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Mixed Stands of Douglas-fir and European Beech Compared to Pure Stands

Patterns and Growth Analyses in Dependence of Site Conditions

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Titel	Mixed Stands of Douglas-fir and European Beech Compared to Pure Stands Patterns and Growth Analyses in Dependence of Site Conditions Mischbestände aus Douglasie und Rotbuche im Vergleich zu Reinbeständen Struktur- und Zuwachsanalyse entlang eines Standortgradienten
Keywords	Triplet experimental setup, Site and age gradient, Overyielding, Growth recovery time, Root stem allometry, Mixing effect Tripletversuch, Standorts- und Altersgradient, Mehrzuwachs, Erholungszeit, Stamm-Wurzel-Allometrie
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My impression is that the topic of mixed stands, especially the mixture of Douglas-fir and European beech, is highly relevant for forest management. That is why I would like to thank Prof. Hans Pretzsch for the possibility to work on this topic, supervising the W44 project and for the many discussions about mixed stands. I also thank Prof. Rainer Matyssek from the Chair of Ecophysiology for being my second referee.

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Especially, I would like to thank Cynthia Schäfer for keeping my back free in the time of dissertations, for discussions about tree physiology and for our nice time at the Chair.

Finally, I am grateful to my parents and my brother for ongoing encouragement.

Preface

With this PhD thesis I want to provide a framework for the four articles that were written during my time at the Chair for Forest Growth and Yield Science. The thesis arose in the context of the project (W44) 'Growth and financial yield of European beech – Douglas-fir – Mixed stand in dependence of site conditions' supported by the Bavarian State Ministry for Food, Agriculture, and Forestry. The project was led by Prof. Hans Pretzsch and edited by me.

Before the main text starts, I want to give a description of the following chapters for a better navigation between articles and PhD thesis.

Generally, the thesis is separated into two sections; a summarizing part of the 'Cumulative thesis', followed by the main section of the thesis. The section 'Cumulative thesis' consists mainly of sections of the articles. It results from the guidelines for a PhD thesis at the Technische Universität München and gives the reader a fast overview of the whole thesis. This is followed by the actual, major section which reflects the thesis 'Mixed stands of Douglas-fir and European beech compared to pure stands' and the attached articles.

The introductions of the articles (I–III) are tailored to the objectives. Therefore, the 'Introduction' of the thesis aims to give a more theoretical explanation of the mixture issues and reviews the studies which also investigated pure and mixed stands of Douglas-fir and European beech.

The chapter 'Material and methods' gives a short presentation of the major applied methods. They are described in much more detail in the respective articles. In the method and material section of the thesis, I take the opportunity to argue why I used the applied methods and what the methodical supplements of this work to existing research are. Due to the peer-reviewed process of the articles, it has been shown which methodical parts are discussable. Therefore, I also want to pick up these points and mention them in this chapter.

The chapter 'Main results and discussion' aims to give an overview of the main findings of the three articles. The aim of the chapter is to put the findings of the three articles into connection to each other. During the course of work, I realized that a few connecting analyses between the articles would help to build a close argumentation line to the mixed stand topic of Douglas-fir and European beech. These analyses were undertaken and added to this chapter. The methods of these additional analyses are described in the appendix.

The thesis finishes with the conclusions, which are separated into conclusions and recommendations for further investigation as well as conclusions for forest practice.

The ranking of the article is based on the three main objectives (productivity – climate sensitivity – root-stem allometry). It starts with the basic article (Article I), which explains the experimental setup in detail and answers the major question of productivity in mixed and pure stands. The fourth article was written for a German journal which is close to forest practice. It is an aggregation of the three previous English articles (I–III). In this respect, it is a good German-language summary of the results of the thesis.

In the study, I always speak about pure and mixed stands. The choice of terms is based on the Glossary of Technical Terms Used in Forestry (Society of American Foresters 1958) and on the number of mixed research studies with the same word choice. Nevertheless, readers who describe pure and mixed stands as monocultures, polycultures, mono-species, mixed-species, mono-specific, or multi-specific stands are also addressed by the study at hand.

Contents

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[1] Article IV is an German-language article which summarized the articles I - III

Part -I-

Cumulative thesis

Picture shows a Douglas-fir and a European beech crown in March. The trees stand on a triplet in Spessart (Bavaria). Warm conditions already allow Douglas-fir to transpire whereas European beech is still before flushing.

Foto einer Rotbuche und einer Douglasie im März. Die Bäume befinden sich in einem Mischbestand eines Triplets im Spessart (Bayern). Die warmen Bedingungen ermöglichen es der Douglasie schon zu transpirieren, währenddessen die Buche noch nicht ausgetrieben hat.

Summary of the thesis

The mixing of tree species enables interactions of the species among each other. This may lead to differences in the performance of these mixed stands from those of pure stands. For the investigation in this study, so-called triplets were used. They built the experimental basis of the thesis and consisted of a pure stand of Douglas-fir, a pure stand of European beech and a mixed stand of both species. Throughout Germany, 18 triplets with 1,987 trees were established in seven different ecological regions from dry to moist site conditions at ages from 30 to 120 years. The thesis compared productivity, structure, drought sensitivity and allometry between the pure and mixed stands.

It was found that species combination produced an overyielding of biomass in mixed stands of 6% or 0.81 Mg ha^{-1} year^{-1}. This overyielding was mainly driven by increased growth of Douglas-firs. Stand structure of pure and mixed stands differed significantly. Mixed stands led to an upper crown layer of dominant Douglas-fir and a lower crown layer of suppressed European beech. This height stratification benefited the light supply of Douglas-fir and stimulates the overyielding. The analysis of tree rings showed that the growth recovery time of Douglas-fir in mixed compared to pure stands is shortened in drought years. In contrast, mixture extend the growth recovery time for European beech compared to pure stand conditions. The different phenological characteristics (evergreen and deciduous) of the species seem to induce this pattern. In springtime, Douglas-fir in mixed stands had higher water availability due to less competition than in pure stands. Measurements of soil water tension also indicated lower water tension in springtime in mixed stands compared to pure stands of Douglas-fir. The analyses of allometry referred to a comparison of diameter growth from stem and lateral coarse roots. The investigations found increasing investment into stem growth (compared to root growth) with increasing degree of surrounding interspecific competition against intraspecific competition. Overall, Douglas-fir and European beech seems to generate a complementary species mixture.

Contribution of the authors and article rights

(I) Improved productivity and modified tree morphology of mixed versus pure stands of European beech *(Fagus sylvatica)* and Douglas-fir *(Pseudotsuga menziesii)* with increasing precipitation and age

Eric A. Thurm: running field work and data analysis and writing the paper.

Hans Pretzsch: initiating the project, contributing to study conception and design, and reviewing the manuscript.

(II) Mixture reduces climate sensitivity of Douglas-fir stem growth

Eric A. Thurm: running field work and data analysis and writing the paper.

Enno Uhl: reviewing and writing the paper.

Hans Pretzsch: initiating the project, contributing to study conception and design, and reviewing the manuscript.

(III) Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir (*Pseudotsuga menziesii*) and European beech (*Fagus sylvatica*)

Eric A. Thurm: running field work and data analysis and writing the paper.

Peter Biber: running data analysis, reviewing and writing the paper.

Hans Pretzsch: initiating the project, contributing to study conception and design, and reviewing the manuscript.

(IV) Douglasie: eine leistungsstarke und klimarobuste Mischbaumart
Buchenbeimischung steigert Wachstum und Stabilität der Douglasie

Eric A. Thurm: running field work and data analysis and writing the paper.

Enno Uhl: reviewing and writing the paper.

Hans Pretzsch: initiating the project, contributing to study conception and design, and reviewing the manuscript.

Summaries of the articles

Summary (Article I – Productivity and Structure)

The mixture of Douglas-fir and European beech has the intrinsic potential to be one of the most productive forest types in Central Europe.

The study investigated how the structure and productivity of mixed stands changed in comparison to pure ones. It analyzed whether there is overyielding in mixed stands and if it was modified due to stand development or along an ecological gradient.

Throughout Germany, 18 research plot triplets with 1987 trees were established in seven different ecological regions from dry to moist site conditions at ages 30 to 120 years. To investigate the growth of the stands, tree cores were collected from 1293 stems.

The study revealed significant overyielding of biomass in mixed stands of 6 % or 0.81 Mg ha$_{-1}$ year$_{-1}$. It was found that: (i) Overyielding in mixed stands was driven by an increase in Douglas-fir growth. (ii) Both species modified their morphology in mixture. Compared to the species in pure stands, Douglas-fir diameters in mixed stands were significantly larger, whereas European beech had a smaller diameter at breast height in the mixture. The effect increased with the age. (iii) The analyses revealed more pronounced overyielding in older stands and on better sites. The findings show that overyielding of Douglas-fir and European beech in mixed stands results from a higher light interception by complementary space occupation.

Summary (Article II – Climate sensitivity)

Due to possible positive and compensatory interaction between species, mixed stands are a commonly accepted silvicultural response to reduce risks arising from climate change. Nonetheless, only a few species combinations have been studied more detailed so far revealing variable mixing effects. Here, we analyze the effect of the mixture of Douglas fir and European beech with regard to the species-specific climate sensitivity of growth. We focus on three hypotheses: (i) Species-specific long term growing performance and climate sensitivity do not differ between monocultures and mixed stands, (ii) species-specific growth reactions to severe drought events do not differ between monocultures and mixed species stands and (iii) species-specific growth reactions on severe drought events are not influenced by differing ecological growing conditions.

To scrutinize the hypothesis, we analyzed tree cores from both species taken from pure and mixed stands covering different site conditions and age classes. Tree ring characteristics were used to analyze the differences in climate related long-term growth responses in pure and mixed stands. Short-term responses were investigated by growth reaction indices on individual tree and stand level involving drought events during the years 1950–2010. Linear mixed models were applied to detect effects of ecological co-variables on the indices.

Results reveal that Douglas-fir in mixed stands exhibit a significant improved growing performance compared to pure stands. European beech seems to react indifferently concerning its performance in mixture compared to pure stands.

Differences in drought stress resistance and growth recovery time mainly arose between the species. Douglas-fir showed a significantly lower resistance and required more time to reach again its initial growth level compared to European beech. In mixture we found a trend that Douglas-fir growth recovery time is shortened and extended for European beech. The analysis along the ecological gradients showed that base-limited soils systems are more drought-tolerant during drought events. Lower basal area as a proxy for reduced stand competition decreased the relative growth loss by drought. We hypothesize that mainly spatial differentiation in height trigger enhanced diameter growth of Douglas-fir in mixture. Temporal differentiation expressed by deferred phenology attenuates climate sensitivity of this conifer. We conclude that in mixed Douglas-fir and European beech stands the former species is stabilized against climatic impacts. On the contrary, climate sensitivity of European beech is increased.

Summary (Article III – Root – stem allometry)

The study investigated partitioning of resources between roots and stems in mono-species and mixed-species stands of Douglas-fir and European beech at four different sites. We combined tree ring analyses of stems and coarse roots in order to scrutinize root-stem allometry with a focus on how it is influenced by species mixture and humidity. The results show that allometry in mixed stands changed in favor of stem growth for both species. Greatest relative allocation into stem growth was observed for individual trees which were completely surrounded by trees of the other species. The data indicate that a decrease of stand density, which was used as a proxy for tree competition, has the same effect on allocation.

To analyze the influence of humidity we used a long and a short-term- index. Based on these we can show that allocation changes with general site conditions and annual humidity variations. We found that on both time scales both species increase resource investment into stem growth if conditions are more humid. Under harsher conditions, allocation shifts into root growth.

The findings contribute to understanding the overyielding in mixed stands. Mixing Douglas-fir and European beech leads to the same allocation patterns as an improvement of site conditions. We suggest that for both species mixture is equivalent to growing on a better site.

Article IV is a German-language summary of Article I – III

Null hypotheses and answers

(I.1) In mixed stands there are no structural changes compared to pure stands.

Both species modified their morphology in mixed stands. Compared to the species in pure stands, Douglas-fir diameters in mixed stands were significantly larger, whereas European beech had a smaller diameter at breast height in mixed stands. The stand density in mixed stands was comparable to the expected stand density from pure stands.

(I.2) In mixed stands no overyielding arises.

The study revealed significant overyielding of biomass in mixed stands of 6% or 0.81 Mg ha^{-1} $year^{-1}$ which was driven by increased Douglas-fir stem diameter growth.

(I.3) Overyielding is unaffected by changing age gradient and productivity gradient.

The analyses revealed more pronounced overyielding in older stands and on better sites.

(I.1) Species-specific long-term growth performance and climate sensitivity do not differ between pure and mixed stands.

Results reveal that Douglas-fir in mixed stands exhibit a significantly improved growth performance, lower mean sensitivity and lower autocorrelation. European beech in mixed stands appear unaffected.

(II.2) Species-specific growth reactions to severe drought events do not differ between pure and mixed stands.

Douglas-fir showed a significantly lower resistance and required more time to return to its initial growth level compared to European beech. In mixed stands we found a trend that the growth recovery time is shortened for Douglas-fir and extended for European beech.

(II.3) Species-specific growth reactions to severe drought events are not influenced by differing ecological growing conditions.

The analysis along the ecological gradients showed that base-limited soil systems are more drought tolerant during drought events. Lower basal area as a proxy for reduced stand competition decreased the relative growth loss by drought.

(III.1) Douglas-fir and European beech have the same root-stem allometry.

Douglas-fir and European beech differ significantly in their root-stem allometry. European beech had a significantly lower allometric scaling factor but a significantly steeper slope than Douglas fir.

(III.2) The mixing of the two species doesn't modify their allocation into coarse roots and stems compared to their growth in pure stands. In this context we also scrutinize the impact of stand density on allometry.

Both species exhibit a significantly higher allocation to stem growth compared to root growth if they compete more against the other species than against their own. The data showed that with increasing stand density, allocation favors root growth over stem growth.

(III.3) Unfavorable general site conditions (low humidity) do not influence the allocation in favor of root growth. Short-term droughts have no analogous effect.

We found that on both timescales both species increase resource investment in stem growth if conditions are more humid. Under harsher conditions, allocation shifts to root growth.

Part -II-

Mixed stands of Douglas-fir and European beech compared to pure stands

The picture shows a Douglas-fir - European beech mixed stand plot of the triplet (trial 1001 4 5 6) in Walkertshofen (Bavaria). The plot is also a part of the long-term experimental trial of the Chair for Forest Growth and Yield Science (TUM). On this mid-age triplet with great site conditions it was measure an overyielding. On the plot of this triplet are installed precipitation collectors and tensiometer. The triplet is one of the triplets that have been intensively sampled in cooperation with the Chair of Soil Science (TUM).

Foto einer Mischbestands-Versuchsfläche aus Douglasien und Buchen von einem Triplet nahe Walkertshofen (Bayern). Die Versuchsfläche ist ebenfalls Bestandteil des langfristigen Versuchsflächennetzes des Lehrstuhls für Waldwachstumskunde (TUM). Die Fläche mit einem mittleren Alter von 55 Jahren verfügt über ausgezeichnete Wuchsbedingungen und es ließ sich ein Mehrzuwachs im Vergleich zu den benachbarten Reinbeständen feststellen. Durch eine Kooperation mit dem Lehrstuhl für Bodenkunde sind auf der Fläche Niederschlagssammler und Tensiometer installiert und es erfolgt dadurch eine gleichzeitige, intensive, bodenkundliche Untersuchung der Mischungsreaktion.

Introduction

Mixed stands

Forest management tries to satisfy the increasing expectations in the field of forestry. Therefore, the establishment of mixed-species stands is becoming a common solution. Several studies provide evidence that mixed stands are able to achieve ecosystem services better than pure stands (Zhang et al. 2012; Gamfeldt et al. 2013; van der Plas et al. 2016; Liang et al. 2016). Nonetheless, the permanently increasing number of case studies about mixed stands show different possibilities regarding how and which improved services arise due to mixed stands. It becomes apparent that there are various outcomes for the different mixtures (Larocque et al. 2013) and that there is no general mechanism behind mixing. The different physiological traits of trees lead to various possibilities of interaction in mixed stands.

Therefore, this work has collected and generated information about Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and European beech (*Fagus sylvatica* L.) in mixed stands, which is currently of great interest in Central European forests. The aim was to understand the patterns in mixed stands and to evaluate how and to what extent this mixture satisfies expectations.

Theory of interspecific competition in forest stands

As mentioned, various interactions of species are possible. That is why, before starting to analyze the interaction between Douglas-fir and European beech, the general classification of possible interactions between neighboring plants will be presented. In theory, interactions are often described as *competition*. This term is confusing because it implies different definitions. Therefore, in the further text, the term *interaction* is preferred to describe an occasion when two or more things (trees) react to each other. The interactions can be separated by their general outcomes (*symbiosis, amensalism, commensalism, protocooperation*, etc.) or their mechanisms (Larocque et al. 2013). Because forest science is mostly interested in understanding the hidden mechanism and quantifying the outcome, the emphasis of the definition is on mechanisms. The deviation of the outcome from the pure additive effect of both species (neutral outcome) is defined as the *mixing effect*. Two mechanisms can lead to a positive mixing effect: *facilitation* or *complementarity*. Facilitation occurs if one species improves the resource supply of the other species or defends the other species against stress. It can be interpreted as a modification of the site at least for one species. Complementarity means that the species uses resources more efficiently at the site, which requires niche differentiation of the species.

Mechanisms which lead to negative outcomes can be defined as *exploitation* and *interference*. Classically, they are grouped together to 'real' competition. Exploitation describes the limiting of a resource by space occupation. Interference summarizes all interactions where species compete directly for a resource (e.g. *allelopathy*).

Finally, the physiological characteristics of the species determine which mechanism arises in mixed stands.

Table 1 Summary and comparison of physiological traits and forestry parameters of Douglas-fir and European beech.

Tabelle 1 *Zusammenfassung und Vergleich von physiologischen Eigenschaften und forstlichen Parametern von Douglasie und Buche.*

Trait	Douglas-fir	European beech	Reference
Family	Pinacea	Fagacea	
Growing in Germany	introduced (1831)	native (3700–1500 BC)	Booth 1882; Magri et al. 2006
Genetic diversity[a] (mean number of alleles per locus)	4 - 31	2 - 4	Konnert et al. 2014; Slavov et al. 2004; Comps et al. 2001
Forest area Germany [ha]	217 604 (2.0%)	1 680 072 (15.4%)	Thünen-Institut 2012b
Maximum age [years]	>500 (max. 1400)	>300 (max. 900)	Hermann 2007 ff; Felbermeier and Mosandl 2007 ff
Height in 100 years (Dominant height of best yield class) [m]	45.0	32.4	Schober 1987; Bergel 1985
Total volume production (Best yield class) [m³]	2016	781	Schober 1987; Bergel 1985
Maximum stand density index (SDI)	920	540	Schober 1987; Bergel 1985
Root system	heat root system	heat root system	Matyssek et al. 2010
Stomatal conductance of leaf water potential at 50% of the maximum ($\Psi g_s 50$) [MPa]	-0.75 – -1.25	-2.12 – -3.17	Woodruff et al. 2008; Aranda et al. 2000; Köcher 2013
Hydric characteristics[b]	isohydric	anisohydric	Klein and Niu 2014
Photosynthesis at saturating light (A_{sat})	13	5.5 (–13.2)	Lewis et al. 2000; Yang et al. 2016; Ellenberg and Leuschner 2010
Light saturation point (µmol m^{-2} s^{-1})	364 – 626	460	Lewis et al. 2000; Ellenberg and Leuschner 2010
Shade-tolerance index[c]	2.78 ±0.18	4.56 ±0.11	Niinemets and Valladares 2006
Shade tolerance	mid-tolerance to intolerant	tolerant	Hermann 2007 ff; Ellenberg and Leuschner 2010

[a] expressing the adaptability of species by genetic diversity is difficult to measure; the mean number of alleles per locus is only advice concerning possible adaptability (Hamrick et al. 1992)

[b] results from $\Psi g_s 50$ based on classification of Klein and Niu (2014)

[c] higher values represent greater shade tolerance

Structural and functional description of Douglas-fir and European beech

To assess which mechanisms apply in mixed stands of Douglas-fir and European beech, Table 1 shows the structural and functional traits of the investigated species. The list aims to summarize a choice of characteristics which are mentioned in the further text to explain the interaction of the two species in mixed stands.

The species Douglas-fir has evolved during repeated long periods of geographic isolation into two varieties, a coastal variety, *var. menziesii*, and an interior variety, *var. glauca*. Both varieties differ greatly in their preferences. In Central Europe, the interior variety turns out to be very sensitive to the needle disease *Rhabdocline pseudotsugae.* This leads to a restriction of planting of the interior variety (Kownatzki and Kriebitzsch 2011; Kleinschmit and Bastien 1992). Nowadays, most plantings take place with the coastal variety. It is much more important for forest management in Central Europe.

Therefore, further investigations and statements in this study refer to the costal variety. For some of the plots a genetic variety analysis exists which confirms that it is the costal variety (Konnert and Cremer 2014). The other plots were visually checked if costal variety or not.

The compatibility of two species is easy to assess if there exist old-growth mixed stands in primary forest. For example the forest community 'Fago-Quercetum' is naturally developed and generates a working mixture on the suitable sites (Ellenberg and Leuschner 2010; Fischer 2003). The conclusion of the compatibility from European beech and Douglas-fir is difficult because the mixture is human-made. An alternative to estimating the compatibility of two species in mixed stands is to compare their physiological traits and their distributions. Already Dengler (1935) mentioned the importance of same site preferences of the species for a working mixed stand. Kownatzki and Kriebitzsch (2011) depicted an overlapping of the bioclimatic envelopes (temperature and precipitation, Kölling 2007) from European beech and Douglas-fir. They concluded that Douglas-fir reached on favorable European beech growing sites the same competition strength as European beech. A helpful trait of Douglas-fir is the good adaptability to acidophilous European beech sites (Albrecht 2008). Table 2 shows the relative amount of European beech association in Douglas-fir stands compared to pure stands and other mixing species.

Table 2 Number of Douglas-fir inventory points where another species is associated. Based on 2 534 Douglas-fir inventory points, overall. Associated species with an amount greater than 1%. Standard deviation in italics and brackets. Mixing proportion calculated by basal area. Data based on third National forest inventory of Germany (Thünen-Institut 2012a).

Tabelle 2 *Übersicht über Douglasien – Inventurflächen in der Bundeswaldinventur und der Vergesellschaftung von Douglasie auf diesen Flächen. Grundlage sind insgesamt 2 534 Inventurflächen. In der Tabelle sind nur Artenvergesellschaftungen dargestellt, die einen Anteil von mehr als 1% an der gesamt Anzahl an den Douglasien Inventurflächen besitzen.*

Associated species	**Relative amount**	**Inventory points**	**Mixing prop. Ass. spec.**	**Mixing prop. of Douglas-fir**
Picea abies	38.0	963	0.36 *(0.42)*	0.25 *(0.25)*
Fagus sylvatica	**28.5**	**723**	0.37 *(0.32)*	0.24 *(0.21)*
Pure *Pseudotsuga menziesii*	**21.1**	**535**		1.00
Pinus sylvestris	15.0	379	0.37 *(0.32)*	0.23 *(0.21)*
Larix decidua	8.1	205	0.34 *(0.25)*	0.23 *(0.17)*
Quercus petraea	7.7	195	0.38 *(0.27)*	0.25 *(0.19)*
Abies alba	6.6	166	0.32 *(0.30)*	0.23 *(0.22)*
Quercus robur	5.8	148	0.31 *(0.23)*	0.21 *(0.17)*
Betula pendula	5.8	146	0.42 *(0.23)*	0.25 *(0.15)*
Acer pseudoplatanus	5.1	128	0.35 *(0.25)*	0.26 *(0.21)*
Larix kaempferi	3.6	91	0.31 *(0.33)*	0.20 *(0.20)*
Fraxinus exelsior	3.1	79	0.38 *(0.23)*	0.25 *(0.15)*
Carpinus betulus	3.0	76	0.37 *(0.22)*	0.23 *(0.14)*
Prunus avium	2.0	51	0.38 *(0.19)*	0.26 *(0.15)*
Quercus rubra	1.7	43	0.28 *(0.35)*	0.24 *(0.27)*
Tilia spec.	1.1	29	0.39 *(0.21)*	0.23 *(0.16)*
Abies grandis	1.1	28	0.34 *(0.30)*	0.23 *(0.22)*
Castanea sativa	1.1	28	0.39 *(0.21)*	0.26 *(0.12)*
Pseudotsuga menziesii		**2534**		**0.24**[a] ***(0.18)***[a]

[a] without pure Douglas-fir inventory points

The natural distribution of Douglas-fir in North America is in the same range of latitude as in Central Europe. However, it is difficult to define the site preferences of the species in Central Europe because climate conditions in its native area are much more oceanic in comparison to Central Europe. The precipitation distribution over the year is different. The native area of Douglas-fir is characterized by a very high precipitation rate in wintertime and short dry periods in summertime. Overall, best growing provenances of Douglas-fir in Central Europe comes from origin with precipitation sums above 2,800 mm per annum (Eilmann et al. 2013). This greatly exceeds the precipitation sum of Douglas-fir planting areas in Central Europe. Nevertheless, the high precipitation supply can be compensated in Central Europe by a more favorable distribution of precipitation to growing periods. Fig. 1 shows climate conditions of growing sites from Douglas-fir in native areas (Gold River, British Columbia, Canada) and Central Europe (Walkertshofen, Bavaria, Germany).

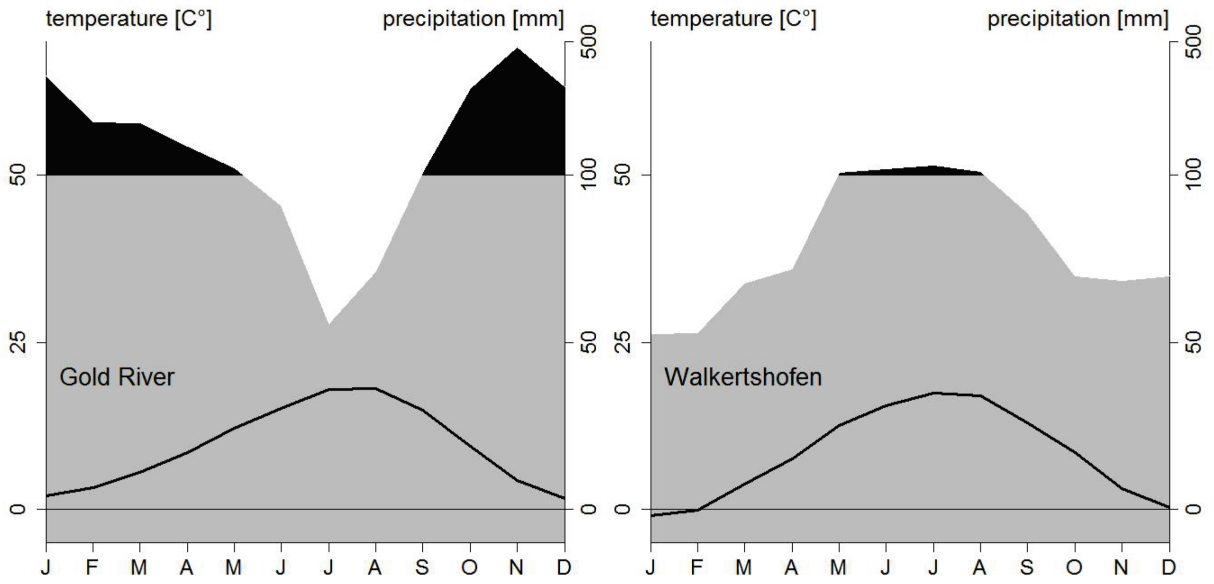

Fig. 1 Climate charts of Douglas-fir growing sites from Gold River (British Columbia, Canada) and Walkertshofen (Bavaria, Germany) according to Walter and Lieth (1967). Climate data represents the average from 1980 – 2010 (Deutscher Wetterdienst 2016; Goverment of Canada 2016).

***Abb. 1** Klimadiagramme nach Walter - Lieth (1967) von einem Douglasien-Standort aus dem ursprünglichen Verbreitungsgebiet Gold River (British Columbia, Kanada) im Vergleich zu einem Douglasien-Standort in Deutschland (Walkertshofen, Bayern). Klimadaten repräsentieren die Zeitspanne von 1980 – 2010 (Deutscher Wetterdienst 2016; Goverment of Canada 2016).*

Fig. 2 pictured a simple model of growth potential from Douglas-fir and European beech in Germany under gradient of annual precipitation sum and annual mean temperature. It can be seen that in the area of favorable growing conditions (precipitation = 1000 mm, temperature = 9°C) of European beech, Douglas-fir shows a great height growth as well. Douglas-fir overtopped European beech by about 7 meters, which is an important trait to resist against the highly competitive European beech.

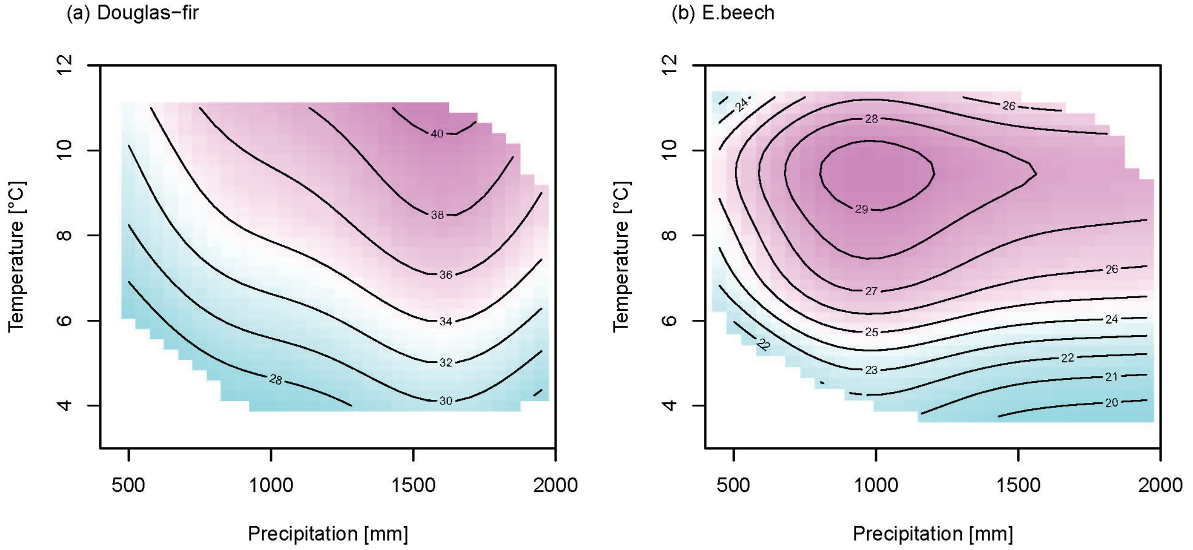

Fig. 2 Mean height at age 100 in dependency of annual precipitation sum and mean temperature for Douglas-fir and European beech. Black isotherms represent the dominant height levels. Purple areas shows the climatic area with best height growth performance.

