil resources do not limit tree growth. Forrester (2014) determined light to be a major limiting factor after canopy closure. For sessile oak, Trouvé et al. (2015) found a modifying influence of stand density on the growth allocation based on long-term experimental data. As light demanding species, oaks try to grow towards the light with increased height growth (Lüpke, 1998). The partial effects of SDI on oaks growing in mixture underline the results for oaks in monospecific stands. In mixture with beech, the effect of stand density is noticeably strong. A steep slope for lower values shows a high positive contribution to tree heights up to an SDI of 500 (Fig. 7a). Furthermore, the visible flatter increase for oak-pine stands indicates the species-specific growth reaction and demonstrates the effect of competition for light on height growth (Fig. 7b). The interspecific competition in mixtures with beech seems to be more apparent than in mixtures with pine. In mixtures with pine, we can assume that oak received enough light to grow due to a higher light transmission of pine (del Río et al., 2014; Jucker et al., 2014), and so does not require accelerated height growth.

The vertical structure of stands and its effect upon oaks tree height varied between different mixture types. Mainly positive effects could be demonstrated in mixed stands. The effect of a multi-layered stand situation is associated with taller oaks in mixed stands, except in an oak-hornbeam mixture. The understory seems to improve oak height growth slightly. We attribute this to an additional positive interspecific effect that favours height growth and is not explained through the stand density of the main stand.

4.2.3. Effects on height growth due to mixture types

We found mixture type specific effects on oak tree height growth. Oak showed a less climate-sensitive reaction in the two-species mixtures compared with monocultures. We assume that our findings are caused by different growth allocation and complementarity effects between tree species. These findings for oak tree heights in mixture with beech are in line with previous studies analysing the dominant height using French forest inventory data (Vallet and Perot, 2016). At the same time, heights appear to be smaller in the mixture with pine that is in line with the reaction to stand density described above. These results for both mixtures are in line with the results of former studies (Pretzsch et al., 2019; Steckel et al., 2019). Pinto et al. (2008) also found different dominant height growth reactions for *Abies alba* due to the admixed species where a positive interaction with stand density was traced back to maintaining access to light. These mixture-dependent reactions are in line with previous studies dealing with mixture effects (Forrester, 2019). From a productivity standpoint, other studies found mixture effects due to the admixed species (Pretzsch et al., 2013a; Pretzsch et al., 2019; Toïgo et al., 2015; Toïgo et al., 2018), even if the effect on productivity is not the same as on height growth. However, one has to bear in mind the change in growth allocation mentioned above when comparing the radial and height growth of trees in different mixed stands or between mixed and monospecific stands. Consequently, this also effects stem taper and hence stem volume where the use of a species-specific function may be biased when ignoring these effects.

Since stand structure can be influenced by forest management, the structural effect identified here provides valuable indications for forest practice on how to promote oak. Stand density regulation in particular seems to be a suitable management option to compensate for negative climatic effects. A delayed introduction of admixed species can reduce silvicultural investments while also ensuring the vitality of mixed species stands. This should also be considered when interpreting site-sensitive growth reactions that can be traced back to climatic factors.

4.3. Implications for current and future height growth-related competitiveness

Adaptive forest management favours stands composed of a mixture of several tree species (Lindner, 2000; Lindner et al., 2010). In addition, the structure of the stands should be heterogeneous in order to increase resistance, resilience and recovery after damages caused by climate changes. In this context, oak is of special importance because it is considered to be thermophilic, drought-tolerant and wind stable (Annighöfer et al., 2015; Kölling and Zimmermann, 2007). Contrary to these positive characteristics, it is competitively inferior to many tree species that grow with it in mixture (Ellenberg and Strutt, 1988; Mosandl and Abt, 2016). Height growth of a tree species is important for its competitiveness in terms of survival within the stands. Our results show that the competitive power of oak, especially in mixture with beech, does not necessarily increase in large areas under climate change. Fig. 8 shows these schematically for the oak-beech (a, b) and oak-pine (c, d) plots. Under current climatic conditions, oak is inferior in particular to beech, its strongest competitor, even in the warmest and driest areas (Fig. 8b). Felbermeier (1993) and Harrer (2004) analysed the growth potential of beech in Bavaria and observed the tallest beeches in the centre of our study region. This indicates the high competitiveness of beech. A superior height growth of beech could be observed in the mixed stands under consideration in particular. We assume that beech seems to benefit additionally from oak in these stands due to species complementarity and facilitation, e.g. the hydraulic lift (Forrester, 2014; Forrester, 2019; Pretzsch et al., 2013a; Pretzsch et al., 2013b). Furthermore, improved height growth of mature beech trees after years with sufficient water availability (Mattes et al., 2013) can increase the species' superiority. Concurrent changes in temperature and precipitation regime nevertheless attest to an increase in the competitiveness and vitality of beech (Ammer et al., 2005). In contrast, oak has been found to be comparatively insensitive to climate (Pretzsch et al., 2013a; Pretzsch et al., 2019; Steckel et al., 2020).

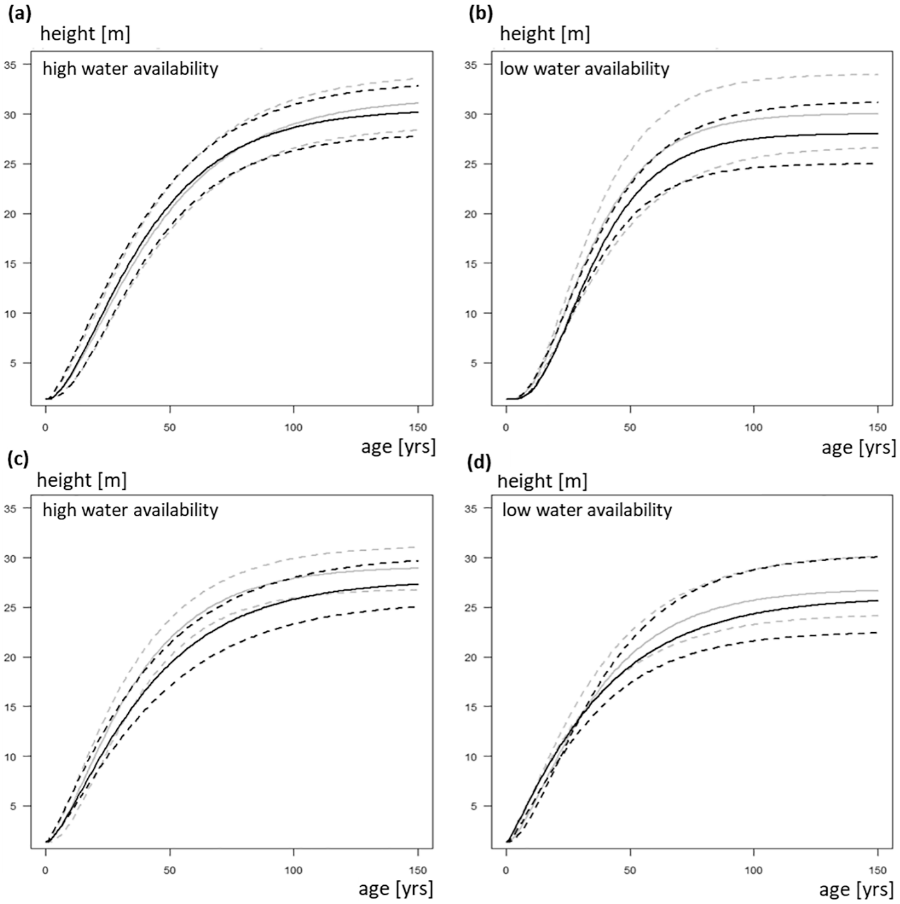

Fig. 8. Height growth trajectories for oak and beech (a, b) and oak and pine (c, d) in mixture for currently moist (a, c; wb > 0 mm) and dry (b, d; wb < 0 mm) site conditions; oak (black), beech or pine (grey), solid line (0.5 quantile), dashed lines (0.25 and 0.75 quantile).

Further studies dealing with the competitiveness of oak compared to other admixed species also show a promotion of oak under higher temperatures, especially compared to beech (Bontemps et al., 2012; Mette et al., 2013). Our findings for beech and oak height growth trajectories are only partly in line with such assumptions. We found shifts of height growth relations due to temperature and water regime which were not in favour of oak when mixed with beech. We attribute this observation to the climatic amplitude of beech. Apparently, most of our study sites are close to the optimum for beech with regard to temperature and water balance. Mette et al. (2013) spoke of a summer temperature above 18 °C for a climatic turning point between beech and oak and Albert and Schmidt (2012) assigned an increased drought stress risk for beech as of a water deficit of −134 mm.

On the basis of our results, we cannot identify a considerable shift in the competitive situation in favour of oak for warm and dry areas under current climatic conditions. Nonetheless, we expect a lower competitiveness of the admixed species, namely beech, for future climatic conditions in view of a higher frequency of extreme climatic events under long-term climatic trends. This is likely to promote the interspecific competitiveness of oak.

4.4. Silvicultural consequences

The overarching objective of current silvicultural practices to adapt forests to climate change should be the establishment of structured, mixed stands of high vitality with the aim to reduce risks and increase biodiversity (Bolte et al., 2009). Therefore, the favouring of oak as a drought-tolerant and thermophilic species should be encouraged. In general, monospecific stands combined with high temperatures and an increasingly low water availability also seems at risk of infestation by species specific insect pests (Castagneyrol et al., 2014). For forest protection, the establishment of monospecific stands should be avoided at all costs. In addition to the high forest protection risks posed by monospecific stands, the climate sensitivity of oak trees can be lowered in mixed stands, which additionally reduce the biotic and abiotic risks. Apart from this, mixed oak stands can result in increased stand productivity (Pretzsch et al., 2013a). Mixed oak stands should be established not only for the aforementioned reasons, but also because of the expected better wood quality of oak (Lüpke, 1998; Saha et al., 2014) or increased biodiversity due to the admixture. The creation of multilayered oak stands with an understory of more shade-tolerant mixed species should be maintained in particular.

One has to remember that both complementary and competition effects can occur in mixed stands. As mentioned above, comparatively high ratios of oak could already be found in warm and dry regions, largely due to silvicultural practices (Leuschner and Ellenberg, 2017; Mosandl and Abt, 2016). These proportions of oak, grown under marginal climatic conditions, could only be maintained or increased by consistent silvicultural assistance in favour of oak. The complementary as well as the competitive effects have to be managed through silvicultural efforts. When considering the observed height growth reaction of oak, a fundamental change in competitive ability is apparently not to be expected. However, in order to be prepared for further climatic changes, a consistent promotion of the oak seems to be appropriate.

Nevertheless, we expect a negative reaction of beech to sharply rising temperatures and especially more frequent extreme drought periods (Bolte, 2016). This should also be accompanied by an improved competitiveness of oak that could mitigate the need of silvicultural efforts. Beside sites that are no longer suitable for less drought-tolerant admixed tree species due to lower water availability, additional sites suitable for oak also seem to appear.

We assume that expected climatic changes indicate the establishment of mixed oak forests that could improve the adaptation capacity of European mixed forests. However, silvicultural management is still crucial for building up and maintaining a sufficient oak proportion and foster vital, vigorous and healthy oaks within mixed stands. These oaks are essential for the continued existence of oak and appropriate tree species proportions. The potential loss of vitality that can be induced by intra- and interspecific competition, drought periods or insect pests should be avoided by silvicultural promotion. From the beginning of the canopy closure, it is important to consistently promote future crop trees with crown thinnings, which help to develop vigorous crowns. The silvicultural assistance mentioned here is most urgently needed on those sites where oak is grown outside its real ecological niche.

5. Conclusion

Our investigations are related to the Federal State of Bavaria. Due to its geographical location in Central Europe, the results can probably be applied to large parts of Europe with comparable conditions. Because of the consideration of oak in mixed stands and the investigation of shifts in site-specific competition between tree species, these results with their large spatial distribution are important for forestry. This is especially true given that pedunculate and sessile oak cover substantial parts of European forests.

The native oak species with their comparatively high climate tolerance can make a decisive contribution to the further development of climate-tolerant mixed stands. We found a climatically and structurally-induced height growth reaction of oak for six mixture types. However, the competitive strength, as measured by the height growth performance of the oak species, hardly seems to increase, even in warm and dry regions under current conditions. The negative effect of the expected water balance seems to eclipse the positive temperature effect, leading to reduced oak heights in future. Based on the results and due to the importance of height growth for competitive strength, it therefore appears that further silvicultural support is needed for a successful establishment and continuity of appropriate oak proportions in mixed stands. This silvicultural support can be the continuous crown thinning or a delayed introduction of the admixed tree species, which could minimise thinning efforts by ensuring all positive effects of mixed species stands at the same time.

Forest inventories reveal climatic and site-specific effects on oak along an ecological gradient. After we have used regionalised, but modelled soil information a more detailed soil assessment is desirable. This may provide additional information for a more detailed evaluation and explanation of unaccounted aspects. For further research, it would also be desirable to include forest management strategies, e.g. thinning. Thus, these effects can directly be analysed and will improve the development of silvicultural guidelines now and in the future.

Funding

This work was supported by the Bavarian State Ministry of Nutrition, Agriculture and Forestry through the project “Growth potential of oak in managed and unmanaged forests dependent on stand structure and site conditions (W045)” [grant number 7831–27295-2017].

CRediT authorship contribution statement

Kilian Stimm: Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Michael Heym:** Software, Data curation, Writing - review & editing. **Enno Uhl:** Conceptualization, Writing - review & editing, Funding acquisition. **Stefan Tretter:** Conceptualization, Resources, Writing - review & editing. **Hans Pretzsch:** Conceptualization, Writing - review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the Thuenen Institute of Forest Ecosystems and the Bavarian State Forest Enterprise for providing the forest inventory data. We also thank the Bavarian State Institute of Forestry for providing regionalised climate and soil data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118780.

References

Aas, G., 2000. Quercus petraea (Matt.) Liebl., Traubeneiche, in: Roloff, A., Weisgerber, H., Lang, U., Stimm, B. (Eds.), Enzyklopädie der Holzgewächse. Wiley-VCH, Weinheim.

Aas, G., 2002. Quercus robur L., Stieleiche. In: Roloff, A., Weisgerber, H., Lang, U., Stimm, B. (Eds.), Enzyklopädie der Holzgewächse. Wiley-VCH, Weinheim, pp. 1–15.

Albert, M., Schmidt, M., 2010. Climate-sensitive modelling of site-productivity relationships for Norway spruce (Picea abies (L.) Karst.) and common beech (Fagus sylvatica L.). Forest Ecology and Management 259, 739–749.

Albert, M., Schmidt, M., 2012. Standort-Leistungs-Modelle für die Entwicklung von waldbaulichen Anpassungsstrategien unter Klimawandel. Archiv f. Forstwesen u. Landsch.ökol. 46, 57–71.

Ammer, C., Albrecht, L., Borchert, H., Brosinger, F., Dittmar, C., Elling, W. et al, 2005. Zur Zukunft der Buche (Fagus sylvatica L.) in Mitteleuropa: Kritische Anmerkungen zu einem Beitrag von Rennenberg et al. (2004). Allgemeine Forst-und Jagdzeitung 176, 60–67.

Annighöfer, P., Beckschäfer, P., Vor, T., Ammer, C., 2015. Regeneration patterns of European oak species (Quercus petraea (Matt.) Liebl., Quercus robur L.) in dependence of environment and neighborhood. PLOS ONE 10, e0134935.

Assmann, E., 1970. The principles of Forest Yield Study: Studies in the Organic Production, Structure. Pergamon Press, Oxford, New York, Toronto, Sydney, Braunschweig, Increment and Yield of Forest Stands.

Bauhus, J., Forrester, D.I., Pretzsch, H., 2017. From Observations to Evidence About Effects of Mixed-Species Stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests: Ecology and Management. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 27–71.

Bolte, A., 2016. Chancen und Risiken der Buche im Klimawandel. AFZ-DerWald 12.

Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.-J., Schall, P., et al., 2009. Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. Scandinavian Journal of Forest Research 24, 473–482.

Bonfils, P., Rigling, A., Brändli, U.-B., Brang, P., Forster, B., Engesser, R. et al, 2015. Die Eiche im Klimawandel: Zukunftschancen einer Baumart. Merkblatt für die Praxis 55.

Bontemps, J.-D., Herve, J.-C., Duplat, P., Dhôte, J.-F., 2012. Shifts in the height-related competitiveness of tree species following recent climate warming and implications for tree community composition: The case of common beech and sessile oak as predominant broadleaved species in Europe. Oikos 121, 1287–1299.

Brandl, S., Falk, W., Klemmt, H.-J., Stricker, G., Bender, A., Rötzer, T., et al., 2014. Possibilities and Limitations of Spatially Explicit Site Index Modelling for Spruce Based on National Forest Inventory Data and Digital Maps of Soil and Climate in Bavaria (SE Germany). Forests 5, 2626–2646.

Brandl, S., Mette, T., Falk, W., Vallet, P., Rötzer, T., Pretzsch, H., 2018. Static site indices from different national forest inventories: Harmonization and prediction from site conditions. Annals of Forest Science 75, 739.

Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E.G., Koricheva, J., 2014. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. J Appl Ecol 51, 134–141.

del Río, M., Condés, S., Pretzsch, H., 2014. Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (Fagus sylvatica L.) mixed stands. Forest Ecology and Management 325, 90–98.

Dolos, K., Mette, T., Wellstein, C., 2016. Silvicultural climatic turning point for European beech and sessile oak in Western Europe derived from national forest inventories. Forest Ecology and Management 373, 128–137.

Ellenberg, H.H., Strutt, G.K., 1988. Vegetation Ecology of Central Europe. Cambridge University Press.

Fajvan, M.A., Rentch, J., Gottschalk, K., 2008. The effects of thinning and gypsy moth defoliation on wood volume growth in oaks. Trees 22, 257–268.

Felbermeier, B., 1993. Der Einfluß von Klimaänderungen auf die Areale von Baumarten. Methodenstudie und regionale Abschätzung für die Rotbuche (Fagus sylvatica L.) in Bayern. Forstlicher Forschungsbericht.

Fischer, H.S., Michler, B., Fischer, A., 2018. Die zukünftige pnV Bayerns: Wie man sich Vorstellungen über die Standortsituation der Zukunft erarbeiten kann. LWF Aktuell 46–49.

Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. Forest Ecology and Management 312, 282–292.