Abb. 2 *Mittelhöhe im Alter von 100 Jahren in Abhängigkeit vom jährlichen Niederschlag und Jahresmitteltemperatur für Douglasie und Buche. Die Schwarzen Isotherme repräsentieren die Mittelhöhenstufen. Lilafarbende Bereiche markieren die klimatischen Bedingungen mit den besten Wuchsvoraussetzungen.*

Mixed stands of Douglas-fir and European beech (state of the art)

When trying to mix the Douglas-fir with different tree species, it has been shown that they are well harmonized with the European beech (Göhre 1958). This observation induced a few studies to analyze this mixture with a view on structure and productivity. There are also a lot of works about the influence of Douglas-fir in pure stands and mixed with European beech on biodiversity, but this is not the topic in this study (for an overview see Tschopp et al. 2014).

Compared to research in pure stands, which has a long tradition in forest science, research in mixed stands is relatively new. Franz (1987) mentioned the need for uniform evaluation basics for mixed stands. Methodical standards from Harper (1977), Vandermeer (1989) and Kelty (1992) prevailed only in newer studies. This methodical lag makes it difficult to find comprehensive studies of Douglas-fir and European beech in mixed and pure stands. Göhre (1958) was one of the first to describe the productivity potential of the mixed stand from both species to productivity in pure stands. His observations were from northeast Germany. He said that the productivity of a mixed stand lay between the productivity of pure stands of Douglas-fir and European beech. The same conclusion was reached by Bartelink (1998) in the Netherlands, Huss (1996) in south Germany (ecoregion 'Schwarzwald'), de Wall et al. (1998)in northwest Germany (ecoregion 'Mitteldeutsches Trias-Berg- und Hügelland' and 'Mittelwestniedersächsisches Tiefland''). Thomas et al. (2015) found an identical yielding of Douglas-fir and mixed stand in west Germany (ecoregion 'Pfälzerwald'; see Gauer and Kroiher (2012) for an overview of the German forest ecoregions). An overall higher productivity of the mixed stands compared to the pure stocked Douglas-fir stand was measured in a study by Lu et al. (2016) in the Netherlands. In further work this result would be defined as 'transgressive overyielding'. However, most of the mentioned studies did not compare the hypothetical productivity of mixed stands resulting from the productivity of a pure stand with the measured productivity in mixed stands (see chapter 'Overyielding'). Bartelink (1998), who applied this comparison with yield table data and measured mixed stands, could model overyielding in mixed stands. He related the mentioned strong influence of mixing proportion to overyielding. However, the use of yield tables enables just a limited statement about the general overyielding. The classification of mixed stands in the yield table of pure stands is restricted because the top height of the species is modified by mixing effects (Pretzsch 1992). Additionally, the calculation of mixing proportion from Bartelink (1998) was based on basal area and did not consider the growing space of the species. This is necessary in mixed stands to consider the 'real' productivity per species (Assmann 1954). The mixing proportion is an important aspect (Dirnberger and Sterba 2014), especially for Douglas-fir and European beech because of the great productivity differences of the species (see Fig. 3).

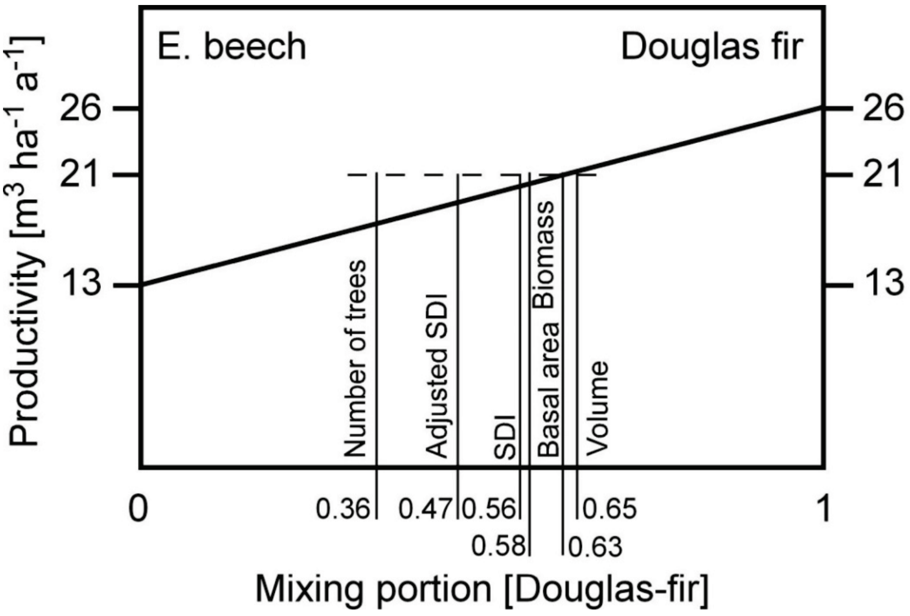

Fig. 3 Influence of the approach of calculating mixing proportion following cross diagrams according to Harper (1977) and Kelty (1992). The left (European beech) and right (Douglas-fir) ordinates in the cross diagrams represent the absolute productivity. The abscissa shows the mixing proportion of Douglas-fir. The solid line from left to right represents the productivity expected for neutral mixing effects on the level of the stand as a whole. The dashed line shows the result of overyielding based on the different approaches of calculation for mixing proportion.

Abb. 3 *Einfluss der unterschiedlichen Mischungsanteilsberechnungen auf den Mehrzuwachs dargestellt mithilfe eines Kreuzdiagrammes nach Harper (1977) und Kelty (1992). Die Y-Achse repräsentiert die absolute Produktivität von Buche (links) und Douglasie (rechts). Die X-Achse stellt den Mischungsanteil der Douglasie dar. Die Diagonale bildet den erwarteten Zuwachs ab; ausgehend von den Reinbeständen und ohne einen Mischungseffekt. Die gestrichelte Linie zeigt die Ergebnisse der Mehrzuwachsanalyse berechnet mit unterschiedlichen Mischungsanteilsansätzen.*

Because of the missing standards in mixed stand research it is difficult to quantify the increased or decreased productivity in mixed stands. The trend is towards the yielding of mixed stands between the pure stands with overyielding.

The comparison of the studies which investigated the structural differences was easier to handle. The studies showed a consistent picture of increased drift between diameter at breast height (DBH) classes from Douglas-fir and European beech in mixed stands with increasing stand development (e.g. Baade 1996; Dreher 1994; de Wall et al. 1998). Douglas-fir showed a greater diameter growth in mixed stands (de Wall et al. 1998; Schelhaas 2008; Thomas et al. 2015). Meanwhile, European beech in mixed stands was unaffected or decreased in diameter growth.

The height stratification is one of the most obvious characteristics in mixed stands. Already Göhre (1958) mentioned the development of a secondary crown layer of European beech under even-aged Douglas-fir. Height measurements showed that height growth of species is nearly unaffected by species mixing (de Wall et al. 1998; Thomas et al. 2015; Schelhaas 2008).

The lower sensitivity response of mixed stands to disturbances like drought events is one major argument in favor of the planting of mixed stands (Kelty 1992; Knoke et al. 2008). However, few species combinations have been investigated so far and the overall behavior is largely unknown, also with regards to productivity. Reyer et al. (2010) researched the drought response of Douglas-fir and European beech in pure and in mixed stands. They modeled pure and mixed stands with a pure stand yield table and analyzed the tree growth with the forest model 4C (FORESEE – Forest Ecosystems in a Changing Environment). Reyer et al. (2010) concluded climate change improved the competitive strength of European beech in mixed stands. As mentioned by productivity, the estimation of tree reaction with yield table data is restricted. Measurements of tree sensitivities for both species in interaction under field conditions are a gap in knowledge.

More and more authors mentioned the necessity to include the belowground and aboveground interactions in the explanation of the mixing effect (Bolte and Villanueva 2005; Shainsky et al. 1992; Jacob et al. 2013). For the species combination of Douglas-fir and European beech, there are three studies which measured direct and indirect root parameters in pure and in mixed stands. Thomas et al. (2015) placed a vertical and a horizontal gradient in the field to collect fine root density. They observed a domination of Douglas-fir in mixed stands in the vertical and horizontal direction. Thomas et al. (2015) concluded an advanced water uptake of Douglas-fir in mixed stands resulting from deeper rooting. Hendriks and Bianchi (1995) collected the fine root density on a vertical gradient inside the stands. They could exhibit a domination of Douglas-fir in mixed stands belowground as well. Their data showed a decreased fine root density in mixed stands in the upper soil area. The fine root density of mixed stands in lower soil areas was comparable to pure stands. Cremer et al. (2016) investigated the concentrations of soil organic carbon. It is an indicator for fine root distribution. The highest carbon concentrations were in the pure Douglas-fir stands, followed by mixed stands and pure stands of European beech. The study showed no general pattern of carbon stratification belowground.

Objectives

Because of its large share of forest area inside and outside its native area, Douglas-fir is a well-researched species (Lavender and Hermann 2014). And even though the methodological approaches are relatively new, there are many mixed research studies of Douglas-fir in their native area with other native species (Binkley 1984; Shainsky et al. 1992; Amoroso and Turnblom 2006). The reason for this is the expectation of greater yielding in mixed stands due to better resource use efficiency, improved stand stability and greater biodiversity. This was the case for the mixture of Douglas-fir and European beech in Central Europe as well. The mixing of Douglas-fir with European beech is of great interest, but there are only a few studies which have investigated the interaction of the two species. That’s why the general aim of the thesis is to increase the knowledge of this species combination.

The *first element* of the study was to quantify the differences of productivity from Douglas-fir and European beech in pure and mixed stands. It should answer the question if there is overyielding in the mixed stands or not. The analyses were undertaken under varying ecological conditions (age and site conditions) because several studies showed that the species interaction is not fixed but changes with ecological conditions (Pretzsch et al. 2013a; Binkley and Greene 1983; Zhang et al. 2012). This enabled a statement about when and where overyielding arises.

The *second element* was the description of the growth response and the structure of the two species in mixed stands. The investigations always compared the response in mixed stands with pure stands. This should give a deeper insight into the interaction of the two species. Therefore, three topics were analyzed:

(1) The description of the structure at stand level and individual tree level. The structure give an unspecific substitute for quantification of resources from trees and stands, and analogously, the supply, capture, and use efficiency of resources (del Río et al. 2016). The differences in structure between pure and mixed stands can give evidence on how mixing effects arise.

(2) The backwards analysis of stem growth under drought event conditions. The predicted climate change makes it necessary to give a forecast of the response of tree species mixtures under warmer conditions. The backwards analyses of tree cores from stems exhibited species interaction under dryer conditions. The response on temporal level can transform, within certain limits, to the spatial level and enables silvicultural recommendations for mixtures. For this, it is also important to analyze the response on stand level as well as individual tree level.

(3) The differences in tree allometry in pure and mixed stands. The allocation of growth in trees is strongly connected with the resource supply of the species. Information about modifications in allometry provides evidence about the limited resources in mixed stands.

Material and Methods

Triplet experimental setup

The experimental basis of the paper is the triplet setup. A triplet is an investigation unit which is built from a pure plot of species A, a pure plot of species B, and a mixed plot of both species. The site, structure, and age conditions between the three plots must be homogenous. In this way, it can exhibit the response of the species under mono-species and mixed-species conditions. A comparison of the two responses shows if there is a mixing effect or not.

The problem was to find such triplets and to separate inhomogeneous conditions from real mixing effects. For example, on the one hand, it is assumed that mixed stands generate higher stand density (Pretzsch and Biber 2016). Therefore, it does not seem helpful to select only pure and mixed plots with identical stand density. On the other hand, the density influences stand performance directly (Pretzsch and Spellmann 1994; Pretzsch 2004). A disregarding of stand density seems to be wrong as well.

This led to a few selection criteria with the aim of providing *ceteris paribus* conditions inside the triplets. The most import criterion was the proximity of the plots inside a triplet. This criterion aims to ensure that the triplets have homogeneous soil and climate conditions, the same genetic material, and comparable management treatments. The soil conditions were checked by means of a site map. For greater distances between the plots, soil conditions were additionally checked by a visual inspection of a sample with boring rod. The tree age inside a triplet has to be equal because stand performance is always age-related. Another important criterion is a comparable structure. Stand structure has a major influence on stand performance. It is assumed that the structure changes in mixed stands (del Río et al. 2016) as well as the mentioned stand density. Therefore, the current study measured only mono-layered stands. Stand density was handled in the same way. In the selection of the plots, we tried to select only fully stocked stands with low thinning intensities. Based on density relationships, the selection of high stand density should ensure a level of stand growth near the maximum (Assmann 1970).

The comparability between plots is a critical point. It is discussed in detail in the introductory paper (Article I).

Mixing proportion

In the selection of the mixed stands, the question of which spatial configuration and which proportion the two species should have arises. Pretzsch (2009) mentioned the major influence of spatial configuration in mixed stands (e.g. large group mixtures, small group mixtures, single-tree mixtures) on stand development. To reach the highest amount of interspecific intersections, the study only selected stands with single-tree mixtures.

The decision about the mixing ratio is also a debatable matter. Radosevich et al. (2006) analyzed mixed and pure stands of Douglas-fir and red alder (*Alnus rubra* Bong.) with different mixing proportions. The information of possible peaks in the mixing effect is a great additional result, but it requires a larger experimental setup. Because of the necessity of homogenous site conditions this setup can only be realized by experimental establishment of mixed stands (Radosevich et al. 2006; DeBell et al. 1997) or by species combination with a large share of the forest area. Because of the small share of Douglas-fir, the current study works with the triplet setup (one mixed stand) and tried to collect visually a 50:50 mixing proportion. As mentioned by the spatial mixing type, it enables the highest interspecific interaction. Naturally, the selections of mixed stands from managed forest contain deviations. In the study at hand the calculation of mixing proportions showed that the mixing proportions of Douglas-fir in mixed stands ranged from 22% to 76% (average = 47%).

The calculation of the mixing proportion is another point which is handled very differently between the studies of mixing research. Dirnberger and Sterba (2014) and Huber et al. (2014) indicated how over- or underyielding can be influenced by the different calculation approaches. Several kinds of calculation are possible: tree number (Amoroso and Turnblom 2006; Forrester et al. 2004), basal area (Puettmann et al. 1992), volume weighted by wood dry mass (Pretzsch et al. 2013a) or biomass, leaf area (Dirnberger and Sterba 2014), and growing space of the trees by adjusted stand density index (SDI) (Dirnberger et al. in review; Pretzsch and Biber 2016). Dirnberger et al. (in review) provided evidence that the adjusted SDI as a stand level calculation approach fits bests with the mixing proportion of tree leaf area at individual tree level. In the study at hand, different calculation approaches for mixing proportion were tested (see also Fig. 3). It became obvious that the adjusted SDI fits best the ecological space occupation in mixed stands as well.

Site and age gradient

Despite the triplet experimental setup, the site and the age gradient is an important methodical tool of the study to understand how the differences in tree performance changed between pure and mixed stands. Bertness and Callaway (1994) predicted that the interaction between species changes with the environmental conditions – the stress-gradient hypothesis. This is the focus of several forest mixed stand studies (Toïgo et al. 2015; Pretzsch et al. 2016; Pretzsch et al. 2013a; Binkley and Greene 1983). The site gradient of the study at hand tried to cover the potential distribution area of Douglas-fir in south Germany. Because of the mainly anthropogenic-driven distribution of Douglas-fir, the realized distribution area is much smaller. This means that some parts of the precipitation and temperature gradient were not included in the field. Finally, the site index measured by top heights of Douglas-firs indicated that the study areas have mid-best to best site conditions for Douglas-fir growth. This seems plausible because growing recommendations for Douglas-fir suggest mainly favorable sites like *Luzulo-Fagetum* (Bayerische Landesanstalt für Wald und Forstwirtschaft 2008). Thereby, the study represents a gradient where Douglas-fir forest management is currently daily business. A detailed description of all sites was presented in Article II (Table 1). A comparison of the triplet homogeneity was analyzed in Article I (Supplementary material 3). Ultimately, the whole experimental setup included 18 triplets.

The age-related changes of tree compartments led to a change of resource uptake which influenced the interaction to neighboring trees (Meinzer 2011). Several studies pointed out that it is important to include age in mixed research because the mixing effect changes during stand development (Cavard et al. 2011; Zhang et al. 2012; Binkley 2003). The investigation of the whole stand development is a general problem of ecosystem science (Leuschner and Scherer 1989). Studies which analyzed the mixing effect in relation to age mainly investigated mono- and polycultures with a low rotation time like non-woody plants (Cardinale et al. 2007) or short rotation tree plantation (Le Maire et al. 2013; Forrester and Smith 2012). Studies on the mixing effect of trees with a longer rotation time are rare and needed long-term experimental plots (Binkley 2003; Lu et al. 2016). An alternative to long-term experimental plots which represents real-time series are chronosequences. They can be used to investigate the stand development as well (Pretzsch 2009). Chronosequences are artificial time series from stands of same site conditions but different age classes. This method was applied in the current study. As a result, it was possible to analyze stand development from 20 to 125 years.

Measurements

To answer the research questions, various types of measurements were applied. Table 3 gives an overview of the measurements at the different trials. The trials have different resolutions of measurements. This is the result of two students’ works, whose measurements were added to the data pool (trial 1004 - Kemmerer et al. 2013 ; trial 1007 - Guske 2013). Additionally, analysis which needs a high measurement effort (laser scanning and root coring) were only undertaken on selected plots.

Table 3 Number of measured trees with the associated measurements method. The bars represented ratio number of measured trees to all trees of a trial.

Tabelle 3 *Anzahl an aufgenommenen Bäumen getrennt nach den unterschiedlichen Messverfahren. Die Balken repräsentieren den Anteil der gemessenen Bäume an allen Bäumen auf der Fläche.*

Number of trial	**1001**	**1002**	**1003**	**1004**	**1005**	**1006**	**1007**	**Total**
Triplets (number)	**3**	**3**	**4**	**1**	**3**	**1**	**3**	**18**
DBH (complete sampling)	301	295	325	215	328	118	405	**1987**
Tree height	300	295	320	74	323	114	327	**1753**
Position of crown	300	295	320	74	322	113	327	**1751**
Crown projection area	301	283	317	184	325	115	0	**1525**
Local basal area	301	295	325	186	327	118	0	**1552**
Cored Tree (2 core per tree)	248	228	234	71	207	78	227	**1293**
Laser scaning	122	212	56	0	0	118	0	**508**
Cored Roots (2 root/ 4 cores per tree)	56	108	36	0	0	0	0	**200**

A part of the sampling was the measuring of the crown projection areas. Because of the high number of crowns, the method of crown measuring was modified in the PhD project. A semiautomatic measurement was developed which supports the method of ‘vertical sighting’ by a laser distance meter (Disto D3aBT, Leica, München, Germany). For this, the laser distance meter was fixed on an aluminum frame together with a tablet (xTablet T7200, MobileDemand, Hiawatha, USA) and a compass (KB-14/360R, Suunto, Finnland) (Fig. 4). Between tablet and laser distance meter a Bluetooth connection exists which transmits the measured values directly into an Excel file. This instrument composition enables fast, precise measurement from crown projection to stem by laser and an easy adjustment of the measuring position to stem direction by the compass. Another advantage is that the measurement can be taken by one person, in contrast to vertical sighting. The accuracy seems to be between vertical sighting and optical plummet, but it was much faster.

Fig. 4 Instrument composition which was used to measure the crown radius of the trees. The mobile tablet, the compass, and the laser distance meter are attached to an aluminum frame. The measured distances are sent by Bluetooth from the laser distance meter to the mobile tablet. The continuous alignment with the stem is done with the compass. The person who taking the measurements, can carry the instrument composition with an attached portable system.

Abb. 4 *Kombination aus Einlese- und Messgeräte, um die Kronenradien der Bäume zu vermessen. Ein outdoorfähiger Tablet - PC, ein Kompass und ein Laserdistanzmesser wurden auf einem Aluminiumrahmen fixiert. Die gemessen Distanzen werden von dem Laserentfernungsmesser per Bluetooth an den Tablet-PC gesendet. Eine kontinuierliche und schnelle Ausrichtung zum Stamm wird durch den Kompass ermöglicht. Die befestigten Tragegurte ermöglichen ein Umschnallen des Gerätes, dadurch kann die Kronenradienmessung von einer Person durchgeführt werden.*

Overyielding

The question how mixing changes productivity is the major issue which has to be answered by forest growth science. The difference in productivity between pure and mixed stands is such a crucial fact, yet to this day it is calculated in different ways in literature. Two experimental designs have been used in studies of competition and productivity: 'additive' and 'substitutive' designs (Harper 1977). These designs result in different assessments of higher or lower productivity in mixed stands (see chapter 'Mixed stands of Douglas-fir and European beech').

The use of a substitutive approach has proven its worth. The substitutive design includes the mixing proportion in the comparison of productivity (Harper 1977; Kelty 2006). The observed mixed stands ($p1.2$) are compared with a hypothetical mixed stand resulting from the productivities of the pure stands ($p1$, $p2$) in relation to the tree-specific mixing proportion in mixed stand($m1, m2$) (Eq. 1).

$$MER = \frac{p1.2}{p1 * m1 + p2 * m2} \qquad \text{(Eq. 1)}$$

This approach was also applied in the study at hand. The inclusion of the mixing proportion into the calculation of overyielding implies the mentioned problem (chapter 'mixing proportion') of how to calculate the mixing proportion. Here, the adjusted SDI was applied.

Climate sensitivity and drought indices

The assessment of drought stability of mixed stands was made by dendrochronological analyses. There are several tools to describe the sensitivity of woody plants under stress like pointer year analysis (Schweingruber et al. 1990), superposed epoch analyses (Lough and Fritts 1987), or correlation coefficients between tree-ring chronologies and climatic data (Biondi and Waikul 2004). Another suitable method are the drought indices by Lloret et al. (2011), which are being used more and more. The drought indices relate tree-ring growth during (*resistance*) and after (*resilience*) drought events to ring growth before a drought event (see Fig. 5). The relation between resilience and resistance is described as *recovery*. Compared to other methods, it enables a simple comparison between tree species. It is therefore predestined for use in mixed research (Pretzsch et al. 2013b).

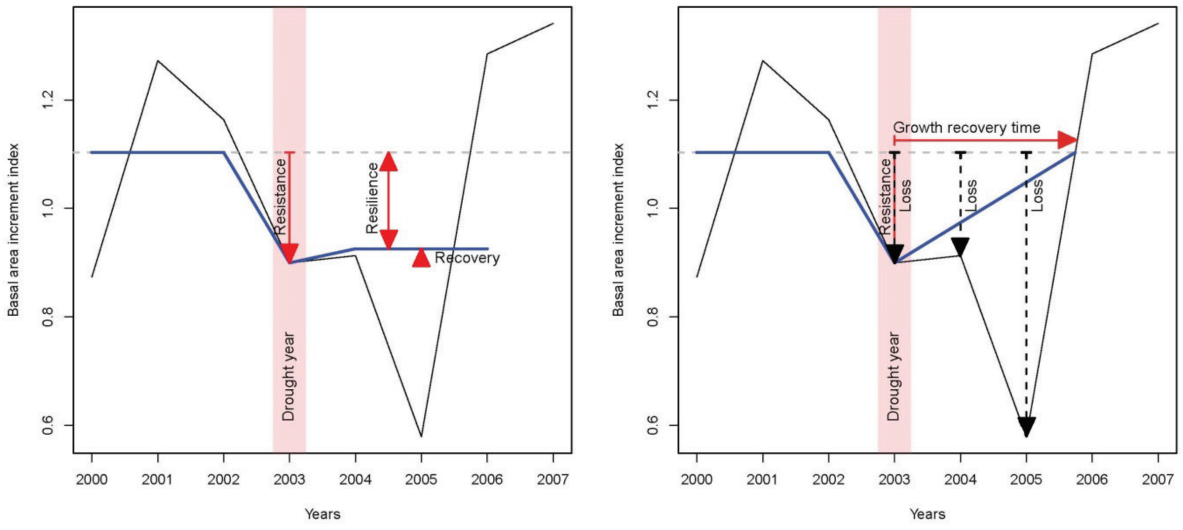

Fig. 5 Drought indices of Lloret et al. (2011) (left) and Thurm et al. (2016) (right) applied to an example tree chronology (black line) for the drought year 2003. The blue line represents the course of the indices; the arrows depict the individual indices.

Abb. 5 *Trockenindizes nach Lloret et al. (2011) (links) und Thurm et al. (2016) (rechts) angewandt auf ein Trockenheitsphase einer Jahrringchronologie. Die blaue Linie zeigt den Verlauf der Indizes; die Pfeile stellen die einzelnen Indizes dar.*

Nonetheless, the description of the resilience is a point which is handled differently in literature. Pimm (1984) refers to resilience as the time a system needs to return to an equilibrium following disturbance. A worldwide analysis of tree-ring growth during drought years provides evidence that trees exhibit a drought ‘legacy effect’ with three to four years’ reduced growth following drought. Based on the description of Pimm (1984), in Article II an additional index was presented. To avoid confusion with Lloret’s declination of resilience, it was called *growth recovery time (GRT)* (Fig. 5). It describes the time after a stress event which a tree needs to return to its pre-growth level (calculation described in Article II). Additionally, it was investigated how much loss of growth arises until drought event (resistance) and growth recovery time, so-called *increment loss due to drought (Loss)* (Fig. 5).

The radial stem growth is subjected to age-related and residual growth trends. Naturally, these trends can cause different increment levels before and after drought events. For example, an age-related increase of growth would lead to an overestimation of growth recovery time. To avoid this mistake, standardization of tree-ring chronology became a basic tool of dendrochronology (Cook and Kairiūkštis 1990; Fritts 1976). The different analyses of tree-ring chronology require different ways of standardization. In the study at hand double detrending was used. The double detrending first removed the age-related trends and secondly the residual growth trends (Holmes et al. 1986).

Because the analysis handled trees from zonal forests of temperate climate, adaptions were made to the classical double detrending. Firstly, basal area increment was used instead of tree-ring width. This two-dimensional measurement better reflects three-dimensional growth of the whole tree (volume) than the one-dimensional growth of tree-ring width (Biondi and Qeadan 2008; LeBlanc 1990). Consequently, the chronologies needed another function to detrend age-related growth. The commonly used linear or negative exponential functions were replaced by Hugershoff's growth function (1936). The second detrending applied a cubic spline with a rigidity of 0.33 times the length of the chronology, as standard. This modification of spline rigidity was mainly undertaken for old growth trees at forest borders with long-term climatic waves (Holmes et al. 1986). Trees from managed forests are more dominated by thinnings. Therefore, a shorter wave length of 15 years was applied. This fitted best the anthropogenic cycles in the investigated forests (see Appendix A in Article II). A prewhitening of chronology series by removing the autocorrelation was not applied to data because the legacy effect of droughts was a major investigation object.

It is clear that tree-ring response studies require a comparison of observed growth to an expected growth baseline. Nevertheless, standardization always includes the risk of eliminating target signals (Cook and Kairiūkštis 1990). The applied detrending base was built on biological explanation and fits best to the sampled data.

Root-stem allometry

Getting usable data from belowground tree compartments is hard work. The complicated excavation and measurements of these compartments has long been a problem. Additionally, strength relationships, like equations for aboveground tree biomass in relation to stem diameter and height, are unknown (Zianis 2005). That is why only a few studies are able to include quantitative, belowground information into the research of mixing effects (Shainsky et al. 1992; Meinen et al. 2009; Bolte and Villanueva 2005). The gap in knowledge about belowground interactions always produces an incomplete interpretation of mixing effects.

A pilot study of the root-stem allometry from Norway spruce (*Picea abies* (L.) H. Karst.) gives a methodical option to solve this problem (Nikolova et al. 2011). The study compared the diameter of two lateral roots to the diameter of the stem. Due to tree cores at the position of root and stem, the diameter ratio of the two compartments can be compared over the time. The relationship between root and stem was described by the overall logarithmic equations for one organ to another (Peters 1983):

$$\log Y_1 = \log\beta + \alpha \log Y_2. \qquad \text{(Eq. 2).}$$

The diameter comparison of root and stem are only a part of the allometry of below- and aboveground biomass. Fine roots, different coarse root types, and branches can differ considerably in their amount and growth dynamics in relation to the measured stem diameter at breast height and the lateral coarse root (Pretzsch et al. 2012). The applied analysis examined at two-dimensional level what has to be considered in the interpretation of allometry (Niklas 1994). Nevertheless, the measured diameters represent a substantial part of the cross section of organs which have to ensure the supply of downstream organs (Shinozaki et al. 1964).

A crucial part of Article II was the confirmation of knowing patterns, like changes in allometry due to site conditions (Keyes and Grier 1981) and density (Poorter et al. 2012), with the results of the method from Nikolova et al. (2011). This confirmation of knowing the patterns by means of method enabled an estimation of new finding patterns (mixture) and their influences on root-stem allometry.

Short and long-term climate indices

Besides the application of precipitation and temperature gradients, two climate indices were used. The climate indices aggregate several climate variables. The climate indices thus produce a value which can be closer to tree response than individual climate variables (Vicente-Serrano et al. 2010).