Forrester, D.I., 2019. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. Forest Ecology and Management 447, 139–157.

Forrester, D.I., Kohnle, U., Albrecht, A.T., Bauhus, J., 2013. Complementarity in mixed-species stands of Abies alba and Picea abies varies with climate, site quality and stand density. Forest Ecology and Management 304, 233–242.

Gadow, K.v., 2003. Waldstruktur und Wachstum.

Grundmann, B.M., Roloff, A., 2009. Use of Forest Tree Species Under Climate Change, in: Feldmann, F. (Ed.), Crop plant resistance to biotic and abiotic factors. Current potential and future demands; proceedings of the 3rd International Symposium on Plant Protection and Plant Health in Europe, held at the Julius-Kühn-Institut, Berlin-Dahlem, Germany, 14-16 May 2009. DPG, Braunschweig. DPG Spectrum Phytomedizin, pp. 53–65.

Harrer, E., 2004. Wachstumstrends der Buche in Bayern.: Untersuchungen zur Auswirkung der Bestandesbehandlung auf das Wachstum der Buche., unpublished final report.

Hertel, D., 1999. Das Feinwurzelsystem von Rein- und Mischbeständen der Rotbuche: Struktur, Dynamik und interspezifische Konkurrenz. Cramer in der Gebr.-Borntraeger-Verl.-Buchh, Berlin. Dissertationes Botanicae 317.

Jacob, D., Goettel, H., Kotlarski, S., Lorenz, P., Sieck, K., 2008. Klimaauswirkungen und Anpassung in Deutschland - Phase 1: Erstellung regionaler Klimaszenarien für Deutschland. Fachbibliothek Umwelt.

Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., et al., 2014. Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. J Ecol 102, 1202–1213.

Klemmt, H.-J., 2007. Standortabhängige Ableitung der Höhenwuchsleistung aus Forstinventurdaten mit Hilfe von Data-Mining-Methoden. Grundlage für die Regionale, Standortbezogene Feinjustierung des forstlichen Wuchsmodells SILVA.

Klemmt, H.-J., Bachmann, M., 2012. Numerische Bewertung der Entnahmenotwendigkeit bei Pflegeeingriffen. LWF Aktuell 11–13.

Kölling, C., 2010. Macht sauer wirklich lustig?: Drei Viertel der Waldböden Bayerns sind kaum versauert, aber das restliche Viertel lässt Probleme erwarten. LWF Aktuell 78, 21–24.

Kölling, C., Zimmermann, L., 2007. Die Anfälligkeit der Wälder Deutschlands gegenüber dem Klimawandel. Gefahrstoffe-Reinhaltung der Luft 67, 259–268.

Krahl-Urban, J., 1959. Die Eichen: forstliche Monographie der Traubeneiche und der Stieleiche. P. Parey.

Leuschner C, Ellenberg H, 2017. Ecology of Central European Forests: Vegetation ecology of central europe, Volume 1 (accessed 21 June 2019).

Leuschner, C., Hertel, D., Coners, H., Büttner, V., 2001. Root competition between beech and oak: a hypothesis. Oecologia 126, 276–284.

Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate change. Tree physiology 20, 299–307.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., et al., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259, 698–709.

von Lüpke, B., 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. Forest Ecology and Management 106, 19–26.

Manthey, M., Leuschner, C., Härdtle, W., 2007. Buchenwälder und Klimawandel.

Marçais, B., Desprez-Loustau, M.-L., 2014. European oak powdery mildew: impact on trees, effects of environmental factors, and potential effects of climate change. Annals of Forest Science 71, 633–642.

Mattes, A., Kahle, H.-P., Spiecker, H., 2013. Höhenwachstumsveränderungen nach Trockenstress: Reagieren Buchen und Traubeneichen unterschiedlich? Beiträge zur Jahrestagung, DVFFA, Sektion Ertragskunde, pp. 95–106.

Mette, T., Dolos, K., Meinardus, C., Bräuning, A., Reineking, B., Blaschke, M., et al., 2013. Climatic turning point for beech and oak under climate change in Central Europe. Ecosphere 4, 1–19.

Mosandl, R., Abt, A., 2016. Waldbauverfahren in Eichenwäldern gestern und heute. AFZ - Der Wald 28–32.

Neufanger, M., 2011. FE-AA-010_Durchfuehrung_von_Betriebsinventuren, Regensburg.

Nothdurft, A., Wolf, T., Ringeler, A., Böhner, J., Saborowski, J., 2012. Spatio-temporal prediction of site index based on forest inventories and climate change scenarios. Forest Ecology and Management 279, 97–111.

Pinto, P.E., Gégout, J.-C., Hervé, J.-C., Dhôte, J.-F., 2008. Respective importance of ecological conditions and stand composition on Abies alba Mill. dominant height growth. Forest Ecology and Management 255, 619–629.

Polley, H., 2011. Aufnahmeanweisung für die dritte Bundeswaldinventur BWI3, 2011–2012.

Pretzsch, H., 2019. Grundlagen der Waldwachstumsforschung. Springer, Berlin Heidelberg, Berlin, Heidelberg.

Pretzsch, H., Biber, P., 2010. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Canadian Journal of Forest Research 40, 370–384.

Pretzsch, H., Biber, P., 2016. Tree species mixing can increase maximum stand density. Can. J. For. Res. 46, 1179–1193.

Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., et al., 2013a. Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. European Journal of Forest Research 132, 263–280.

Pretzsch, H., Schütze, G., Uhl, E., 2013b. Resistance of European tree species to drought stress in mixed *versus* pure forests: Evidence of stress release by inter-specific facilitation: Drought stress release by inter-specific facilitation. Plant Biology 15, 483–495.

Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., et al., 2019. Stand growth and structure of mixed-species and monospecific stands of Scots pine (Pinus sylvestris L.) and oak (Q. robur L., Quercus petraea (Matt.) Liebl.) analysed along a productivity gradient through Europe. European Journal of Forest Research.

R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. Journal of Agricultural Research 46, 627–638.

Richards, F.J., 1959. A Flexible Growth Function for Empirical Use. J Exp Bot 10, 290–301.

Rubtsov, V.V., 1996. Influence of repeated defoliations by insects on wood increment in common oak (Quercus robur L). Ann. For. Sci. 53, 407–412.

Saha, S., Kuehne, C., Bauhus, J., 2014. Intra- and interspecific competition differently influence growth and stem quality of young oaks (Quercus robur L. and Quercus petraea (Mattuschka) Liebl.). Annals of Forest Science 71, 381–393.

Schütz, J.-P., 1993. High-quality oak silviculture in Switzerland: concepts of education and production in the marginal range of European oak. Ann. For. Sci. 50, 553–562.

Spathelf, P., van der Maaten, E., van der Maaten-Theunissen, M., Campioli, M., Dobrowolska, D., 2014. Climate change impacts in European forests: the expert views of local observers. Annals of Forest Science 71, 131–137.

Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G. et al, 2020. Species mixing reduces drought susceptibility of Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. Forest Ecology and Management.

Steckel, M., Heym, M., Wolff, B., Reventlow, D.O.J., Pretzsch, H., 2019. Transgressive overyielding in mixed compared with monospecific Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) stands – Productivity gains increase with annual water supply. Forest Ecology and Management 439, 81–96.

Strona, G., Mauri, A., San-Miguel-Ayanz, J., 2016. A high-resolution pan-European tree occurrence dataset.

Thuenen-Institut, 2017. BWI Daten.

Toïgo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.-C., Longuetaud, F., et al., 2018. Difference in shade tolerance drives the mixture effect on oak productivity. J Ecol 106, 1073–1082.

Toïgo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C., Courbaud, B., 2015. Overyielding in mixed forests decreases with site productivity. J Ecol 103, 502–512.

Trouvé, R., Bontemps, J.-D., Seynave, I., Collet, C., Lebourgeois, F., 2015. Stand density, tree social status and water stress influence allocation in height and diameter growth of Quercus petraea (Liebl.). Tree physiology 35, 1035–1046.

Turc, L., 1961. Estimation of irrigation water requirements, potential evapotranspiration: a simple climatic formula evolved up to date. 13–49. Annals of Agronomy 12, 13–49.

Vallet, P., Perot, T., 2016. Tree diversity effect on dominant height in temperate forest. Forest Ecology and Management 381, 106–114.

Vospernik, S., 2017. Possibilities and limitations of individual-tree growth models – A review on model evaluations. Die Bodenkultur: Journal of Land Management, Food and Environment 68, 283.

Wood, S.N., 2017. Generalized Additive Models: An Introduction with R, (2nd edition). Chapman and Hall/CRC.

Zang, C., Rothe, A., Weis, W., Pretzsch, H., 2011. Zur Baumarteneignung bei Klimawandel: Ableitung der Trockenstress-Anfälligkeit wichtiger Waldbaumarten aus Jahrringbreiten. Allgemeine Forst-und Jagdzeitung 182, 98–112.

Zeller, L., Liang, J., Pretzsch, H., 2018. Tree species richness enhances stand productivity while stand structure can have opposite effects, based on forest inventory data from Germany and the United States of America. For. Ecosyst. 5, 3.

B - Article II

Title:

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

Authors:

Kilian Stimm, Michael Heym, Ralf-Volker Nagel, Enno Uhl, Hans Pretzsch

Journal:

Forests 2022, Volume 13, Issue 5, 724

Impact Factor:

3.282

forests

MDPI

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

Kilian Stimm [1,2,*], Michael Heym [1,2], Ralf-Volker Nagel [3], Enno Uhl [1,2] and Hans Pretzsch [1]

[1] Chair of Forest Growth and Yield Science, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; michael.heym@lwf.bayern.de (M.H.); enno.uhl@tum.de (E.U.); hans.pretzsch@tum.de (H.P.)
[2] Bavarian State Institute of Forestry, Hans-Carl-von-Carlowitz-Platz 1, 85354 Freising, Germany
[3] Department A (Forest Growth), Northwest German Forest Research Institute, Grätzelstraße 2, 37079 Göttingen, Germany; ralf.nagel@nw-fva.de
* Correspondence: kilian.stimm@tum.de

check for updates

Citation: Stimm, K.; Heym, M.; Nagel, R.-V.; Uhl, E.; Pretzsch, H. 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. *Forests* **2022**, *13*, 724. https://doi.org/10.3390/f13050724

Academic Editors: Ion Catalin Petritan, Jarosław Paluch and Timothy A. Martin

Received: 15 February 2022
Accepted: 1 May 2022
Published: 5 May 2022

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 [°C] (1970–2000); Alt—altitude above sea level [m.a.s.l.]; mean values, min and max values in italics below.

	N	*n*	S [ha]	Per	Int [yrs]	hq 100 [m]	Prec [mm]	Temp [°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 ha^{-1} $year^{-1}$.

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

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.

$$cpa = 0.07 \times dbh^{1.70} \tag{2}$$

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)).

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

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].

$$SDI = \sum_{1}^{m} n_m \times \left(\frac{25}{d_{q_m}}\right)^{-1.605} \times E_m \tag{4}$$

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 ($Prop_{\mathrm{oak}}$, 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.

$$Prop_{oak} = \frac{SDI_{oak}}{SDI} \tag{5}$$

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)).

$$rel\_d_f = {}^{dbh_f}\!\big/_{dbh_{max}} \tag{6}$$

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)).

$$cvh = {}^{sd\_h}\!\big/_{\overline{h}} \tag{7}$$

where *sd_h* and $\overline{h}$ 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.

		PAIV	***Vol***	**Age**	***SDI***	$Prop_{oak}$	***SI***	***GDC***	***cvh***
[*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.

		iv/cpa	**Age**	***rel_d***	***cpa***
[*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.

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

where *PAIV* is the stand productivity in m^3 ha^{-1} $year^{-1}$. *V* is the standing volume in m^3 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)).

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

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.

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

where *iv/cpa* is the single tree productivity in dm^3 m^{-2} 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.

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

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

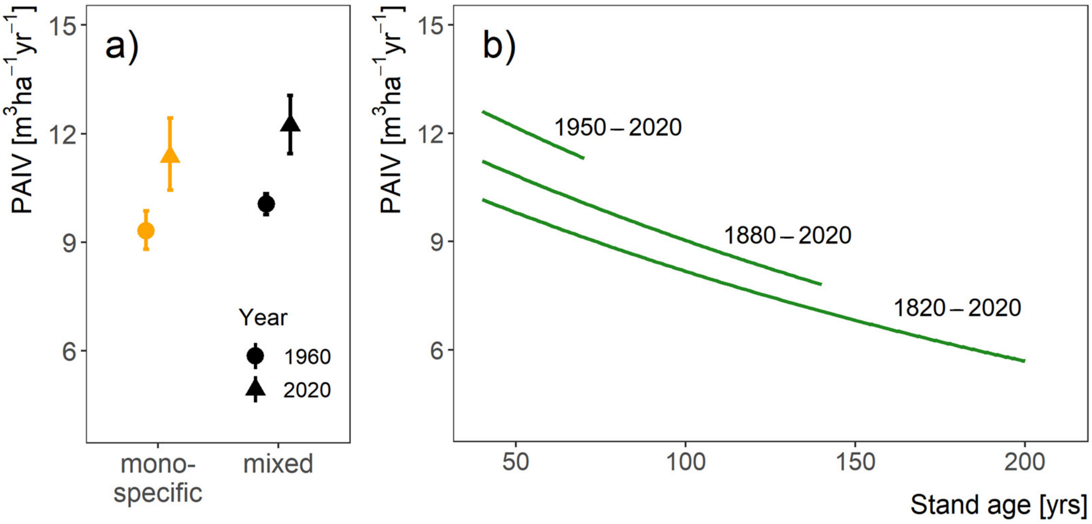

Figure 1. Stand productivity for monospecific and mixed oak stands at the age of 100 for different Calendar years (**a**); stand productivity for monospecific oak stands as a function of stand age after culmination (not shown) for different growing periods (**b**); all other variables were set to their 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 ha^{-1} $year^{-1}$ 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 m^3 ha^{-1} $year^{-1}$ on the less productive sites to 12.8 m^3 ha^{-1} $year^{-1}$ 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 m^3 ha^{-1} $year^{-1}$ 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.

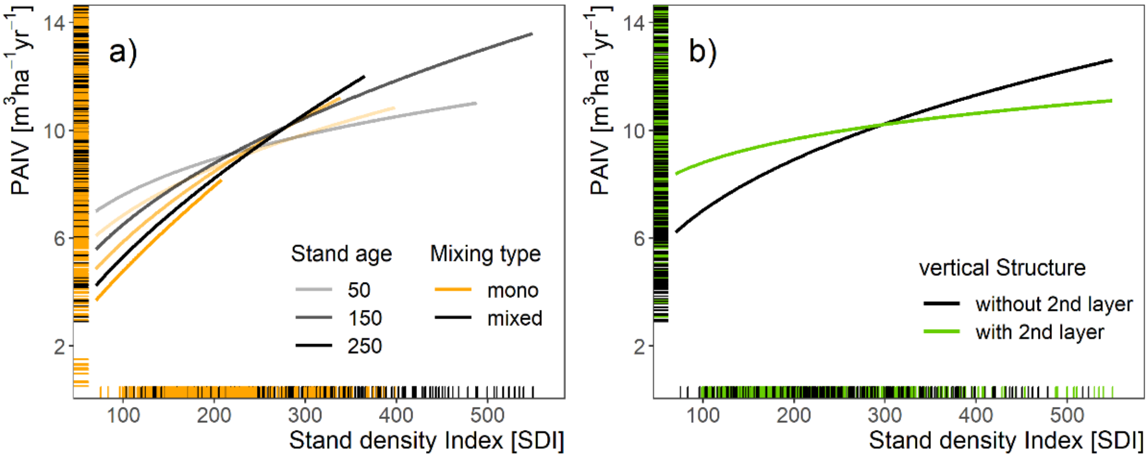

Figure 2. Stand productivity for monospecific and mixed oak stands as a function of stand density, stand age and mixing type (**a**) and as a function of stand density and vertical structure (**b**); rugs on the x-and y-axis indicate the observed values of *SDI* and stand productivity, respectively;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

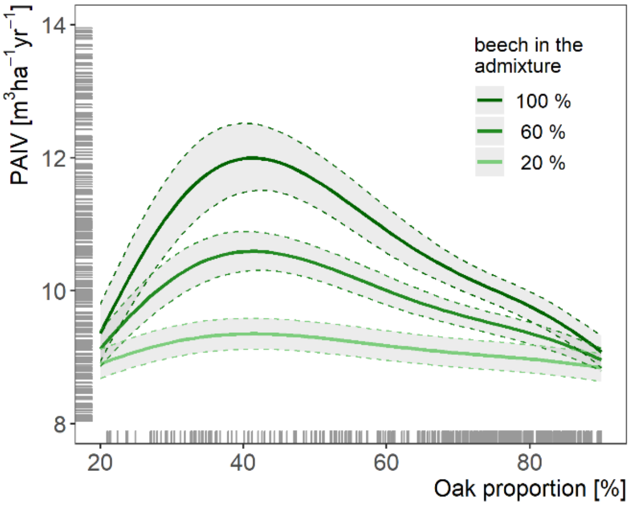

Figure 3. Non-linear smooth functions (GAMM) of stand productivity for mixed oak stands as a function of oak proportions and proportion of beech in the admixture; rugs on the x-and y-axis indicate the observed values of oak proportions and stand productivity, respectively; for the underlying model statistics 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	*p*-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	*rel_d*	2.636	0.037	<0.001	***	ε_{ijft}	0.46
a_4	MT [mono]	−0.061	0.011	<0.001	***		
a_5	*cvh*	0.260	0.061	<0.001	***	*n* obs	67.479
a_6	ln (Age) * ln (*SDI*)	−0.782	0.027	<0.001	***	pseudo-R^2 (m/c)	0.38/0.70
a_7	ln (Age) * *rel_d*	−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) * *cvh*	−0.231	0.093	0.013	*		
a_{10}	*rel_d* * MT [mono]	0.669	0.048	<0.001	***		
a_{11}	*rel_d* * ln (*SDI*)	−0.126	0.058	0.030	*		
a_{12}	*rel_d* * *cvh*	2.953	0.197	<0.001	***		
a_{13}	*cvh* * ln (*SDI*)	−0.341	0.109	0.002	**		
a_{14}	MT [mono] * ln (*SDI*)	0.136	0.027	<0.001	***		
a_{15}	MT [mono] * *cvh*	0.273	0.085	0.001	**		