A short-term index, the standardized precipitation-evapotranspiration index (SPEI), was used to identify drought years (Vicente-Serrano et al. 2010) and exhibited influence of weather conditions on root-shoot allometry. The SPEI is able to consider past climate values of a system by varying timescale (0–24 months) with different kernel function types (e.g. Gaussian, triangular, circular). This respected the water-holding capacity of a system (Vicente-Serrano et al. 2010). The length of the timescale determines the ecosystem, e.g. boreal areas have very long timescales whereas semiarid areas have short timescales (Vicente-Serrano et al. 2013). The length of timescale for this study was determined by the correlation of increment drop in tree-ring chronologies with SPEI under different timescales (Fig. 6). Because of this peak of accordance the timescale in the study was fixed at five months.

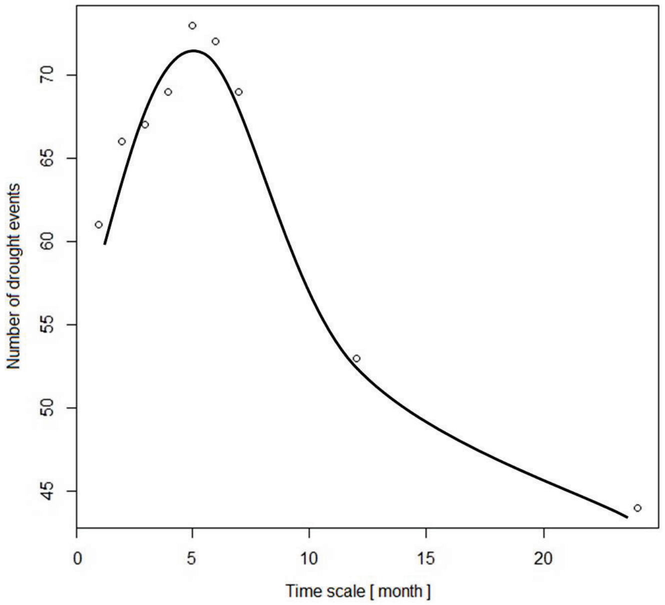

Fig. 6 Correlation of drought events and varying timescale of standardized precipitation-evapotranspiration index. The classification of drought events was made by the detection of significant drops of increment in year rings from the majority of trees in a triplet.

Abb. 6 *Abhängigkeit zwischen Trockenheitsevents und Zeitskala des berechneten standardisierten Niederschlag - Evapotranspiration Index SPEI, um die optimale Dauer der Zeitskala zu bestimmen. Trockenheitsevents wurden definiert, wenn es neben dem negativen SPEI (10 % Quantil) bei der Mehrheit der Bäume eines Bestandeskollektives zu einem signifikanten Zuwachseinbruch kam.*

The climate-vegetation-productivity index (ICVP) by Paterson (1956) was used as the long-term index. In contrast to the climate index of Martonne (1926), ICVP tries to consider indirectly the evapotranspiration of an analyzed area. ICVP includes the length of growing period and a solar radiation factor E which downgrades or upgrades the index in dependence of distance to the pole. However, the equation of Paterson (1956) can be a bit imprecise locally because it was designed for a worldwide resolution. The thesis at hand used a modification of the Paterson (1956) equation to be more precise on the local scale. It is an adaption of E by considering the ‘real’ sun duration at a site by measured sun hours of climate stations. The approach was developed by Gandullo and Serrada (1977). The equations are presented in detail in Article III.

Statistics

As mentioned in the chapters *‘Triplet experimental setup’* and *‘Measurements’*, backward analyses of chronosequences and tree-ring series was an essential data base of this thesis. Repeated measurements which are taken on the same statistical unit (longitudinal study) have to be viewed with caution to avoid artificial significances. The statistical technique of mixed modeling has become an important tool for ecologists to handle such nested data (Zuur et al. 2009). The study at hand mainly applied linear mixed models to describe statistical differences in data. It is debatable whether generalized adaptive mixed models (‘GAMM’) or boosted regression trees, which also fix the problem of nested data, show a more detailed course of dependent variables. Particularly the response of ecological systems to ecological conditions is inherently nonlinear (Burkett et al. 2005). Therefore, the data of overyielding and drought sensitivity was also examined with generalized adaptive mixed models but the results showed almost linear courses. The little more accurate modeling of the data by adaptive models brought no significant benefit compared to the simpler interpretation of linear models.

A main analysis of the thesis was to test the mixing effect (overyielding, sensitivity and root-stem allometry) under varying site conditions. However, the sampled plot covered various ecological conditions; the potential distribution of the species was not fully covered (see chapter ‘Site and age gradient’). That could be one of the reasons why the modeling course was almost linear.

However, the circumscription of the articles included some connecting analysis that imperatively required a non-linear analysis like the species distribution modeling (chapter ‘Structural and functional description of Douglas-fir and European beech’), the stand diameter and height distribution (chapter ‘Structural patterns’) and the matrix potential over the year (chapter ‘Climate sensitivity’). Their analyses were made with generalized adaptive models (GAM) and generalized adaptive mixed models (GAMM). They are described in detail in Appendices A, C, and E.

All statistical analyses were performed in the statistical environment R version 3.2.2 (R Core Team 2015).

Main Results and Discussion

Overyielding

The major aim of the thesis was the quantification of productivity difference between pure and mixed stands. Based on the sampled triplets, the improved growth in mixed stands compared to what would have been expected from pure stands has been shown. Thus the results of other studies can be confirmed. The overyielding in the study at hand was 8% (mean annual increment of aboveground volume - MERV) or 1.63 m³ ha^{-1} a^{-1} (Fig. 7). The mixed stand had a mean annual increment of 21.1 m^3 ha^{-1} a^{-1}. The pure Douglas-fir stand had a mean increment of 26.1 m^3 ha^{-1} a^{-1}. The pure European beech stand had a mean increment of 13.6 m^3 ha^{-1} a^{-1}. The overyielding was mainly driven by the improved growth of Douglas-fir.

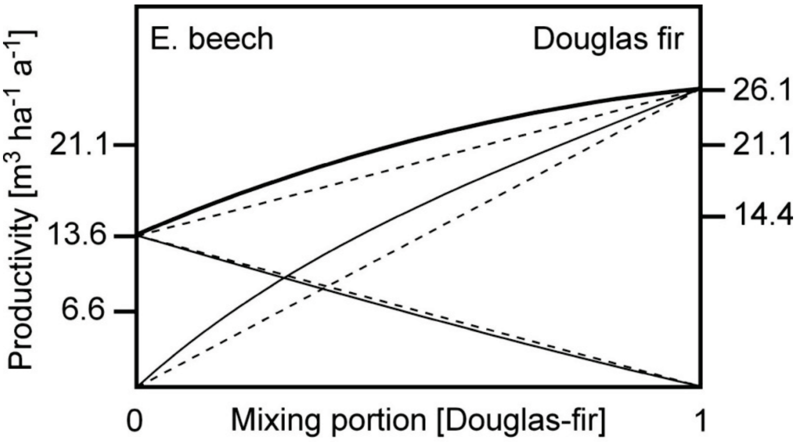

Fig. 7 Cross diagrams according to Harper (1977) and Kelty (1992) displaying the mixing effect on the productivity of Douglas-fir and European beech for volume increment. The abscissa shows the mixing portion of Douglas-fir. The left (European beech) and right (Douglas-fir) ordinates in the cross diagrams represent the absolute productivity. Dashed lines represent the productivity expected for neutral mixing effects on the level of the stand as a whole and on the level of the two contributing species. The solid lines show the observed productivity of whole stands (upper bold curve) and species-specific proportions at productivity (lower thin curves).

***Abb. 7** Kreuzdiagramm nach Harper (1977) und Kelty (1992), um den Mischungseffekt auf den Zuwachs von Douglasie und Buche darzustellen. Die Y-Achse stellt den Mischungsanteil der Douglasie im Bestand dar, die Y- Achse zeigt die absolute Produktivität. Somit steht die linke Y-Achse für die Produktivität im Buchen-Reinbestand und die rechte Y-Achse für die Produktivität im Douglasien-Reinbestand. Die gestrichelten Linien zeigen die zu erwartende Produktivität (ohne Mischungseffekt) in den Mischbeständen ausgehend von der Produktivität in den Reinbeständen, für den gesamten Bestand (obere, gestrichelte Linie) und baumarten-spezifisch (gestrichelte Diagonalen). Die durchgehenden Kurven stellen die gemessene Produktivität für den gesamten Mischbestand (dicke, obere Kurve) und baumarten-spezifisch (Kurven unterhalb) dar.*

The question arises whether overyielding results from increased density of stand per hectare or the increased growth of individual trees. Pretzsch and Biber (2016) provide evidence that the overyielding of various tree mixtures results from greater stand density. However, they found that this was not the case for Douglas-fir and European beech. A comparison of species-specific stand density indices from pure and mixed stands in Article I (Supplementary material 1) indicated that there were no differences between Douglas-fir (pure = 1032, mixed = 1022, $p > 0.5$) and European beech (pure = 725; mixed = 627, $p > 0.5$). But data of the study at hand showed that overyielding was mainly driven by significantly greater increment growth of individual trees of Douglas-fir (Fig. 8). European beech did not show a significant effect of growth resulting from mixing. This is consistent with the result that overyielding was generated by Douglas-fir (Fig. 7).

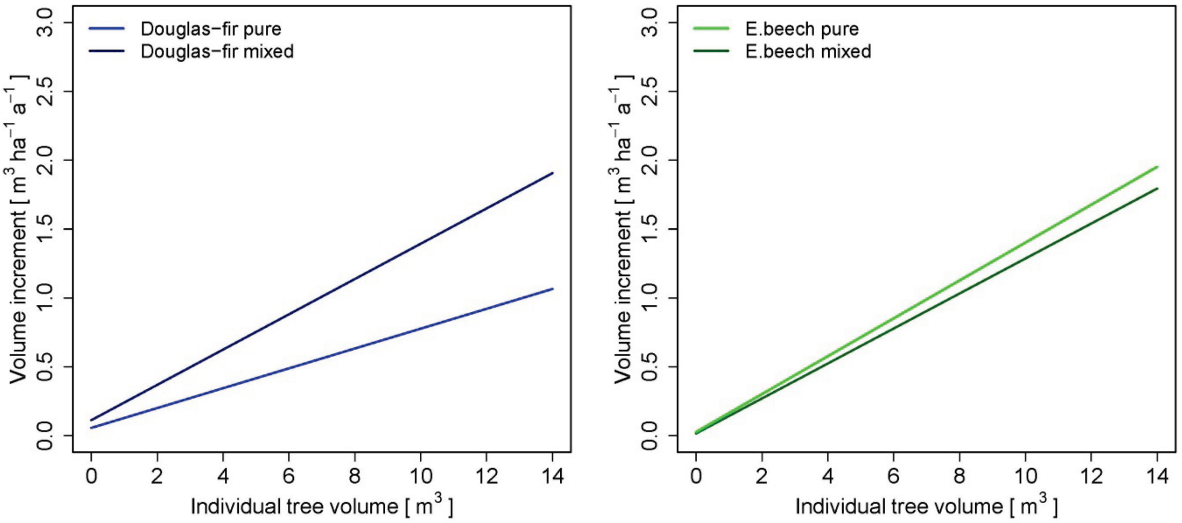

Fig. 8 Relationship of tree volume and volume increment of Douglas-fir (left) and European beech (right) separated in pure and mixed stands. Lines represented linear mixed models. Model description is given in Appendix B.

Abb. 8 *Zusammenhang zwischen Baumvolumen und Volumenzuwachs für Douglasie und Rotbuche unterteilt nach Rein- und Mischbestand. Die Linien entsprechen linear gemischten Modellen, welche in Anhang B beschrieben sind.*

Structural patterns (stand level and tree level)

The increased individual tree growth should be found in the diameter distribution of the plots as well. Fig. 9 and 10 summarize the diameter distribution of all plots by a relative scale. As mentioned in the introduction, the diameters of Douglas-fir and European beech separated in mixed stands. This was also verified in this study (Fig. 9). In comparison to pure stands, Douglas-fir in mixed stands had greater diameters, whereas European beech have a greater abundance in smaller diameter classes in mixed stands.

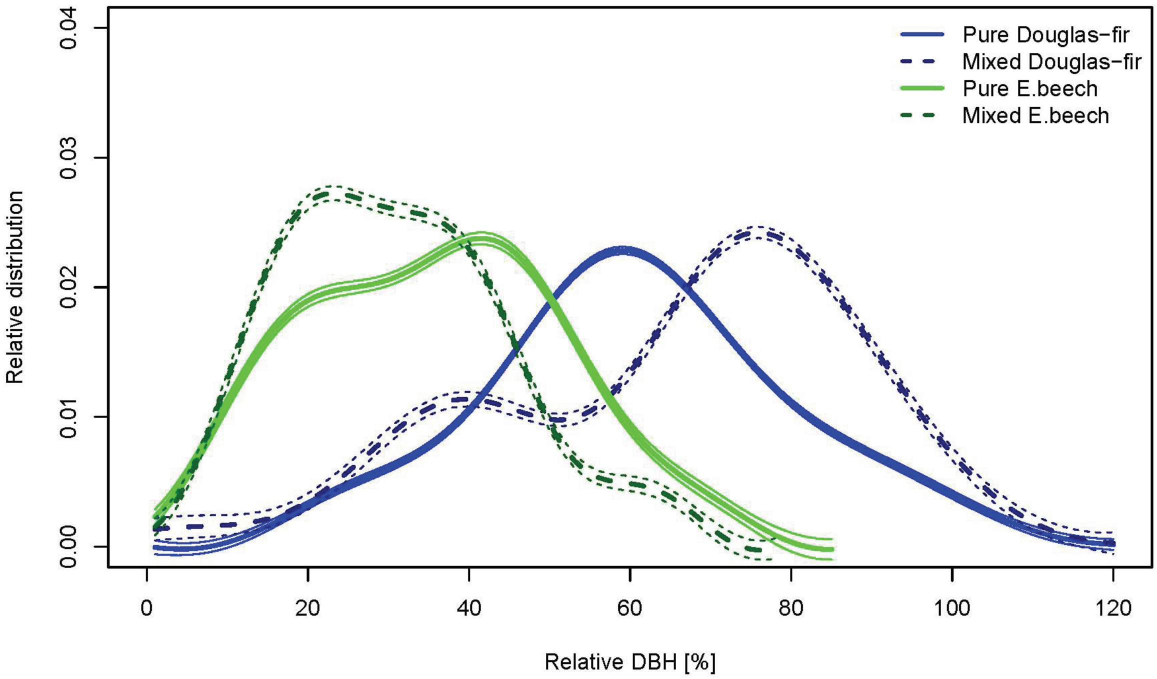

Fig. 9 Relative diameter distribution of Douglas-fir and European beech in pure and mixed stands of all 18 triplets. Bold lines represent the average, relative distribution smoothed by splines; narrow lines show the 95% confidence intervals. A generalized additive mixed model was applied. Detailed description in Appendix C.

***Abb. 9** Relative Durchmesserverteilung von Douglasie und Buche im Rein- und Mischbestand zusammengefasst aus allen 18 Triplets. Die dicken Linien repräsentieren die durchschnittliche Verteilung, welche mit Splines angepasst worden sind; die dünnen Linien zeigen die dazugehörigen 95% Konfidenzintervalle. Die Anpassung erfolgte mit einem generalisierten, additiven, gemischten Model, welches in Anhang C beschrieben ist.*

This separation of diameter classes increases with age. It was found that the diameter collectives of Douglas-fir and European beech stands separate more and more (Fig. 10 a, c, e). However, the effect is more pronounced in mixed stands. Fig. 10 b, d, f show the *measured* distribution of the mixed stands compared with the *hypothetical* distribution of mixed stands by merging the pure stands with the mixing proportion of mixed stands. The characteristic mixed stand distribution arose more and more with age. Finally, (Fig. 10 f) the mixed stands showed their peak of abundance in smaller DBH classes compared to what would have been expected from pure stands. The distribution curve have a more positive skewness. The pure stands exhibited a more symmetrical distribution, nearly Gaussian normal distribution. This was also depicted by Pretzsch and Schütze (2016) in an analysis of kurtosis and skewness from various species mixtures.

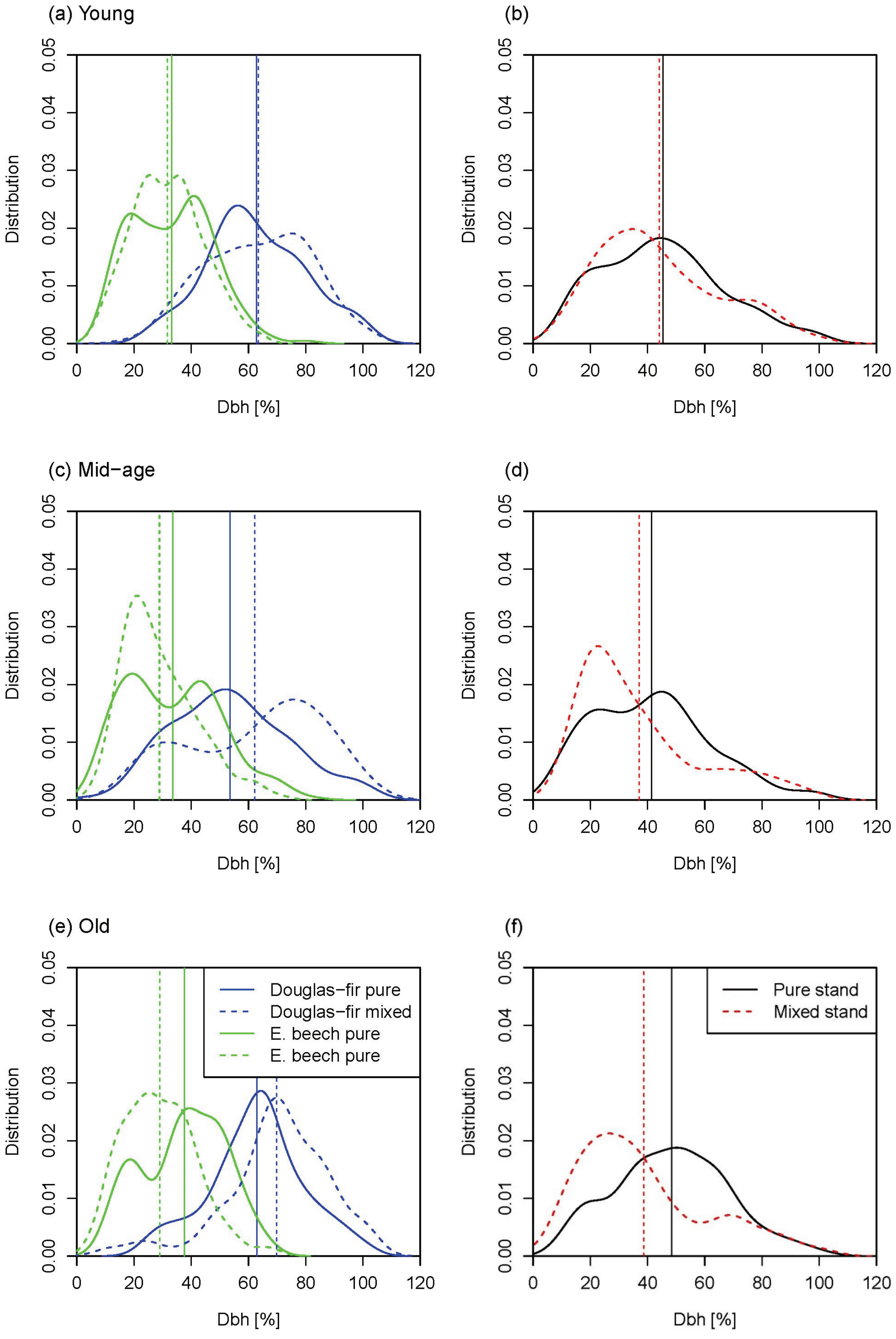
(a) Young
(b)
(c) Mid−age
(d)
(e) Old
(f)
Distribution
0.00
0.01
0.02
0.03
0.04
0.05
Dbh [%]
0
20
40
60
80
100
120
Douglas−fir pure
Douglas−fir mixed
E. beech pure
E. beech pure
Pure stand
Mixed stand

Fig. 10 Relative diameter distribution of Douglas-fir and European beech in pure and mixed stands of all 18 triplets separated into different age classes. Fig. a, c, and e show the density without mixing proportion. Fig b, d, and f show the diameter distribution of measured mixed stands compared to hypothetical mixed stands generated from the distribution of pure stands adjusted by mixing proportion. The densities function was applied to the whole tree diameter dataset.

Abb. 10 *Relative Durchmesserverteilung von Douglasie und Buche im Rein- und Mischbestand zusammengefasst aus allen 18 Triplets getrennt nach unterschiedlichen Altersklassen. Abb. a, c und e zeigen die Verteilung ohne Mischungsanteil. Abb. b, d und f stellen die Verteilung der gemessen Mischbestände, denen der erwarteten Häufigkeiten im Mischbeständen anhand der Reinbestände gegenüber. Die Dichtefunktion wurde auf den gesamten Baumdatensatz angewandt.*

The height stratification of the overtopping Douglas-fir and the understory European beech is the most obvious characteristic of this mixture. The separation of height classes can be seen in Fig. 11. Thurm and Pretzsch (2016) determined that this is the crucial trait for overyielding in the species combination. Douglas-fir, with its high light use efficiency (Lewis et al. 2000), benefit from the upper part of the crown with full radiation. European beech, with a lower light compensation point (Ellenberg and Leuschner 2010), can still hold their productivity level in the lower height zones. This means a vertical gradient of leaf physiology which was measured by Douglas-fir and Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). This mixture showed comparable height stratification like the mixture of Douglas-fir and European beech. The optimization of carbon uptake at the canopy level (Mooney and Gulmon 1979) can be strengthened by combining species with different leaf physiologies (Lewis et al. 2000). This physiological adjustment to the prevailing light environment leads to gains in total carbon uptake compared to uniform structured canopies (Givnish 1988).

In comparison to pure stands, European beech in mixed stands showed slightly greater abundances at lower tree heights, as well as Douglas-fir. However, the height comparisons with the linear mixed models (Article I supplementary material 5) showed no significant differences.

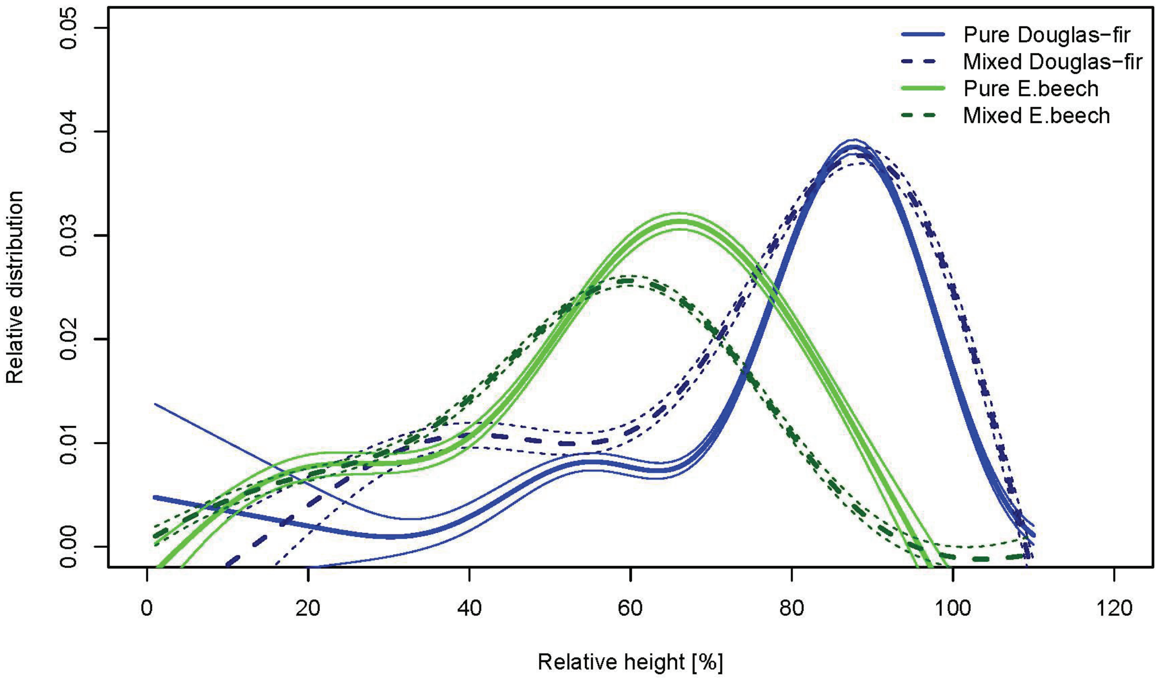

Fig. 11 Relative tree height distribution of Douglas-fir and European beech in pure and mixed stands of all 18 triplets. Bold lines represent the average, relative distribution smoothed by splines; narrow lines show the 95% confidence intervals. A generalized additive mixed model was applied. Detailed description in Appendix C.

***Abb. 11** Relative Baumhöhenverteilung von Douglasie und Buche im Rein- und Mischbestand zusammengefasst aus allen 18 Triplets. Die dicken Linien repräsentieren die durchschnittliche Verteilung, welche mit Splines angepasst worden sind; die dünnen Linien zeigen die dazugehörigen 95% Konfidenzintervalle. Die Anpassung erfolgte mit einem generalisierten, additiven, gemischten Model, welches in Anhang C beschrieben ist.*

The vertical gradient in the canopy could also be observed in occupation of the individual height zones. Fig. 12 shows the species profile index (Pretzsch 1995), which indicates the relative number of trees in different tree height zones in stands. The mixed stand showed the greatest occupation of all the height zones. This might be due to the mentioned physiological gradient in leaves (Lewis et al. 2000; Thomas et al. 2015).

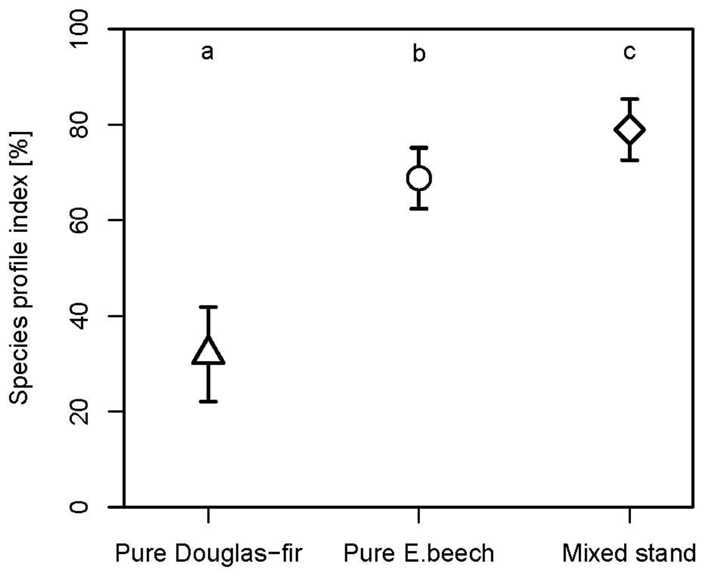

Fig. 12 Mean species profile index according Pretzsch (1995) for 18 triplets and retrospective for 20 years. Mean values were eliminated from random effects due to linear mixed models. Error bars represent the 95% confidence intervals. For a detailed model description see Appendix D.

Abb. 12 *Mittler Artprofilindex nach Pretzsch (1995) der 18 Triplets über einen Betrachtungszeitraum von 20 Jahren. Die zufälligen Effekte wurden innerhalb des linearen, gemischten Modells berücksichtigt. Die Fehlerbalken repräsentieren die 95% Konfidenzintervalle. Eine detaillierte Beschreibung befindet sich im Anhang D.*

The mixing of the species led to different diameter growth compared to pure stands, whereas the height growth was not influenced significantly by mixing. Therefore, a different height–diameter ratio arose in mixed stands which exhibited significantly tapered Douglas-firs and significantly slender European beeches. This was also found by Schelhaas (2008). The modified ratio might be a result of the dominance of Douglas-fir and the suppression of European beech (Abetz 1976; Bauhus et al. 2000). Alongside these competition considerations, the greater taper of Douglas-fir could also be a response to the increased wind load in mixed stands. The exposed, upper part of the Douglas-fir crowns in mixed stands leads to a greater contact surface for the wind. Mason (2002) noted that the decreasing h/d values in mixed stands is a tree response to increase the wind-firmness of the stands. The modified h/d ratio is probably a combination of competition and wind-firmness.

Climate sensitivity

Another advantage of mixing should be the stabilization of the trees against drought events (Kelty 1992; Lebourgeois et al. 2013; Pretzsch et al. 2013b). This could partly be confirmed by the tree-ring data in the study at hand (Fig. 13). The resistance in drought years of Douglas-fir and European beech was unaffected by mixing but the growth recovery time was influenced. Doulas-fir growth recovery time was shortened in mixed stands whereas European beech recovery time was extended.