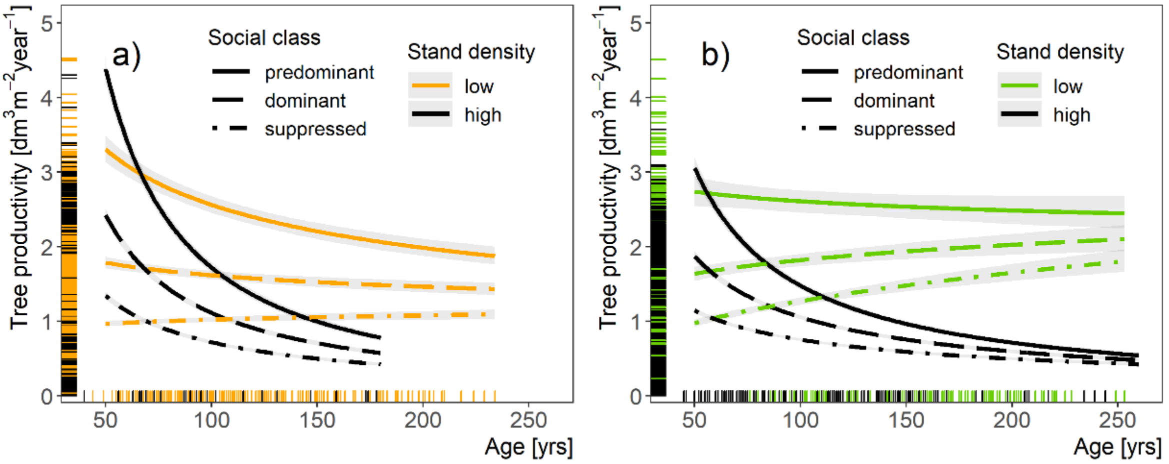

Figure 4. Productivity of oak trees growing in monospecific (**a**) and mixed species (**b**) stands as a function of Age, stand density and social class; low stand density = *SDI* of 100, high stand density = *SDI* of 350; rugs on the x-and y-axis indicate the observed values of age and tree productivity,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

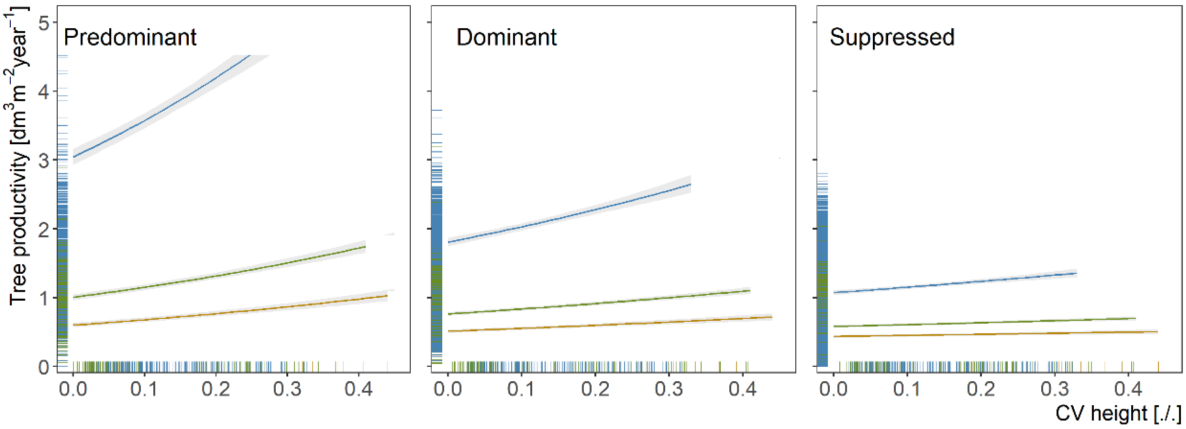

Figure 5. Productivity of oak trees as a function of coefficient of variation of tree heights and age for predominant (*rel_d* > 0.9), dominant (*rel_d* < 0.9 and >0.7) and suppressed (*rel_d* < 0.7) oaks in monospecific stands; rugs on the x-and y-axis indicate the observed values of *cvh* and tree 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	*p*-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	***	*n* obs	740
a_5	Age * ln (*SDI*)	−0.001	0.000	0.093	ns	pseudo-R^2 (m/c)	0.45/0.60
a_6	MT [mixed] * ln (*SDI*)	0.051	0.019	0.007	**	RMSE	0.06

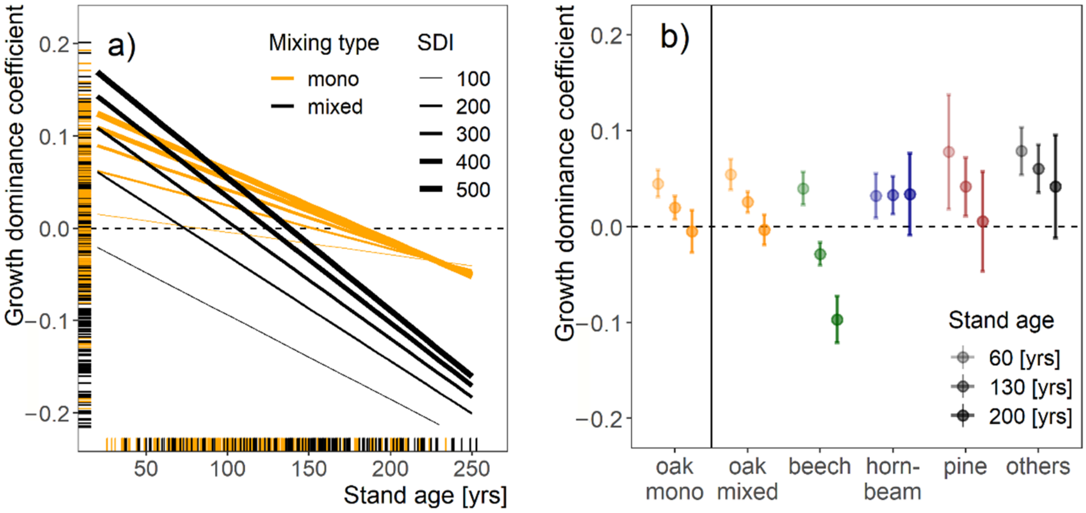

Figure 6. Growth dominance coefficient on stand level (**a**) in dependence of stand age and stand density for monospecific and mixed oak stands and the species-specific Growth dominance coefficient (**b**) for oak in monospecific and mixed stands, as well as beech, hornbeam pine and other tree species 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

Author Contributions: Conceptualization, K.S., E.U. and H.P.; methodology, K.S.; formal analysis, K.S.; investigation, K.S.; resources, R.-V.N. and H.P.; data curation, K.S. and M.H.; writing—original draft preparation, K.S.; writing—review and editing, K.S., M.H., E.U. and H.P.; visualization, K.S.; supervision, H.P.; funding acquisition, E.U. and H.P. All authors have read and agreed to the published version of the manuscript.

Funding: This publication is part of the project "Growth potential of oak in managed and unmanaged forests dependent on stand structure and site conditions (W045)" [grant number 7831–27295-2017] that was supported by the Bavarian State Ministry of Nutrition, Agriculture and Forestry. The experimental plots are part of the network of long-term yield trials of Bavaria which is funded by the Bavarian State Ministry of Nutrition, Agriculture and Forestry [grant number W007 7831-26625-2017].

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data used in this study are available on request from the corresponding author.

Acknowledgments: We would like to thank the Bavarian State Institute of Forestry (LWF) for providing the data of the strict forest reserves and the Northwest German Forest Research Institute (NW-FVA) for completing the long-term research plot data.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Bolte, A.; Ammer, C.; Löf, M.; Madsen, P.; Nabuurs, G.-J.; Schall, P.; Spathelf, P.; Rock, J. Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. *Scand. J. For. Res.* **2009**, *24*, 473–482. [CrossRef]
2. Lindner, M. Developing adaptive forest management strategies to cope with climate change. *Tree Physiol.* **2000**, *20*, 299–307. [CrossRef] [PubMed]
3. Lindner, M.; Maroschek, M.; Netherer, S.; Kremer, A.; Barbati, A.; Garcia-Gonzalo, J.; Seidl, R.; Delzon, S.; Corona, P.; Kolström, M.; et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manag.* **2010**, *259*, 698–709. [CrossRef]
4. Brockerhoff, E.G.; Barbaro, L.; Castagneyrol, B.; Forrester, D.I.; Gardiner, B.; González-Olabarria, J.R.; Lyver, P.O.; Meurisse, N.; Oxbrough, A.; Taki, H.; et al. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodivers. Conserv.* **2017**, *26*, 3005–3035. [CrossRef]
5. Pretzsch, H.; del Río, M.; Biber, P.; Arcangeli, C.; Bielak, K.; Brang, P.; Dudzinska, M.; Forrester, D.I.; Klädtke, J.; Kohnle, U.; et al. Maintenance of long-term experiments for unique insights into forest growth dynamics and trends: Review and perspectives. *Eur. J. For. Res.* **2019**, *138*, 165–185. [CrossRef]
6. Pretzsch, H.; Biber, P.; Schütze, G.; Uhl, E.; Rötzer, T. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* **2014**, *5*, 4967. [CrossRef]

7. Pretzsch, H.; Bielak, K.; Block, J.; Bruchwald, A.; Dieler, J.; Ehrhart, H.-P.; Kohnle, U.; Nagel, J.; Spellmann, H.; Zasada, M.; et al. Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur. J. For. Res.* **2013**, *132*, 263–280. [CrossRef]
8. Pretzsch, H.; Steckel, M.; Heym, M.; Biber, P.; Ammer, C.; Ehbrecht, M.; Bielak, K.; Bravo, F.; Ordóñez, C.; Collet, C.; et al. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* **2019**, *139*, 349–367. [CrossRef]
9. Río, M.; Sterba, H. Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. *Ann. For. Sci.* **2009**, *66*, 502. [CrossRef]
10. Liang, J.; Crowther, T.W.; Picard, N.; Wiser, S.; Zhou, M.; Alberti, G.; Schulze, E.-D.; McGuire, A.D.; Bozzato, F.; Pretzsch, H.; et al. Positive biodiversity-productivity relationship predominant in global forests. *Science* **2016**, *354*, aaf8957. [CrossRef]
11. Vandermeer, J.H. *The Ecology of Intercropping*; Cambridge University Press: Cambridge, UK, 1989; ISBN 9780521345927.
12. Pretzsch, H.; Block, J.; Dieler, J.; Dong, P.H.; Kohnle, U.; Nagel, J.; Spellmann, H.; Zingg, A. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann. For. Sci.* **2010**, *67*, 712. [CrossRef]
13. Pretzsch, H.; Biber, P. Tree species mixing can increase maximum stand density. *Can. J. For. Res.* **2016**, *46*, 1179–1193. [CrossRef]
14. Condés, S.; Del Rio, M.; Sterba, H. Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. *For. Ecol. Manag.* **2013**, *292*, 86–95. [CrossRef]
15. Brunner, A.; Forrester, D.I. Tree species mixture effects on stem growth vary with stand density—An analysis based on individual tree responses. *For. Ecol. Manag.* **2020**, *473*, 118334. [CrossRef]
16. Zeller, L.; Pretzsch, H. Effect of forest structure on stand productivity in Central European forests depends on developmental stage and tree species diversity. *For. Ecol. Manag.* **2019**, *434*, 193–204. [CrossRef]
17. Forrester, D.I. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. *For. Ecol. Manag.* **2019**, *447*, 139–157. [CrossRef]
18. Forrester, D.I.; Pretzsch, H. Tamm Review: On the strength of evidence when comparing ecosystem functions of mixtures with monocultures. *For. Ecol. Manag.* **2015**, *356*, 41–53. [CrossRef]
19. Manso, R.; Morneau, F.; Ningre, F.; Fortin, M. Effect of climate and intra- and inter-specific competition on diameter increment in beech and oak stands. *Forestry* **2015**, *88*, 540–551. [CrossRef]
20. del Río, M.; Condés, S.; Pretzsch, H. Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. *For. Ecol. Manag.* **2014**, *325*, 90–98. [CrossRef]
21. Ammer, C. Diversity and forest productivity in a changing climate. *New Phytol.* **2019**, *221*, 50–66. [CrossRef]
22. del Río, M.; Pretzsch, H.; Alberdi, I.; Bielak, K.; Bravo, F.; Brunner, A.; Condés, S.; Ducey, M.J.; Fonseca, T.; von Lüpke, N.; et al. Characterization of the structure, dynamics, and productivity of mixed-species stands: Review and perspectives. *Eur. J. For. Res.* **2016**, *135*, 23–49. [CrossRef]
23. Forrester, D.I. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *For. Ecol. Manag.* **2014**, *312*, 282–292. [CrossRef]
24. Binkley, D. A hypothesis about the interaction of tree dominance and stand production through stand development. *For. Ecol. Manag.* **2004**, *190*, 265–271. [CrossRef]
25. Binkley, D.; Kashian, D.M.; Boyden, S.; Kaye, M.W.; Bradford, J.B.; Arthur, M.A.; Fornwalt, P.J.; Ryan, M.G. Patterns of growth dominance in forests of the Rocky Mountains, USA. *For. Ecol. Manag.* **2006**, *236*, 193–201. [CrossRef]
26. Pothier, D. Relationships between patterns of stand growth dominance and tree competition mode for species of various shade tolerances. *For. Ecol. Manag.* **2017**, *406*, 155–162. [CrossRef]
27. Fernández-Tschieder, E.; Binkley, D. Linking competition with Growth Dominance and production ecology. *For. Ecol. Manag.* **2018**, *414*, 99–107. [CrossRef]
28. Pretzsch, H. The social drift of trees. Consequence for growth trend detection, stand dynamics, and silviculture. *Eur. J. For. Res.* **2021**, *140*, 703–719. [CrossRef]
29. Albert, M.; Nagel, R.-V.; Nuske, R.; Sutmöller, J.; Spellmann, H. Tree Species Selection in the Face of Drought Risk—Uncertainty in Forest Planning. *Forests* **2017**, *8*, 363. [CrossRef]
30. Leuschner, C.; Ellenberg, H. *Ecology of Central European Forests: Vegetation Ecology of Central Europe*; Springer: Cham, Switzerland, 2017; Volume 1, ISBN 978-3-319-43040-9.
31. Pretzsch, H.; Schütze, G.; Uhl, E. Resistance of European tree species to drought stress in mixed *versus* pure forests: Evidence of stress release by inter-specific facilitation: Drought stress release by inter-specific facilitation. *Plant Biol.* **2013**, *15*, 483–495. [CrossRef]
32. Steckel, M.; del Río, M.; Heym, M.; Aldea, J.; Bielak, K.; Brazaitis, G.; Černý, J.; Coll, L.; Collet, C.; Ehbrecht, M.; et al. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.)—Site water supply and fertility modify the mixing effect. *For. Ecol. Manag.* **2020**, *461*, 117908. [CrossRef]
33. Attocchi, G. *Silviculture of Oak for High-Quality Wood Production: Effects of Thinning on Crown Size, Volume Growth and Stem Quality in Even-Aged Stands of Pedunculate Oak (Quercus robur L.) in Northern Europe*; Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences: Alnarp, Sweden, 2015; ISBN 978-91-576-8277-2.
34. Kenk, G.K. New perspectives in German oak silviculture. *Ann. For. Sci.* **1993**, *50*, 563–570. [CrossRef]

35. von Lüpke, B. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *For. Ecol. Manag.* **1998**, *106*, 19–26. [CrossRef]
36. Löf, M.; Brunet, J.; Filyushkina, A.; Lindbladh, M.; Skovsgaard, J.P.; Felton, A. Management of oak forests: Striking a balance between timber production, biodiversity and cultural services. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manag.* **2016**, *12*, 59–73. [CrossRef]
37. Mölder, A.; Meyer, P.; Nagel, R.-V. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. *For. Ecol. Manag.* **2019**, *437*, 324–339. [CrossRef]
38. Bayerische Staatsforsten AöR. *Waldbauhandbuch Bayersiche Staatsforsten: Richtlinie zur Baumartenwahl*; Bayerische Staatsforsten: Regensburg, Germany, 2020.
39. Bayerisches Staatsministerium für Ernährung, Landwirtschaft und Forsten. *Baumarten für den Klimawald; Leitlinien der Bayerischen Forstverwaltung*; Bayerisches Staatsministerium für Ernährung, Landwirtschaft und Forsten: Munich, Germany, 2020.
40. Leroy, B.M.L.; Lemme, H.; Braumiller, P.; Hilmers, T.; Jacobs, M.; Hochrein, S.; Kienlein, S.; Müller, J.; Pretzsch, H.; Stimm, K.; et al. Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems: An experimental approach. *Ecol. Solut. Evid.* **2021**, *2*, e12045. [CrossRef]
41. Field, E.; Castagneyrol, B.; Gibbs, M.; Jactel, H.; Barsoum, N.; Schönrogge, K.; Hector, A. Associational resistance to both insect and pathogen damage in mixed forests is modulated by tree neighbour identity and drought. *J. Ecol.* **2020**, *108*, 1511–1522. [CrossRef]
42. Maleki, K.; Zeller, L.; Pretzsch, H. Oak often needs to be promoted in mixed beech-oak stands—The structural processes behind competition and silvicultural management in mixed stands of European beech and sessile oak. *iForest* **2020**, *13*, 80–88. [CrossRef]
43. Stimm, K.; Heym, M.; Uhl, E.; Tretter, S.; Pretzsch, H. Height growth-related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance still required in mixed-species stands? *For. Ecol. Manag.* **2021**, *482*, 118780. [CrossRef]
44. Beinhofer, B. Comparing the financial performance of traditionally managed beech and oak stands with roomy established and pruned stands. *Eur. J. For. Res.* **2010**, *129*, 175–187. [CrossRef]
45. Weaver, G.T.; Spiecker, H. Silviculture of high-quality oaks: Questions and future research needs. *Ann. Sci For.* **1993**, *50*, 531–534. [CrossRef]
46. Aas, G. Quercus petraea (Matt.) Liebl., Traubeneiche. In *Enzyklopädie der Holzgewächse*; Roloff, A., Weisgerber, H., Lang, U., Stimm, B., Eds.; Wiley-VCH: Weinheim, Germany, 2000.
47. Aas, G. Quercus robur L., Stieleiche. In *Enzyklopädie der Holzgewächse*; Roloff, A., Weisgerber, H., Lang, U., Stimm, B., Eds.; Wiley-VCH: Weinheim, Germany, 2002; pp. 1–15.
48. Jüttner, O. Eichenertragstafeln. In *Ertragstafeln der Wichtigsten Baumarten*; Schober, R., Ed.; JD Sauerländer´s Verlag: Frankfurt am Main, Germany, 1955; pp. 12–25, 134–138.
49. Johann, K. DESER-Norm 1993. Normen der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten zur Aufbereitung von waldwirtschaftlichen Dauerversuchen. *Ber. Der Jahrestag. Des Dtsch. Verb. Forstl. Sekt. Ertragskunde* **1993**, 96–104.
50. Schwaiger, F.; Poschenrieder, W.; Biber, P.; Pretzsch, H. Species Mixing Regulation with Respect to Forest Ecosystem Service Provision. *Forests* **2018**, *9*, 632. [CrossRef]
51. West, P.W. Calculation of a Growth Dominance Statistic for Forest Stands. *For. Sci.* **2014**, *60*, 1021–1023. [CrossRef]
52. Reineke, L.H. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* **1933**, *46*, 627–638.
53. Kramer, H.; Akça, A. *Leitfaden zur Waldmesslehre*, 3rd ed.; Sauerländer: Frankfurt am Main, Germany, 1995; ISBN 9783793908807.
54. Burschel, P.; Huss, J. *Grundriß des Waldbaus: Ein Leitfaden für Studium und Praxis*, 2nd ed.; Parey: Berlin, Germany, 1997; ISBN 3826330455.
55. Zuur, A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. (Eds.) *Mixed Effects Models and Extensions in Ecology with R*; Springer: New York, NY, USA, 2009; ISBN 978-0-387-87457-9.
56. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2018.
57. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [CrossRef]
58. Wood, S.N. *Generalized Additive Models: An Introduction with R*, 2nd ed.; Chapman and Hall/CRC: Boca Raton, FL, USA, 2017; ISBN 9781315370279.
59. Wickham, H. *Ggplot2: Elegant Graphic.cs for Data Analysis*, 2nd ed.; Springer: New York, NY, USA, 2016; ISBN 978-3-319-24277-4.
60. Spiecker, H. Overview of Recent Growth Trends in European Forests. In *Forest Growth Responses to the Pollution Climate of the 21st Century*; Sheppard, L.J., Cape, J.N., Eds.; Springer: Dordrecht, The Netherlands, 1999; pp. 33–46, ISBN 978-94-017-1578-2.
61. Bontemps, J.-D.; Hervé, J.-C.; Dhôte, J.-F. Long-Term Changes in Forest Productivity: A Consistent Assessment in Even-Aged Stands. *For. Sci.* **2009**, *55*, 549–564. [CrossRef]
62. Bontemps, J.-D.; Hervé, J.-C.; Duplat, P.; Dhôte, J.-F. Shifts in the height-related competitiveness of tree species following recent climate warming and implications for tree community composition: The case of common beech and sessile oak as predominant broadleaved species in Europe. *Oikos* **2012**, *121*, 1287–1299. [CrossRef]

63. Pretzsch, H.; Biber, P.; Schütze, G.; Bielak, K. Changes of forest stand dynamics in Europe. Facts from long-term observational plots and their relevance for forest ecology and management. *For. Ecol. Manag.* **2014**, *316*, 65–77. [CrossRef]
64. Hilmers, T.; Avdagić, A.; Bartkowicz, L.; Bielak, K.; Binder, F.; Bončina, A.; Dobor, L.; Forrester, D.I.; Hobi, M.L.; Ibrahimspahić, A.; et al. The productivity of mixed mountain forests comprised of Fagus sylvatica, Picea abies, and Abies alba across Europe. *For. An. Int. J. For. Res.* **2019**, *92*, 512–522. [CrossRef]
65. Vannoppen, A.; Kint, V.; Ponette, Q.; Verheyen, K.; Muys, B. Tree species diversity impacts average radial growth of beech and oak trees in Belgium, not their long-term growth trend. *For. Ecosyst.* **2019**, *6*, 252. [CrossRef]
66. Fajvan, M.A.; Rentch, J.; Gottschalk, K. The effects of thinning and gypsy moth defoliation on wood volume growth in oaks. *Trees* **2008**, *22*, 257–268. [CrossRef]
67. Forrester, D.I.; Bauhus, J. A Review of Processes Behind Diversity—Productivity Relationships in Forests. *Curr. For. Rep.* **2016**, *2*, 45–61. [CrossRef]
68. Pretzsch, H.; Schütze, G. Effect of tree species mixing on the size structure, density, and yield of forest stands. *Eur. J. For. Res.* **2016**, *135*, 1–22. [CrossRef]
69. Dieler, J.; Uhl, E.; Biber, P.; Müller, J.; Rötzer, T.; Pretzsch, H. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. *Eur. J. For. Res.* **2017**, *136*, 739–766. [CrossRef]
70. Pretzsch, H. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manag.* **2014**, *327*, 251–264. [CrossRef]
71. Torresan, C.; del Río, M.; Hilmers, T.; Notarangelo, M.; Bielak, K.; Binder, F.; Boncina, A.; Bosela, M.; Forrester, D.I.; Hobi, M.L.; et al. Importance of tree species size dominance and heterogeneity on the productivity of spruce-fir-beech mountain forest stands in Europe. *For. Ecol. Manag.* **2020**, *457*, 117716. [CrossRef]
72. Hein, S.; Dhôte, J.-F. Effect of species composition, stand density and site index on the basal area increment of oak trees (*Quercus* sp.) in mixed stands with beech (*Fagus sylvatica* L.) in northern France. *Ann. For. Sci.* **2006**, *63*, 457–467. [CrossRef]
73. Pretzsch, H.; Schütze, G. Crown allometry and growing space efficiency of Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biol.* **2005**, *7*, 628–639. [CrossRef]
74. Dieler, J.; Pretzsch, H. Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. *For. Ecol. Manag.* **2013**, *295*, 97–108. [CrossRef]
75. Zapater, M.; Hossann, C.; Bréda, N.; Bréchet, C.; Bonal, D.; Granier, A. Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. *Trees* **2011**, *25*, 885–894. [CrossRef]
76. Pretzsch, H. *Grundlagen der Waldwachstumsforschung*; Springer: Berlin/Heidelberg, Germany, 2019.
77. Pretzsch, H. The course of tree growth. Theory and reality. *For. Ecol. Manag.* **2020**, *478*, 118508. [CrossRef]
78. Del Río, M.; Schütze, G.; Pretzsch, H. Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biol.* **2014**, *16*, 166–176. [CrossRef] [PubMed]
79. Vanhellemont, M.; Bijlsma, R.-J.; de Keersmaeker, L.; Vandekerkhove, K.; Verheyen, K. Species and structural diversity affect growth of oak, but not pine, in uneven-aged mature forests. *Basic Appl. Ecol.* **2018**, *27*, 41–50. [CrossRef]
80. Pretzsch, H.; Biber, P. A re-evaluation of Reineke's rule and stand density index. *For. Sci.* **2005**, *51*, 304–320.
81. de Groote, S.R.; Vanhellemont, M.; Baeten, L.; van den Bulcke, J.; Martel, A.; Bonte, D.; Lens, L.; Verheyen, K. Competition, tree age and size drive the productivity of mixed forests of pedunculate oak, beech and red oak. *For. Ecol. Manag.* **2018**, *430*, 609–617. [CrossRef]
82. Toïgo, M.; Perot, T.; Courbaud, B.; Castagneyrol, B.; Gégout, J.-C.; Longuetaud, F.; Jactel, H.; Vallet, P.; Hector, A. Difference in shade tolerance drives the mixture effect on oak productivity. *J. Ecol.* **2018**, *106*, 1073–1082. [CrossRef]
83. Baret, M.; Pepin, S.; Ward, C.; Pothier, D. Long-term changes in stand growth dominance as related to resource acquisition and utilization in the boreal forest. *For. Ecol. Manag.* **2017**, *400*, 408–416. [CrossRef]
84. Knoke, T.; Ammer, C.; Stimm, B.; Mosandl, R. Admixing broadleaved to coniferous tree species: A review on yield, ecological stability and economics. *Eur. J. For. Res.* **2008**, *127*, 89–101. [CrossRef]
85. Paul, C.; Brandl, S.; Friedrich, S.; Falk, W.; Härtl, F.; Knoke, T. Climate change and mixed forests: How do altered survival probabilities impact economically desirable species proportions of Norway spruce and European beech? *Ann. For. Sci.* **2019**, *76*, 1–15. [CrossRef]
86. Puettmann, K.J.; Messier, C. Simple Guidelines to Prepare Forests for Global Change: The Dog and the Frisbee. *NWSC* **2019**, *93*, 209. [CrossRef]
87. Brändle, M.; Brandl, R. Species richness of insects and mites on trees: Expanding Southwood. *J. Anim. Ecol.* **2001**, *70*, 491–504. [CrossRef]
88. Manos, P.S.; Stanford, A.M. The Historical Biogeography of Fagaceae: Tracking the Tertiary History of Temperate and Subtropical Forests of the Northern Hemisphere. *Int. J. Plant Sci.* **2001**, *162*, S77–S93. [CrossRef]
89. van der Plas, F.; Ratcliffe, S.; Ruiz-Benito, P.; Scherer-Lorenzen, M.; Verheyen, K.; Wirth, C.; Zavala, M.A.; Ampoorter, E.; Baeten, L.; Barbaro, L.; et al. Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. *Ecol. Lett.* **2018**, *21*, 31–42. [CrossRef] [PubMed]
90. Penone, C.; Allan, E.; Soliveres, S.; Felipe-Lucia, M.R.; Gossner, M.M.; Seibold, S.; Simons, N.K.; Schall, P.; van der Plas, F.; Manning, P.; et al. Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecol. Lett.* **2019**, *22*, 170–180. [CrossRef] [PubMed]

91. Pretzsch, H.; Zenner, E.K. Toward managing mixed-species stands: From parametrization to prescription. *For. Ecosyst.* **2017**, *4*, 1–17. [CrossRef]
92. Pretzsch, H.; Poschenrieder, W.; Uhl, E.; Brazaitis, G.; Makrickiene, E.; Calama, R. Silvicultural prescriptions for mixed-species forest stands. A European review and perspective. *Eur. J. For. Res.* **2021**, *140*, 1267–1294. [CrossRef]
93. Pretzsch, H.; del Río, M. Density regulation of mixed and mono-specific forest stands as a continuum: A new concept based on species-specific coefficients for density equivalence and density modification. *Forestry* **2020**, *93*, 1–15. [CrossRef]
94. Thurm, E.A.; Pretzsch, H. Growth–density relationship in mixed stands—Results from long-term experimental plots. *For. Ecol. Manag.* **2021**, *483*, 118909. [CrossRef]
95. Petritan, I.C.; Marzano, R.; Petritan, A.M.; Lingua, E. Overstory succession in a mixed Quercus petraea–Fagus sylvatica old growth forest revealed through the spatial pattern of competition and mortality. *For. Ecol. Manag.* **2014**, *326*, 9–17. [CrossRef]
96. Mosandl, R.; Abt, A. Waldbauverfahren in Eichenwäldern gestern und heute. *AFZ-Der Wald* **2016**, *20*, 28–32.
97. Krahl-Urban, J. *Die Eichen: Forstliche Monographie der Traubeneiche und der Stieleiche*; P. Parey: Hamburg, Germany, 1959.

C - Article III

Title:

Chances and Limitations of Mixed Oak Regeneration under Continuous Canopy Cover — Evidence from Long-Term Observations

Authors:

Kilian Stimm, Enno Uhl, Hans Pretzsch

Journal:

Forests 2022, Volume 13, Issue 12, 2052

Impact Factor:

3.282

forests

MDPI

Article

Chances and Limitations of Mixed Oak Regeneration under Continuous Canopy Cover—Evidence from Long-Term Observations

Kilian Stimm [1,2,*], Enno Uhl [1,2] and Hans Pretzsch [1]

[1] Chair of Forest Growth and Yield Science, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising, Germany
[2] Bavarian State Institute of Forestry, Hans-Carl-von-Carlowitz-Platz 1, D-85354 Freising, Germany
* Correspondence: kilian.stimm@tum.de

Abstract: Traditionally, due to its light ecology, oak is regenerated on clear cuts or areas where the crown coverage is heavily reduced. Thus, the regeneration phase is relatively short. Recently, selective long-term regeneration phases avoiding large gaps in the canopy but fostering mixed-species stands have been advocated as being more in keeping with close-to-nature forestry in Central European forests. However, examples of the successful regeneration of oak in mixtures following this type of regeneration are largely missing. Here, we report the results of long-term experiments located in three different forest types, where oak was long-term regenerated under different mixing and canopy cover situations. The observation periods reached from 26 to 36 years. We focused on the dynamics of stem number reduction, as well as the height and biomass development of oaks and their interaction with interspecific competition and canopy density. The probability of oaks occurring in the regeneration basically decreased over the duration of the regeneration period. Despite this, considerable regeneration biomass growth could be observed, especially in the case of the lower standing volume of the mature stand. The development of beech as the main competitor is scarcely slowed down by the canopy cover compared to oak. Increasing canopy cover noticeably impeded oak regeneration in the considered mixed stands. The model results suggest that a reduction in competition within the regeneration by lowering the proportion of beech below 30% enhanced the success of oak regeneration in the long run even in small patches. The productivity of the remaining stand was primarily driven by standing volume. However, a negative trend of its productivity emerged with high regeneration biomasses. The study results show that small-scale oak regeneration with prolonged regeneration duration is possible in principle. However, oak regeneration requires active and continuous silvicultural assistance, which has to be adjusted to the specific site conditions.

Keywords: oak species; regeneration; close-to-nature silviculture; mixed stands; long-term experiments

check for updates

Citation: Stimm, K.; Uhl, E.; Pretzsch, H. Chances and Limitations of Mixed Oak Regeneration under Continuous Canopy Cover—Evidence from Long-Term Observations. *Forests* **2022**, *13*, 2052. https://doi.org/10.3390/f13122052

Academic Editors: Pil Sun Park and Timothy A. Martin

Received: 29 September 2022
Accepted: 30 November 2022
Published: 2 December 2022

1. Introduction

Sessile (*Quercus petraea* (Matt.) Liebl) and pedunculate (*Quercus robur* L.) oaks are two of the most widespread native broadleaved tree species in Central Europe [1] and are expected to be suitable for coping with the predicted climatic changes in the future [2–4]. Based on their broad ecological amplitude and high drought tolerance, they can be an important component of climate-resilient mixed species forests [5,6], which are considered as an option to meet the challenges of climate change [7–10].

Furthermore, the genus oak, with its large species abundance [11,12], enhances forest biodiversity, which has recently become an increasingly important management goal [13–15]. More generally, both oak species seem to be suitable for multifunctional forest management [14,16], including valuable wood production as one major management goal of oak silviculture [17–19]. Frequently, oak is either simultaneously or at a later stage underplanted with more shade-tolerant tree species, such as European beech (*Fagus sylvatica* L.) or hornbeam (*Carpinus* *betulus* L.), which are commonly used as serving trees to ensure high-quality oak wood production [17,18].

However, in addition to the multitude of positive characteristics that oak species provide as a component of multifunctional forest management [14], they require silvicultural assistance on most sites due to more competitive admixed tree species [20,21]. Thus, their current occurrence in temperate forests in Central Europe is strongly dependent on the past human land use systems and forest management practices [18,22–24]. Furthermore, both oak species occur naturally as dominant tree species primarily in their own ecological niches, in stands with extreme or distinctive site conditions [20].

One decisive component of an appropriate future oak participation in mature mixed stands is determined by the type of regeneration. So far, due to the comparatively high light requirements of oaks compared to those of admixed tree species, stand establishment has usually been carried out with large crown openings combined with short- to mid-term regeneration periods [18,25]. Consequently, in recent years, these large-scale shelterwood and clearcutting systems have also been increasingly criticized in the course of oak management [26,27].

In particular, in the course of close-to-nature silviculture clear cuts should be largely avoided [28,29]. In addition, other core principles of close-to-nature silviculture are the promotion of site-adapted tree species, the establishment of structured mixed stands, and the promotion of natural regeneration [30]. These principles can be implemented in practice, especially by using single-tree selection, group selection, or shelterwood systems [28]. However, the utilization of natural processes, as a core element of close-to-nature silviculture in particular, puts native oaks at an additional disadvantage compared to their mostly more shade-tolerant admixed tree species [18,23,31,32]. This appears to further weaken oaks in their relative competitive strength on many sites, often resulting in a decline in vitality or loss of oaks in young and mature stands.

In this context, previous studies particularly addressed light availability and its effect on the success of oak regeneration [18,33–35]. Lüpke [18] suggested the need for at least 15% of full light for survival and 40% for the optimal height growth of oak. Furthermore, the light requirements of oaks were higher in the later development stages [33,36], which indicates continuous silvicultural interferences in the canopy cover. However, Ligot et al. [34] demonstrated that beech outperformed oak throughout the light gradient and concluded that silvicultural control of the canopy cover is not sufficient in mixed oak and beech regenerations. Consequently, to keep survival rates high the management of mixed oak regenerations has to consider competing woody species [37,38] and ground vegetation [39–41].

Most studies cover short- to mid-term regeneration periods. Long-term studies for oak that cover regeneration periods of up to 20 years and longer are scarcely available [33,38]. However, prolonged regeneration after the first years of successful stand initiation is often decisive for future tree species composition and wood quality in the mature stand. This is especially true for close-to-nature silviculture and long regeneration periods of 30 years or more. In addition, the results of the studies are often limited to specific site conditions and cannot be readily applied to other stand situations or site conditions [38].

The objective of this study is to assess the success and constraints of the regeneration of oak established in mixtures under continuous canopy cover. In detail, we first analyze the survival probability of oaks over time and hypothesize that survival is dependent on the forest site. Secondly, we evaluate the course of species-specific regenerated tree density and biomass. Here, we test the hypothesis that the development of density and biomass is species-specific and modified by the degree of canopy cover. In the next step, we quantify the height growth rates of oaks to answer the hypothesis that the height growth of oaks is negatively influenced by canopy cover and interspecific competition. Lastly, we analyze the effect of advanced regeneration on the productivity of the remaining stand following the hypothesis that high rates of regeneration biomass reduce the productivity of the remaining stand. From the result, we deduce the silvicultural recommendations for the successful regeneration of oaks within continuous cover forestry.