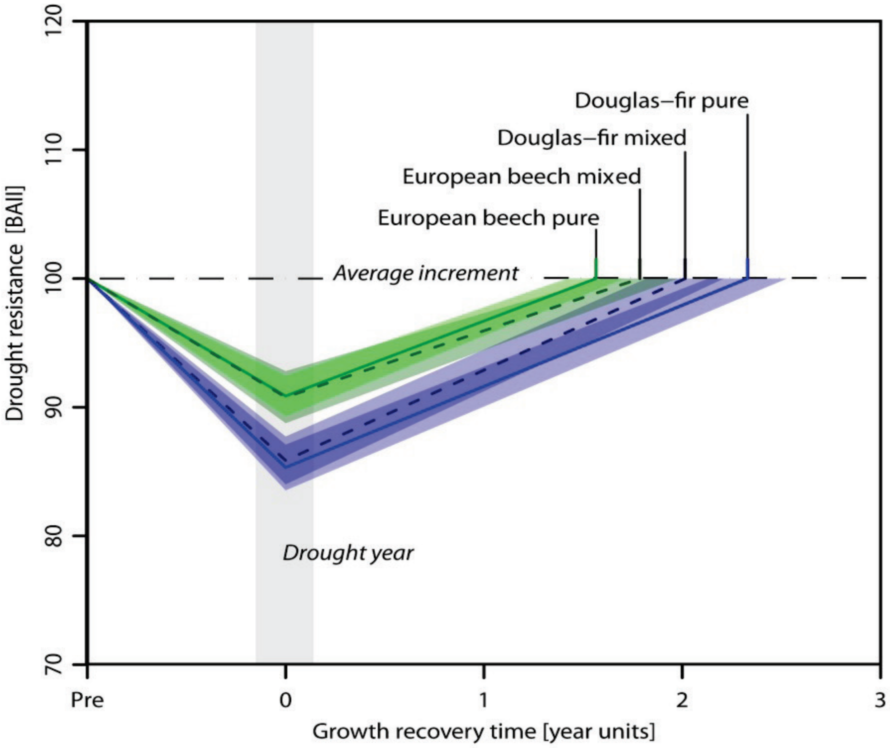

Fig. 13 Mean drought response on individual tree level for all drought events represented by the indices resistance and growth recovery time for European beech (green) and Douglas-fir (blue) in pure (solid) and mixed stands (dashed). The colored bands behind the lines show the respective 95% confidence interval.

Abb. 13 *Darstellung des Trockenstressverhaltens von Douglasie (blaue) und Buche (grüne) anhand von den Indizes Resistenz und Erholungszeit gemittelt für Trockenevents aus den Jahren 1950 bis 2010. Die Baumarten wurden auf Einzelbaumebene betrachtet und getrennt nach Rein- und Mischbestandssituation. Die farbigen, transparenten Bänder stellen die 95% Konfidenzintervalle dar.*

Thurm et al. (2016) assumed that the water supply in pure and mixed stands is comparably low in drought years. In a case study in Rhineland-Platine, Thomas et al. (2015) provided evidence that the Douglas-fir is able to use water from deeper soil horizons. The conclusion was based on the significantly greater number of findings of negative $\delta^{18}O$ values in Douglas-fir twigs. From this it appears that Douglas-fir and European beech in mixed stands might be able to complementarily use water from different soil horizons. Nevertheless, European beech and Douglas-fir have heart root systems (Matyssek et al. 2010). Both species are able achieve the same soil depth in dependency of the soil type (Crow 2005). Additionally, such stratification of roots always demands water holding zones, which enables such water partitioning. Furthermore, it has to be considered that the higher productivity in mixed stands requires a generally greater water demand.

An explanation for the changed growth recovery times might be found in the phenology of the species. A hypothesis could be that the advantage of mixed stands arises in springtime one year after drought. Douglas-fir as a coniferous species is able to transpire nearly throughout the whole year if weather conditions are favorable (Waring and Running 1978). Because of its deciduous character, the transpiration time of European beech is restricted to the growing period. During early springtime, in mixed stands only Douglas-fir transpires because European beech is not flushed. Therefore, Douglas-fir has higher water availability due to less competition compared to pure stands. The necessary reparation and regeneration of organs and cells after a drought year (Matyssek et al. 2010) is improved for Douglas-fir by the favorable conditions of water supply. When European beech starts to transpire in spring, the water supply is already reduced by the Douglas-firs. This may explain the shortened growth recovery time of Douglas-fir and the extended recovery time of European beech in mixed stands. Moore et al. (2011) observed this temporal partitioning of water utilization by Douglas-fir and red alder. Goisser et al. (2016) and Schume et al. (2004) showed this partitioning in European beech and Norway spruce as well.

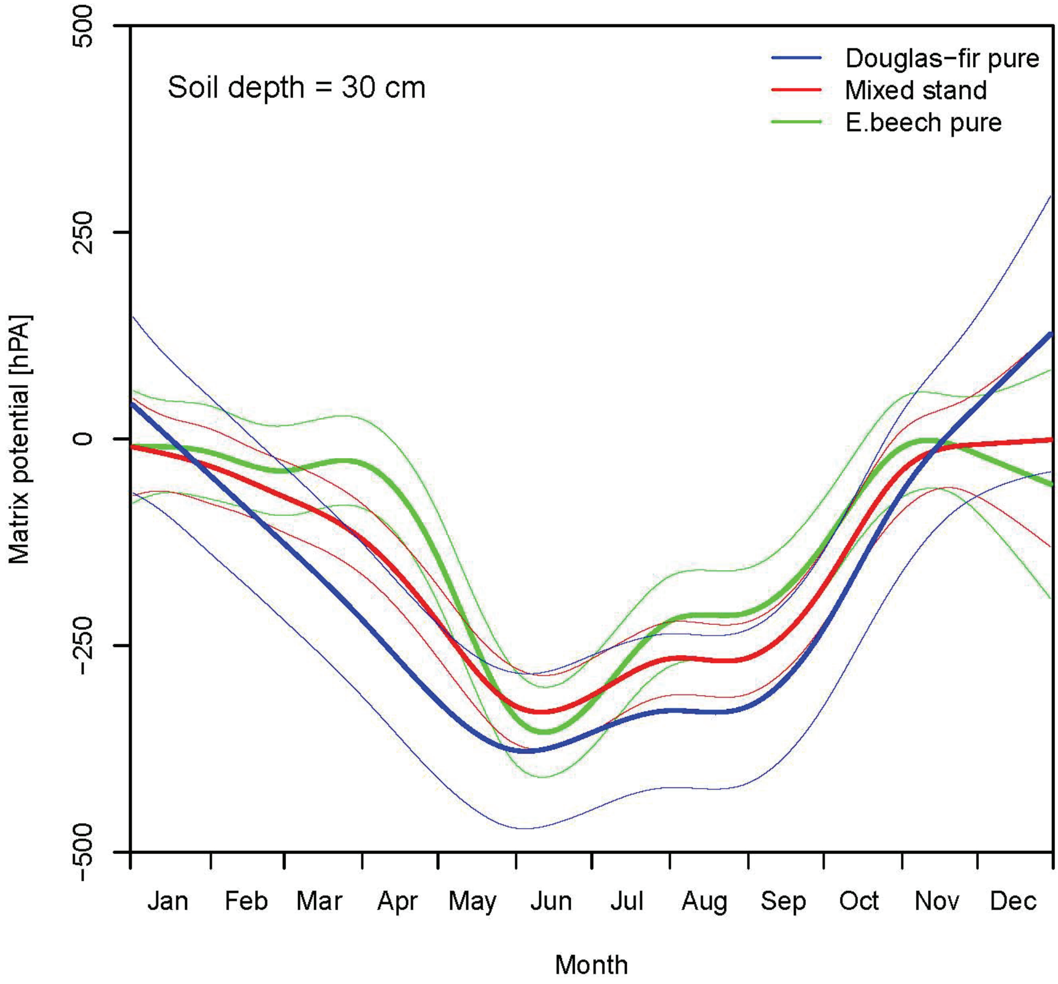

Fig. 14 Matrix potential in 30 cm soil depth in the different mixing types over the year. Measured data from 2013 to 2015 on four triplets of the thesis at hand. Bold curves were fitted with generalized additive mixed models. Small lines show the respective 95% confidence interval. Model description in Appendix E.

Abb. 14 *Verlauf des Matrixpotential über ein Jahr, gemessen in 30 cm Bodentiefe in unterschiedlichen Mischungstypen. Die Daten stammen von vier Triplets der vorliegenden Studie. Die Kurven (dick) wurden mithilfe von generalisierten, additiven, gemischten Modellen angepasst. Die schmalen Linien repräsentieren die jeweiligen 95% Konfidenzintervalle. Die Modelbeschreibung befindet sich in Anhang E.*

The hypothesis is supported by the course of the matrix potential in soil. A study by Cremer and Prietzel (2016) observed the monthly matrix potential between October 2013 and October 2015. The observation was undertaken on a section of the plots from the study at hand. A negative value of matrix potential indicates soil dryness. In Fig. 14 the early, continuous decrease of water content in pure Douglas-fir stands can be seen. This reflects the gradual starting of transpiration with increasing temperature (Mayr et al. 2003). The course of the mixed stand is flatter due to the lower proportion of transpiring trees in spring. Pure European beech stands decrease the least, but abruptly, which can be explained by the simultaneous flushing of European beech.

This short-term pattern could also be observed by the parameters ‘mean sensitivity’ and ‘autocorrelation’, which are characteristics of tree-ring chronology. They describe the response of the tree chronology in a long-term view. The mean sensitivity quantifies the year-to-year variability. It was nearly unaffected by the mixing. The autocorrelation indicates to what extent the increment of year n is correlated with year n-1. The analysis showed a significant, unusually low autocorrelation of Douglas-fir in mixed stands. It supports the hypothesis that the improved water supply in springtime makes Douglas-fir more independent from weather conditions from one year before.

Besides the mixing effect, the drought sensitivity of Douglas-fir and European beech can also be influenced or overruled by other effects like individual tree habitus (Čermák et al. 1993; Meinzer 2011), stand structure (Rais et al. 2014), and environmental conditions (Löw et al. 2006; Mencucci 2003). The data of the current thesis suggests that smaller tree height and stronger hydraulic pathways improved drought resistance (Hacke et al. 2001; Matyssek et al. 2010; Meinzer 2011). Increasing stand density also caused an increased loss of stem growth under drought events, which can also be shown by Rais et al. (2014). Additionally, base-rich sites seem to reduce the risk of drought stress.

Coarse root-stem allometry

The analysis of root-stem allometry should offer the influence of mixture on the partitioning of growth inside the trees. Fig. 15 shows the effect of mixture on individual trees of both investigated species. The degree of intra- or interspecific competition for the individual tree was triggered due to the proportion of basal area by surrounding trees. European beech as well as Douglas-fir showed a clear tendency to increase stem growth when the tree was surrounded not by its own species but by the other species. The mixture seems to improve stem growth in ratio to root growth.

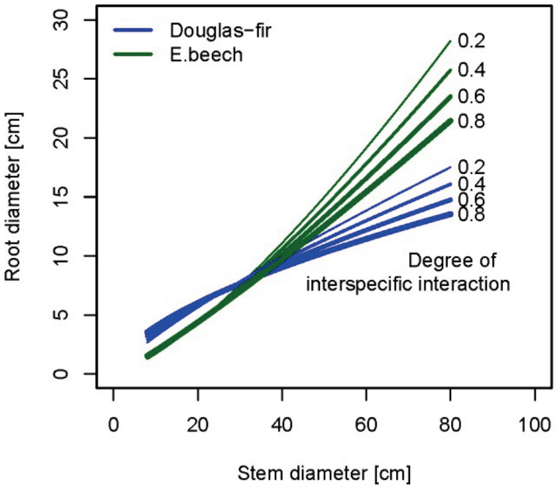

Fig. 15 Root-stem allometry in dependence of interspecific interaction (0 - no interspecific interaction, 1 - maximum interspecific interaction) for Douglas-fir (blue) and European beech (green). Degree of interspecific interaction is represented by percentage of the tree species on the basal area which surround the individual tree. Model coefficients and equation are shown in Article III (Table 3, Eq. 7).

Abb. 15 *Wurzel-Stamm Allomtrie in Abhängigkeit von der interspezifischen Konkurrenz (0 – keine interspezifische Konkurrenz, 1 – nur interspezifische Konkurrenz) für Douglasie (blau) und Rotbuche (grün). Der Grad der interspezifischen Konkurrenz ergibt sich aus den prozentualen Artenanteilen der umgebenden Bäume an der Stamm-Grundfläche. Die Modelkoeffizienten und die Gleichung sind in Artikel III (Tabelle 3, Formel 7) abgebildet.*

Additional analysis investigated the influence of short-term (weather in growing period) and long-term humidity (site conditions) and stand density. The results provided evidence that root growth increased under dry weather conditions, dryer site conditions, and greater competition due to higher stand density. The response of the root stem allometry of these conditions could also be confirmed in other studies (Poorter et al. 2012; Reich 2002). These conditions can be summarized as unfavorable conditions. Against this background it seems to be interesting that mixing increased root growth, which leads to the conclusion that the mixture (European beech and Douglas-fir) is a favorable condition for the tree. Kozovits et al. (2005) analyzed the root-stem biomass from saplings of European beech and Norway spruce. They could not find a significant effect of mixture on the modification of allometry. This may be linked to the young research objectives. In the current results, it is also exhibited that the modification of root-stem allometry increased with the tree size (Fig. 15). In addition, that the mixing effect needs time to develop was shown in other studies as well (Binkley 2003; Thurm and Pretzsch 2016; Zhang et al. 2012).

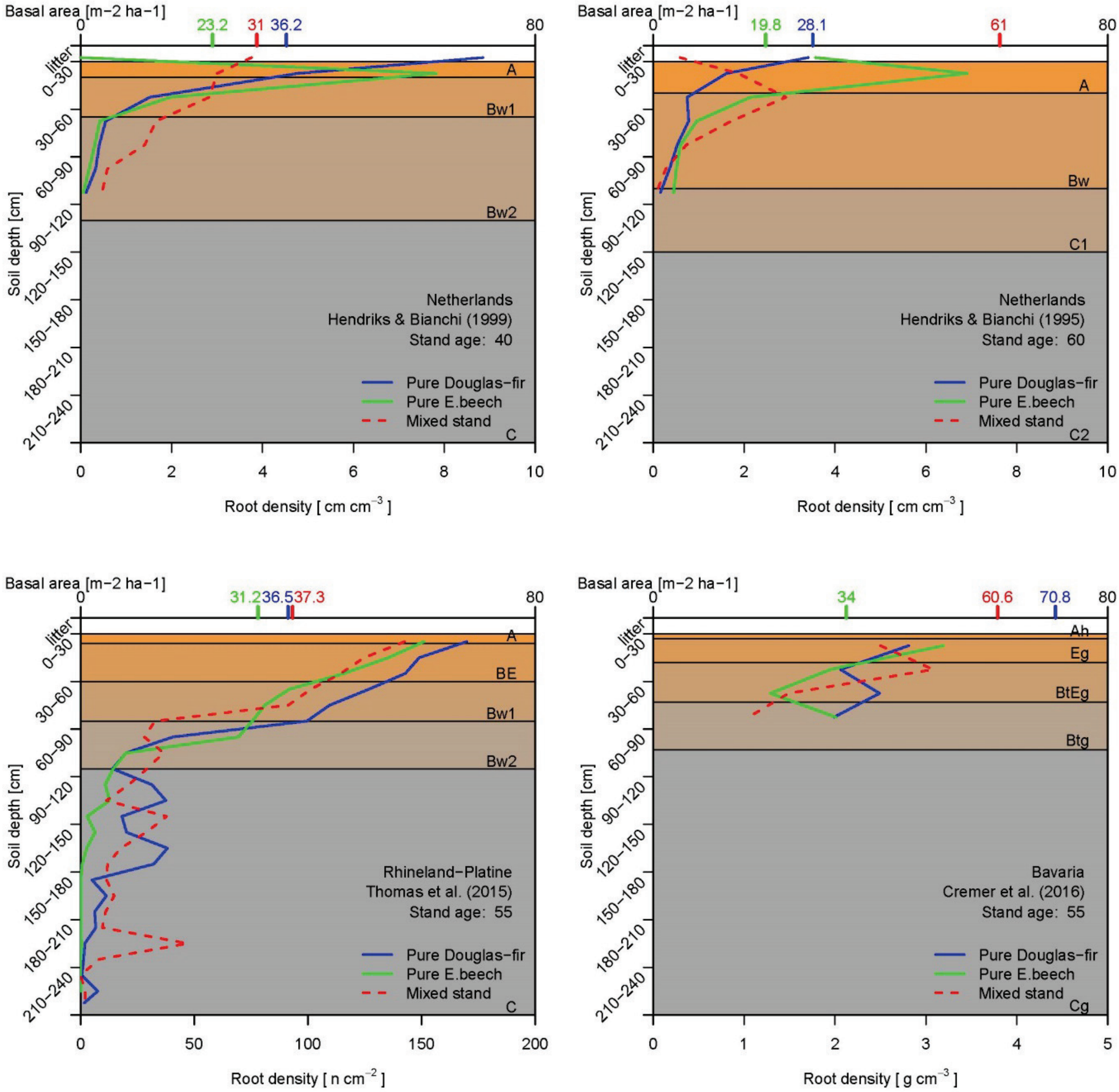

Fig. 16 Fine root density data of the three studies (four triplets). The fine root density was investigated in all studies but in different measurement units (units added to x-axis). The colored horizontal layers represent the respective soil horizons of the triplets (aggregate and classified by FAO (2006)). The soil horizons are named at the right border of the diagrams. The second x-axis (associated as aboveground) showed the basal area of the respective stands (colored ticks) on a scale from 0 to 80 m² ha^{-1}.

Abb. 16 *Feinwurzeldaten aus drei unterschiedlichen Studien (vier Triplets). Die Feinwurzeldichte wurde in den Studien auf unterschiedliche Weise erhoben, daher verfügen die x-Achsen über unterschiedliche Einheiten. Die farbigen Schichten innerhalb der Diagramme zeigen die unterschiedlichen Bodenhorizonte auf (aggregiert und klassifiziert nach FAO, 2006). Die Bodenhorizontbezeichnungen befinden sich am rechten Rand der Diagramme. Die zweite obere X-Achse (als bildliche Abgrenzung zur oberirdischen Biomasse) stellt die Grundflächen der jeweiligen aufstockenden Bestände dar, anhand einer Skala von 0 bis 80 m² ha*$^{-1}$.

An open question of the analysis was whether the method of sampling lateral coarse roots represented the partitioning of growth between the upper and the lower part of the tree. The pros and cons of the method were discussed in detail in Article III. An explanation for the identified result of decreased lateral root growth in mixed stands might be increased root growth in deeper soil horizons. Bolte and Villanueva (2005) could show a clear deep stratification of fine roots from Norway spruce and European beech in mixed stands. In Article III it was concluded by different arguments that this stratification in soil for Douglas-fir and European beech seems to be implausible, but measurements were not taken to prove this. Therefore, a meta-analysis was applied which summarized the fine root data in relation to soil depth from three studies (Hendriks and Bianchi 1991, 1995; Feldmeier 2011; Thomas et al. 2015; Cremer et al. 2016; Cremer and Prietzel unpublished data). The studies measured fine root density in pure Douglas-fir, pure European beech, and mixed stands of both species. They thus had the same triplet experimental setup as the study at hand.

Interestingly, the fine root density of mixed stands in Fig. 16 was depicted low in the upper soil (0 – 30 cm soil depth) on the different sites. This reaction is contrary to the stand cited above, where mixed stands showed the greatest basal area per hectare or basal area near to Douglas-fir pure stands. Upper soil contained more suitable conditions for roots because nutrients, soil strength, aeration, and temperature are more favorable there than at depth (Sands and Mulligan 1990). The lower intensity of fine roots in mixed stands may result from a reduced need for water and nutrient uptake. As can be seen from the results, both species showed a complementary use of water in mixed stands.

Pretzsch et al. (2014) could show that Douglas-fir and European beech have different contents of nutrients under the same soil conditions. It is suggested that the species used the different nutrients in different intensities. This would also build a complementary usage. The unused nutrients of one species would be accessible for the other species, which could also be found in tropical mixed and pure forests of Brazil (Gama-Rodrigues et al. 2007).

The modified water use was mentioned in the chapter ‘Climate sensitivity’. It seems to be that a greater availability of water and nutrients in mixed stands shifts the limiting factor out of the soil. This is consistent with the findings of root-stem allometry.

Conclusion for further investigations

Holistic description

The thesis examined several topics of mixed research. Knowledge was extended on (1) a more precise description of overyielding (2) and on which sites it arises; (3) structural stand descriptions were confirmed and improved, (4) descriptions of climate sensitivity were made and influence factors on root-stem allometry were presented. However, more research of some topics is necessary to obtain a complete overview of the interaction between Douglas-fir and European beech.

In the thesis, interactions in mixed stands were deduced by ecophysiological traits. The information about photosynthesis at saturating light or stomatal conductance of the species came from literature without a background of mixed conditions. Measurements of physiological tree parameters in pure and mixed stands are meaningful to improve the description of the mixing effect. This must be the most important next step of research.

Another important point is the quantification of the overyielding. The current approach calculated the biomass production of the mixed stands with the same biomass equation as in pure stands. The calculation of biomass is based on the DBH and height of the individual trees. The current thesis and other studies could provide evidence that tree allometry changes in mixed stands. Therefore, it must be the goal to establish biomass equations which respect the modified allometry of the trees in mixed stands. Especially the crown seems to be an influential compartment in mixed stands. Further measurements with terrestrial or airborne laser scans may help to fix this problem. During the study, terrestrial laser scan measurements were taken on the triplets as well. However, methodical standards of mixed and pure stand comparisons are needed to get reliable statements from the data. However, biomass is not only a question of size; the weight (e.g. wood weight per cm^3) can be a variable parameter in mixed stands as well. Further study of the issue would be of interest.

The overyielding finding in the study at hand was based on the aboveground production of the mixed stands. The study could also show changed allometries between aboveground and belowground compartments. The description of the belowground biomass in mixed stands is currently a little researched field, which must be included in the description of mixed stands. Additionally, continuing research on the function of mycorrhiza appears fully justified because several studies suggest that mycorrhiza physically connect tree species and thereby manage their interaction.

Another topic is the quantification of overyielding in relation to environmental conditions. It has been shown that the overyielding was greatly influenced by stand age and site conditions. An extension of the site gradient to areas of species marginality would bring additional, important information about mixing effects. Especially the description of the relation between overyielding and site conditions from line to a curve, as also Bertness and Callaway (1994) predicted, would increase knowledge about mixed stands (discussed in Article I).

Another stage of research must be the complete description of income and outcome from mixed stands. Measurements of light, water and the nutrient cycles exist of the triplet but primary production was not related to resource supply and resource capture in the thesis. Nevertheless, the question of use efficiency has to be answered against the background of climate change and increasing requirements of citizens to the forests. The collected dataset of the thesis would allow a justification the theory of multiple resource use efficiency.

Comparing patterns

The current thesis described several mechanisms between Douglas-fir and European beech. To verify the finding mechanisms, it can also be interesting for further research to analyze the two species in other species combinations. For Douglas-fir there have been many analyses in combination with red alder, but the species show different mechanisms in mixed stands. Western hemlock and Douglas-fir seems to be a mixture which has comparable mechanisms as Douglas-fir and European beech, despite the coniferous-coniferous combination (discussed in Article I). Comparable investigation might be interesting. Another interesting species combination might be Douglas-fir and small-leaved lime (*Tilia cordata* Mill.). The characteristics of small-leaved lime might generate an equally complementary mixture with Douglas-fir as with European beech. It would also be a possible alternative for Central European forests. For European beech, the mixture with the spruce seems to trigger comparable mechanisms. Nevertheless, this comparatively well-studied mixture of species shows some differences to Douglas and European beech. In this mixture European beech tended to profit more from the combination than Norway spruce. The mixture of European beech and European silver fir suggests more comparability and is worth investigation.

Extended experimental setup

The mentioned possible mixtures need a great experimental setup which includes several species combinations under the same site and age conditions. This stage will be impossible with selected stands from managed forests and chronosequences, requiring instead the extensive establishment of a pure and mixed experimental trial.

The current study analyzed the mechanisms between the two species. Multiple mixture research would exponentially increase the number of interactions. It will be difficult to crystallize the individual mechanisms. Nevertheless, it has been shown that an increasing number of species in a stand increases the output of ecosystem services. Therefore, it must also be the goal to understand mechanisms and quantify the productivity of multiple species combinations. For this it is indispensable to create an experimental design which includes several species with different mixing proportions. Maybe, the ‘septet’ would be the further experimental design to analyze a three-species mixture.

Conclusion for forest practice

The investigation of Douglas-fir and European beech in mixed stands presented them as a complementary species combination. Due to the height stratification of the species and their complementary physiological features, mixed stands enable an improved utilization of incoming light. Thus, an overyielding arose in mixed stands which was not reached by the simple addition of the productivities in pure stands. For use in practice, it is important to know that overyielding increased with age, because height stratification needs time to develop. It is therefore necessary to adapt the rotation time of mixed stands. 120 years seems to be a reasonable rotation time. It has been shown in several studies that the mixing effect needs time to develop, regardless of the underlying mechanism. Thus, it can be taken as a general recommendation for mixed stands to manage them until greater ages.

Greater height stratification between the species enables a better utilization of incoming light. Therefore, it is necessary to have a high stand density so that this partitioning of light can work. The productivity gain would fail if trees stand in a single-tree situation. A stand with low density would not generate the mixing effect. The development of the two crown layers demands an intense mixing of the species. Only a high structuring in stands led to an optimal use of resources. It can be concluded that a mixture of one to three Douglas-firs surrounded by European beeches seems to be an optimal mixture.

However, this does not mean a tree-wise mixture in planting. The data showed that in the beginning of stand development European beech is able to grow faster than Douglas-fir. Therefore, it is recommended to plant or regenerate Douglas-firs in small groups (approximately 10 m x 10 m). Depending on expected failure in planting, the mixing proportion should reach a 50:50 proportion of crown projection area in old stands.[2] The managing of the mixture becomes much easier when Douglas-fir grows out of the crown layer from European beech with increasing age. European beech demands no intensive support in the understory due to its high shade tolerance. Additionally, its ability to fill gaps in thinned trees is a major benefit of this mixture. In higher stand development,

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[2] A practicable method in the field is to check the 50:50 mixing proportion by stocking level. Stocking level is calculated by measured basal area, relative to yield table full-stocking basal area of the species. As full-stocking, the basal area of remaining stand plus thinned stand can be taken. Thus, the method included the same fundamental idea of the adjusted SDI which is applied in the study at hand. For example, the mixture of European beech and Douglas-fir has an equivalence coefficient of 1.67 according to the yield tables (first yield class) of Bergel (1985) and Schober (1987). This is nearly identical to the equivalence coefficient of 1.63 resulting from the maximum stand density of pure stands in this study. The mixing proportion based on the stocking level would come to the comparable result as the adjusted SDI.

Douglas-fir loses the feature to use the full productivity capacity of the site. The upper Douglas-fir crown layer becomes more open. European beech is able to use these released resources and fill the crown gaps. The mentioned high density is also important to preserve this mechanism.

Besides the overyielding, it was shown that the mixture of European beech improved the drought stability of Douglas-fir. Thus, the mixture is a good possibility to shift away from coniferous trees in forests without increasing the risk of productivity loss under expected climate change. The stabilizing effect of the mixture allows Douglas-fir to grow on sites that will no longer be suitable in the future under pure conditions due to an increasing number of drought events.

Whether Douglas-fir is more or equally risky for wind throw as Norway spruce is currently a topic of discussion. Storm risk is a parameter which is influenced by many variables. The data from this study indicate that Douglas-firs in mixed stands have lower h/d ratios, which suggests improved wind stability. This is just a suggestion but the positive effect of mixing against windthrow was also made by other studies for other species mixtures.

Finally, the analysis of root stem allometry revealed the favorability of mixing for the individual trees of both species. The results show that the mixture is more suitable for the species than pure stand conditions. This pattern ran through the different sections of growth investigation. Summing up, Douglas-fir and European beech complement each other in stands of interest to forestry management.

Appendix

Appendix A – Ecological niche model

Fig. 2 is based on the German national forest inventory dataset. The site index of the trees was determined by the mean height with yield tables of Bergel (1985) and Schober (1987). The relation between mean height and climate was fitted with a generalized additive model (*gam*, R package 'mgcv'). The independent climate variables were multiannual precipitation sum and mean temperature (1980 - 2010) (Deutscher Wetterdienst 2016). The smoother of climate variables was fixed by 6 for precipitation and 5 for temperature to avoid oversensitive adaption of the spline. The grid of models was visualized with *vis.gam*. It was scaled into the unit square along with the view variables and then grid nodes more than 0.2 from the predictor variables were excluded. z represents the average site index of a climatic grid.

$$Hq_z = a_0 + f_1(Precipitation_z) + f_2(Temperature_z) + \varepsilon_z$$

	Dependent variable:			
	Mean height (Hq)			
	Douglas-fir		**E. beech**	
Parametric coefficients:				
Estimate	34.3940	***	26.437	***
	(0.2469)		*(0.121)*	
Approximate significance of smooth terms:				
s(Precipitation)				
Estimated degrees of freedom	3.619	***	3.64	***
s(Temperature)				
Estimated degrees of freedom	1.939	***	4.42	***
R²	0.166		0.397	
Observations	383		510	

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Italics and in brackets the std. error

Appendix B – Individual tree increment

The relationship of tree volume and volume increment (Fig. 9) was modeled by the equation

$$IV_{ijt} = a_0 + a_1 \cdot V_{ijt} + a_2 \cdot Mixture_{ij} + a_3 \cdot Mixture_{ij} \cdot V_{ijt} + b_i + b_{ij} + \varepsilon_{ijt} \qquad \text{(Eq. 4)}$$

The fixed effect $Mixture$ was included as a binary variable (1: pure stand, 0: mixed stand). a_0 … a_3 represent the coefficients of the fixed effects. Random effects b are considered triplet i, plot j, tree k. The index t stands for the year a measurement belongs to. The symbol ε represents i.i.d. errors.

	Dependent variable:	
	Volume increment	
	Douglas-fir	**E. beech**
Volume	0.128***	0.127***
	(0.003)	*(0.002)*
Mixture(Pure)	-0.056	0.011 .
	(0.038)	*(80.006)*
Volume* Mixture(Pure)	-0.021***	-0.020***
	(0.004)	*(80.003)*
Intercept	0.113***	0.016**
	(0.027)	*(0.005)*
Observations	2 885	4 430

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Italics and in brackets the std. error

Appendix C – Adaptive models of DBH and tree height

The curves in Fig. 9 and 11 were generated by splines which applied to the density function of diameter and height distribution. The splines were fitted by generalized additive models. The averaging by spline has the consequence that the integrals of the curves lose their characteristics of direct measure for distribution. Nevertheless, they are able to present the form of the diameter and height classes and describe the distribution with a certain degree of fuzziness. The indices are the same as in Eq. 4.

The applied equations were:

$$DBH\ distribution_{ijk} = a_0 + f_1(relativeDBH_k) + \varepsilon_{ijk} \qquad \text{(Eq. 5)}$$

$$Height\ distribution_{ijk} = a_0 + f_1(relativeHeight_k) + \varepsilon_{ijk} \qquad \text{(Eq. 6)}$$

	Dependent variable: *DBH distribution*			
	Douglas-fir		**E. beech**	
	Pure	Mixed	Pure	Mixed
Parametric coefficients:				
Estimate	0.0096 ***	0.0120 ***	0.0133 ***	0.0139 ***
	(0.0001)	*(0.0001)*	*(0.0001)*	*(0.0001)*
Approximate significance of smooth terms:				
s(relativeDBH)				
Estimated degrees of freedom	8.906 ***	8.915 ***	8.930 ***	8.921 ***
R²	0.679	0.428	0.478	0.542
Observations	9216	9216	9216	9216

	Dependent variable: *Height distribution*			
	Douglas-fir		**E. beech**	
	Pure	Mixed	Pure	Mixed
Parametric coefficients:				
Estimate	0.0178 ***	0.0222 ***	0.0182 ***	0.0143 ***
	(0.0002)	*(0.0002)*	*(0.0002)*	*(0.0001)*
Approximate significance of smooth terms:				
s(relativeHeight)				
Estimated degrees of freedom	5.998 ***	3.999 ***	4.983 ***	4.998 ***
R²	0.392	0.239	0.183	0.313
Observations	9216	9216	9216	9216

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Italics and in brackets the std. error

Appendix D – Species profile index

The calculation of the species profile index SPI against mixing types was done with the equation:

$$SPI_{ijt} = a_0 + a_1 \cdot Mixed\ stand_{ijt} + a_2 \cdot E.beech\ pure\ stand_{ijt} + \ b_i + b_{ij} + \varepsilon_{ijt} \qquad \text{(Eq. 7)}$$

The mixing types (Douglas-fir pure stand, E. beech pure stand, and mixed stand) were included as fixed effects and coded as binary variables which switch between 1 and 0 depending on which mixing type is fitted. The random effects were coded as in Appendix B. A generalized linear hypothesis test was used for contrasting all mixing type effects, as obtained by the linear mixed model, against each other. We applied the R-package 'multcomp' (Hothorn et al. 2008).

	Dependent variable:
	Species profile index
Mixed stand	46.996***
	(3.263)
E. beech pure stand	36.815***
	(3.254)
Intercept	31.963***
	(5.049)
Observations	253

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Italics and in brackets the std. error

Appendix E – Adaptive models of matrix potential

The matrix potential over the course of a year based on tensiometer measurements from four triplets (1001_4 5 6, 1004_ 4 5 6, 1003_4 5 6, 1003_7 8 9) between October 2013 and October 2015. The measurements were taken monthly at 30 cm soil depth. The independent variable was the day of the year DOY. The course of the matrix potential was fitted by a generalized additive mixed model (*gamm*, Rpackage 'mgcv'). Random effects were trial l and triplet i. The models were fitted for the single mixing types (Douglas-fir pure stand, European beech pure stand, and mixed stand). The applied equation was:

$$Matrix\ potential_{lit} = a_0 + f_1(DOY_t) + b_l + b_i + \varepsilon_{lit} \qquad \text{(Eq. 8)}$$

	Dependent variable:					
	Matrix potential					
	Douglas-fir		**E. beech**		**Mixed stand**	
Parametric coefficients:						
Estimate	-211.2	***	-132.09	***	-161.19	***
	(42.60)		*(21.59)*		*(14.49)*	
Approximate significance of smooth terms:						
s(DOY)						
Estimated degrees of freedom	6.255	***	8.056	***	7.23	***
R²	0.265		0.338		0.300	
Observations	593		602		626	

References

Abetz P (1976) Beiträge zum Baumwachstum. Der h/d-Wert - mehr als ein Schlankheitsgrad. Forst- u. Holzwirt 31:389–393

Albrecht L (2008) Waldbau mit der Douglasie in Unterfranken. LWF Wissen(59):39–43

Amoroso MM, Turnblom EC (2006) Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Can. J. For. Res. 36(6):1484–1496. doi: 10.1139/X06-042

Aranda I, Gil L, Pardos JA (2000) Water relations and gas exchange in Fagus sylvatica L. and Quercus petraea (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. Trees 14(6):344–352. doi: 10.1007/s004680050229

Assmann E (1954) Die Standraumfrage und die Methodik von Mischbestandsuntersuchungen. Allg. Forst Jagdztg 5(125):149–153

Assmann E (1970) The principles of forest yield study. Pergamon, Oxford, New York

Baade U (1996) Anlage und Auswertung einer Douglasien-Buchen-Wuchsreihe im Wuchsbezirk Geest- Mitte. Diplomarbeit, Universität Göttingen

Bartelink HH (1998) Simulation of growth and competition in mixed stands of Douglas-fir and beech. Landbouwuniversiteit Wageningen, Wageningen

Bauhus J, Khanna PK, Menden N (2000) Aboveground and belowground interactions in mixed plantations of Eucalyptus globulus and Acacia mearnsii. Can. J. For. Res. 30(12):1886–1894. doi: 10.1139/x00-141

Bayerische Landesanstalt für Wald und Forstwirtschaft (ed) (2008) Die Douglasie- Perspektiven im Klimawandel, Freising

Bergel D (1985) Douglasien-Ertragstafel für Nordwestdeutschland. Nieders. Forstl. Versuchsanst., Abt. Waldwachstum, Göttingen

Bertness MD, Callaway RM (1994) Positive interactions in communities. Trends in Ecology & Evolution 9(5):191–193. doi: 10.1016/0169-5347(94)90088-4

Binkley D (1984) Importance of size—density relationships in mixed stands of douglas-fir and red alder. Forest Ecology and Management 9(2):81–85. doi: 10.1016/0378-1127(84)90075-6

Binkley D (2003) Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Can. J. For. Res. 33(11):2274–2279. doi: 10.1139/x03-158

Binkley D, Greene S (1983) Production in mixtures of conifers and red alder: the importance of site fertility and stand age. In: Ballard R, Gessel. S (eds) International Union of Forestry Research Organizations Symposium on Forest Site and Continuous Productivity, pp 112–117

Biondi F, Qeadan F (2008) A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Research 64(2):81–96. doi: 10.3959/2008-6.1

Biondi F, Waikul K (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers & Geosciences 30(3):303–311. doi: 10.1016/j.cageo.2003.11.004

Bolte A, Villanueva I (2005) Interspecific competition impacts on the morphology and distribution of fine roots in European beech (Fagus sylvatica L.) and Norway spruce (Picea abies (L.) Karst.). European Journal of Forest Research 125(1):15–26. doi: 10.1007/s10342-005-0075-5

Booth J (1882) Die Naturalisation ausländischer Waldbäume in Deutschland. Springer Berlin Heidelberg, Berlin, Heidelberg

Burkett VR, Wilcox DA, Stottlemyer R, Barrow W, Fagre D, Baron J, Price J, Nielsen JL, Allen CD, Peterson DL (2005) Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. Ecological complexity 2(4):357–394

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences 104(46):18123–18128. doi: 10.1073/pnas.0709069104

Cavard X, Bergeron Y, Chen HYH, Paré D, Laganière J, Brassard B (2011) Competition and facilitation between tree species change with stand development. Oikos 120(11):1683–1695. doi: 10.1111/j.1600-0706.2011.19294.x

Čermák J, Matyssek R, Kučera J (1993) Rapid response of large, drought-stressed beech trees to irrigation. Tree Physiology 12(3):281–290. doi: 10.1093/treephys/12.3.281

Comps B, Gömöry D, Letouzey J, Thiébaut B, Petit RJ (2001) Diverging Trends Between Heterozygosity and Allelic Richness During Postglacial Colonization in the European Beech. Genetics 157(1):389–397

Cook E, Kairiūkštis L (1990) Methods of dendrochronology: Applications in the environmental science. Kluwer Academic Publishers; International Institute for Applied Systems Analysis, Dordrecht, Netherlands, Boston

Cremer M, Kern NV, Prietzel J (2016) Soil organic carbon and nitrogen stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce. Forest Ecology and Management 367:30–40. doi: 10.1016/j.foreco.2016.02.020

Cremer M, Prietzel J (unpublished data) Fine root density in Douglas-fir and European beech mixed and pure stands

Cremer M, Prietzel J (2016) Soil matrix potential of Douglas-fir European beech pure and mixed stands. unpublished raw data

Crow P (2005) The influence of soils and species on tree root depth. Information note / Forestry Commission, FCIN078. Forestry Commission, Edinburgh

de Wall K, Dreher G, Spellmann H, Pretzsch H (1998) Struktur und Dynamik von Buchen-Douglasien-Mischbeständen. forstarchiv 69(5):179–191

DeBell DS, Cole TG, Whitesell CD (1997) Growth, Development, and Yield in Pure and Mixed Stands of Eucalyptus and Albizia. Forest Science 43(2):286–298

del Río M, Pretzsch H, Alberdi I, Bielak K, Bravo F, Brunner A, Condés S, Ducey MJ, Fonseca T, Lüpke N von, Pach M, Peric S, Perot T, Souidi Z, Spathelf P, Sterba H, Tijardovic M, Tomé M, Vallet P, Bravo-Oviedo A (2016) Characterization of the structure, dynamics, and productivity of mixed-species stands: Review and perspectives. Eur J Forest Res. doi: 10.1007/s10342-015-0927-6

Dengler A (1935) Waldbau auf ökologischer Grundlage Ein Lehr- und Handbuch, 2nd edn. Verlag von Julius Springer, Berlin

Deutscher Wetterdienst (2016) Grids germany-annual: sunshine duration 1951-2016. ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/annual/sunshine_duration/. Accessed 18 March 2016

Dirnberger G, Sterba H, Condés S, Ammer C, Annighöfer P, Avdagić A, Bielak K, Brazaitis G, Coll L, Heym M, Hurt V, Kurylyak V, Motta R, Pach M, Ponette Q, Ruiz Peinado R, Skrzyszewski J, Šrámek V, de Streel G, Svoboda M, Zlatanov T, Pretzsch H (in review) Species proportions by area in mixtures of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.). Euopean Journal of Forest Research

Dirnberger GF, Sterba H (2014) A comparison of different methods to estimate species proportions by area in mixed stands. Forest Syst 23(3):534. doi: 10.5424/fs/2014233-06027

Dreher G (1994) Struktur und Wuchsdynamik von Buchen-Douglasien Mischbeständen im Mittel-Westniedersächsischen Tiefland. Diplomarbeit, Universität Göttingen

Eilmann B, de Vries, Sven M. G., den Ouden J, Mohren, Godefridus M. J., Sauren P, Sass-Klaassen U (2013) Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (Pseudotsuga menziesii (Mirb.)) provenances. Forest Ecology and Management 302(0):133–143. doi: 10.1016/j.foreco.2013.03.031

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht: 203 Tabellen, 6., vollst. neu bearb. und stark erw. Aufl. UTB, vol 8104. Ulmer, Stuttgart

FAO (2006) Guidelines for soil description, 4th ed. Food and Agriculture Organization of the United Nations, Rome

Felbermeier B, Mosandl R (2007 ff) Fagus sylvatica. In: Lang UM, Roloff A, Schütt P, Stimm B, Weisgerber H (eds) Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie /begründet von Peter Schütt. Andreas Roloff; Horst Weisgerber; Ulla M. Lang; Bernd Stimm. Wiley-VCH, Weinheim, pp 1–20

Feldmeier S (2011) Vertikale Wurzelverteilung von Buche (Fagus sylvatica) und Douglasie (Pseudotsuga menziesii) in Rein- und Mischbeständen. Bachleor-thesis, Universität Trier

Fischer A (2003) Forstliche Vegetationskunde: Eine Einführung in die Geobotanik ; 31 Tabellen, 3., aktualisierte Aufl. UTB, vol 8268. Ulmer, Stuttgart

Forrester DI, Bauhus J, Khanna PK (2004) Growth dynamics in a mixed-species plantation of Eucalyptus globulus and Acacia mearnsii. Synthesis of the physiological, environmental, genetic and silvicultural determinants of the growth and productivity of eucalypts in plantations 193(1–2):81–95. doi: 10.1016/j.foreco.2004.01.024

Forrester DI, Smith RGB (2012) Faster growth of Eucalyptus grandis and Eucalyptus pilularis in mixed-species stands than monocultures. Forest Ecology and Management 286:81–86. doi: 10.1016/j.foreco.2012.08.037

Franz F (1987) Zum Aufbau eines neuzeitlichen Informationssystems für die Forstwirtschaft. forstarchiv 58(4):131–137

Fritts HC (1976) Tree rings and climate. Acad. Pr, London

Gama-Rodrigues ACd, Barros NFd, Comerford NB (2007) Biomass and nutrient cycling in pure and mixed stands of native tree species in southeastern Bahia, Brazil. Rev. Bras. Ciênc. Solo 31(2):287–298. doi: 10.1590/S0100-06832007000200011

Gamfeldt L, Snall T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Froberg M, Stendahl J, Philipson CD, Mikusinski G, Andersson E, Westerlund B, Andren H, Moberg F, Moen J, Bengtsson J (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. Nat Commun 4:1340. doi: 10.1038/ncomms2328

Gandullo JM, Serrada R (1977) Mapa de productividad potencial forestal de la España peninsular. Monografias INIA (Spain). no. 16.

Gauer J, Kroiher F (eds) (2012) Waldokologische Naturraume Deutschlands: Forstliche Wuchsgebiete und Wuchsbezirke – Digitale Topographische Grundlagen – Neubearbeitung Stand 2011, Sonderheft Nr. 359. Landbauforschung vTI Agriculture and Forestry Research

Givnish TJ (1988) Adaptation to Sun and Shade: a Whole-Plant Perspective. Functional Plant Biol 15(2):63–92

Göhre K (1958) Die Douglasie und ihr Holz. Akademie Verlag, Berlin

Goisser M, Geppert U, Rötzer T, Paya A, Huber A, Kerner R, Bauerle T, Pretzsch H, Pritsch K, Häberle KH, Matyssek R, Grams T (2016) Does belowground interaction with Fagus sylvatica increase drought susceptibility of photosynthesis and stem growth in Picea abies? Forest Ecology and Management 375:268–278. doi: 10.1016/j.foreco.2016.05.032

Goverment of Canada (2016) Canadian Climate Normals 1981-2010 Station Data. http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?searchType=stnProx&txtRadius=200&selCity=&selPark=&optProxType=custom&txtCentralLatDeg=49&txtCentralLatMin=45&txtCentralLatSec=0&txtCentralLongDeg=126&txtCentralLongMin=04&txtCentralLongSec=0&stnID=246&dispBack=0. Accessed 31 August 2016

Guske A (2013) Vergleichende Produktivitätsuntersuchung von Rein- und Mischbeständen der Baumarten Buche und Douglasie. Master thesis, Technische Universität München

Hacke GU, Sperry SJ, Pockman TW, Davis DS, McCulloh AK (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126(4):457–461. doi: 10.1007/s004420100628

Hamrick JL, Godt MJW, Sherman-Broyles SL (1992) Factors influencing levels of genetic diversity in woody plant species. In: Population genetics of forest trees. Springer, pp 95–124

Harper JL (1977) Population biology of plants. Academic Press, London

Hendriks C, Bianchi F (1991) Root density and root length development in pure and mixed stands of Douglas fir and Beech

Hendriks C, Bianchi F (1995) Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. Netherlands Journal of Agricultural Science 1995(43):321–331

Hermann RK (2007 ff) Pseudotsuga menziesii. In: Lang UM, Roloff A, Schütt P, Stimm B, Weisgerber H (eds) Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie /begründet von Peter Schütt. Andreas Roloff; Horst Weisgerber; Ulla M. Lang; Bernd Stimm. Wiley-VCH, Weinheim, pp 1–18

Holmes RL, Adams RK, Fritts HC (1986) Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin with procedures used in the chronology development work including users manuals for computer programs COFECHA and ARSTAN

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. Biom. J. 50(3):346–363. doi: 10.1002/bimj.200810425

Huber MO, Sterba H, Bernhard L (2014) Site conditions and definition of compositional proportion modify mixture effects in Picea abies – Abies alba stands. Can. J. For. Res. 44(10):1281–1291. doi: 10.1139/cjfr-2014-0188

Hugershoff R (1936) Die mathematischen Hilfsmittel der Kulturingenieurs und Biologen: Herleitung von gesetzmäßigen Zusammenhängen als Manuskript veröffentlicht, Dresden

Huss J (1996) Die Douglasie als Mischbaumart. AFZ-DerWald 51:1112–1116

Jacob A, Hertel D, Leuschner C (2013) On the significance of belowground overyielding in temperate mixed forests: Separating species identity and species diversity effects. Oikos 122(3):463–473. doi: 10.1111/j.1600-0706.2012.20476.x

Kelty M (1992) Comparative productivity of monocultures and mixed-species stands. In: Kelty M, Larson B, Oliver C (eds) The Ecology and Silviculture of Mixed-Species Forests, vol 40. Springer Netherlands, pp 125–141

Kelty MJ (2006) The role of species mixtures in plantation forestry. Improving Productivity in Mixed-Species Plantations 233(2–3):195–204. doi: 10.1016/j.foreco.2006.05.011

Kemmerer J, Warger K, Heller T (2013) Zuwachsleistung von Mischbeständen in Abhängigkeit von Umweltbedingungen: Mischung Douglasie-Buche, Ebersberger Forst. Bachelor project, Technische Universität München

Keyes MR, Grier CC (1981) Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11(3):599–605. doi: 10.1139/x81-082

Klein T, Niu S (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct Ecol 28(6):1313–1320. doi: 10.1111/1365-2435.12289

Kleinschmit J, Bastien JC (1992) IUFRO's role in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco.) tree improvement. Silvae genetica 41(3):161–173

Knoke T, Ammer C, Stimm B, Mosandl R (2008) Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. Eur J Forest Res 127(2):89–101. doi: 10.1007/s10342-007-0186-2

Köcher P (2013) Hydraulic traits and their relevance for water use strategies in five broad-leaved tree species of a temperate mixed forest. Niedersächsische Staats- und Universitätsbibliothek Göttingen, Göttingen

Kölling C (2007) Klimahüllen für 27 Waldbaumarten. AFZ-DerWald 23:1242–1245

Konnert M, Cremer E (2014) Isoenzymatische Untersuchungen von Douglasienvorkommen im Rahmen des Projektes B74: Zwischenbericht ASP

Konnert M, Cremer E, Fussi B (2014) Genetische Variation wichtiger Waldbaumarten in Bayern. LWF Wissen 74:14–21

Kownatzki D, Kriebitzsch W-U (2011) Zum Douglasienanbau in Deutschland: Ökologische, waldbauliche, genetische und holzbiologische Gesichtspunkte des Douglasienanbaus in Deutschland und den angrenzenden Staaten aus naturwissenschaftlicher und gesellschaftspolitischer Sicht. Landbauforschung vTI agriculture and forestry research - Sonderheft, vol 344. Johann Heinrich von Thünen-Institut (vTI), Bundesforschungsinstitut für Ländliche Räume, Wald und Fischerei, Braunschweig

Kozovits AR, Matyssek R, Blaschke H, Göttlein A, Grams TEE (2005) Competition increasingly dominates the responsiveness of juvenile beech and spruce to elevated CO2 and/or O3 concentrations throughout two subsequent growing seasons. Global Change Biology 11(9):1387–1401

Larocque GR, Luckai N, Adhikary SN, Groot A, Bell FW, Sharma M (2013) Competition theory — science and application in mixed forest stands: review of experimental and modelling methods and suggestions for future research. Environ. Rev. 21(2):71–84. doi: 10.1139/er-2012-0033

Lavender DP, Hermann RK (2014) Douglas-fir: The genus Pseudotsuga. Oregon State University, College of Forestry, Forest Research Laboratory, Corvallis, Or.

Le Maire G, Nouvellon Y, Christina M, Ponzoni FJ, Gonçalves J, Bouillet J-P, Laclau J-P (2013) Tree and stand light use efficiencies over a full rotation of single- and mixed-species Eucalyptus grandis and Acacia mangium plantations. Forest Ecology and Management 288:31–42. doi: 10.1016/j.foreco.2012.03.005

LeBlanc DC (1990) Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Can. J. For. Res. 20(9):1399–1407. doi: 10.1139/x90-185

Lebourgeois F, Gomez N, Pinto P, Mérian P (2013) Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. Forest Ecology and Management 303:61–71. doi: 10.1016/j.foreco.2013.04.003

Leuschner C, Scherer B (1989) Fundamentals of an applied ecosystem research project in the Wadden Sea of Schleswig-Holstein. Helgoländer Meeresuntersuchungen 43(3):565–574. doi: 10.1007/BF02365912

Lewis JD, McKane RB, Tingey DT, Beedlow PA (2000) Vertical gradients in photosynthetic light response within an old-growth Douglas-fir and western hemlock canopy. Tree Physiology 20(7):447–456. doi: 10.1093/treephys/20.7.447

Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, McGuire AD, Bozzato F, Pretzsch H, de-Miguel S, Paquette A, Herault B, Scherer-Lorenzen M, Barrett CB, Glick HB, Hengeveld GM, Nabuurs G-J, Pfautsch S, Viana H, Vibrans AC, Ammer C, Schall P, Verbyla D, Tchebakova N, Fischer M, Watson JV, Chen HYH, Lei X, Schelhaas M-J, Lu H, Gianelle D, Parfenova EI, Salas C, Lee E, Lee B, Kim HS, Bruelheide H, Coomes DA, Piotto D, Sunderland T, Schmid B, Gourlet-Fleury S, Sonke B, Tavani R, Zhu J, Brandl S, Vayreda J, Kitahara F, Searle EB, Neldner VJ, Ngugi MR, Baraloto C, Frizzera L, Balazy R, Oleksyn J, Zawila-Niedzwiecki T, Bouriaud O, Bussotti F, Finer L, Jaroszewicz B, Jucker T, Valladares F, Jagodzinski AM, Peri PL, Gonmadje C, Marthy W, O’Brien T, Martin EH, Marshall AR, Rovero F, Bitariho R, Niklaus PA, Alvarez-Loayza P, Chamuya N, Valencia R, Mortier F, Wortel V, Engone-Obiang NL, Ferreira LV, Odeke DE, Vasquez RM, Lewis SL, Reich PB (2016) Positive biodiversity-productivity relationship predominant in global forests. Science 354(6309). doi: 10.1126/science.aaf8957

Lloret F, Keeling EG, Sala A (2011) Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120(12):1909–1920. doi: 10.1111/j.1600-0706.2011.19372.x

Lough JM, Fritts HC (1987) An assessment of the possible effects of volcanic eruptions on North American climate using tree-ring data, 1602 to 1900 A.D. Climatic Change 10(3):219–239. doi: 10.1007/BF00143903

Löw M, Herbinger K, Nunn AJ, Häberle K-H, Leuchner M, Heerdt C, Werner H, Wipfler P, Pretzsch H, Tausz M, Matyssek R (2006) Extraordinary drought of 2003 overrules ozone impact on adult beech trees (Fagus sylvatica). Trees 20(5):539–548. doi: 10.1007/s00468-006-0069-z

Lu H, Mohren GM, den Ouden J, Goudiaby V, Sterck FJ (2016) Overyielding of temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species mixtures over time in the Netherlands. Forest Ecology and Management 376:321–332. doi: 10.1016/j.foreco.2016.06.032

Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gomory D, Latalowa M, Litt T, Paule L, Roure JM, Tantau I, van der Knaap, W O, Petit RJ, Beaulieu J-L de (2006) A new scenario for the quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. New Phytol 171(1):199–221. doi: 10.1111/j.1469-8137.2006.01740.x

Martonne Ed (1926) Une Nouvelle fonction climatologique. L’Indice d’aridité. Impr. Gauthier-Villars, Paris

Mason WL (2002) Are irregular stands more windfirm? Forestry 75(4):347–355. doi: 10.1093/forestry/75.4.347

Matyssek R, Fromm J, Rennenberg H, Roloff A (2010) Biologie der Bäume: Von der Zelle zur globalen Ebene ; 32 Tabellen. UTB Biologie, Agrar- und Forstwissenschaften, Landschaftsplanung, vol 8450. Ulmer, Stuttgart

Mayr S, Schwienbacher F, Bauer H (2003) Winter at the Alpine Timberline. Why Does Embolism Occur in Norway Spruce But Not in Stone Pine? Plant Physiology 131(2):780–792. doi: 10.1104/pp.011452

Meinen C, Hertel D, Leuschner C (2009) Biomass and morphology of fine roots in temperate broad-leaved forests differing in tree species diversity: is there evidence of below-ground overyielding? Oecologia 161(1):99–111. doi: 10.1007/s00442-009-1352-7

Meinzer FC (ed) (2011) Size- and age-related changes in tree structure and function. Tree physiology, vol 4. Springer, Dordrecht

Mencucci M (2003) The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant, Cell & Environment 26(1):163–182. doi: 10.1046/j.1365-3040.2003.00991.x

Mooney HA, Gulmon SL (1979) Environmental and Evolutionary Constraints on the Photosynthetic Characteristics of Higher Plants. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) Topics in Plant Population Biology. Macmillan Education UK, London, pp 316–337

Moore GW, Bond BJ, Jones JA (2011) A comparison of annual transpiration and productivity in monoculture and mixed-species Douglas-fir and red alder stands. Forest Ecology and Management 262(12):2263–2270. doi: 10.1016/j.foreco.2011.08.018

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76(4):521–547. doi: 10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

Niklas KJ (1994) Plant allometry: The scaling of form and process. Univ. of Chicago Press, Chicago

Nikolova PS, Zang C, Pretzsch H (2011) Combining tree-ring analyses on stems and coarse roots to study the growth dynamics of forest trees: a case study on Norway spruce (Picea abies [L.] H. Karst). Trees 25(5):859–872. doi: 10.1007/s00468-011-0561-y

Paterson SS (1956) Forest area of the world and its potential productivity, Göteborg

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307(5949):321–326. doi: 10.1038/307321a0

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. New Phytologist 193(1):30–50. doi: 10.1111/j.1469-8137.2011.03952.x

Pretzsch H (1992) Konzeption und Konstruktion von Wuchsmodellen für Rein- und Mischbestände. Forstliche Forschungsberichte München

Pretzsch H (1995) Zum Einfluß des Baumverteilungsmusters auf den Bestandeszuwachs. Allg. Forst Jagdztg 166(9/10):190–201

Pretzsch H (2004) Gesetzmäßigkeiten zwischen Bestandesdichte und Zuwachs. Lösungsansatz am Beispiel von Reinbeständen aus Fichte (Picea abies [L.] Karst.) und Buche (Fagus sylvatica L.). Allg. Forst Jagdztg 175(12):225–234

Pretzsch H (2009) Forest dynamics, growth and yield: From measurement to model. Springer, Berlin, London

Pretzsch H, Biber P (2016) Tree species mixing can increase maximum stand density. Can. J. For. Res.:1–15. doi: 10.1139/cjfr-2015-0413

Pretzsch H, Bielak K, Block J, Bruchwald A, Dieler J, Ehrhart H-P, Kohnle U, Nagel J, Spellmann H, Zasada M, Zingg A (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. Eur J Forest Res 132(2):263–280. doi: 10.1007/s10342-012-0673-y

Pretzsch H, Block J, Dieler J, Gauer J, Göttlein A, Moshammer R, Schuck J, Weis W (2014) Nährstoffentzüge durch die Holz- und Biomassenutzung in Wäldern. Teil 1: Schätz-funktionen für Biomasse und Nährelemente und ihre Anwendung in Szenariorechnungen. Allg. Forst Jagdztg 185(11/12):261–285

Pretzsch H, del Río M, Schütze G, Ammer C, Annighöfer P, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Drössler L, Fabrika M, Forrester DI, Kurylyak V, Löf M, Lombardi F, Matović B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Skrzyszewski J, Sramek V, Sterba H, Svoboda M, Verheyen K, Zlatanov T, Bravo-Oviedo A (2016) Mixing of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) enhances structural heterogeneity, and the effect increases with water availability. Forest Ecology and Management 373:149–166. doi: 10.1016/j.foreco.2016.04.043

Pretzsch H, Schütze G (2016) Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur J Forest Res 135(1):1–22. doi: 10.1007/s10342-015-0913-z

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. Plant Biology 15(3):483–495. doi: 10.1111/j.1438-8677.2012.00670.x

Pretzsch H, Spellmann H (1994) Leistung und Struktur des Douglasien-Durchforstungsversuchs Lonau 135. Forst und Holz 49(3)

Pretzsch H, Uhl E, Biber P, Schütze G, Coates KD (2012) Change of allometry between coarse root and shoot of Lodgepole pine (Pinus contorta DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia. Scandinavian Journal of Forest Research 27(6):532–544. doi: 10.1080/02827581.2012.672583

Puettmann KJ, Hibbs DE, Hann DW (1992) The Dynamics of Mixed Stands of Alnus Rubra and Pseudotsuga Menziesii: Extension of Size—Density Analysis to Species Mixture. Journal of Ecology 80(3):449–458. doi: 10.2307/2260690

R Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Radosevich SR, Hibbs DE, Ghersa CM (2006) Effects of species mixtures on growth and stand development of Douglas-fir and red alder. Can. J. For. Res. 36(3):768–782. doi: 10.1139/x05-280

Rais A, van de Kuilen, Jan-Willem G., Pretzsch H (2014) Growth reaction patterns of tree height, diameter, and volume of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) under acute drought stress in Southern Germany. Eur J Forest Res 133(6):1043–1056. doi: 10.1007/s10342-014-0821-7

Reich PB (2002) Root-shoot relations: optimality in acclimation and adaptation or the ‘Emperor’s New Clothes’. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: The hidden half, 3rd ed., rev. and expanded. M. Dekker, New York, pp 205–220

Reyer C, Lasch P, Mohren GJ, Sterck F (2010) Inter-specific competition in mixed forests of Douglas-fir (Pseudotsuga menziesii) and common beech (Fagus sylvatica) under climate change — a model-based analysis. Annals of Forest Science 67(8):805. doi: 10.1051/forest/2010041

Sands R, Mulligan DR (1990) Water and nutrient dynamics and tree growth. Forest Ecology and Management 30(1-4):91–111. doi: 10.1016/0378-1127(90)90129-Y

Schelhaas MJ (2008) The wind stability of different silvicultural systems for Douglas-fir in the Netherlands: A model-based approach. Forestry 81(3):399–414. doi: 10.1093/forestry/cpn028

Schober R (1987) Ertragstafeln wichtiger Baumarten bei verschiedener Durchforstung, 3., neubearb. u. erw. Aufl. Sauerländer, Frankfurt am Main

Schume H, Jost G, Hager H (2004) Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. Journal of Hydrology 289(1–4):258–274. doi: 10.1016/j.jhydrol.2003.11.036

Schweingruber FH, Eckstein D, Serre-Bachet F, Bräker OU (1990) Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8:9–38

Shainsky LJ, Newton M, Radosevich SR (1992) Effects of intra- and inter-specific competition on root and shoot biomass of young Douglas-fir and red alder. Can. J. For. Res. 22(1):101–110. doi: 10.1139/x92-014

Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A Quantitative Analysis of Plant Form - The Pipe Model Theory I. Basic Analyses. Japanese Journal of Ecology 14(3):97–105

Slavov GT, Howe GT, Yakovlev I, Edwards KJ, Krutovskii KV, Tuskan GA, Carlson JE, Strauss SH, Adams WT (2004) Highly variable SSR markers in Douglas-fir: Mendelian inheritance and map locations. Theor Appl Genet 108(5):873–880. doi: 10.1007/s00122-003-1490-y

Society of American Foresters (1958) Forestry terminology: A glossary of technical terms used in forestry, 3. ed. Soc. of Amer. Foresters, Washington, D.C.