We make use of experimental plots where regeneration has been monitored and measured for up to 36 years. The experimental plots have been established in monospecific pine and mixed oak stands. The regeneration was initiated by planting in the case of the pine stands. In the mixed oak stands, the crown cover was reduced selectively over the existing natural regeneration. Following the aforementioned objectives, the study focused on four main questions:

i. What are the survival probabilities of oak in small-scale and long-term regenerated stands and do they differ between different forest types?
ii. What is the long-term development of the regenerated tree species' density and the effect of canopy cover on regeneration biomass?
iii. How does canopy cover and interspecific competition modify the heights of regenerated oaks?
iv. Is there a feedback effect of advanced regeneration on the productivity of the mature stand?

2. Materials and Methods

2.1. Long-Term Experiments

We used the data of 12 regenerated experimental plots, each located in a different stand; they are a part of four long-term experiments in southern and central Germany (Figure 1). The size of the individual experimental plots varies between 0.1 and 1.0 ha. The investigated stands are located in three different woodland regions and sites, namely Spessart, Steigerwald, and Nuremberg, which are further referred to using their experiment codes BUS, EBR, and NUE, respectively. The stands represent mixed oak and monospecific Scots pine stands. The mixed mature stands are composed of sessile oak and European beech in the case of BUS and sessile oak and European beech and Scots pine (*Pinus sylvestris* L.) in the case of EBR (Table 1); these are denoted as oak, beech, and pine in the following. The mixed stands in BUS and EBR were mainly regenerated naturally; the planting of oaks occurred only marginally. In contrast, the monospecific pine stands in the Nuremberg region were regenerated by sowing and underplanting oak and beech, respectively. The experimental plots were established to test the different overstorey stand densities and their effect on regeneration by applying single-tree and group selection systems. The considered stands cover a broad range of small-scale canopy gaps, from approximately 0.01 to 0.25 ha, and different light situations.

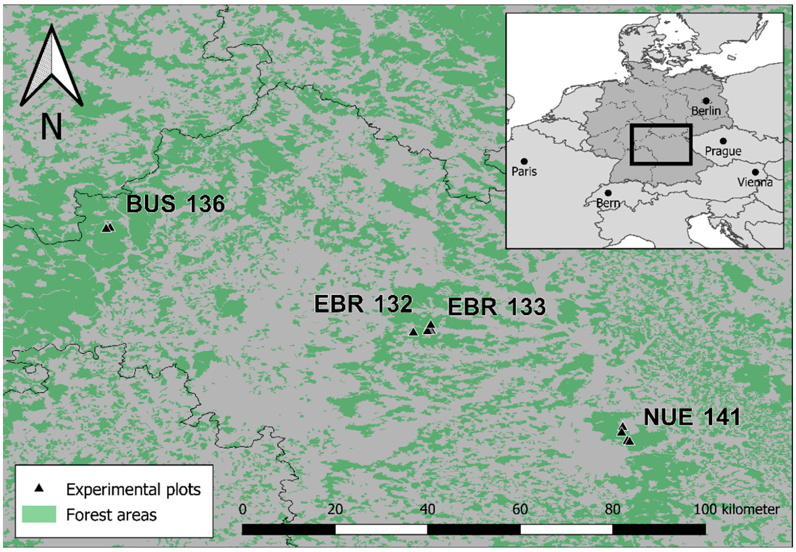

Figure 1. Geographic location of the experimental plots in southern and central Germany.

Table 1. General description of the long-term experiments; Exp—experiment (code); Nr—experiment number; n—number of plots; Size—plot sizes [ha]; Comp—species composition; RT—type of regeneration; Surveys—measurement years; Per—regeneration period [yrs]; Lat—latitude; Lon—longitude; P—annual precipitation [mm yr^{-1}]; T—annual mean temperature [°C]; Alt—altitude [m.a.s.l.].

Exp	Nr	n	Size	Comp [1]	RT [2]	Surveys	Per	Lat	Lon	Soil	P	T	Alt
BUS	136	2	0.5	Oa-Be	nat	1986, 1995, 2012	26	50.129	9.593	Cambisol	796	7.8	445
EBR	132	1	0.5	Oa-Be-Pi	nat	1982, 1993, 2019	36	49.836	10.547	Cambisol	683	8.1	338
EBR	133	5	1.0	Oa-Be-(Pi)	nat/art	1983, 1999, 2019	36	49.853	10.547	Cambisol—(Pseudogley)	675	7.9	385
NUE	141	4	0.1	Pi	nat/art	1991, 1998, 2019	28	49.499	11.144	Cambisol/Pseudogley	759	8.7	333

[1] Oa—sessile oak; Be—European beech; Pi—Scots pine; [2] nat—natural regeneration; art—artificially regenerated.

The first measurements of the experimental plots were carried out between 1982 and 1991. In total, the mature stands and their respective regeneration have been measured three times since then. Thus, a unique database on the development of oak regeneration under different conditions covering a 36-year regeneration period was established.

2.2. Yield Data of the Mature Stand

To quantify wood volume V (m^3 ha^{-1}), stand basal area BA (m^2 ha^{-1}), dominant tree diameter D_{100} (cm), dominant height H_{100} (m), and the periodic annual basal area and wood volume increment PAIBA (m^2 ha^{-1} yr^{-1}), as well as PAIV (m^3 ha^{-1} yr^{-1}), respectively, the DESER-standards [42] were applied. The stand basal area BA and standing wood volume V at the beginning of the measurements ranged from 5.1 to 28.7 m^2 ha^{-1} and from 83.5 to 428.5 m^3 ha^{-1}. The respective periodic annual basal area and volume increment varied from 0.1 to 0.2 m^2 ha^{-1} yr^{-1} and 1.0 to 5.2 m^3 ha^{-1} yr^{-1} (Table 2).

Table 2. Yield data of the main stand for the first and latest survey; S—tree species; Age—stand age [yrs]; N—number of trees [n ha^{-1}]; H_{100}—dominant height [m]; D_{100}—dominant diameter [cm]; BA—basal area [m^2 ha^{-1}]; V—volume [m^3 ha^{-1}]; CC—canopy cover [%]; PAIBA—periodic annual basal area increment [m^2 ha^{-1} yr^{-1}]; PAIV—periodic annual volume increment [m^3 ha^{-1} yr^{-1}]; Per—observation period [yrs].

			First Survey							Last Survey									
Exp (Nr)	Plot	S	Age	N	H_{100}	D_{100}	BA	V	CC	Age	N	H_{100}	D_{100}	BA	V	PAIBA	PAIV	CC	Per
EBR (132)	1	Pi	147	21	30.9	53.3	4.65	66.14	37	184	12	33.27	65.01	4.15	63.15	0.05	0.76	30	36
		Be	147	42	31.34	45.12	6.66	110.2		184	21	33.05	69.6	7.93	138.81	0.1	1.76		
		Oa	147	4	31.59	46.9	0.72	12.26		184	4	32.78	67.4	1.49	26.99	0.02	0.38		
		total		67			12.03	188.61			37			13.56	228.94	0.17	2.9		
EBR (133)	2	Pi	143	8	27.03	51.64	1.66	20.98	60	178	2	32.07	52.2	0.39	5.79	0.01	0.11	43	36
		Be	143	77	32.44	47.15	12.24	209.08		178	53	34.78	64.37	15.44	282.88	0.19	4.09		
		Oa	143	14	29.02	46	2.33	36.71		178	13	32.65	62.1	3.94	71.18	0.05	1.05		
		total		99			16.23	266.78			68			19.77	359.84	0.24	5.24		
	4	Be	164	44	34.88	49.35	8.42	159.51	22	199	33	35.1	70.11	12.74	237.99	0.16	3.35	43	36
		Oa	164	12	33.55	46.74	2.06	37.18		199	12	33.33	61.5	3.56	65.38	0.04	0.87		
		Hb	164	1	24.38	30.7	0.07	0.92		199	1	28.44	42.5	0.14	2.11	0	0.04		
		total		57			10.55	197.61			46			16.44	305.48	0.2	4.27		
	6	Pi	162	11	27.09	53.14	2.4	30.21	62	197	9	28.68	60.38	2.44	32.49	0.02	0.18	54	36
		Be	162	44	28.72	46.56	4.92	71.82		197	34	31.29	60.43	5.64	107.13	0.07	1.51		
		Oa	162	67	28.67	43.7	9.46	145.15		197	62	30.91	54.69	14.58	241.67	0.15	3.33		
		Hb	162	10	23.53	22.54	0.24	1.81		197	10	20.37	28.98	0.49	4.73	0	0.07		
		total		132			17.02	249			115			23.98	386.03	0.24	5.08		
	7	Sp	146	1	27.55	47	0.17	2.18	22	181	16	28.5	50.85	3.25	42.9	0.03	0.55	30	36
		Pi	146	24	27.02	41.36	3.22	40.31			0	-	-	-	-	-	-		
		Be	146	25	30.12	44.64	3.91	62.53		181	19	27.76	58.43	5.09	74.79	0.06	0.72		
		Oa	146	18	25.97	40.38	2.3	32.22		181	17	26.44	57.23	4.37	64.48	0.06	1.04		
		total		68			9.61	137.25			52			12.72	182.17	0.15	2.31		
	8	Be	153	13	32.81	48.84	2.44	42.33	25	188	4	26.21	64.18	1.29	18.11	0.01	0.11	9	36
		Oa	153	19	29.34	41.73	2.6	40.89		188	15	27.67	55.3	3.6	55.22	0.05	0.85		
		Hb	153	1	21.72	18	0.03	0.26			0	-	-	-	-	-	-		
		total		33			5.06	83.48			19			4.9	73.33	0.06	0.96		
BUS (136)	1	Be	192	40	24.97	43.52	2.52	30.58	67	218	4	27.01	39.6	0.42	5.52	0.02	0.3	38	26
		Oa	192	66	29.31	60.12	18.74	305.77		218	52	31.34	70.58	20.34	356.57	0.19	3.82		
		total		106			21.26	336.35			56			20.76	362.09	0.21	4.11		
	2	Be	202	106	28.08	44.76	7.03	88.29	67	228	26	27.78	49.97	3.78	53.8	0.08	0.94	41	26
		Oa	202	74	28.18	61	21.63	340.19		228	48	30.92	68.54	17.71	305.72	0.16	3.24		
		total		180			28.66	428.48			74			21.48	359.52	0.24	4.17		
NUE (141)	1	Pi	88	400	24.1	35.76	27.07	287.45	66	116	144	26.77	39.99	16.69	203.99	0.23	3.52	35	28
	2	Pi	97	400	25.52	35.95	29.53	332.25	77	125	233	30	43.83	29.25	389.24	0.45	7.44	57	28
	3	Pi	125	189	27.57	47.56	27.62	346.41	63	153	111	30.19	52.67	23.59	327.32	0.29	4.95	42	28
	4	Pi	130	133	31.65	48.8	22.46	324.85	57	158	44	29.79	54.33	10.3	141.56	0.1	1.03	23	28

Oa—sessile oak; Be—European beech; Pi—Scots pine; Hb—hornbeam; Sp—Norway spruce.

In addition, the canopy cover CC (%) was calculated for all the surveys. Based on 8 measurements per tree crown, the maps were plotted with crown shape approximations by cubic splines. From this, the corresponding area covered by tree crowns was calculated for the total stand and the regeneration squares (see Section 2.3), respectively. The canopy cover varied from 22 to 77% in the first survey and from 9 to 57% in the last survey (Table 2).

2.3. Regeneration Data

The regeneration on each experimental plot was fully inventoried three times using a grid of 5 × 5 m squares. Thus, the data of 1 916 squares were obtained per survey, making 5748 in total. Of these, 4112, 1200, and 432 were located in EBR, BUS, and NUE, respectively. A total of 482,012 saplings (trees) or 275,300 oaks were recorded during the regeneration surveys. For the analyses, the regeneration data, tree height, and biomass were aggregated and summarized by each square, survey, and tree species. In addition to the most abundant tree species, oak, beech, hornbeam, and pine, all the other occurring tree species were summarized under the term "Others" (Table S1). All occurring regeneration plants were recorded. Saplings smaller than 2 m were assigned to 4 height classes (0–50 cm, 51–100 cm, 101–150 cm, 151–200 cm). Additionally, for plants taller than 2 m, the diameter at breast height (dbh) was measured. For saplings taller than 1.3 m and smaller than 2 m, the dbh were estimated as a function of the height using a logarithmic model.

The regeneration biomass was calculated for each tree using the formula of Forrester et al. [43].

$$ln(bm) = ln(\beta_0) + \beta_1 \, ln(D) + \varepsilon \tag{1}$$

where the calculated biomass (*bm*) was the aboveground biomass of the individual tree in kg. *D* was the diameter in cm of the corresponding tree. β_0 and β_1 were the species-specific function parameters.

A descriptive summary of the plot and species-specific regeneration data for the first and last surveys is provided in Table 3.

Table 3. Regeneration data for the first and latest survey; S—tree species; A—age of regeneration [yrs]; d—plant density [n ha^{-1}]; bm—regeneration biomass [kg ha^{-1}]; h—mean height [m].

			First Survey				Last Survey			
Exp (Nr)	**Plot**	**S**	**A**	**d**	**bm**	**h**	**A**	**d**	**bm**	**h**
EBR (132)	1	Pi	4	3504	182	0.67	40	4	202	16.07
		Be		18,308	2033	1.05		3492	55,745	7.41
		Oa		22,104	562	1.07		271	11,015	13.45
		Hb		3383	605	1.21		354	9235	7.99
		Others		350	33	1.55		4	26	8.19
EBR (133)	2	Pi	6	366	22	0.89	42	0	-	-
		Be		15,464	1767	1.11		3709	27,696	7.1
		Oa		8892	165	0.87		5	68	11.48
		Hb		130	16	1.74		6	716	15.48
		Others		697	118	2.85		59	3305	12.06
	4	Pi	22	6	0	0.62	58	0	-	-
		Be		30,554	6100	3.19		2394	91,381	11.4
		Oa		1 140	15	1.44		6	279	13.97
		Hb		197	28	1.64		6	1038	18
		Others		284	60	4.71		98	32,299	19.89
	6	Pi	6	100	4	0.36	42	5	125	9.27
		Be		15,791	1056	0.65		5280	49,307	5.72
		Oa		119,009	833	0.32		98	921	7.12
		Hb		69	9	0.87		95	2033	9.87
		Others		153	15	1.07		77	8714	10.21

Table 3. *Cont.*

			First Survey				Last Survey			
Exp (Nr)	**Plot**	**S**	**A**	**d**	**bm**	**h**	**A**	**d**	**bm**	**h**
	7	Pi	11	2198	161	1.44	47	59	4672	13.24
		Be		19,284	2863	1.71		3972	49,136	7.13
		Oa		17,402	479	1.84		613	43,182	14.41
		Hb		2925	594	1.67		453	7973	9.51
		Others		3609	477	2.03		184	9655	9.54
	8	Pi	13	70	5	1.36	49	16	2340	16.55
		Be		7634	891	1.53		3203	29,103	5.72
		Oa		41,570	1483	1.89		2500	102,447	10.07
		Hb		3642	897	2.14		1553	33,505	7.81
		Others		219	27	2.37		22	6699	14.86
BUS (136)	1	Be	5	15,878	1052	0.67	31	11,628	12,644	2.8
		Oa		54,286	1686	0.3		6678	10,142	3.52
	2	Be	3	12,245	812	0.64	29	8175	23,505	3.9
		Oa		13,302	411	0.25		5	26	7.13
NUE (141)	1	Pi	3	31,911	849	0.3	31	2133	2753	2.77
		Be		1278	130	0.32		1478	8653	6.35
		Oa		18,889	785	0.45		2444	6696	3.1
		Others		544	162	0.47		356	1714	4.67
	2	Pi	5	86,967	2429	0.32	33	122	92	2.81
		Be		1122	129	0.43		3567	46,948	8.17
		Oa		42,911	1742	0.53		822	3120	5.09
		Others		156	47	0.38		222	950	6.14
	3	Pi	9	2300	157	0.88	37	0	-	-
		Be		5011	1095	1.75		2622	76,353	10.96
		Oa		40,211	4230	1.56		89	3900	14.34
		Others		7089	3060	1.22		322	13,313	10.41
	4	Pi	9	1800	128	0.89	37	0	-	-
		Be		322	54	0.94		500	3888	3.58
		Oa		23,911	2517	1.54		1733	100,861	11.58
		Others		1633	670	1.22		256	6497	6.86

Oa—sessile oak; Be—European beech; Pi—Scots pine; Hb—hornbeam.

2.4. Statistical Analyses

To describe the occurrence probability of oak in long-term and small-scale regenerated stands in general (*i*), a logistic model was set up across all the investigated stands. Oak abundance was set as a function of the duration of the regeneration period (*dur*) and the corresponding experimental site (*site*). The predicted probability was based on the occurrence of oaks in the respective regeneration square. Each square was categorized by the binary variable as either 1 (oak occurs) or 0 (oak does not occur).

$$\begin{gathered} logit[E(Y_{ijk} \mid dur_{ik}, site_i)] = \\ p_{ijk}/1 - p_{ijk} = a_0 + a_1\, dur_{ik} + a_2\, site_i + b_i + b_{ij} + \varepsilon_{ijk} \end{gathered} \tag{2}$$

Indices i, j, and k denoted the plot, the regeneration square, and the survey, respectively. a_0, a_1, and a_2 represented the estimated fixed effects parameters. With the regeneration squares lying next to each other and repeatedly recorded, the corresponding random effects were b_i and b_{ij}, to account for the spatial and temporal autocorrelation. ε_{ijk} are i.i.d. errors (ε_{ijk}~N(0;σ_3^2)).

To answer the further research questions (ii–iv), linear mixed effects models were set up to account for the potential autocorrelation due to the assumed spatial and temporal dependencies, as described above [44]. In each case, the models were adjusted for the individual experimental site. The respective models with the considered interactions between the covariates were determined by the research questions and applied equally for each experimental site.