Thomas FM, Bögelein R, Werner W (2015) Interaction between Douglas fir and European beech: Investigations in pure and mixed stands = Wechselwirkungen zwischen Douglasie und Rotbuche : Untersuchungen an Rein- und Mischbeständen. Forstarchiv : forstwissenschaftliche Fachzeitschrift 86(4):83–91

Thünen-Institut (2012a) Dritte Bundeswaldinventur - Ergebnisdatenbank: BWI-Basisdaten. https://bwi.info/Download/de/BWI-Basisdaten. Accessed 11 September 2016

Thünen-Institut (2012b) Dritte Bundeswaldinventur - Ergebnisdatenbank: Waldfläche (gemäß Standflächenanteil) [ha] nach Land und Baumartengruppe (rechnerischer Reinbestand). 77Z1JI_L235of_2012_bi / 2014-6-10 16:7:59.927. https://bwi.info. Accessed 14 July 2016

Thurm EA, Pretzsch H (2016) Productivity and structural properties of mixed versus pure stands of European beech (Fagus sylvatica L.) and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) depends on environmental conditions. Ann. For. Sci.:1–15. doi: 10.1007/s13595-016-0588-8

Thurm EA, Uhl E, Pretzsch H (2016) Mixture reduces climate sensitivity of Douglas-fir stem growth. Forest Ecology and Management(376):205–220. doi: 10.1016/j.foreco.2016.06.020

Toïgo M, Vallet P, Tuilleras V, Lebourgeois F, Rozenberg P, Perret S, Courbaud B, Perot T (2015) Species mixture increases the effect of drought on tree ring density, but not on ring width, in Quercus petraea–Pinus sylvestris stands. Forest Ecology and Management 345:73–82. doi: 10.1016/j.foreco.2015.02.019

Tschopp T, Holderegger R, Bollmann K (2014) Auswirkungen der Douglasie auf die Waldbiodiversität: Eine Literaturübersicht, vol 20. Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf

van der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Hector A, Ampoorter E, Baeten L, Barbaro L, Bauhus J, Benavides R, Benneter A, Berthold F, Bonal D, Bouriaud O, Bruelheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Coomes D, Coppi A, Bastias CC, Muhie Dawud S, Wandeler H de, Domisch T, Finer L, Gessler A, Granier A, Grossiord C, Guyot V, Hattenschwiler S, Jactel H, Jaroszewicz B, Joly F-X, Jucker T, Koricheva J, Milligan H, Muller S, Muys B, Nguyen D, Pollastrini M, Raulund-Rasmussen K, Selvi F, Stenlid J, Valladares F, Vesterdal L, Zielinski D, Fischer M (2016) Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nat Commun 7:11109. doi: 10.1038/ncomms11109

Vandermeer JH (1989) The ecology of intercropping. Cambridge University Press, Cambridge [England], New York

Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Climate 23(7):1696–1718. doi: 10.1175/2009JCLI2909.1

Vicente-Serrano SM, Gouveia C, Camarero JJ, Begueria S, Trigo R, Lopez-Moreno JI, Azorin-Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Moran-Tejeda E, Sanchez-Lorenzo A (2013) Response of vegetation to drought time-scales across global land biomes. Proc Natl Acad Sci U S A 110(1):52–57. doi: 10.1073/pnas.1207068110

Walter H, Lieth H (1967) Klimadiagramm-Weltatlas: Von Heinrich Walter und Helmut Lieth. G. Fischer, Jena

Waring RH, Running SW (1978) Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant Cell Environ 1(2):131–140. doi: 10.1111/j.1365-3040.1978.tb00754.x

Woodruff DR, Meinzer FC, Lachenbruch B (2008) Height-related trends in leaf xylem anatomy and shoot hydraulic characteristics in a tall conifer: safety versus efficiency in water transport. New Phytologist 180(1):90–99. doi: 10.1111/j.1469-8137.2008.02551.x

Yang N, Zavišić A, Pena R, Polle A (2016) Phenology, photosynthesis, and phosphorus in European beech (Fagus sylvatica L.) in two forest soils with contrasting P contents. J. Plant Nutr. Soil Sci. 179(2):151–158. doi: 10.1002/jpln.201500539

Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. Journal of Ecology 100(3):742–749. doi: 10.1111/j.1365-2745.2011.01944.x

Zianis D (2005) Biomass and stem volume equations for tree species in Europe. Silva Fennica Monographs, vol 4. Finnish Soc. of Forest Science, Helsinki

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer New York, New York, NY

Article -I-

Improved productivity and modified tree morphology of mixed versus pure stands of European beech *(Fagus sylvatica)* and Douglas-fir *(Pseudotsuga menziesii)* with increasing precipitation and age

in ***Annals of Forest Science (2016)***

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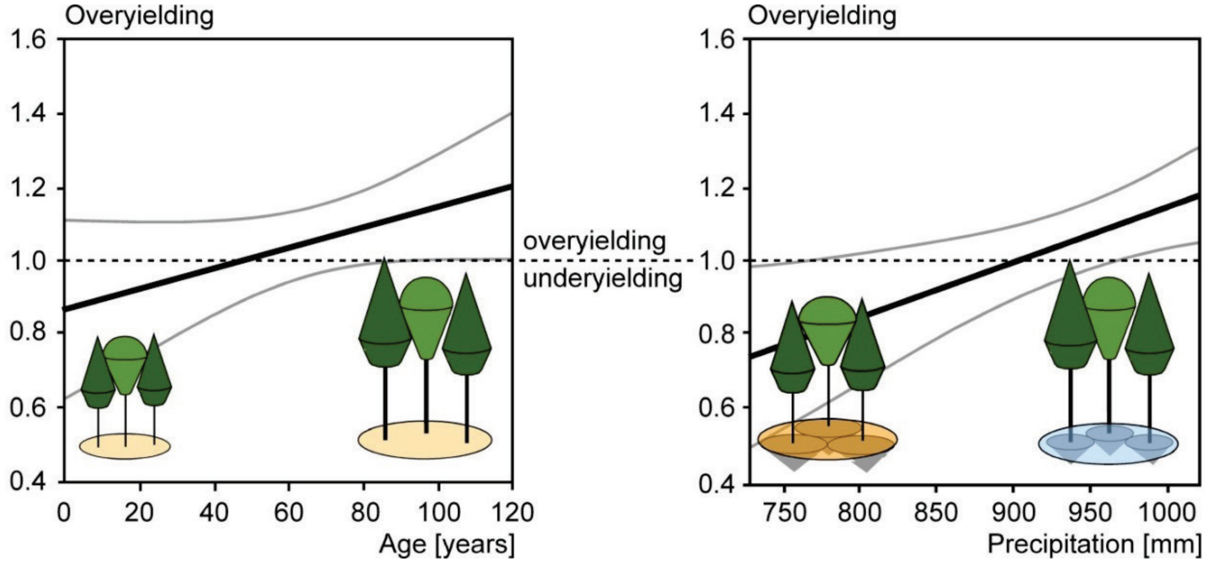


Key message

The mixture of Douglas-fir and European beech produced more biomass compared to what would have been expected from a weighted average of pure stands. Overyielding of the mixed stands improved with increasing stand age and under better site conditions.

Abstract

Context • The mixture of Douglas-fir and European beech has the intrinsic potential to be one of the most productive forest types in Central Europe.

Aims • The study investigated how the structure and productivity of mixed stands changed in comparison to pure ones. It analyzed whether there is overyielding in mixed stands and if it was modified due to stand development or along an ecological gradient.

Methods • Throughout Germany, 18 research plot triplets with 1,987 trees were established in seven different ecological regions from dry to moist site conditions at ages from 30 to 120 years. To investigate the growth of the stands, tree cores were collected from 1,293 stems.

Results • The study revealed significant overyielding of biomass in mixed stands of 6% or 0.81 Mg ha^{-1} $year^{-1}$. It was found that: (i) Overyielding in mixed stands was driven by an increase in Douglas-fir growth. (ii) Both species modified their morphology in mixture. Compared to the species in pure stands, Douglas-firs diameters in mixed stands were significantly larger, whereas European beech had a smaller diameter at breast height in the mixture. The effect increased with the age. (iii) The analyses revealed more pronounced overyielding in older stands and on better sites.

Conclusion • The findings show that overyielding of Douglas-fir and European beech in mixed stands results from a higher light interception by complementary space occupation.

Keywords: Mixing effect; Overyielding; Triplet experimental setups; Age gradient; Ecological gradient; Height stratification

1. Introduction

Recently, the mixture of Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco) and European beech (*Fagus sylvatica* L.) has greatly increased in relevance (Thünen-Institut 2012). Silviculture with Douglas-fir is a very controversial topic in Germany. On the one hand, it is considered as one of the most successfully introduced tree species in Europe because it is known for its high wood quality, growth and adaptability to heterogeneous environments (Kleinschmit and Bastien 1992). Douglas-fir is superior in its productivity in comparison to other species in Central Europe (Pretzsch 2005). Therefore, the high productivity of this tree species offers the potential to counteract the expected wood supply gaps in the future (Mantau et al. 2008). On the other hand, it is often criticized that Douglas-fir, as a neophyte, leads to a floristic and faunistic impoverishment in European forests (Knoerzer and Reif 1996; Meyer 2011). It is known that introducing additional tree species in pure stands can increase overall biodiversity (Felton et al. 2010; Cavard et al. 2011) and decrease the risk of pest outbreaks (Kelty 1992; Montagnini et al. 1995; Jactel and Brockerhoff 2007). Thus, a practical compromise might be the management of Douglas-fir in mixed stands.

Due to its specific growing behavior, there are not many candidate species to mix with Douglas-fir to get an even-aged, single-tree mixture (Göhre 1958). Its slow growth after planting places it in danger of being overgrown by other species. After it is established, its vigorous growth can easily drive other species into suppression. So, the species considered for admixture should be both vigorous in growth and shade-tolerant at the same time.

In its natural North American range, Douglas-fir is a sub-climax species. Natural pure stands mainly arise as a result of forest fires (Hermann 2007). Over the course of stand development, the Douglas-firs are joined by shade-tolerant species like western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Western red cedar (*Thuja plicata* Donn ex D. Don) in the understory. These mixtures might also work in Central Europe but considering biodiversity issues, indigenous species are mostly preferred to mix with Douglas-fir in Europe.

European beech is often considered an appropriate Central European deciduous species to mix with Douglas-fir (Göhre 1958; Otto 1987). The climatic requirements of both species overlap in Central Europe (Kölling 2007). Given the shade-tolerance of European beech, it is able to build a second stand layer below the predominant Douglas-fir. European beech retains its vitality and fills developing gaps in the canopy in older stands (Göhre 1958). The horizontal structure and resulting tree size pattern seems to be an important issue to understand mixing effects (del Río et al. 2015).

With regard to the known high productivity potential of Douglas-fir in pure stands and the relevance of its mixture with European beech, it is important to improve knowledge about the growth and yield of such mixed stands. While there are many studies dealing with the question of over- or underyielding in mixed stands (e.g. Kelty 1992; Piotto 2008; Pretzsch et al. 2013), there are, to our knowledge, only two extensive studies dealing with Douglas-fir and European beech (Bartelink 1998, Thomas et al. 2015). Both studies showed a higher increment in mixed stands compared to what would have been expected from a weighted average of pure stands. Bartelink (1998) included an age gradient in his study, but did not analyze the impact of the age on overyielding. Studies with other mixtures pointed out that age influenced overyielding (Binkley 2003; Forrester et al. 2004; Amoroso and Turnblom 2006). That is why the current study analyzes if it is possible that over- or underyielding in Douglas fir–European beech stands changes with stand age.

Studies on mixed stand effects revealed that, independent of tree species, over- or underyielding is dependent on site conditions (Binkley 2003; Pretzsch et al. 2010; Forrester et al. 2013). The shift of facilitation to competition along an improving environmental gradient (Callaway and Walker 1997) leads to overyielding on poorer sites in some studies (Pretzsch et al. 2010; Binkley 2003; Toïgo et al. 2014). In other studies, complementary effects were especially evident on better sites and resulted in a higher yield with improving site conditions (Forrester et al. 2013; Forrester and Albrecht 2014).

Based on previous studies the following questions were investigated: (i) How does the structure change in mixed stands compared to pure stands? (ii) Does overyielding arise in mixed stands? How does this overyielding change along an (iii) age and (iv) productivity gradient?

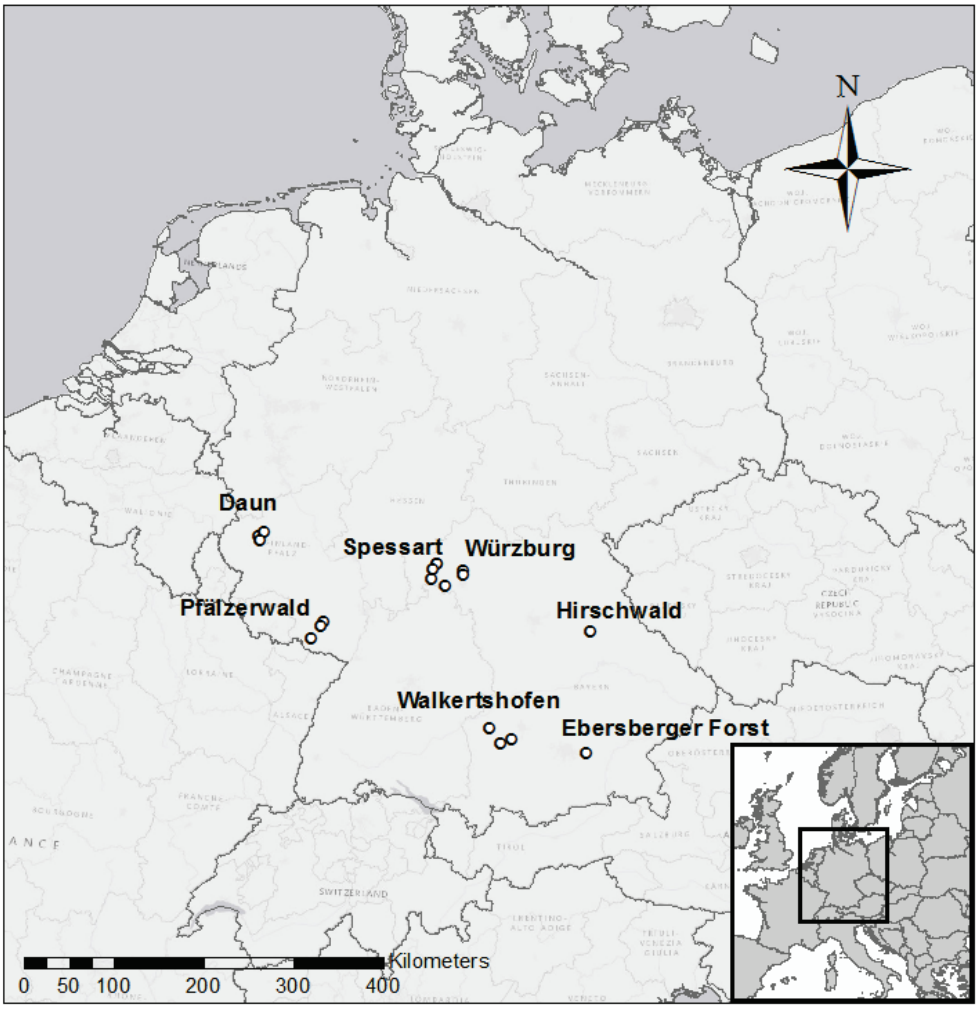


Fig. 1 Geographic location of the 18 triplets at seven different ecological regions in Germany; each of the 18 sites (black points) include three plots: a pure stand of Douglas-fir, a pure stand of European beech and a mixed stand of both species.

Abb.1 *Geopgraphische Lage der 18 Triplets in den sieben unterschiedlichen Ökoregionen in Deutschland; jeder der 18 Triplets (schwarze Punkte) beinhaltet 3 Versuchflächen: einen Douglasien - Reinbestand, einen Rotbuchen - Reinbestand und einen Mischbestand aus beiden Baumarten.*

2. Material and methods

2.1. Study sites

Site characteristics

In Southern Germany, seven ecological regions – five in Bavaria and two in Rhineland-Palatinate – were selected for experimental setup (Fig. 1). Table 1 summarizes important climate and soil characteristics. The experiment collection was concentrated in the colline level (330 m – 580 m a. s. l.) and covered a span of 430 km. The mean annual temperature ranged from 7.5 to 9.3°C (average = 8.4°C) with an annual mean precipitation between 718 mm and 1070 mm (average = 935 mm) (Deutscher Wetterdienst 2015). The experiment included drier, warmer sites in the ecological region of *Fränkische Platte* and moister, colder sites like the *Schwäbisch-Bayerische Schotterplatten- und*

Altmoränenlandschaft. The base supply of the soil ranged from base-rich to base-poorer sites. The water supply of the established plots, described by the combination of water-holding capacity, precipitation and transpiration, ranged from very fresh (equate with much moisture) to moderate-dry (Landesforst Rheinland-Pfalz 2014; Bayerische Landesanstalt für Wald und Forstwirtschaft 2013).

Table 1 Site characteristics of the seven experimental locations in their ecological regions (Gauer and Kroiher 2012), climate data (Deutscher Wetterdienst 2015), base-richness and water supply (Landesforst Rheinland-Pfalz 2014; Bayerische Landesanstalt für Wald und Forstwirtschaft 2013).

***Tabelle 1** Standortseigenschaften der sieben Versuchsanlagen mit den jeweiligen Ökoregionen (Gauer und Kroiher 2012), Klimadaten (Deutscher Wetterdienst 2015), Basenausstattung und Wasserversorgung (Landesforst Rheinland-Pfalz 2014; Bayerische Landesanstalt für Wald und Forstwirtschaft 2013).*

Experimental location	Ecological region	Geographic position		Elevation	Mean annual precipitation (1981 - 2014)	Mean annual temperature (1981 - 2014)	Base-richness from base-poor (1) to base-rich(5)	Water supply from very dry (1) to very fresh(7)
		N-latitude	E-longitude					
				m above sea level (min - max)	mm yr-1 (min - max)	°C (min - max)		
Walkertshofen	Tertiäres Hügelland	48°15'18.33''	10°44'49.15''	556 (523 - 597)	961 (890 - 1011)	8.2 (8.1 - 8.4)	3	7
Würzburg	Fränkische Platte	49°56'10.05''	9°56'17.51''	310 (272 - 343)	749 (718 - 792)	8.8 (8.5 - 9.2)	4	3
Spessart	Spessart	49°50'37.96''	9°27'56.62''	384 (279 - 384)	1001 (878 - 1070)	8.5 (7.9 – 9.0)	3-4	4-7
Ebersberger Forst	Schwäbisch-Bayerische Schotterplatten- und Altmoränen-landschaft	48°07'16.78''	11°51'09.88''	532	1044	8.5	4	7
Daun	Osteifel	50°10'23.86''	6°44'36.33''	486 (471 - 500)	978 (880 - 1066)	7.9 (7.5 - 8.2)	3	6
Hirschwald	Frankenalb und Oberpfälzer Jura	49°20'34.74''	11°54'34.98''	474 (462 - 482)	821	8.0	3	5
Pfälzerwald	Pfälzerwald	49°19'10.67''	7°48'23.27''	445 (416 - 457)	967 (894 – 832)	8.6 (8.3 - 8.8)	2	5

Experimental design of plots

The samples were subdivided into stands of three age levels per ecological region: young (around 30 years), mature (around 60 years) and old (older than 90 years). The age levels of the ecological regions were used to build chronosequences (also see de Wall et al. 1998). In two of the seven ecological regions, only one age level was established. In the ecological region *Spessart*, we sampled four triplets because mature triplets were already installed. Altogether, 18 triplets were analyzed (open circles in Fig. 1). The triplet setup is a well-established method for mixture research (e.g. Amoroso and Turnblom 2006, Pretzsch et al. 2010) and consisted of a pure stand of Douglas-fir (${}_{\mathrm{Df}}$), a pure stand of European beech(${}_{\mathrm{Eb}}$) and a mixed stand of both species(${}_{\mathrm{Df,Eb}}$). The selection of the triplets was made in managed forest stands without experimental background. The plots of a triplet were located in close proximity. The median distance from the center of the pure to the center of the mixed plot was 86 m for Douglas-fir and 260 m for European beech. In the majority of triplets, the three plots were inside the same compartment. They were more or less even-aged (see Online Resource 1) and had similar site conditions (also seen in Online Resource 2). The soil similarity of the triplets was checked by a comparison of the site map. When the plots were not inside the same compartment, the similarity of the soil was visually checked by a sample with a boring rod. The distances between the plots of a triplet were not great enough to have a significant influence on climate. Minor climatic differences might result from the intersection of the plots with the gridded climate data. For the analyses we used the average site conditions of a triplet. Overall 54 plots were part of the study. All site conditions from all plots within an ecological region are assumed to be similar (also seen in Online Resource 2).

In the selection of the plots, we tried to select only fully stocked stands with low thinning intensity. The maximum stand density should ensure that all stands produce their maximum yield and enables a comparison between the different mixing types. Because we investigated backwards a time period of 20 years, the mechanism of self-thinning and thinning took effect in the development of the stands. Therefore, we also collected the dead trees and the stumps of the felled trees and their time point of death and reconstructed fully stocked stands for the whole time period.

We selected the plots with the requirement to include only the two investigated species. The plots were sections of planted stands or anthropogenic initiated natural regeneration. Therefore, pure stands consisted completely of one species. The proportion of foreign tree species in pure and mixed stands was 1.2 percent of the overall basal area. These individual trees were only suppressed trees. We added them to the stand productivity of Douglas-fir or European beech, depending on whether they were broadleaf or coniferous species.

When selecting the plots we tried to consider a buffer zone of more than one tree length, to exclude edge effects or mixing effects with other tree species. The minimum requirement was that the neighboring trees continued the species composition of the plot.

The mixed plots were selected by the criterion of single tree mixture. The mixing proportion (m) was calculated using the stand density index (SDI) introduced by Reineke (1933). The stand density differences between the species were adjusted by an equivalence coefficient e_1 computed by the ratio between the SDI of pure Douglas-fir stands ($\mathrm{SDI}_{\mathrm{Df}}$) and pure beech stands ($\mathrm{SDI}_{\mathrm{Eb}}$) (Sterba et al. 2014; Pretzsch et al. 2015). The equivalence coefficient (average 1.63) was computed for every triplet. Douglas-fir and European beech in mixed stands were abbreviated with $_{\mathrm{Df,(Eb)}}$ and $_{\mathrm{(Df),Eb}}$.

$$m_{\mathrm{Df,(Eb)}} = \frac{\mathrm{SDI}_{\mathrm{Df,(Eb)}}}{\mathrm{SDI}_{\mathrm{Df,(Eb)}} + \mathrm{SDI}_{\mathrm{(Df),Eb}} \cdot \mathrm{e1}} \quad (1)$$

The mean ratio of mixture was 0.47 : 0.53 (Douglas-fir : European beech) and ranged between 0.22 and 0.76 for Douglas-fir.

The 54 plots comprised a span of size between 0.01 ha and 0.24 ha (mean = 0.06 ha). The sizes of the plots were dependent on the age of the trees. Each pure stand contained 20 dominant trees and each mixed stand contained 20 dominant trees per species. For all of the 1,987 trees, diameter at breast height (DBH), positions of the crown and tree height (h) were measured (Online Resource 1). Two cores were taken from all dominant trees and, when available, from five suppressed trees. Altogether, cores of 1,293 trees (2,586 cores) were gathered (Online Resource 3) and measured with a digital positiometer (Biritz GmbH, Gerasdorf bei Wien, Austria). Cross-dating of the year rings was undertaken with the software TSAPWin Scientific 4.69d (Rinntech, Heidelberg, Germany).

In addition to the standing trees, all stumps on the plots were registered. Their diameters were measured in order to comprehend the thinning in the past and thus to not underestimate the increment of the whole stands. With the root collar diameters from the living trees and their DBHs, the DBHs from the stumps could be reconstructed. We estimated the approximate date of tree felling by visual attribution of the decay. The assessment of the stumps was carried out in five decay classes based on the classification by Krüger (2013).

2.2 Stand history – increment calculation

The annual diameter increment (i_d) of stumps and undrilled trees were calculated by fitting the function $\ln(i_\mathrm{d}) = \mathrm{a} + b \cdot \ln(DBH)$. The reconstruction time span was usually 20 years. For young trees of an age of less than or equal to 30 years the time span was 10 years. The current tree heights and the positions of the crowns were measured with a Vertex IV (Haglöf, Långsele, Sweden). Previous height developments were described by the Michailov height curve system, which was parametrized by measured tree heights of the chronosequences. Wherever no chronosequences were available, height development was calculated by yield tables (Bergel 1985; Schober 1987). With the given size and tree number per plot the volume of the plots could be extrapolated by the reconstructed diameters and heights. The increment results from the difference in the volume from one period to the previous period plus removal stand (thing and self-thinning).

For each of the 18 triplets the most common growth and yield parameters were computed according to the DESER Norm (Johann 1993) in five-year periods for the last three decades using standard software of the Chair for Forest Growth and Yield Science (Biber 2013). In the end, a data pool of 66 survey periods of the triplets periods existed.

The aboveground biomass was calculated by functions based on Pretzsch et al. (2014). The biomass of the individual tree (B_{it}) was calculated by the diameter at breast height (DBH) and the tree height (h):

$$B_{\mathrm{it}} = e^{\mathrm{a}_0} \cdot DBH^{\mathrm{a}_1} \cdot h^{\mathrm{a}_2}, \tag{2}$$

with a_0 = -2.996, a_1 = 2.123 and a_2 = 0.694 for European beech and a_0 = -3.211, a_1 =2.008 and a_2 = 0.730 for Douglas-fir.

The biomass increment was obtained by the biomass of a tree in the current period subtracted by the previous period. The increment of the stand arose from all trees of a plot scaled up to one hectare.

2.3 Structure

The height (h), diameter at breast height (DBH) and the ratio between both (h/d ratio) showed the structural differences between trees in pure and mixed stands. They were included in the analysis as the quadratic mean diameter tree of the plots, backwards in five-year intervals.

To characterize the species-specific dynamics along the age gradient, we fitted height growth curves for both species in mixed stands (also described by del Río et al. 2015). For this, we used the tree heights and positions of crowns in mixed stands in the year of sampling. The fitting was done by means of the Chapman-Richard growth function.

2.4 Mixing effects

The description of the mixing effect has often been considered and is commonly accepted (Huber et al. 2014). So here only the formulas are presented. For a more detailed overview see Pretzsch et al. (2010). As already used by Pretzsch et al. (2010), periodic mean annual increment of volume (PAIV) and aboveground biomass (PAIW) were used as a measure of productivity in this study. The description of over- or underyielding, the mixing effect, was made by the comparison of expected mixed stand $\hat{p}_{\mathrm{Df,Eb}}$ based on pure stand versus observed mixed stand $p_{\mathrm{Df,Eb}}$. So absolute (MEA) and relative (MER) mixing effect was quantified by

$$MEA_{\mathrm{Df,Eb}} = p_{\mathrm{Df,Eb}} - \hat{p}_{\mathrm{Df,Eb}} \text{ and } MER_{\mathrm{Df,Eb}} = \frac{p_{\mathrm{Df,Eb}}}{\hat{p}_{\mathrm{Df,Eb}}} \tag{3}$$

and was calculated for increment of volume (MEAV, MERV) and aboveground biomass (MEAW, MERW). The absolute mixing effect is defined as cubic meters (MEAV) or tons (MEAW) per hectare and year. The expected mixed stand productivity (Eq. 4) if there were no mixture effects is calculated by weighting the pure stands' productivities by the species' proportions in the mixed stands.

$$\hat{p}_{\mathrm{Df,Eb}} = p_{\mathrm{Df}} \cdot m_{\mathrm{Df,(Eb)}} + p_{\mathrm{Eb}} \cdot m_{\mathrm{(Df),Eb}} \tag{4}$$

To compare the intraspecific differences of Douglas-fir and European beech between pure and mixed stands (Eq. 5), the productivity in mixed stands ($pp_{\mathrm{Df,(be)}}$, $pp_{\mathrm{(Df),be}}$) was scaled up to one hectare.

$$p_{\mathrm{Df,(Eb)}} = pp_{\mathrm{Df,(Eb)}} \cdot m_{\mathrm{Df,(Eb)}} \text{ and } p_{\mathrm{(Df),Eb}} = pp_{\mathrm{(Df),Eb}} \cdot m_{\mathrm{(Df),Eb}} \qquad (5)$$

The ratio of the scaled-up productivity in the mixed stand and the productivity in the pure stand of the same species (Eq. 6) identified the species-specific over- and underyielding in the mixed stand.

$$MER_{\mathrm{Df,(Eb)}} = \frac{p_{\mathrm{Df,(Eb)}}}{p_{\mathrm{Df}}} \text{ and } MER_{\mathrm{(Df),Eb}} = \frac{p_{\mathrm{(Df),Eb}}}{p_{\mathrm{Eb}}} \qquad (6)$$

2.5 Statistics

This study was based on measured and reconstructed data. Because of this nesting in data, we used linear mixed-effects regression models. The nesting levels of experiment location and triplet within the experiment location could be included as random effects.

The first questions, the differences of structure and productivity between pure and mixed stands, were tested by:

$$Y_{ijkt} = a_0 + a_1 \cdot mixture_{ijk} + a_2 \cdot age_{ijkt} + a_3 \cdot mixture_{ijk} \cdot age_{ijkt} + b_i + b_{ij} + b_{ijk} + (c_i + c_{ij} + c_{ijk}) \cdot age_{ijkt} + \varepsilon_{ijkt} \, . \qquad (7)$$

Y_{ijt} stands for the structural and productivity variables (height, DBH, h/d ratio, mean periodic increment of volume and aboveground biomass) to be tested. The differences of pure and mixed stands were included by the explanatory variables of $mixture$. We added an interaction of $mixture$ and age to consider changing behavior of the variables along the stand age gradient. The indexes *i, j, k* and *t* represent an experimental location, a triplet, a plot and a point in time, respectively. The fixed-effect coefficient is represented by *a*. Random effects of experimental location, triplet and plot level were included in *b* for the intercept and c for the age. Differences in height and h/d ratio were not based on reconstructed data. Therefore, we excluded the random-effect plot *k* in these models. The symbol ε represents the independent and identically distributed random error. Model selection was based on the Akaike Information Criterion (Burnham and Anderson 1998) and biological plausibility of the results.

The question about the influence of age and site conditions on overyielding was investigated by the relative periodic mean annual increment of aboveground biomass (MERW). It was used instead of the mean annual increment of volume (MERV) because aboveground biomass is closer to the biological explanation approach.

To verify the influence of age and ecological conditions on MERW, the following explanatory variables were included into linear mixed models: age, site index, water supply, base-richness, mean annual temperature and mean annual precipitation (also seen in Table 1). Site index was the dominant top height at the age of 100 years of Douglas-fir in pure stands. Interactions of explanatory variables were expected between site index and age and between precipitation and water supply. The analysis was split into two approaches. The first one included the ecological conditions via the site index (SI) of Douglas fir as one single variable:

$$MERW_{ijt} = a_0 + a_1 \cdot age_{ijt} + a_2 \cdot SI_{ij} + a_3 \cdot age_{ijt} \cdot SI_{ij} + b_i + b_{ij} + \varepsilon_{ijt} \qquad (8)$$

The second model included the ecological conditions in more detail:

$$MERW_{ijt} = a_0 + a_1 \cdot age_{ijt} + a_2 \cdot precipitation_{ij} + a_3 \cdot temperature_{ij} + a_4 \cdot base - richness_{ij} + a_5 \cdot water\ supply_{ij} + \ a_6 \cdot water\ supply_{ij} \cdot precipitation_{ij} + b_i + b_{ij} + \varepsilon_{ijt} \qquad (9)$$

This model was fitted with MERW for the whole stand ($MERW_{Df,Eb}$) as well as for both species separately ($MERW_{Df,(Eb)}$, $MERW_{(Df),Eb}$).

All models were processed with the *lmer* function in the R package *lme4* (Bates et al. 2015). Model selection from the extensive model of the gradients was made with the additional help of automated model selection (*dredge*) from the R package *MuMln* (Barton 2015). The significances of the fixed effects were tested by an F-Test with Satterthwaite’s approximation (Kuznetsova et al. 2015). To calculate the marginal coefficient of determination for the mixed-effect models, *r.squaredGLMM* from the *MuMln* package was used. The command is based on the coefficient of determination calculation of Nakagawa and Schielzeth (2013). All statistical analyses were performed in the statistical environment R version 3.2.1 (R Core Team 2015).

3. Results

3.1 Structure

By comparing the species tree height (h) and diameter at breast height (DBH), it could be determined that Douglas-fir, regardless of whether mixed or pure, was generally taller (h = 33.1 m, $p < 0.001$) and thicker (DBH = 46.1 cm, $p < 0.001$) than European beech (h = 23.8 m; DBH = 23.6 cm) (Online Resource 1). The species-specific height difference also becomes evident in terms of the site index in pure stands: At age 100, Douglas-fir had a dominant top height of 47.2 m while European beech was only 36.9 m (Online Resource 4).

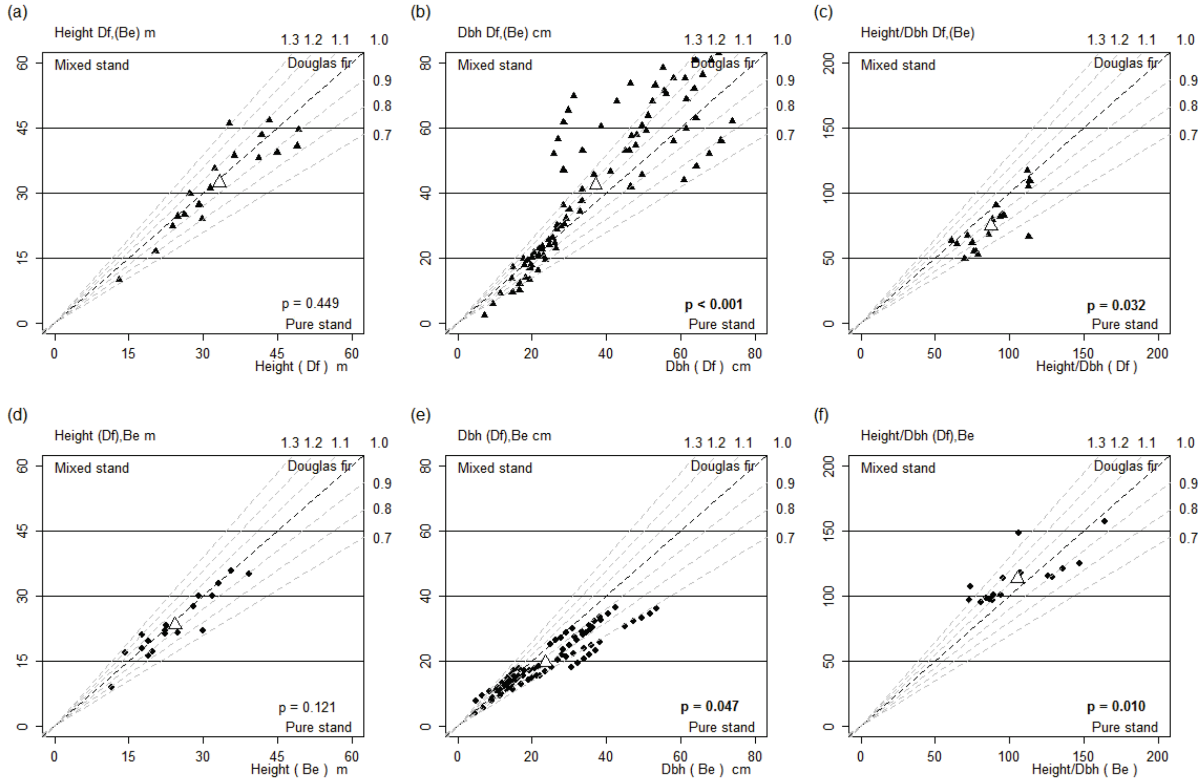


Fig. 2 Comparison between pure and mixed stand of height (a, d), diameter at breast height (b, e) and h/d ratio(c, f) of Douglas-fir (triangles, above) and European beech (circles, below). White symbols describe the mean value. Listed is the decisive significant in connection with the mixture (variable: mixture or correlation of mixture and age). The values represent the measured and reconstructed data of the quadratic mean diameter tree. The whole descriptive statistic for significance is given in Online Resource 5.

***Abb. 2** Vergleich zwischen Rein- und Mischbestand in Bezug auf die Baumhöhe (a,d), Brusthöhendurchmesser (b,e) und H/D Verhältnis von Douglasie (Dreiecke, oberhalb) und Rotbuche (Kreise, unterhalb). Weiße Symbole repräsentieren die Mittelwerte. Aufgeführt ist die ausschlaggebende Signifikanz aus den jeweiligen Modellen in Hinblick auf die Mischung (Variable: Mischung oder Korrelation von Alter und Mischung). Die Daten repräsentieren sowohl gemessene als auch rekonstruierte Daten des Grundflächenmittelstammes. Die gesamte Modellstatistik ist im Anhang 5 aufgeführt.*

Fig. 2 shows the structural comparison between pure and mixed stands by height, DBH and the ratio of height and diameter (h/d ratio). The significances and how the structural parameters react along the age gradient can also be seen in Online Resource 5. The data indicated that the height of

Douglas-fir in mixed stands (32.5 m) was similar to in pure stands (33.3 m, $p > 0.05$) (Fig. 2a), whereas the DBH was significantly larger (42.6 cm to 37.1 cm, $p < 0.001$)(Fig. 2b). So the taper which was described here by the h/d ratio (Fig. 2c) showed a higher taper for Douglas-fir in mixture (87.4 to 75.0, $p < 0.05$). A contrary picture for European beech could be observed. The DBH was significantly smaller (19.5 cm to 23.7 cm, $p < 0.001$) (Fig. 2e) and slender in mixed stands (105.3 to 113.4, $p < 0.05$) (Fig. 2f). The tree height of mixed stands was also similar to pure stands (23.3 m to 24.3 m, $p > 0.05$) (Fig. 2d).

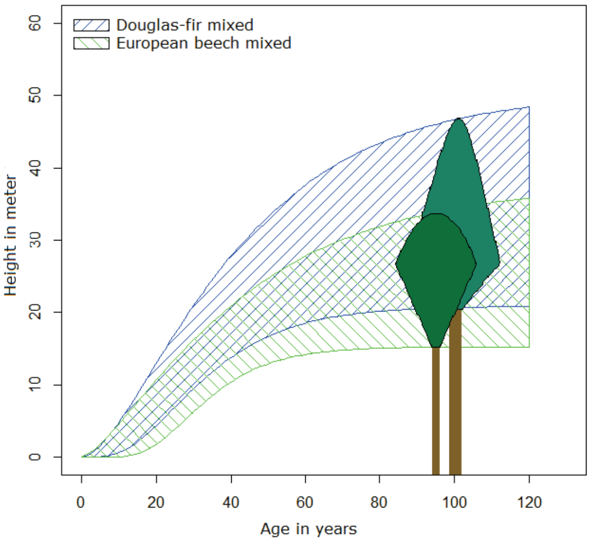


Fig. 3 Crown development from Douglas-fir and European beech of 20% of the highest tree in mixed stand along the age gradient. The data were measured tree heights and position of crowns at the survey points, which were averaged by the Chapman-Richards model ($a(1\text{-}exp(-k\ t))^p$), Douglas-fir (height: a=53.25, k=0.027, p=1.57; crown: a=19.27, k=0.08, p=8.98), European beech (height: a=49.44, k=0.012, p=1.00; crown: a=15.13, k=0.08, p=10.00). Significance of the parameter can be seen in Online Resource 7.

Abb.3 *Kronenentwicklung von Douglasie und Rotbuche der höchsten Bäume (20% Quantil) im Mischbestand entlang des Altergradienten. Die Daten bestehen aus gemessene Baum- und Kronenhöhen. Die Modellkurve ist eine an die Daten angepasste Chapman-Richards model* ($a(1\text{-}exp(-k\ t))^p$)*, Douglasie (Höhe: a=53.25, k=0.027, p=1.57; Kronenanfang: a=19.27, k=0.08, p=8.98), Rotbuche (Höhe: a=49.44, k=0.012, p=1.00; Kronenanfang: a=15.13, k=0.08, p=10.00). Signifikanzen der einzelnen Parameter sind in Anhang 7 nachzulesen.*

Fig. 3 shows the height development of the highest trees in mixed stands along an age gradient. It shows the large height difference between Douglas-fir and European beech in mixed stands. At younger ages, the differences between European beech and Douglas-fir were marginal, with European beech slightly leading. After 20 years the differences increased in favor of Douglas-fir until its maximum of 11.4 m at the age of 90 years.

3.2 Overyielding

The species-specific mean volume increment in pure stands differs greatly in the present study. A mean volume increment ($PAIV_{Df}$) of 26.12 m³ ha^{-1} yr^{-1} for pure Douglas-fir and ($PAIV_{Eb}$) 13.59 m³ ha^{-1} yr^{-1} for pure European beech (see Online Resource 4) was found. The mixed stand lay with 21.08 m³ ha^{-1} yr^{-1} between the two. Important for the analysis of overyielding was the comparison between the productivity which would be expected in mixed stands with the weighted average of the neighboring pure stands and the observed productivity in mixed stands (MEA). Overall the mixing effect of annual volume increment ($MEAV_{Df,Eb}$) was spread from 73% above to 55% below the expected productivity. On average the mixed stands produced 1.63 m³ ha^{-1} yr^{-1} ($p < 0.05$) more than expected from pure stands (Fig. 4a, see also Online Resource 4). This means a mixture leads to overyielding, which amounts to a significant, positive mixing effect of 8%.

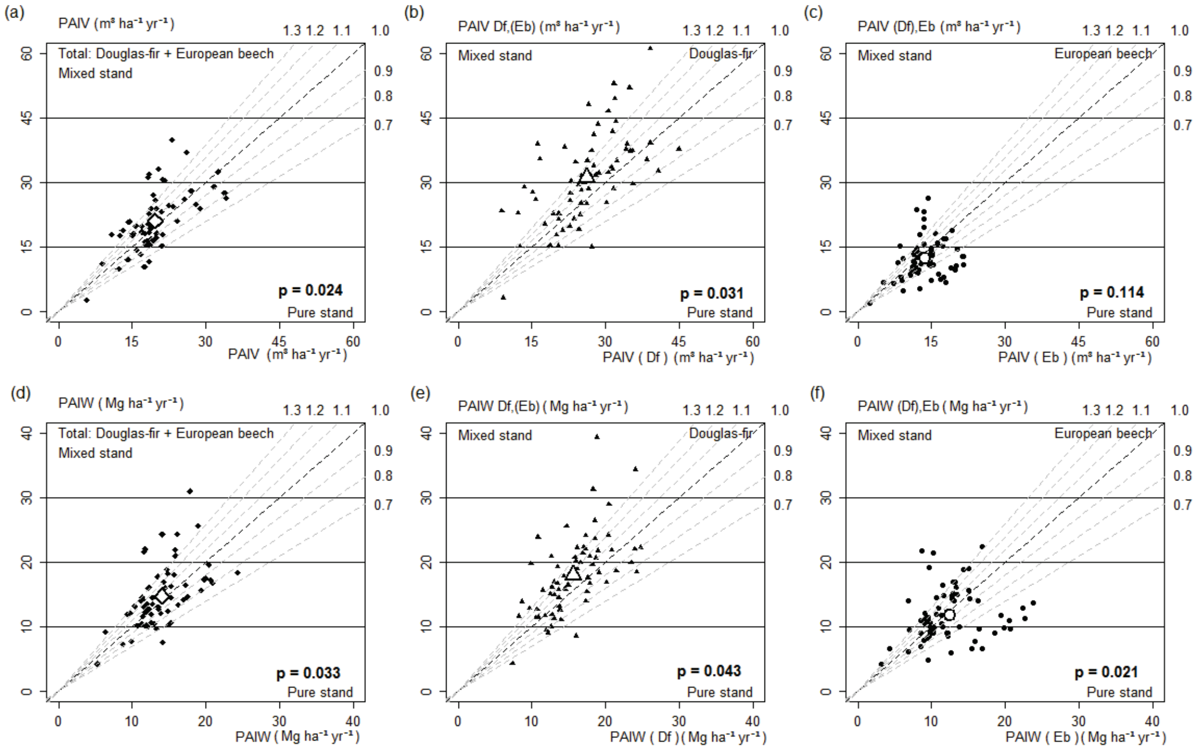


Fig. 4 Comparison between pure and mixed stands of the periodic mean annual increment of volume (above) and aboveground biomass (below) for the whole stand – diamonds (a, d), Douglas-fir – triangle (b, e) and European beech – circle(c, f). White symbols describe the mean value of pure and mixed stands. Listed is the decisive significant in connection with the mixture (mixture or correlation of mixture and age). The values represent the measured and reconstructed data. The whole descriptive statistic for significance is given in Online Resource 5.

***Abb. 4** Vergleich zwischen Rein- und Mischbestand in Bezug auf die periodischen, mittleren jährlichen Zuwächse des Volumens (oberhalb) und der Biomasse (unterhalb). Weiße Symbole repräsentieren die Mittelwerte. Aufgeführt ist die ausschlaggebende Signifikanz aus den jeweiligen Modellen in Hinblick auf die Mischung (Variable: Mischung oder Korrelation von Alter und Mischung). Die Daten repräsentieren sowohl gemessene als auch rekonstruierte Daten des Grundflächenmittelstammes. Die gesamte Modellstatistik ist im Anhang 5 aufgeführt.*

In detail, there was a significant difference in how overyielding in mixed stands arose. The cross diagrams (Fig. 5, see also Online Resource 6) show that overyielding was contributed to by Douglas-fir. It produced 20% more volume in mixed than in pure stands (5.09 m^3 h^{-1} yr^{-1}, $p < 0.05$) (Fig. 4b), whereas European beech in mixed stands tended to lose increment compared to pure stands ($p > 0.05$) (Fig. 4c). It produced 8% less volume than in pure stands, which means an inferiority of 1.25 m^3 ha^{-1} yr^{-1} (Fig. 4c). The large productivity differences between Douglas-fir and European beech in pure stands ($PAIV_{Df}$: $PAIV_{Eb}$ 1 : 2.09) increased even in mixed stands. Douglas-fir grew 2.97 times more than European beech (Online Resource 4), which showed that productivity overyielding was determined by the increment of Douglas-fir.

It was shown that the productivity differences of volume increment between the two species reduced in the calculation with the aboveground biomass production. Douglas-fir grew 1.39 times more in pure stands ($PAIW_{Df}$: $PAIW_{Eb}$) and 1.59 times more in mixture ($PAIW_{Df,(Eb)}$: $PAIW_{(Df),Eb}$). The absolute annual growth of aboveground biomass in pure stands was 15.6 Mg ha^{-1} yr^{-1} for Douglas-fir ($PAIW_{Df}$) and 12.4 Mg ha^{-1} yr^{-1} for European beech ($PAIW_{Eb}$). Nevertheless, at 14.73 Mg ha^{-1} yr^{-1} an average overyielding in biomass production of 6% or 0.81 Mg ha^{-1} yr^{-1} ($p < 0.05$) was established in mixed stands (Fig. 4d, see also Online Resource 4). Overyielding was driven in general by Douglas-fir, but we found that higher age also leads to additional overyielding for European beech in mixed stands, while lower ages are connected to underyielding ($p < 0.05$). However, in the average age span of our triplets (60–80 years) there were no differences in increment whether European beech occurs in pure or in mixed stands.

3.3 Dependency of overyielding on age and site conditions

The explanatory variables remaining in the final models are shown in Table 2. The first model (model 1) contains all explanatory variables that were initially chosen. Age and site index were positively correlated with overyielding. The negative interactions between age and site index results from the decreasing influence of age with improving site index. The second model was based on stand description by site characteristics. It shows slightly more variance ($R^2 = 0.34$) than the first model ($R^2 = 0.26$). In the second model, the main explanatory variables are precipitation and temperature. Rising precipitation and temperature improved the mixing effect. Age was incorporated into the model but was not significant. Nevertheless, the AIC (-14.536) indicated that the age gave a benefit to the model compared to model without age (AIC -13.889). In both models it was shown that improving site conditions, in the first one by site index and in the second one by mean annual precipitation and temperature, led to a greater relative mixing effect.

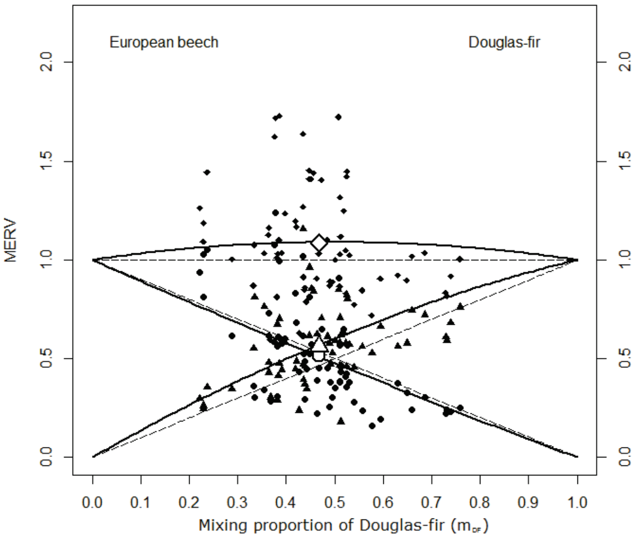


Fig. 5 Cross diagrams according to Harper (1977) and Kelty (1992) displaying the mixing effect on the productivity of Douglas-fir and European beech for volume increment. The left (European beech) and right (Douglas-fir) ordinates in the cross diagrams represent the relative productivity. The abscissa shows the mixing portion of Douglas-fir ($m_{Df,(Be)}$). Broken lines represent the productivity expected for neutral mixing effects on the level of the stand as a whole (horizontal 1.0 line) and on the level of the two contributing species (decreasing with respect to increasing lines). The solid lines show the observed productivity from whole stand (upper bold curve) and species-specific (lower thin curves). Black symbols represent the single observation of the whole stand (diamond), Douglas-fir (triangle) and European beech (circle). The means are marked with a white symbol.

***Abb. 5** Kreuzdiagramm nach Harper (1977) und Kelty (1992) um den Mischungseffekt auf den Zuwachs von Douglasie und Buche darzustellen. Die Y-Achse stellt den Mischungsanteil der Douglasie im Bestand dar, die Y- Achse zeigt die absolute Produktivität. Somit steht die linke Y-Achse für die Produktivität im Buchen-Reinbestand und die rechte Y-Achse für die Produktivität im Douglasien-Reinbestand. Die gestrichelten Linien zeigen die erwartete Produktivität (ohne Mischungseffekt) in den Mischbeständen ausgehend von der Produktivität in den Reinbeständen, für den gesamten Bestand (obere, gestrichelte Linie) und baumarten-spezifisch (gestrichelte Diagonalen). Die durchgehenden Kurven stellen die gemessene Produktivität für den gesamten Mischbestand (dicke, obere Kurve) und baumarten-spezifisch (Kurven unterhalb) dar.*

In addition to the explanation of the relative mixing effect of the stand, models three and four try to explain how Douglas-fir ($MERW_{Df,(Eb)}$) and European beech ($MERW_{(Df),Eb}$) react to environmental conditions in mixed stands. The model of Douglas-fir showed no significant explanatory variables ($R^2 = 0.11$). Only the temperature was incorporated in the model. The European beech model was more insightful ($R^2 = 0.31$). The two explanatory variables of overyielding were base-richness and age. Age also correlated positively as in the whole stands. Base-richness reduced the mixing effect.

Table 2 Influence of the environmental gradients on the relative mixing effect based on aboveground biomass increment for the stand (MERW$_{Df,Eb}$) and separated for Douglas-fir (MERW$_{Df,(Eb)}$) and European beech (MERW$_{(Df),Eb}$).

Tabelle 2 *Einfluss des Umweltgradient auf den Mischungseffekt basierend auf den oberirdische Biomassezuwachs für den Gesamtbestand (MERW$_{Df,Eb}$) und getrennt nach Douglasie (MERW$_{Df,(Eb)}$) und Rotbuche (MERW$_{(Df),Eb}$).*

	Response variable:			
	MERW$_{Df,Eb}$		MERW$_{Df,(Eb)}$	MERW$_{(Df),Eb}$
Model/ Equation	(**1**/8)	(**2**/9)	(**3**/9)	(**4**/9)
SI$_{(Df)}$	**0.083***			
47.2	*(0.033)*			
Age	**0.060***	0.003		**0.006 .**
69.1	*(0.023)*	*(0.002)*		*(0.003)*
SI$_{(Df)}$ * Age	**-0.001***			
47.2 * 69.1	*(0.0005)*			
Precipitation		**0.002***		
939		*(0.001)*		
Temperature		**0.329***	**0.329 .**	
8.4		*(0.143)*	*(0.180)*	
Water supply				
4.3				
Base-richness				**-0.024***
3.0				(0.012)
Constant	**-3.100 .**	**-3.298***	-1.596	**1.356****
	(1.584)	*(1.549)*	*(1.505)*	*0.407*
Observations	66	66	66	66
Log Likelihood	13.501	14.268	-5.572	7.241
Akaike Inf. Crit.	-13.002	-14.536	21.144	-2.482
Bayesian Inf. Crit.	2.326	0.792	32.093	10.656
R^2	0. 26	0.34	0.11	0.31

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Italics and in brackets the std. error

4. Discussion

4.1 Use of triplet experimental setup

The study could determine a significant average overyielding of 6% more biomass increment per year in mixture, but this mixing effect was spread with a standard deviation of 28% (standard error = 3.42). Besides the discussion of how ecological gradients influenced this overyielding, it must be discussed which influence the method has, especially the triplet selection, on the variance of overyielding. Triplet experimental setups have been proven in many studies to be a good method to detect the mixing effect (e.g. Dirnberger and Sterba 2014; Pretzsch et al. 2015). Besides the advantage of the direct comparability of species reaction in pure and mixed stands, triplets always entail the risk of heterogeneity (e.g. age, soil conditions, genetic material) inside the triplet.

The proximity of the plots inside the triplet was a main criterion for selection to minimize any heterogeneity. The soil conditions were controlled visually and by site maps. Yet it could not be excluded that there were differences in base-richness and water supply because of soil microsites.

However, it cannot be assumed that the difference is systematical. Another point was the silvicultural influences. Some studies designed experimental setups which were especially established for the research of pure to mixed stands (Forrester et al. 2004; Amoroso and Turnblom 2006). This has the advantage that they can ensure the same stand history. To answer the question how age influences the mixing effect, it was necessary to cover the whole (or rather a longer) time span of the stand. Such long-term plots do not exist for Douglas-fir and European beech. That is why we used chronosequences to cover the whole rotation time.

Currently, the proportion of Douglas-fir in German forests is very low. Only two percent of German forest is forested with Douglas-fir. It was difficult to find plots which had not been thinned over the last 20 years. Completely unthinned stands would bring the advantage that we ‘only’ had to collect the dead trees and reconstruct their exclusion from the tree collective. In managed forests, this self-thinning mechanism is anticipated by forest management. Therefore, we also recorded the felled trees to reconstruct fully stocked stands over the whole investigation time. The thinning bore the risk of not investigating the tree response at the maximum possible stand density. Nevertheless, the growth–density relationship gives us a buffer because in high-density stands the tree collective is able to compensate for the productivity loss of the felled trees through more productivity of the remaining trees (Assmann 1970). This enabled comparable productivities of stand densities close to the maximum stand density. A comparison of yield table of fully stocked stands under given ages (Bergel 1985; Schober 1987) with our pure plots indicated that the mean SDIs are more or less equal (2% higher SDI in selected plots). Non-experimental plot stands may be a doubtful point of reference. Nevertheless, the use of plots in managed forest is a useful benchmark as it often represents the silvicultural business as usual.

A comparable stand history was another main reason for the necessity of proximity of the stands, so that it could be expected that the same seed material was used which grows under the same forestry management system. In some cases the current study could use plots which were less than 20 meters apart. These plots were much easier to handle than plots which definitely grow on the same soil but lie 1 km apart. It can be said that for further research the proximity of the stands is of particular importance for the selection of the triplets.

4.2 Mixing proportion

As expected, our study showed a great difference of increment between Douglas-fir and European beech. We noted that overyielding is strongly influenced by the approach of the calculation of mixing proportion. The calculation of mixing proportion was handled very differently in other studies. Mixing proportion can be calculated for example by tree number (Forrester et al. 2004; Amoroso and

Turnblom 2006), basal area (Puettmann, K. J. et al. 1992), volume weighted by wood dry mass (Pretzsch et al. 2013) or biomass and leaf area (Dirnberger and Sterba 2014). In this study, different approaches for mixing proportions (tree number, basal area, volume weighted by wood dry mass, adjusted SDI) were calculated and compared. In the choice of plots the mixing proportion was estimated visually with the goal of a 50:50 proportion. It was surprising how volume shifted the mixing proportion in favor of Douglas-fir, whereas the number of trees shifted the mixing proportion in favor of European beech. Dirnberger and Sterba (2014) and Huber et al. (2014) could also show how strongly the different calculation approaches of mixing proportion influenced over- or underyielding. Finally, the adjusted SDI was taken to determine the mixing proportion, as it proved to be close to tree leaf area (Dirnberger and Sterba 2014) and results in a mixture of 0.47: 0.53 (Douglas-fir: E. beech).

Two increment characteristics (volume and aboveground biomass) were compared in this study. It was mentioned that increasing productivity differences between the two species lead to an increasing of influence in the calculation of mixing proportion. The advantage of the aboveground biomass was that the increment ratio between Douglas-fir and European beech decreased. So the similar overyieldings in volume (1.08) and biomass (1.06) suggest that the choice of adjusted SDI was near to reality.