First, the regeneration density (d) was estimated for each species as a function of regeneration age, as described by the following model function.

$$ln(d_{ijk}) = a_0 + a_1 \times ln(A) + a_2 \times S + a_3 \times (ln(A) \times S) + b_i + b_{ij} + \varepsilon_{ijk} \tag{3}$$

where A is the respective regeneration age and S is the regenerated tree species. The corresponding random effects were b_i and b_{ij}, to account for the spatial and temporal autocorrelation. ε_{ijk} are i.i.d. errors (ε_{ijk} ~ N(0;σ_3^2).

Second, the regeneration biomass (bm) was set as a function of regeneration age and canopy cover (CC), as described by the following adjusted model function.

$$ln(bm_{ijk}) = a_0 + a_1 \times ln(A) + a_2 \times S + a_3 \times CC + a_4 \times (S \times CC) + b_{\mathrm{i}} + b_{ij} + \varepsilon_{ijk} \tag{4}$$

Third, the maximum heights (h) were estimated using the extended model, which additionally accounted for the interspecific competition within the regeneration. Therefore, the proportion of the admixed tree species, which was in all cases primarily constituted by beech, was additionally included in the model (BE_perc). The following model was set up:

$$\begin{gathered} ln(h_{ijk}) = a_0 + a_1 \times ln(A) + a_2 \times S + a_3 \times CC + a_4 \times BE\_perc + a_5 \times (S \times CC) + \\ a_6 \times (S \times BE\_perc) + b_i + b_{ij} + \varepsilon_{ijk} \end{gathered} \tag{5}$$

To describe the effect of the regeneration biomass on the productivity of the overstorey ($PAIV$), the periodic annual increment was estimated as a function of the standing volume and the total regeneration biomass on a plot level.

$$ln(PAIV_{ik}) = a_0 + a_1 \times ln(V_{ik}) + a_2 \times bm\_reg_{ik} + a_3 \times (ln(V_{ik}) \times bm\_reg_{ik}) + b_i + \varepsilon_{ik} \tag{6}$$

Here, the independent variables were the standing volume of the overstorey (V) and the aggregated biomass of regeneration on a plot level (bm_reg). The corresponding random effect was b_i, to account for temporal autocorrelation. ε_{ik} are i.i.d. errors (ε_{ik}~N(0; σ_2^2).

All statistical analyses were performed using the statistical program R and the package lme4 [45,46].

3. Results

3.1. Oak Occurrence Probabilities

At the end of the observation periods, oak was present on 34%, 44%, and 71% of the regeneration squares in EBR, BUS, and NUE, respectively, which represents a decline in oak in 55%, 52%, and 29% of the squares after 36, 26, and 28 years. Correspondingly, the regeneration period had a most significant effect on oak occurrence in the considered small-scale regenerated stands. With an odds ratio (OR) of 0.89 ($p < 0.001$), the probability of oak presence in the regeneration decreased with the increasing regeneration period. Similarly, there were significant differences between the three forest types. The highest oak occurrence was found in the monospecific pine stands in NUE (OR = 35.44) (Figure 2). Thus, survival was much lower in the beech–oak–pine stands in EBR (OR = 0.33) (Figure 2). The reference was the oak–beech stands in BUS. Overall, in NUE, the oak presence was still high after 30 years, even in the long-term and small-scale regenerated stands. For the mixed oak stands in EBR and BUS, the estimated decrease was much earlier and more pronounced (Figure 2).

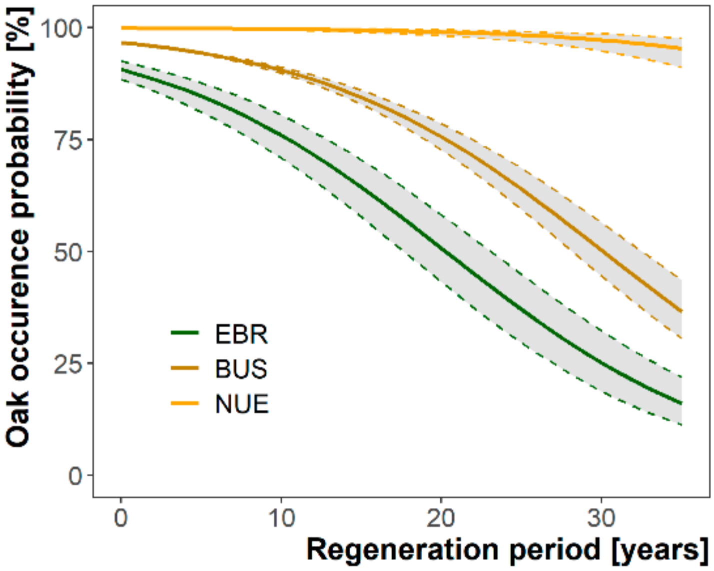

Figure 2. Estimated occurrence probability of oak for the studied sites depending on the regeneration period (Equation (2); for model statistics see Table S2).

3.2. Regeneration Density and the Effect of Canopy Cover on Regeneration Biomass

The regeneration tree density decreased significantly with the duration of the regeneration period or the respective regeneration age. The estimated trajectories showed species-specific differences (Figure 3). With the exception of pine in NUE, the oak tree numbers decreased the most with age on all sites relative to all admixed tree species. The estimated coefficients were -1.26, -0.35, and -1.27 in EBR, BUS, and NUE, respectively. In contrast, the density reduction was the lowest for beech in all the investigated stands, although a slight increase was observed for beech in BUS. The reduced estimates appeared to be due to masting during the observation period (Table 4).

The biomass of the regenerated plants was affected by canopy cover. Closed canopy stand situations mostly resulted in lower regeneration biomasses. For the experimental site EBR and the oak, beech, pine, and hornbeam species, respectively, the effect was significant. In NUE, only oak biomass was significantly and negatively affected by canopy cover (Table 5). However, in BUS, the effect was not significant for either the oak or the beech species.

Accordingly, oak biomass increased by 12.1 t ha^{-1}, 1.3 t ha^{-1}, and 7.3 t ha^{-1} in EBR, BUS, and NUE, respectively, at the age of 30 from non- to fully canopied stand situations.

When there was no canopy cover, the oaks in EBR reached approximately the biomass of the beech regeneration. In BUS, however, the values of the beech biomass were not reached by oak in any canopy cover situation. In contrast, in NUE, the oak biomass exceeded the beech biomass in almost every canopy cover situation (Figure 4).

Table 4. Model statistics for tree density as a function of regeneration age (A) (Equation (3)); the reference tree species is oak; Est—estimated value; SE—standard error; *p*—*p*-value; significant values are written in bold.

	EBR		BUS		NUE	
Fixed Effects	**Est (SE)**	***p***	**Est (SE)**	***p***	**Est (SE)**	***p***
(Intercept)	**12.09** (0.16)	**<0.001**	**10.28** (0.28)	**<0.001**	**12.43** (0.25)	**<0.001**
ln (A)	−**1.26** (0.03)	**<0.001**	−**0.35** (0.05)	**<0.001**	−**1.27** (0.07)	**<0.001**
Be	−**1.24** (0.12)	**<0.001**	−**1.00** (0.17)	**<0.001**	−**4.94** (0.26)	**<0.001**
Be × ln (A)	**0.61** (0.04)	**<0.001**	**0.39** (0.10)	**<0.001**	**1.26** (0.10)	**<0.001**
Pi	−**3.63** (0.17)	**<0.001**	-	-	−0.28 (0.2)	0.316
Pi × ln (A)	**0.65** (0.06)	**<0.001**	-	-	−**0.26** (0.11)	**0.020**
Hb	−**3.61** (0.15)	**<0.001**	-	-	-	-
Hb × ln (A)	**0.81** (0.05)	**<0.001**	-	-	-	-
Others	−**4.45** (0.14)	**<0.001**	-	-	−**4.04** (0.30)	**<0.001**
Others × ln (A)	**0.92** (0.05)	**<0.001**	-	-	**0.70** (0.11)	**<0.001**
Random Effects						
σ^2	1.16		1.55		1.00	
$\tau_{00\ \mathrm{Squ:P}}$	0.03		0.33		0.04	
$\tau_{00\ \mathrm{P}}$	0.11		0.12		0.11	
N_{Squ}	256		200		36	
N_{P}	6		2		4	
N measurements	10,599		2101		1405	
AIC	31,971.7		7215.1		4084.5	

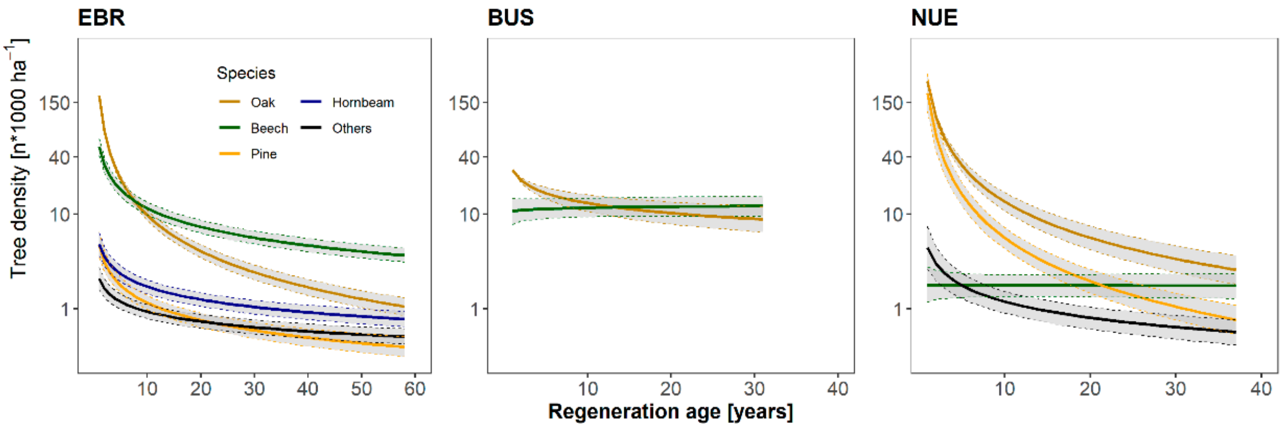

Figure 3. Estimated tree densities of the regenerated tree species (Equation (3)); note the logarithmic scaling of the *y*-axis and the different scaling of the *x*-axes.

3.3. Influence of Canopy Cover and Interspecific Competition on Oaks' Maximum Heights

In addition to the canopy cover of the old stand, the observed maximum heights of the regeneration were additionally influenced by the interspecific competition. The interspecific competition with the oak regeneration in the studied stands was almost exclusively by the admixed beech (see Figure 4); thus, the beech admixture was considered to be the competition factor (Table 6).

For the mixed stands in BUS and EBR, respectively, the effect of canopy cover was significant (Table 6). In particular, the effects were different between the considered tree species, as shown below for the oak and admixed beech (Table 6, Figure 5).

Table 5. Model statistics for biomass development as a function of regeneration age (A) and canopy cover (CC) (Equation (4)); the reference tree species is oak; Est—estimated value; SE—standard error; *p*—*p*-value; significant values are written in bold.

	EBR		BUS		NUE	
Fixed Effects	**Est (SE)**	***p***	**Est (SE)**	***p***	**Est (SE)**	***p***
(Intercept)	−**3.71** (0.29)	**<0.001**	−**3.99** (0.34)	**<0.001**	−**3.04** (0.47)	**<0.001**
ln (A)	**2.11** (0.08)	**<0.001**	**1.93** (0.10)	**<0.001**	**1.90** (0.12)	**<0.001**
CC	−**2.90** (0.13)	**<0.001**	−0.26 (0.19)	0.168	−**0.95** (0.38)	**0.013**
Be	**0.24** (0.08)	**0.002**	**0.76** (0.17)	**<0.001**	−**0.93** (0.38)	**0.015**
Be × CC	**2.69** (0.15)	**<0.001**	0.01 (0.24)	0.955	0.99 (0.54)	0.065
Pi	−**1.32** (0.17)	**<0.001**	-	-	−**2.51** (0.55)	**<0.001**
Pi × CC	**2.46** (0.32)	**<0.001**	-	-	**1.53** (0.75)	**0.041**
Hb	−**1.13** (0.09)	**<0.001**	-	-	-	-
Hb × CC	**2.64** (0.21)	**<0.001**	-	-	-	-
Others	0.22 (0.17)	0.194	-	-	−**1.85** (0.40)	**<0.001**
Others × CC	0.81 (0.42)	0.056	-	-	0.84 (0.58)	0.144
Random Effects						
σ^2	2.61		2.15		2.50	
$\tau_{00\ \mathrm{Squ:P}}$	0.10		0.18		0.00	
$\tau_{00\ \mathrm{P}}$	0.07		0.01		0.09	
N_{Squ}	256		200		36	
N_{P}	6		2		4	
N measurements	5195		1307		772	
AIC	19,983.3		4829.5		2931.8	

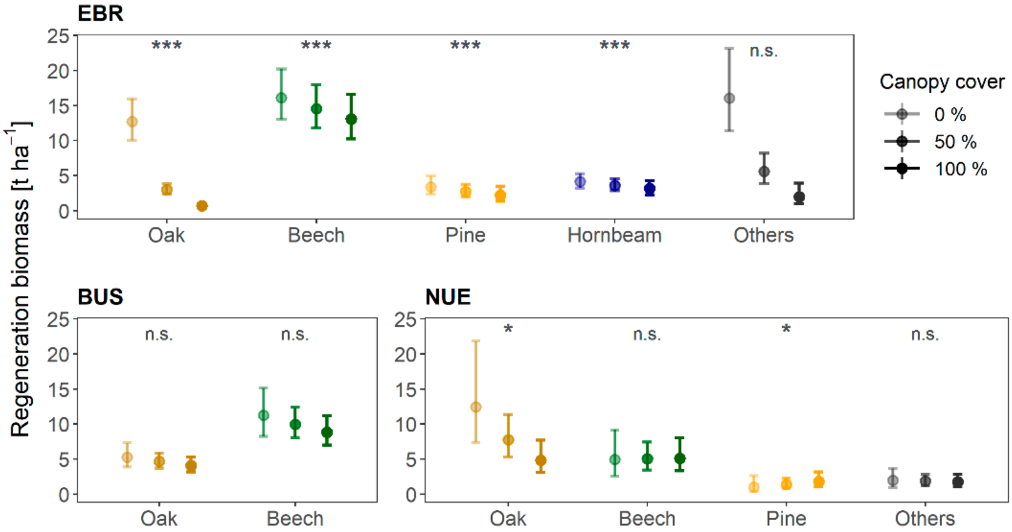

Figure 4. Regenerated biomass of oak, beech, pine, hornbeam, and other broadleaf tree species as a function of canopy cover at the age of 30 (Equation (4)); asterisks denote the significance levels of the canopy cover effect, *** $p < 0.001$, * $p < 0.05$, n.s. not significant.

The heights of the oaks were negatively affected by the canopy cover of all the investigated stands. The estimated coefficients were −0.80, −0.50, and −0.2 for EBR, BUS, and NUE, respectively. However, in the monospecific stands, this coefficient estimate was not significant. The strongest negative effect of the canopy cover could therefore be found for the mixed stands of EBR. There, the 50% canopy cover reduced the oak heights by 33% compared to the non-canopied stand situations, which corresponds to an average reduction of 1.7 m at the regeneration age of 15 years. For BUS and NUE, the oaks were 23% and 11% smaller, respectively (Figure 5).

Consequently, the canopy cover had a stronger effect on the oak than on the beech regeneration at all the sites (Table 6, Figure 5). Assuming a canopy cover of 50% indicates that beech trees outperform oak trees at a regeneration age of 15 years by 1.5 m and 1.4 m in the mixed oak stands in BUS and EBR, respectively. Even for the stand situations without a canopy cover, a certain advantage for beech is shown for both experimental sites. A negative height relation between oak and beech is always evident.

In the monospecific pine stands (NUE), both tree species reached comparable heights, with a visible, but not significant, height advantage for oak. There, the characteristics of oak as a light-demanding tree species became more evident. A canopy cover below 60% resulted in a positive height relation with oak as compared to beech.

The canopy cover of the mature stand and the interspecific competition in the regeneration showed strong effects on the heights of the oak regeneration. Increasing the beech admixture led to decreasing heights of the neighboring oaks (Figure 6). This effect was observed across all experimental sites. For the most vigorous sites in EBR, the height relation of oak compared to beech was still positive up to a beech proportion of 47% in the non-canopied stand situations. At a canopy cover of 50%, the positive height relation could only be observed at beech proportions of 20%. In BUS, these values were 30% and 14% and in NUE 19% and 16%, respectively.

Table 6. Results on the height model as a function of regeneration age (A), canopy cover (CC), and proportion of beech regeneration (BE_perc) (Equation (5)); the reference species is oak; Est—estimated value; SE—standard error; *p*—*p*-value. Significant values are written in bold.

	EBR		BUS		NUE	
Fixed Effects	**Est (SE)**	***p***	**Est (SE)**	***p***	**Est (SE)**	***P***
(Intercept)	−0.20 (0.10)	0.251	−**2.60** (0.30)	**<0.001**	−**1.70** (0.40)	**<0.001**
ln (A)	**0.77** (0.00)	**<0.001**	**1.24** (0.00)	**<0.001**	**1.20** (0.10)	<0.001
CC	−**0.80** (0.10)	**<0.001**	−**0.50** (0.10)	**<0.001**	−0.20 (0.30)	0.387
Be_perc	−**0.70** (0.10)	**<0.001**	−**0.40** (0.10)	**0.001**	−**1.90** (0.70)	**0.008**
Be	−**0.50 (0.00)**	**<0.001**	−**0.50** (0.10)	**<0.001**	−0.40 (0.30)	0.077
Be × Be_perc	**1.13** (0.10)	**<0.001**	**1.52** (0.10)	**<0.001**	**2.25** (0.70)	**0.001**
Be × CC	**0.58** (0.10)	**<0.001**	**0.48** (0.10)	**<0.001**	0.12 (0.30)	0.703
Pi	0.01 (0.10)	0.932	-	-	−0.80 (0.40)	0.052
Pi × Be_perc	−0.20 (0.20)	0.546	-	-	0.15 (1.00)	0.880
Pi × CC	**0.69 (0.20)**	**<0.001**	-	-	−0.20 (0.50)	0.631
Hb	−**0.50 (0.10)**	**<0.001**	-	-	-	-
Hb × Be_perc	**0.66** (0.10)	**<0.001**	-	-	-	-
Hb × CC	**0.66** (0.10)	**<0.001**	-	-	-	-
Others	−0.10 (0.10)	0.147	-	-	−**1.10** (0.30)	**<0.001**
Others × Be_perc	**0.43** (0.20)	**0.010**	-	-	0.90 (0.80)	0.242
Others × CC	0.12 (0.20)	0.425	-	-	0.33 (0.40)	0.354
Random Effects						
σ^2	0.27		0.33		0.53	
$\tau_{00\ Squ:P}$	0.03		0.07		0.06	
$\tau_{00\ P}$	0.03		0.18		0.06	
N_{Squ}	256		200		36	
N_{P}	6		2		4	
N measurements	3519		1266		464	
AIC	5752.0		2423.0		1103.3	

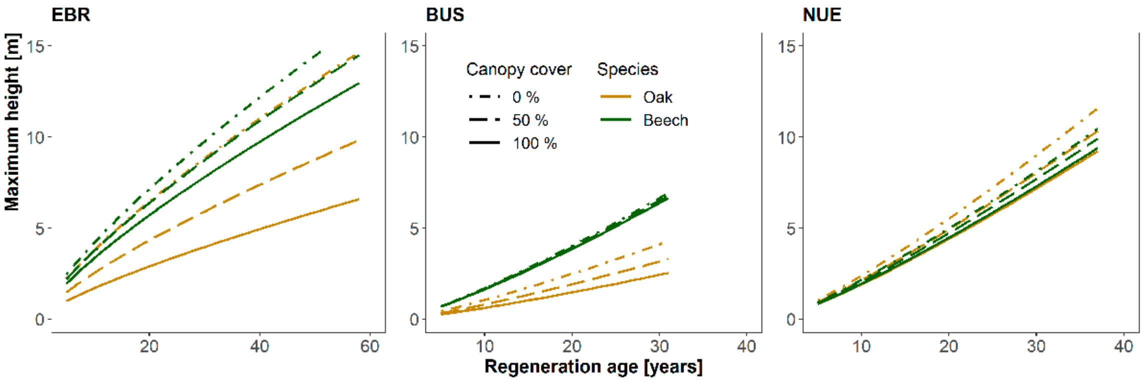

Figure 5. Estimated maximum heights of oak and beech regeneration as a function of regeneration age and canopy cover (Equation (5)); shown are the height trajectories of oak and the most competitive beech species. Note the different scaling of the *x*-axes.

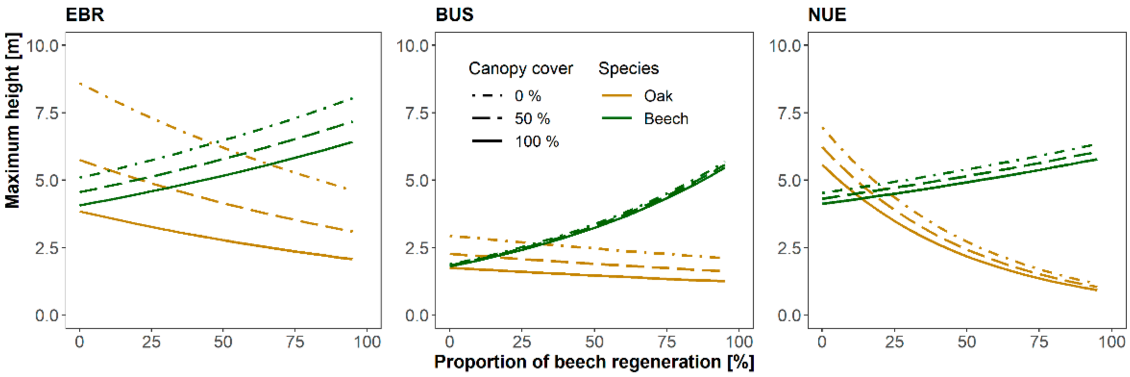

Figure 6. Estimated maximum heights of oak and beech regeneration as a function of the proportion of beech regeneration and canopy cover at the age of 20 (Equation (5)); shown are the height trajectories of oak and the most competitive beech species. Note the different scaling of the *x*-axes.

3.4. Feedback of Regeneration on Main Stand Productivity

The periodic annual increment was mainly dependent on the stand volume, which was statistically significant (Table 7). An increase in standing volume by 100 m^3 ha^{-1} in the mature stand resulted in higher stand increments by an average of 1.8 to 2.7 m^3 ha^{-1} $year^{-1}$ (Figure 7).

Table 7. Results of the model on periodic annual increment of the main stand as a function of the standing volume (V) and the regeneration biomass (bm_reg) (Equation (6)); Est—estimated value; SE—standard error; *p*—*p*-value; significant values are written in bold.

Fixed Effects	**Est (SE)**	***p***
(Intercept)	−**7.23** (1.79)	**<0.001**
bm_reg	0.03 (0.03)	0.358
ln (V)	**1.58** (0.33)	**<0.001**
ln (V) × bm_reg	−0.01 (0.01)	0.279
Random Effects		
σ^2	0.23	
$\tau_{00\ P}$	0	
N_{P}	7	
N measurements	24	
AIC	62.5	

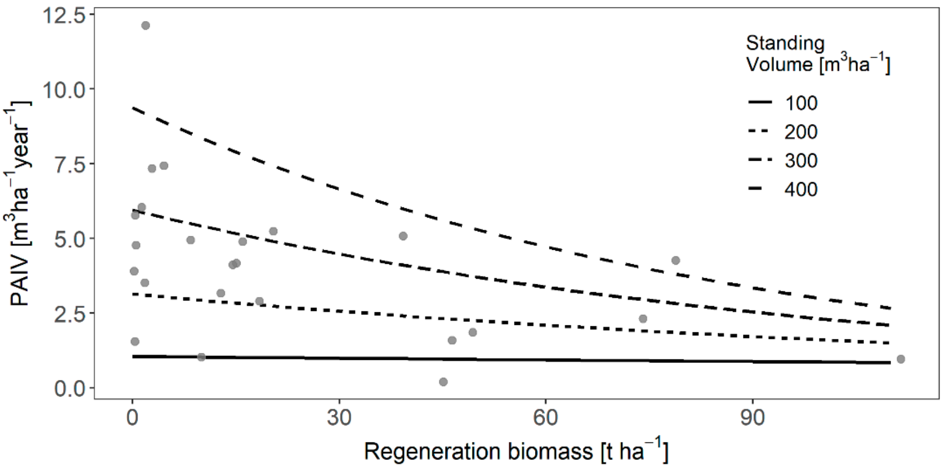

Figure 7. Periodic annual increment of the main stand as a function of regeneration biomass (not significant) and volume (most significant) (Equation (6)).

The effect of the regeneration biomass was not significant. However, a negative trend was visible, which was amplified with the increasing stand volumes in the main stand (Figure 7). The periodic annual increment of the main stand seemed to decrease by an average of 23% and 40% at a regeneration biomass of 30 and 60 t ha^{-1}, respectively. In absolute values, this corresponded to reductions in the old-growth stand increments of 1.0 and 1.8 m^3 ha^{-1} year^{-1}, respectively, as compared to the non-regenerated stands. This trend was more pronounced in the percentage, as well as in the absolute terms, of the stands with higher standing volumes compared to the stands with low standing volume.

4. Discussion

4.1. Valuable Insights from Long-Term Observations as Research Basis

A recent literature review [38] concluded that oak regeneration is in principle possible even in small areas, but at the same time, it noted that the underlying data for this conclusion are still very limited, especially when the long-term developments of oak regeneration are considered. With the present study, the regeneration data covering a period beyond 15 years and reaching up to 36 years could be used. To our knowledge, the present study is the only study of oak regeneration that covers an observation period of more than 25 years.

Furthermore, full surveys of stand regeneration in experimental stands of up to 1.0 ha in size are very rare. Here, a unique dataset encompassing half a million single data of regenerated trees could be used. In connection with the information available for the mature trees, the data cover a wide range of regeneration situations, i.e., gap sizes, species mixture, and canopy cover characteristics, as well as site conditions (see Section 2.1).

4.2. Long-Term Development and Survival of the Regeneration

The results showed that close-to-nature silviculture with long-term (>25 years) and small-scale (0.01–0.25 ha) regeneration methods can be one option for the regeneration of oak. However, the range of regeneration development within the stands and between sites was wide, ranging from the total loss of oak to an increase in oak proportions over the entire regeneration period (see Table 2). High percentages of oak in the regeneration at the beginning of the regeneration period favor the success of oak regeneration, but do not necessarily lead to a corresponding percentage of oak at the beginning of the stem exclusion stage (see Tables 2 and 3). The conclusions drawn from previous studies, namely that oak regeneration can succeed even with small-scale regeneration methods [33,38,39], could be corroborated for the long run by the present results. However, it was also revealed that at certain sites, beech is able to become dominant or even outcompete oak sooner or later [18,34,47,48].

This insight was also evident when considering the survival rates of oak. In particular, the decreasing survival probabilities indicated the need for silvicultural assistance in the given stand situations (see Figure 2). Accordingly, the participation of oak in a mixture with beech was not stable throughout the regeneration period and confirmed the results of some studies [18,19,39,49], which can also be found in the early silvicultural principles for oak management [18,25,50]. Differences between experimental sites and forest stand types were clearly recognizable and should be considered in pre-commercial thinnings. Small-scale and long-term regeneration methods are especially promising in low-growth sites and/or monospecific pine stands. The competitive ability of oaks seemed to benefit from the higher light availability under more light-transmitting pine canopies. Lower site quality additionally reduced beech growth. The observed survival probabilities of 30% and more after 20 years of regeneration initialization (see Figure 2) also showed the remarkable potential of young oaks when small-scale regeneration methods were applied. However, when interpreting the results, it should also be noted that the survival rates represent the occurrence and not the dominance of oak in the regeneration.

The observed regeneration biomass showed an enormous growth potential. Even the apparently low-growing sites in NUE showed a considerable growth potential of oak and reached maximum biomass values that were similar to those of the more vigorous sites in EBR (see Figure 4). However, without appropriate silvicultural interferences in the main stand and pre-commercial thinnings in the advanced regeneration in favor of oak, this potential remained unused. Uniformly high or increasing stand volume in the main stand counteracted this (see Tables 2 and 3). This was also true for the development of the appreciable oak proportions after early regeneration until the stem exclusion stage.

Equally apparent was the potential of natural oak regeneration, which was the basis of the observed oak regeneration in the majority of stands. Together with the findings by Löf et al. [41], who evaluated the costs for oak natural regeneration and found them to be the lowest, this results in an additional potential for operational savings or at least compensation.

4.3. Influence of Canopy Cover and Interspecific Competition

Sessile oak, as a light-demanding tree species, reacted more strongly to the canopy cover reduction than beech at all the sites. Thus, the results match those of several studies that observed a similar trend [18,35,51]. Interestingly, beech was still superior to oak irrespective of the canopy cover in the considered mixed stands in EBR and BUS (see Figure 5). This observation suggested that successful oak regeneration in the mixed regenerations was apparently not possible by controlling the canopy cover alone. A similar conclusion was drawn by Modrow et al. [35], who recommended controlling mixed tree species regardless of the regeneration gap size. At the same time, this resulted in the greatest scope for promoting oak in EBR, which may indicate that competition for light rather than soil-based resources was occurring at this site, whereas in BUS the nutrients seemed limiting. In NUE, the effect of canopy cover reduction was the lowest, which suggests that water and nutrients may be the limiting factors. Furthermore, NUE was the only experimental site where oak appeared to be superior to beech in height growth. These height relations indicated that oak's superiority compared to beech was strongly dependent on monospecific pine stands with sparse site conditions. However, it is precisely these stands that should be urgently adapted to the rapidly changing climate [52]. These observations were also made for even younger oak regenerations [34,53]. Accordingly, oak requires the support of the silvicultural regulation of woody competitors for successful establishment in many sites [18,49,54].

The revealed competition of beech with the height development of oak regeneration deepens the conclusions drawn from studies considering shorter regeneration periods, which suggest a reduction in competition in favor of oak [35,38]. For example, Hauskeller-Bullerjahn [55] found that height growth in oak was reduced by 24% on average by competition and 30% of full light. The competition exerted by the admixture of beech was, in addition to the control of canopy cover, the most important factor for the successful establishment of oak in the considered stands. The observed competition effect by beech seemed to be influenced, on the one hand, by higher light availability and thus less by the influence of canopy cover [56] and, on the other hand, by increased root competition [57] due to lower nutrient and water availability.

Accordingly, high oak percentages at the beginning of the regeneration period and correspondingly lower beech competition showed positive effects on the development of oak regeneration (see Table 3). The increase in beech proportions in the regeneration resulted in a decrease in the positive competition relation of oak towards beech. This appeared to be due to the interspecific competitive pressure of beech on oak [36]. Therefore, the relations between oak and the mixed (competitor) species should be given special attention when creating the mixture. This is important for the success of the specific species mixture and the appropriate maintenance efforts, taking into account the natural development. For example, Meesenburg et al. [58] recommend a group mixture of tree species, which should have a minimum size of 0.3 ha. As a conclusion of the present study, oak regeneration can be successfully practiced even in smaller areas, assuming that the silvicultural goal is oak and that the thinnings are focused on assisting oak.

4.4. Influence of Regeneration on Old-Growth Productivity

Due to the long-term regeneration periods, with regeneration ages reaching 58 years, regeneration biomasses up to more than 100 t ha^{-1} could be observed in the investigated stands (see Table 3). At the same time, the remaining main stand continued to produce wood increments throughout the entire regeneration period. This is particularly important for deciding on the silvicultural approach.

Productivity was thus primarily determined by the standing volume (see Table 7). The effect of regeneration biomass on the productivity of the main stand was not significant. However, a negative trend was visible (see Figure 7). Accordingly, as biomass increased old-growth productivity decreased. In particular, this appeared to be due to increased belowground competition for resources between old growth and regeneration [59,60]. This conclusion is further supported by the observation that the effect was more pronounced with higher standing volumes. Conversely, this also meant that high regeneration biomasses could partially compensate for the resulting increment losses, due to the volume reduction by the harvesting of single mature trees.

However, so that the influence of regeneration on the overstorey can be conclusively assessed, further studies on the observed trend should be carried out. Particularly for the management of multi-layered stands, the consideration of the feedback of advanced regeneration on the remaining stand seems to be highly relevant.

4.5. Silvicultural Consequences

How oak stands or forests in general are managed is basically very much determined by the production objective in the respective stand. This also applies to the proportion of oak in the tree species portfolio of future forest stands. If oak is to be maintained or established in appreciable proportions for timber production [14,19] or as an ecological admixture [24], appropriate pre-commercial thinnings are necessary. The chosen silvicultural approach is therefore not a static system but should change with the site and stand conditions as well as with the corresponding operational objective. In principle, sessile oaks can make a valuable contribution in establishing climate-stable and structured mixed stands [4,5]. In this regard, it is important to emphasize the potential of oak for converting monospecific pine stands into mixed pine–oak stands.

The single tree and group selection systems considered in this study are one option for the establishment of oak while maintaining a balanced forest interior climate at the same time. Current climatic trends indicate that clear-cut climates should be avoided in any case. The outlined results therefore show a way to maintain or establish oak in the tree species portfolio as well as the small-scale regeneration methods in the long term.

For this to succeed, it is recommended that the standing volume of mature stands, including the serving tree layers in the area to be regenerated, should be consistently reduced. In this case, gap size or the area to be regenerated may be 0.1 ha. Depending on site conditions, the remaining stand volume should optimally be less than 250 m^3 ha^{-1} in mixed beech–oak stands and 300 m^3 ha^{-1} in monospecific pine stands, respectively (see Table 2). During the regeneration period, a renewed volume build-up must be avoided. The priority goal in the respective patches has to be the regeneration of oak. Ideally, there is no advanced regeneration of admixed tree species. If mixed tree species are present, increased management in favor of oak must be calculated since regulation of the old stand alone is not sufficient. Mixed tree species proportions, especially those of beech, that exceed 30% significantly impair oak in early regeneration until the stem exclusion stage.

Against the backdrop of rapidly advancing climate change, preparing European forests by creating mixed and structured stands is the order of the day. In particular, mixed stands with oak participation can make an important contribution to more resilient stands in the future.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13122052/s1, Table S1: list of tree species, summarized under the general term "Others", Table S2: model statistics of oak survival rates.

Author Contributions: Conceptualization, K.S., E.U. and H.P.; methodology, K.S.; formal analysis, K.S.; investigation, K.S.; resources, H.P.; data curation, K.S.; writing—original draft preparation, K.S.; writing—review and editing, K.S., E.U. and H.P.; visualization, K.S.; supervision, H.P.; funding acquisition, E.U. and H.P. All authors have read and agreed to the published version of the manuscript.

Funding: This publication is part of the project "Growth potential of oak in managed and unmanaged forests dependent on stand structure and site conditions (W045)" [grant number 7831–27295-2017] that was supported by the Bavarian State Ministry of Nutrition, Agriculture and Forestry. The experimental plots are part of the network of long-term yield trials of Bavaria which are funded by the Bavarian State Ministry of Nutrition, Agriculture and Forestry [grant number W007 7831-26625-2017].

Data Availability Statement: The data used in this study are available on request from the corresponding author.

Acknowledgments: We would like to thank the Bavarian Forest Enterprise (BaySF), particularly the branch offices in Nuremberg and Ebrach and the community of Burgsinn for providing the research opportunities.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Eaton, E.; Caudullo, G.; Oliveira, S.; de Rigo, D. Quercus robur and *Quercus petraea* in Europe: Distribution, habitat, usage and threats. In *European Atlas of Forest Tree Species*; San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A., Eds.; Publications Office of the European Union: Luxembourg, 2016; pp. 160–163, ISBN 978-92-79-52833-0.
2. Mette, T.; Dolos, K.; Meinardus, C.; Bräuning, A.; Reineking, B.; Blaschke, M.; Pretzsch, H.; Beierkuhnlein, C.; Gohlke, A.; Wellstein, C. Climatic turning point for beech and oak under climate change in Central Europe. *Ecosphere* **2013**, *4*, 1–19. [CrossRef]
3. Mette, T.; Brandl, S.; Kölling, C. Climate Analogues for Temperate European Forests to Raise Silvicultural Evidence Using Twin Regions. *Sustainability* **2021**, *13*, 6522. [CrossRef]
4. Schroeder, H.; Nosenko, T.; Ghirardo, A.; Fladung, M.; Schnitzler, J.-P.; Kersten, B. Oaks as Beacons of Hope for Threatened Mixed Forests in Central Europe. *Front. For. Glob. Chang.* **2021**, *4*, 78. [CrossRef]
5. Albert, M.; Nagel, R.-V.; Nuske, R.; Sutmöller, J.; Spellmann, H. Tree Species Selection in the Face of Drought Risk—Uncertainty in Forest Planning. *Forests* **2017**, *8*, 363. [CrossRef]
6. Pretzsch, H.; Bielak, K.; Block, J.; Bruchwald, A.; Dieler, J.; Ehrhart, H.-P.; Kohnle, U.; Nagel, J.; Spellmann, H.; Zasada, M.; et al. Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur. J. For. Res.* **2013**, *132*, 263–280. [CrossRef]
7. Ammer, C. Unraveling the Importance of Inter- and Intraspecific Competition for the Adaptation of Forests to Climate Change. In *Progress in Botany Vol. 78*; Cánovas, F.M., Lüttge, U., Matyssek, R., Eds.; Springer International Publishing: Cham, Switzerland, 2017; pp. 345–367, ISBN 978-3-319-49489-0.
8. Bolte, A.; Ammer, C.; Löf, M.; Madsen, P.; Nabuurs, G.-J.; Schall, P.; Spathelf, P.; Rock, J. Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. *Scand. J. For. Res.* **2009**, *24*, 473–482. [CrossRef]

9. Lindner, M.; Maroschek, M.; Netherer, S.; Kremer, A.; Barbati, A.; Garcia-Gonzalo, J.; Seidl, R.; Delzon, S.; Corona, P.; Kolström, M.; et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manag.* **2010**, *259*, 698–709. [CrossRef]
10. Puettmann, K.J.; Messier, C. Simple Guidelines to Prepare Forests for Global Change: The Dog and the Frisbee. *NWSC* **2019**, *93*, 209. [CrossRef]
11. Brändle, M.; Brandl, R. Species richness of insects and mites on trees: Expanding Southwood. *J. Anim. Ecol.* **2001**, *70*, 491–504. [CrossRef]
12. Manos, P.S.; Stanford, A.M. The Historical Biogeography of Fagaceae: Tracking the Tertiary History of Temperate and Subtropical Forests of the Northern Hemisphere. *Int. J. Plant Sci.* **2001**, *162*, S77–S93. [CrossRef]
13. Brockerhoff, E.G.; Barbaro, L.; Castagneyrol, B.; Forrester, D.I.; Gardiner, B.; González-Olabarria, J.R.; Lyver, P.O.; Meurisse, N.; Oxbrough, A.; Taki, H.; et al. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodivers Conserv.* **2017**, *26*, 3005–3035. [CrossRef]
14. Löf, M.; Brunet, J.; Filyushkina, A.; Lindbladh, M.; Skovsgaard, J.P.; Felton, A. Management of oak forests: Striking a balance between timber production, biodiversity and cultural services. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manag.* **2016**, *12*, 59–73. [CrossRef]
15. van der Plas, F.; Ratcliffe, S.; Ruiz-Benito, P.; Scherer-Lorenzen, M.; Verheyen, K.; Wirth, C.; Zavala, M.A.; Ampoorter, E.; Baeten, L.; Barbaro, L.; et al. Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. *Ecol. Lett.* **2018**, *21*, 31–42. [CrossRef] [PubMed]
16. Weaver, G.T.; Spiecker, H. Silviculture of high-quality oaks: Questions and future research needs. *Ann. Sci.* **1993**, *50*, 531–534. [CrossRef]
17. Attocchi, G. *Silviculture of Oak for High-Quality Wood Production: Effects of Thinning on Crown size, Volume Growth and Stem Quality in Even-Aged Stands of Pedunculate oak (Quercus robur L.) in Northern Europe*; Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences: Alnarp, Sweden, 2015; ISBN 978-91-576-8277-2.
18. von Lüpke, B. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *For. Ecol. Manag.* **1998**, *106*, 19–26. [CrossRef]
19. Mölder, A.; Sennhenn-Reulen, H.; Fischer, C.; Rumpf, H.; Schönfelder, E.; Stockmann, J.; Nagel, R.-V. Success factors for high-quality oak forest (*Quercus robur*, *Q. petraea*) regeneration. *For. Ecosyst.* **2019**, *6*, 262. [CrossRef]
20. Ellenberg, H.H.; Strutt, G.K. *Vegetation Ecology of Central Europe*; Cambridge University Press: Cambridge, UK, 1988; ISBN 9780521236423.
21. Manthey, M.; Leuschner, C.; Härdtle, W. Buchenwälder und Klimawandel. *Nat. Landsch.* **2007**, *82*, 441–445.
22. Aas, G. Quercus petraea (Matt.) Liebl., Traubeneiche. In *Enzyklopädie der Holzgewächse*; Roloff, A., Weisgerber, H., Lang, U., Stimm, B., Eds.; Wiley-VCH: Weinheim, Germany, 2000.
23. Krahl-Urban, J. *Die Eichen: Forstliche Monographie der Traubeneiche und der Stieleiche*; P. Parey: Hamburg, Germany, 1959.
24. Mölder, A.; Meyer, P.; Nagel, R.-V. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. *For. Ecol. Manag.* **2019**, *437*, 324–339. [CrossRef]
25. Fleder, W. Vom unterfränkischen Verjüngungsbetrieb. *Allg. Forstz.* **1983**, *38*, 1013–1014.
26. Jedicke, E.; Hakes, W. Management von Eichenwäldern im Rahmen der FFH-Richtlinie. *Nat. Landsch.* **2005**, *37*, 37–45.
27. Meyer, P. Forstwirtschaft und Naturschutz—Konfliktpotenzial und Synergien am Beispiel von Natura 2000. In *Natura 2000 im Wald—Lebensraumtypen, Erhaltungszustand, Management, Naturschutz und Biologische Vielfalt*; Lehrke, S., Ellwanger, G., Buschmann, A., Frederking, W., Paulsch, C., Schröder, E., Ssymank, A., Eds.; Landwirtschaftsverlag: Münster, Germany, 2013; pp. 177–197.
28. Brang, P.; Spathelf, P.; Larsen, J.B.; Bauhus, J.; Boncina, A.; Chauvin, C.; Drossler, L.; Garcia-Guemes, C.; Heiri, C.; Kerr, G.; et al. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* **2014**, *87*, 492–503. [CrossRef]
29. Puettmann, K.J.; Wilson, S.M.; Baker, S.C.; Donoso, P.J.; Drössler, L.; Amente, G.; Harvey, B.D.; Knoke, T.; Lu, Y.; Nocentini, S.; et al. Silvicultural alternatives to conventional even-aged forest management—What limits global adoption? *For. Ecosyst.* **2015**, *2*, 8. [CrossRef]
30. Spathelf, P.; Bolte, A.; van der Maaten, E.C.D. Is Close-to-Nature Silviculture (CNS) an adequate concept to adapt forests to climate change? *Landbauforsch.-Appl. Agric. For. Res.* **2015**, *65*, 161–170. [CrossRef]
31. Maleki, K.; Zeller, L.; Pretzsch, H. Oak often needs to be promoted in mixed beech-oak stands—The structural processes behind competition and silvicultural management in mixed stands of European beech and sessile oak. *iForest* **2020**, *13*, 80–88. [CrossRef]
32. Mosandl, R.; Abt, A. Waldbauverfahren in Eichenwäldern gestern und heute. *AFZ-Der Wald* **2016**, *20*, 28–32.
33. Březina, I.; Dobrovolný, L. Natural regeneration of sessile oak under different light conditions. *J. For. Sci.* **2011**, *57*, 359–368. [CrossRef]
34. Ligot, G.; Balandier, P.; Fayolle, A.; Lejeune, P.; Claessens, H. Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. *For. Ecol. Manag.* **2013**, *304*, 391–398. [CrossRef]
35. Modrow, T.; Kuehne, C.; Saha, S.; Bauhus, J.; Pyttel, P.L. Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes. *Eur. J. For. Res.* **2019**, *116*, 346. [CrossRef]
36. Annighöfer, P.; Beckschäfer, P.; Vor, T.; Ammer, C. Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. *PLoS ONE* **2015**, *10*, e0134935. [CrossRef]

37. Kanjevac, B.; Krstić, M.; Babić, V.; Govedar, Z. Regeneration Dynamics and Development of Seedlings in Sessile Oak Forests in Relation to the Light Availability and Competing Vegetation. *Forests* **2021**, *12*, 384. [CrossRef]
38. Kohler, M.; Pyttel, P.; Kuehne, C.; Modrow, T.; Bauhus, J. On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests—A literature review. *Ann. For. Sci.* **2020**, *77*, 101. [CrossRef]
39. Kuehne, C.; Pyttel, P.; Modrow, T.; Kohnle, U.; Bauhus, J. Seedling development and regeneration success after 10 years following group selection harvesting in a sessile oak (*Quercus petraea* [Mattuschka] Liebl.) stand. *Ann. For. Sci.* **2020**, *77*, 71. [CrossRef]
40. Löf, M. Establishment and growth in seedlings of Fagus sylvatica and *Quercus robur*: Influence of interference from herbaceous vegetation. *Can. J. For. Res.* **2000**, *30*, 855–864. [CrossRef]
41. Löf, M.; Barrere, J.; Engman, M.; Petersson, L.K.; Villalobos, A. The influence of fencing on seedling establishment during reforestation of oak stands: A comparison of artificial and natural regeneration techniques including costs. *Eur. J. For. Res.* **2021**, *140*, 807–817. [CrossRef]
42. Johann, K. DESER-Norm 1993. Normen der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten zur Aufbereitung von waldwirtschaftlichen Dauerversuchen. *Ber. Jahrestag. Dtsch. Verb. Forstl. Sekt. Ertragskunde* **1993**, 96–104.
43. Forrester, D.I.; Tachauer, I.; Annighoefer, P.; Barbeito, I.; Pretzsch, H.; Ruiz-Peinado, R.; Stark, H.; Vacchiano, G.; Zlatanov, T.; Chakraborty, T.; et al. Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. *For. Ecol. Manag.* **2017**, *396*, 160–175. [CrossRef]
44. Zuur, A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. *Mixed Effects Models and Extensions in Ecology with R*; Springer: New York, NY, USA, 2009; ISBN 978-0-387-87457-9.
45. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2018.
46. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Soft.* **2015**, *67*, 1–48. [CrossRef]
47. Petritan, A.M.; Bouriaud, O.; Frank, D.C.; Petritan, I.C. Dendroecological reconstruction of disturbance history of an old-growth mixed sessile oak-beech forest. *J. Veg. Sci.* **2017**, *28*, 117–127. [CrossRef]
48. Dietz, L.; Gégout, J.-C.; Dupouey, J.-L.; Lacombe, E.; Laurent, L.; Collet, C. Beech and hornbeam dominate oak 20 years after the creation of storm-induced gaps. *For. Ecol. Manag.* **2022**, *503*, 119758. [CrossRef]
49. Manso, R.; Ligot, G.; Fortin, M. A recruitment model for beech–oak pure and mixed stands in Belgium. *For. Int. J. For. Res.* **2020**, *93*, 124–132. [CrossRef]
50. Vanselow, K. Die Waldbautechnik der Eiche im bayerischen Spessart in geschichtlicher Betrachtung. *Forstwiss. Cent.* **1960**, *79*, 270–286. [CrossRef]
51. von Lüpke, B. Einfluss unterschiedlicher Hiebsformen auf die Naturverjüngung eines Traubeneichen-Buchen-Mischbestandes. *Forstarchiv* **2008**, *79*, 4–15.
52. Leuschner, C.; Förster, A.; Diers, M.; Culmsee, H. Are northern German Scots pine plantations climate smart? The impact of large-scale conifer planting on climate, soil and the water cycle. *For. Ecol. Manag.* **2022**, *507*, 120013. [CrossRef]
53. von Lüpke, B.; Hauskeller-Bullerjahn, K. Beitrag zur Modellierung der Jungwuchsentwicklung am Beispiel von Traubeneichen-Buchen-Mischverjüngungen. *Allg. Forst. U J. Ztg* **2004**, *175*, 61–69.
54. Mölder, A.; Nagel, R.-V.; Meyer, P.; Schmidt, M.; Rumpf, H.; Spellmann, H. Historischer Rückblick auf die Verjüngung von Eichen im Spessart des 19. Jahrhunderts–Bedeutung der angewandten Verfahren für die heutige Eichenwirtschaft. *Forstarchiv* **2017**, *88*, 67–78.
55. Hauskeller-Bullerjahn, K. Wachstum Junger Eichen Unter Schirm. Ph.D. Dissertation, Universität Göttingen, Göttingen, Germany, 1997.
56. Skrzyszewski, J.; Pach, M. Crookedness of pedunculate oak (*Quercus robur* L.) growing under a canopy of Scots pine (*Pinus sylvestris* L.). *Scand. J. For. Res.* **2015**, *30*, 688–698. [CrossRef]
57. Leuschner, C.; Hertel, D.; Coners, H.; Büttner, V. Root competition between beech and oak: A hypothesis. *Oecologia* **2001**, *126*, 276–284. [CrossRef]
58. Meesenburg, H.; Schmidt, M.; Sutmöller, J.; Albert, M. Klimaanpassung ist Vorsorge für den Wald. *proWald* **2015**, *11*, 4–10.
59. Pretzsch, H.; Biber, P.; Uhl, E.; Dauber, E. Long-term stand dynamics of managed spruce–fir–beech mountain forests in Central Europe: Structure, productivity and regeneration success. *Forestry* **2015**, *88*, 407–428. [CrossRef]
60. Knapp, E. Zur Wuchsleistung der Unterbaubuche im ungleichaltrigen Kiefern-Buchen-Mischbestand vor und nach ihrer Übernahme als Hauptbestand auf Standorten des nordostdeutschen Tieflandes. *Ber. Jahrestag.* **1991**, 96–110.

D - Publication List

Articles – peer-reviewed

Stimm, K., Heym, M., Uhl, E., Tretter, S., Pretzsch, H. (2021) Height-Growth related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance in mixed-species stands still required? *Forest Ecology and Management*

Stimm, K., Heym, M., Nagel, R.-V., Uhl, E., Pretzsch, H. (2022) 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. *Forests*

Stimm, K., Uhl, E., Pretzsch, H. (2022) Chances and Limitations of Mixed Oak Regeneration under Continuous Canopy Cover – Evidence from Long-Term Observations. *Forests*

Heym, M., Uhl, E., Moshammer, R., Dieler, J., **Stimm, K**., Pretzsch, H. (2021) Utilising forest inventory data for biodiversity assessment. *Ecological Indicators*

Leroy, B.M.L., Lemme, H., Braumiller, P., Hilmers, T., Jacobs, M., Hochrein, S., Kienlein, S., Müller, J., Pretzsch, H., **Stimm, K**., Seibold, S., Jaworek, J., Hahn, W.A., Müller-Kroehling, S., Weisser, W.W. (2021) Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems: An experimental approach. *Ecological solutions and evidence*

del Río, M., Pretzsch, H., Bončina, A., Avdagić, A., Bielak K., Binder, F., Coll, L., Hilmers, T., Höhn, M., Kašanin-Grubin, M., Klopčič, M., Neroj, B., Pfatrisch, M., Stajić, B., **Stimm, K.**, Uhl, E. (2022) Assessment of Indicators for Climate Smart Management in Mountain Forests. In: *Tognetti, R., et al. (eds.), Climate-Smart Forestry in Mountain Regions, Managing Forest Ecosystems*

Pretzsch, H., Hilmers, T., Uhl, E., del Río, M., Avdagić, A., Bielak K., Bončina, A., Coll, L., Giammarchi, F., **Stimm, K.**, Tonon, G., Höhn, M., Kašanin-Grubin, M., Tognetti, R. (2022) Efficacy of Trans-geographic Observational Network Design for Revelation of Growth Pattern in Mountain Forests Across Europe. In: *Tognetti, R., et al. (eds.), Climate-Smart Forestry in Mountain Regions, Managing Forest Ecosystems*

Articles – non-peer-reviewed

Stimm, K., Heym, M., Hübner, C., Pretzsch, H. (2019) Zum Einzelbaumwachstum von Eichen (*Quercus petraea* (Matt.) Liebl. Und *Quercus robur* L.) in Rein- und Mischbeständen in Abhängigkeit von der lokalen Bestandsstruktur. *Beiträge zur Jahrestagung. DVFFA - Sektion Ertragskunde*

Stimm, K., Heym, M., Förster, B., Uhl, E., Tretter, S., Pretzsch, H. (2020) Bestandsdynamik und Verjüngung in Eichen-Naturwaldreservaten. *AFZ-DerWald*

Stimm, K., Heym, M., Uhl, E., Tretter, S., Pretzsch, H. (2021) Klimasensitives Höhenwachstum der Eiche. *AFZ-DerWald*

Stimm, K., Ambs, D., Uhl, E., Pretzsch, H. (2021) Ziele und Wege der Eichenbewirtschaftung in Europa. *Forstliche Forschungsberichte München 221, S. 31-46*

Stimm, K., Heym, M., Uhl, E., Nagel, R.-V., Pretzsch, H. (2021) Zur Produktivität von Eichen in Rein- und Mischbeständen in Abhängigkeit von Bestandsstruktur und Standort – vom Bestand zum Einzelbaum. *Forstliche Forschungsberichte München 221, S. 126-142*

Stimm, K., Uhl, E., Pretzsch, H. (2021) Zur langfristigen Verjüngungsdynamik der Eichen (*Quercus petraea* MATT. Liebl und *Quercus robur* L.) in Kieferrein- und Eichenmischbeständen – Struktur, Wachstum, waldbauliche Behandlung. *Forstliche Forschungsberichte München 221, S. 162-182*

Stimm, K., Heym, M., Blaschke, M., Uhl, E., Tretter, S., Pretzsch, H. (2021) Zur Bestandsdynamik und Verjüngungssituation in Naturwaldreservaten mit Eichenbeteiligung. *Forstliche Forschungsberichte München 221, S. 183-201*

Uhl, E., **Stimm, K.** (2021) Langfristige Wachstumstrends von Eichenbeständen in Deutschland. *Forstliche Forschungsberichte München 221, S. 116-125*

Scientific report (Editor)

Stimm, K. (Ed.) (2021) Die Eiche. Facetten zu Ökologie, Naturschutz, Wachstum und waldbaulichen Perspektiven. *Forstliche Forschungsberichte München 221.*