4.3 Structure

The first question was whether there are any structural differences between the two species grown together compared to grown in monocultures. In the present study, the tree height–diameter ratio from mixed to pure stand differed significantly for Douglas-fir and European beech. The tree height–diameter ratio can be used as an indicator of changing competition in even-aged stands (Abetz 1976). The reason is that trees under increased competition allocate more carbon to height than to diameter growth in order to keep their crown in the canopy (Bauhus et al. 2000; Forrester et al. 2004). As a result, a higher h/d ratio indicates greater competition for light. The lower h/d ratio of Douglas-fir and greater h/d ratio of European beech in mixed stands compared to pure stands could be a sign of decreased competition for light for Douglas-fir and increased competition for European beech.

The differences of stem taper in mixed stands compared to pure stands can also be observed by the mixture of Douglas-fir and shade-tolerant western hemlock, where Douglas-fir overtopped the mixed species (Amoroso and Turnblom 2006; Erickson et al. 2009). Both could measure increasing h/d ratios for Douglas-fir and decreasing h/d ratios for the suppressed western hemlock in mixture.

Erickson et al. (2009) found that the individual tree volume of Douglas-fir in mixed stands increased while the tree volume of western hemlock didn't change significantly.

The reverse situation was found by Radosevich et al. (2006) in a simultaneously planted mixture of Douglas-fir with red alder (*Alnus rubra* [Bong.]). Here Douglas-firs in mixed stands were either as small as or smaller in diameter than those trees measured in pure stands. This reverse allocation pattern of trunk growth could be determined because Douglas-fir, at younger ages, will be suppressed by red alder. At older ages, the dominance situation changes in favor of Douglas-fir (Binkley 2003). The influence of the h/d ratio was not analyzed in this study. For European beech mixed with Norway spruce (*Picea abies* (L.) H. Karst.), Dieler and Pretzsch (2009) found that the h/d ratio of European beech increased in mixed stands, whereas the h/d ratio of Norway spruce did not change. The increased taper of European beech in mixture resulted from an increased DBH.

In addition to the dimensional change from pure to mixed stands, our study showed how large the height differences of Douglas-fir and European beech are and how they change along the stand development (Fig. 3). De Wall et al. (1998) also found similar height differences of Douglas-fir and European beech mixed stands along chronosequences. They described that the fast growth of Douglas-fir led to separation in height zones by a dominant Douglas-fir and a suppressed European beech. In the present study the highest Douglas-firs overtopped the highest beeches at the age of 90 years by 11.4 m. Therefore, the predominated Douglas-fir possessed a low lateral restriction of the crowns that increased with age. For the younger stands (around 15 years), the special situation arose that European beech outgrew Douglas-fir. This was also mentioned by Göhre (1958). It could be a critical situation for Douglas-fir because strong shading by European beech could lead to a demixing of Douglas-fir.

4.4 Productivity

We found overyielding in mixed stands in our study. This corresponds with the results of Bartelink (1998). Thomas et al. (2015) concluded that, for the mixture of Douglas-fir and European beech, there is no overyielding. This contrasting result arose because of a different definition of overyielding. Their aboveground biomass increment in mixed stands didn't overtop the most productive pure stand, the Douglas-fir stands. This is defined as transgressive overyielding (Harper 1977). In our definition, with a comparison of the expected mixed stand from the combination of pure stands, Thomas et al. (2015) would have overyielding as well.

Similar to Bartelink (1998) and Thomas et al. (2015), the present study found that mixed stands did not exceed the absolute productivity of Douglas-fir pure stands. But why did the mixing effect not generate average transgressive overyielding? A reason could be the large differences between growth rates of Douglas-fir and European beech. A mixing effect, regardless of how it developed, had to be much stronger to compensate for these differences (Forrester 2014).

The overyielding in the present study resulted in an increased productivity of Douglas-fir. The results of Amoroso and Turnblom (2006) and Erickson et al. (2009) have also shown that overyielding contributed to Douglas-fir. In their studies they compared Douglas-fir in mixed stands with western hemlock. The growth situation in young stands of Douglas-fir and red alder was the reverse. Radosevich et al. (2006) showed that overyielding was driven by red alder. Binkley (2003) showed that this situation can change. With increasing age and height dominance, Douglas-fir contributes more and more to overyielding in mixed stands (Binkley 2003).

For the mixture of European beech there are studies which found overyielding driven by European beech (Pretzsch et al. 2010) or by the admixed species (Pretzsch et al. 2013). It seems to be that interaction between European beech to admixed species can vary.

4.5 Explanation of mixing effect

Light

As mentioned above, the height stratification in Douglas-fir–European beech mixed stands is an important factor. Thereby, a forest type developed where an intermediate shade-tolerant species like Douglas-fir (Barnes and Spurr 1998) exists beside the very shade-tolerant European beech (Ellenberg and Leuschner 2010). Normally the shade-tolerant European beech outcompetes the native, intermediate species over the course of stand development (Thomas et al. 2015; Röhrig et al. 2006). In pure stands, Douglas-firs are surrounded in the crown stratum by individuals of the same species in the same height zones. An interspecific competition situation for light arises (‘interference’), which could be seen in higher h/d ratios. In mixed stands, we found a physical exclusion of individual Douglas-firs which outgrew the closed canopy layer of European beech. Douglas-fir with its high light-saturated net photosynthetic rates (Lewis et al. 2000) could efficiently use this improved light access. European beech with a lower light compensation point (Ellenberg and Leuschner 2010) can still exist in the lower height zones. Overall, it seems to be that the two species differentiate each other by niches of different radiation intensity. It may result in maximum light interception of the available light at the site. Menalled et al. (1998) could provide evidence that the height stratifications of Douglas-fir and suppressed western hemlock resulted in sufficient radiation interception in the upper canopy. This allows higher productivity of the shade-intolerant Douglas-fir and yet adequate transmission of radiation to the shade-tolerant western hemlock. Thomas et al. (2015) measured the relative fraction of sun leaves of European beech mixed with Douglas-fir. They also concluded a more efficient usage of incoming light. Vandermeer (1989) called this interaction complementarity.

Soil

In the present study, it was asked how site quality influenced the mixture. Due to the fact that the belowground situation was not directly measured, the assumptions about the belowground competition in the present study were only speculative. Improving site fertility was detected in both models as a driver of increasing overyielding. This was in line with findings of a global biodiversity study based on forest inventory data (Liang et al. 2016). In the first model of the study at hand (Eq. 8), site fertility was determined by the site index. In the second model (Eq. 9), increasing precipitation and temperature drove overyielding. Case and Peterson (2005) found that precipitation and temperature (model 2) mainly drove the growth variation of Douglas-fir. Therefore, we interpreted the site index of Douglas-fir as a proxy for precipitation and temperature. The improved site conditions probably led to increased height differences, which reinforced the complementary effect between Douglas-fir and European beech.

Studies on Douglas-fir–red alder (Binkley and Greene 1983; Binkley 2003) and European beech–Norway spruce (Pretzsch et al. 2010) mixtures found that under poor site conditions, the mixing effect declined. These studies assumed that the mixing effect arose because one species, the ‘facilitator’, improved soil conditions for the other species. In the case of Douglas-fir mixed stands, it is well-researched that the presence of nitrogen-fixing red alder on nitrogen-poor sites improved soil conditions and ecosystem productivity (Tarrant and Miller 1963; Binkley and Greene 1983; Binkley 2003). Tree litter in mixed stands of Douglas-fir and red alder decomposed faster than in pure stands (Fyles and Fyles 1993). In the case of European beech–Norway spruce mixtures, Norway spruce benefited from the improved decomposition conditions and turnover of the mixed litter (Berger und Berger 2014). The influence of litter and its decomposition on mixtures of Douglas-fir and European beech has not been researched yet. Whether this positive reaction would also occur for Douglas-fir–European beech mixtures is doubtful. This is because Douglas-fir already has intermediate decomposable litter (Edmonds 1980; Augusto et al. 2002).

Another facilitative effect in Douglas-fir–European beech mixtures could be that the soil profile has been ‘opened’ for European beech by decreasing Douglas-fir root density in older ages (Hendriks and Bianchi 1995). However, this rooting strategy needs much more replication to be accepted (Rothe and Binkley 2001). Besides this facilitation between the two species, Hendriks and Bianchi (1995) showed that root density in deeper soil strata was higher in mixed than in pure stands. They conclude that nutrient and water uptake is more efficient in mixed stands. Therefore, complementary effects are not only present in the canopy, but in the soil as well.

Our analyses of the influence of the ecological parameters on the productivity of European beech showed a significant increase in productivity with reduced base-richness. Thomas et al. (2015) found a competitive superiority of Douglas-fir over European beech at root level. Their site fertility is comparable to our average site fertility. It might be that European beech reinforces competitive strength in root stratum on base-poor sites. Hendriks and Bianchi (1995) confirmed the importance of the belowground competition in addition to the aboveground competition for Douglas-fir–European beech mixtures. Their study showed the shift of competition strength between the two species only along an age gradient. The influence of changing site conditions on belowground competition is still unknown. Pretzsch et al. (2010) already stated that along a site gradient competitive strength can shift from one species to the other.

Nevertheless, the present study assumed that overyielding was less influenced by declined base-richness for European beech because Douglas-fir was mainly responsible for productivity.

The limiting resource for our study seems to be light, rather than soil. Forrester (2014) concluded that the major growth-limiting resource determines the mixing effect. Other studies which showed that different factors, such as poorer sites (e.g. Pretzsch et al. 2010; Toïgo et al. 2014), increased overyielding did not contradict our results. They only show the influence of the present factors under given locations and tree species mixtures.

The selected study sites represent average and best climate conditions (Table 1) in comparison to climate conditions in Germany (Deutscher Wetterdienst 2015). This could be seen by the site indices of top height as well (Online Resource 4). In the study there was a lack of poorer, arid sites to embrace a complete ecological gradient for the whole of Central Europe. A facilitative effect might have appeared more under poor site conditions. The present study assumed that along a greater ecological site gradient, positive interactions in mixed stands are rather quadratic than linear, as Bertness and Callaway (1994) predicted.

Age

Our findings show that the age had a relevant influence on overyielding. This was shown by the steep rise of age in models one and two (Table 2). Although not all explanatory variables were significant, like age in model 2, the AIC indicated that their presence in combined effect with the other variables was important. In addition, all parameters (DBH and increment) which included an interaction of age and mixture showed that positive mixing effects arise only in older stands (Online Resource 5).

The present study and also de Wall et al. (1998) came to the conclusion that the increasing age of Douglas-fir–European beech stands leads to a vertical separation of the species in the canopy zone. As mentioned above, we suspected that structuring leads to overyielding. So higher stand ages could have a positive effect on productivity. Other studies also concluded that overyielding increases with increasing age (Zhang et al. 2012). Independent of the reason for overyielding, it might be that the positive mixing effect takes time to appear. In our study the break-even point of mixture seems to be 60 years.

5. Conclusion

The mixture of Douglas-fir and European beech emerges as a stable mixture type, which does not lead to the loss of one of the species without silvicultural intervention. That is noteworthy because it is a species composition of a native with an introduced species. This mixture creates considerable height stratification, which is unusual for native Central European forest types. The accrued overyielding in mixture was determined by the age dynamics of the stands. Failing to consider the age dynamics could lead to a miscalculation of the mixing effect. Further mixture research should consider the influence of age.

The gradient of the site conditions shows that overyielding is particularly expected in favorable locations. Further research should extend the gradient to extreme sites. That would enable a more comprehensive site conclusion about the whole site spectrum.

Douglas-fir–European beech mixed stands can be recommended for forest management. It is an option that combines the demand for mixed stands with the need for coniferous wood production. The benefits that come with increasing age of the mixture should be brought into the focus of silviculture.

References

Abetz P (1976) Beiträge zum Baumwachstum. Der h/d-Wert - mehr als ein Schlankheitsgrad. Forst- u. Holzwirt 31:389–393

Amoroso MM, Turnblom EC (2006) Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Can. J. For. Res. 36(6):1484–1496. doi: 10.1139/X06-042

Assmann E (1970) The principles of forest yield study. Pergamon, Oxford, New York

Augusto L, Ranger J, Binkley D, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59(3):233–253. doi: 10.1051/forest:2002020

Barnes BV, Spurr SH (1998) Forest ecology, 4th ed. Wiley, New York

Bartelink HH (1998) Simulation of growth and competition in mixed stands of Douglas-fir and beech. Landbouwuniversiteit Wageningen, Wageningen

Barton K (2015) MuMIn: Multi-model inference

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: Linear mixed-effects models using Eigen and S4

Bauhus J, Khanna PK, Menden N (2000) Aboveground and belowground interactions in mixed plantations of Eucalyptus globulus and Acacia mearnsii. Can. J. For. Res. 30(12):1886–1894. doi: 10.1139/x00-141

Bayerische Landesanstalt für Wald und Forstwirtschaft (2013) Bayerisches Standortinformationssystem (BaSIS): Basenausstattung; Wasserhaushalt

Bergel D (1985) Douglasien-Ertragstafel für Nordwestdeutschland. Nieders. Forstl. Versuchsanst., Abt. Waldwachstum, Göttingen

Berger TW, Berger P (2014) Does mixing of beech (Fagus sylvatica) and spruce (Picea abies) litter hasten decomposition? Plant and Soil 377(1-2):217–234. doi: 10.1007/s11104-013-2001-9

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol. Evol. 9(5):191–193. doi: 10.1016/0169-5347(94)90088-4

Biber P (2013) Kontinuität durch Flexibilität – Standardisierte Datenauswertung im Rahmen eines waldwachstumskundlichen Informationssystems. Allg. Forst Jagdztg. 184(7/8):167–177

Binkley D (2003) Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Can. J. For. Res. 33(11):2274–2279. doi: 10.1139/x03-158

Binkley D, Greene S (1983) Production in mixtures of conifers and red alder: the importance of site fertility and stand age. In: Ballard R, Gessel. S (eds) International Union of Forestry Research Organizations Symposium on Forest Site and Continuous Productivity, pp 112–117

Burnham KP, Anderson DR (1998) Model selection and inference: A practical information-theoretic approach. Springer, New York

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78(7):1958–1965. doi: 10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2

Cavard X, Macdonald SE, Bergeron Y, Chen HYH (2011) Importance of mixedwoods for biodiversity conservation: Evidence for understory plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. Environ. Rev. 19:142–161. doi: 10.1139/a11-004

de Wall K, Dreher G, Spellman H, Pretzsch H (1998) Struktur und Dynamik von Buchen-Douglasien-Mischbeständen. forstarchiv 69(5):179–191

del Río M, Pretzsch H, Alberdi I, Bielak K, Bravo F, Brunner A, Condés S, Ducey MJ, Fonseca T, Lüpke N von, Pach M, Peric S, Perot T, Souidi Z, Spathelf P, Sterba H, Tijardovic M, Tomé M, Vallet P, Bravo-Oviedo A (2016) Characterization of the structure, dynamics, and productivity of mixed-species stands: Review and perspectives. Eur. J. For. Res. doi: 10.1007/s10342-015-0927-6

Deutscher Wetterdienst (2015) Grids germany-monthly: mean temperature and precipitation. ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/monthly/. Accessed 10 July 2015

Dieler J, Pretzsch H (2009) Baummorphologie von Fichte und Buche im Rein- und Mischbestand. In: DVFFA (ed) Sektion Ertragskunde, Jahrestagung 2009

Dirnberger GF, Sterba H (2014) A comparison of different methods to estimate species proportions by area in mixed stands. Forest Syst. 23(3):534. doi: 10.5424/fs/2014233-06027

Edmonds RL (1980) Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver fir ecosystems in western Washington. Can. J. For. Res. 10(3):327–337. doi: 10.1139/x80-056

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht: 203 Tabellen, 6. Aufl. UTB, vol 8104. Ulmer, Stuttgart

Erickson HE, Harrington CA, Marshall DD (2009) Tree growth at stand and individual scales in two dual-species mixture experiments in southern Washington State, USA. Can. J. For. Res. 39(6):1119–1132. doi: 10.1139/X09-040

Felton A, Lindbladh M, Brunet J, Fritz Ö (2010) Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. For. Ecol. Manage. 260(6):939–947. doi: 10.1016/j.foreco.2010.06.011

Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. For. Ecol. Manage. 312:282–292. doi: 10.1016/j.foreco.2013.10.003

Forrester DI (2015) Transpiration and water-use efficiency in mixed-species forests versus monocultures: effects of tree size, stand density and season. Tree Physiol. 35(3):289–304. doi: 10.1093/treephys/tpv011

Forrester DI, Albrecht AT (2014) Light absorption and light-use efficiency in mixtures of Abies alba and Picea abies along a productivity gradient. For. Ecol. Manage. 328:94–102. doi: 10.1016/j.foreco.2014.05.026

Forrester DI, Bauhus J, Khanna PK (2004) Growth dynamics in a mixed-species plantation of Eucalyptus globulus and Acacia mearnsii. Synthesis of the physiological, environmental, genetic and silvicultural determinants of the growth and productivity of eucalypts in plantations For. Ecol. Manage. 193(1–2):81–95. doi: 10.1016/j.foreco.2004.01.024

Forrester DI, Kohnle U, Albrecht AT, Bauhus J (2013) Complementarity in mixed-species stands of Abies alba and Picea abies varies with climate, site quality and stand density. For. Ecol. Manage. 304:233–242. doi: 10.1016/j.foreco.2013.04.038

Fyles JW, Fyles IH (1993) Interaction of Douglas-fir with red alder and salal foliage litter during decomposition. Can. J. For. Res. 23(3):358–361. doi: 10.1139/x93-052

Gauer J, Kroiher F (eds) (2012) Waldokologische Naturraume Deutschlands: Forstliche Wuchsgebiete und Wuchsbezirke – Digitale Topographische Grundlagen – Neubearbeitung Stand 2011, Sonderheft Nr. 359. Landbauforschung vTI Agriculture and Forestry Research

Göhre K (1958) Die Douglasie und ihr Holz. Akademie Verlag, Berlin

Harper JL (1977) Population biology of plants. Academic Press, London

Hendriks CMA, Bianchi F (1995) Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. Netherlands Journal of Agricultural Science 1995(43):321–331

Hermann RK (2007) Pseudotsuga menziesii. In: Lang UM, Roloff A, Schütt P, Stimm B, Weisgerber H (eds) Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie /begründet von Peter Schütt. Andreas Roloff; Horst Weisgerber; Ulla M. Lang; Bernd Stimm. Wiley-VCH, Weinheim, pp 1–18

Huber MO, Sterba H, Bernhard L (2014) Site conditions and definition of compositional proportion modify mixture effects in Picea abies – Abies alba stands. Can. J. For. Res. 44(10):1281–1291. doi: 10.1139/cjfr-2014-0188

Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. Ecol. Lett. 10(9):835–848. doi: 10.1111/j.1461-0248.2007.01073.x

Johann K (1993) DESER-Norm 1993. Normen der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten zur Aufbereitung von waldwachstumskundlichen Dauerversuchen. Proc Dt Verb Forstl Forschungsanst, Sek Ertragskd, in Unterreichenbach-Kapfenhardt:96–104

Kelty M (1992) Comparative productivity of monocultures and mixed-species stands. In: Kelty M, Larson B, Oliver C (eds) The Ecology and Silviculture of Mixed-Species Forests, vol 40. Springer Netherlands, pp 125-141

Kleinschmit J, Bastien JC (1992) IUFRO’s role in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco.) tree improvement. Silvae genetica 41(3):161–173

Knoerzer D, Reif A (1996) Die Naturverjüngung der Douglasie im Bereich des Stadtwaldes von Freiburg. AFZ-DerWald(20):1117–1120

Kölling C (2007) Klimahüllen für 27 Waldbaumarten. AFZ-DerWald 23:1242–1245

Krüger I (2013) Potential of above- and belowground coarse woody debris as a carbon sink in managed and unmanaged forests. dissertation, Universität Bayreuth

Kuznetsova A, Brockhoff B, Christensen HB (2015) lmerTest: Tests in Linear Mixed Effects Models

Landesforst Rheinland-Pfalz (2014) Forsteinrichtung Rheinland-Pfalz: Basenaustattung, Wasserhaushalt

Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, McGuire AD, Bozzato F, Pretzsch H, de-Miguel S, Paquette A, Hérault B, Scherer-Lorenzen M, Barrett CB, Glick HB, Hengeveld GM, Nabuurs GJ, Pfautsch S, Viana H, Vibrans AC, Ammer C, Schall P, Verbyla D, Tchebakova N, Fischer M, Watson JV, Chen HYH, Lei X, Schelhaas M-J, Lu H, Gianelle D, Parfenova EI, Salas C, Lee E, Lee B, Kim HS, Bruelheide H, Coomes DA, Piotto D, Sunderland T, Schmid B, Gourlet-Fleury S, Sonké B, Tavani R, Zhu J, Brandl S, Vayreda J, Kitahara F, Searle EB, Neldner VJ, Ngugi MR, Baraloto B, Frizzera L, Bałazy R, Oleksyn J, Zawiła-Niedźwiecki T, Bouriaud O, Bussotti F, Finér L, Jaroszewicz B, Jucker T, Valladares V, Jagodzinski AM, Peri PL, Gonmadje C, Marthy W, O'Brien T, Martin EH, Marshall AR, Rovero F, Bitariho R, Niklaus PA, Alvarez-Loayza P, Chamuya N, Valencia R, Mortier F, Wortel V, Engone-Obiang NL, Ferreira LV, Odeke DE, Vasquez RM, Lewis SL, Reich PB (2016) Positive Biodiversity–Productivity Relationship Predominant in Global Forests. Science. ISSN 0036-8075 (In Press)

Mantau U, Steierer F, Hetsch S, Prins K (eds) (2008) Wood resources availability and demands - implications of renewable energy policies: A first glance at 2005, 2010 and 2020 in European countries.

Meyer P (2011) Naturschutzfachliche Bewertung der Douglasie. forstarchiv 82:157–158

Montagnini F, González E, Porras C, Rheingans R (1995) Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. The Commonwealth Forestry Review:306–314

Morin X, Fahse L, Scherer-Lorenzen M, Bugmann H (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol. Lett. 14(12):1211–1219. doi: 10.1111/j.1461-0248.2011.01691.x

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4(2):133–142. doi: 10.1111/j.2041-210x.2012.00261.x

Otto H (1987) Skizze eines optimalen Douglasienanbaues in Norddeutschland. Forst- u. Holzwirt 42:515–522

Piotto D (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. For. Ecol. Manage.255(3-4):781–786. doi: 10.1016/j.foreco.2007.09.065

Pretzsch H, Bielak K, Block J, Bruchwald A, Dieler J, Ehrhart H, Kohnle U, Nagel J, Spellmann H, Zasada M, Zingg A (2013) 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. Forest. Res. 132(2):263–280. doi: 10.1007/s10342-012-0673-y

Pretzsch H, Block J, Dieler J, Dong PH, Kohnle U, Nagel J, Spellmann H, Zingg A (2010) Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. For. Sci. 67(7):712. doi: 10.1051/forest/2010037

Pretzsch H, Block J, Dieler J, Gauer J, Göttlein A, Moshammer R, Schuck J, Weis W (2014) Nährstoffentzüge durch die Holz- und Biomassenutzung in Wäldern. Teil 1: Schätz-funktionen für Biomasse und Nährelemente und ihre Anwendung in Szenariorechnungen. Allg. Forst Jagdztg. 185(11/12):261–285

Pretzsch H, del Río M, Ammer C, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Dirnberger G, Drössler L, Fabrika M, Forrester DI, Godvod K, Heym M, Hurt V, Kurylyak V, Löf M, Lombardi F, Matović B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Schütze G, Schweig J, Skrzyszewski J, Sramek V, Sterba H, Stojanović D, Svoboda M, Vanhellemont M, Verheyen K, Wellhausen K, Zlatanov T, Bravo-Oviedo A (2015) Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe. Eur. J. Forest. Res. doi: 10.1007/s10342-015-0900-4

Puettmann, K. J., Hibbs, D. E., Hann, D. W. (1992) The Dynamics of Mixed Stands of Alnus Rubra and Pseudotsuga Menziesii: Extension of Size--Density Analysis to Species Mixture. J. Ecol. 80(3):449–458. doi: 10.2307/2260690

R Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Radosevich SR, Hibbs DE, Ghersa CM (2006) Effects of species mixtures on growth and stand development of Douglas-fir and red alder. Can. J. For. Res. 36(3):768–782. doi: 10.1139/x05-280

Röhrig E, Bartsch N, Lüpke B von, Dengler A (2006) Waldbau auf ökologischer Grundlage: 91 Tabellen, 7. Aufl., vol 8310. UTB, Stuttgart

Rothe A, Binkley D (2001) Nutritional interactions in mixed species forests: a synthesis. Can. J. For. Res. 31(11):1855–1870. doi: 10.1139/x01-120

Schober R (1987) Ertragstafeln wichtiger Baumarten bei verschiedener Durchforstung, 3. Aufl. Sauerländer, Frankfurt am Main

Sterba H, Del Rio M, Brunner A, Condes S (2014) Effect of species proportion definition on the evaluation of growth in pure vs. mixed stands. Forest Syst. 23(3):547. doi: 10.5424/fs/2014233-06051

Tarrant RF, Miller RE (1963) Accumulation of Organic Matter and Soil Nitrogen Beneath A Plantation of Red Alder and Douglas-Fir1. Soil Sci. Soc. Am. J. 27(2):231. doi: 10.2136/sssaj1963.03615995002700020041x

Thomas FM, Bögelein R, Werner W (2015) Interaction between Douglas fir and European beech: Investigations in pure and mixed stands. forstarchiv 86(4):83–91

Thünen-Institut (2012) Dritte Bundeswaldinventur - Ergebnisdatenbank: Veränderung der Waldfläche [ha] nach Bestockungstyp und Beimischung. 69Z1PN_L321mf_0212_L322c / 2015-2-23 14:30:40.110. https://bwi.info. Accessed 9 July 2015

Toïgo M, Vallet P, Perot T, Bontemps J, Piedallu C, Courbaud B (2014) Over-yielding in mixed forests decreases with site productivity. J Ecol. 103(2): 502-512. doi: 10.1111/1365-2745.12353

Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. J. Ecol. 100(3):742–749. doi: 10.1111/j.1365-2745.2011.01944.x

Online Resource 1 Mean values of the stands of the 18 triplets at the 7 experimental locations, height and diameter at breast height were taken from quadratic mean tree. Periodic mean annual volume increment and growing stock based on the last five years before measurement. The species-specific PAIV and the grow stock scaled up to a hectare by mixing proportion.

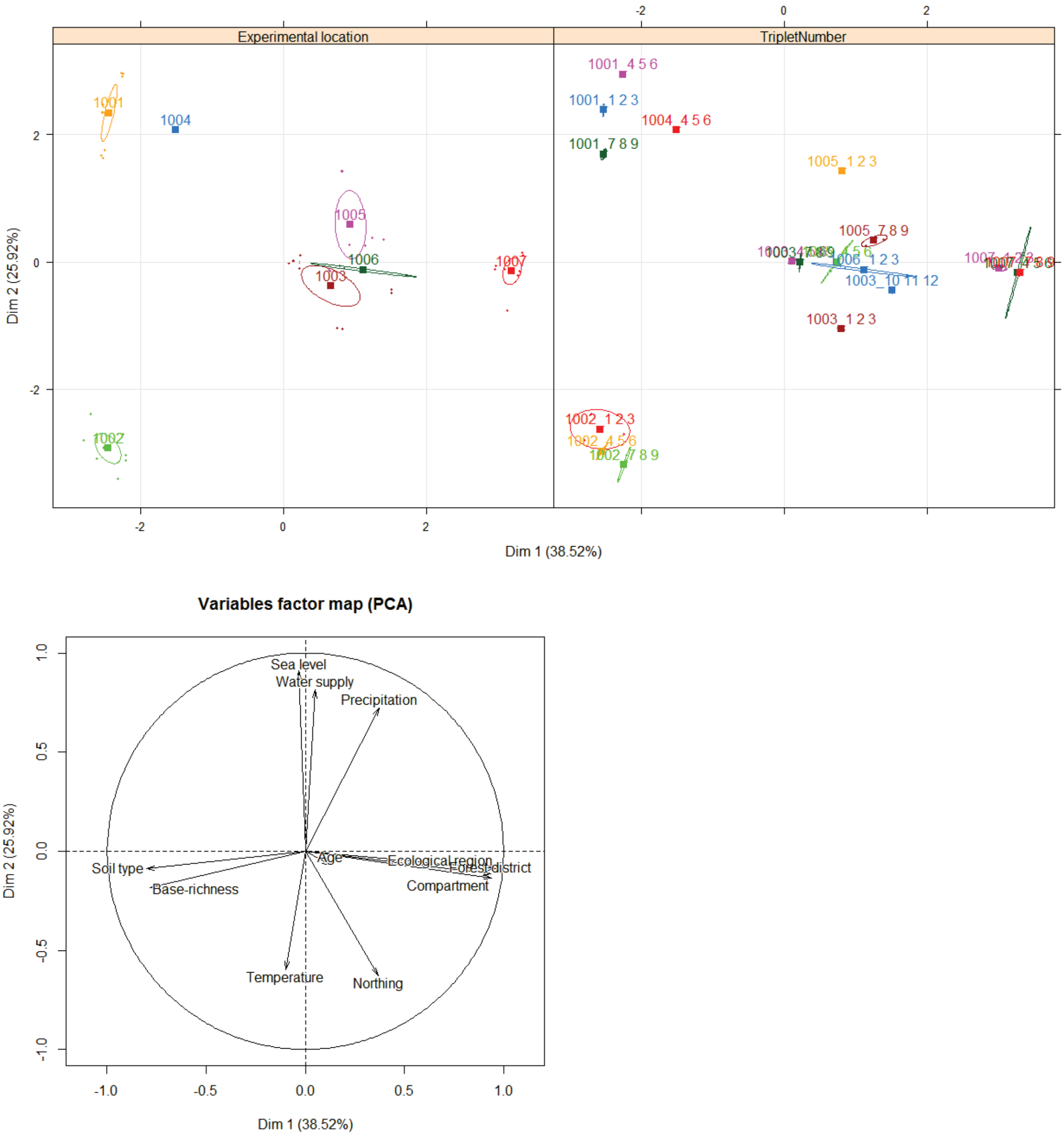
Experimental location	Triplet	Sampling year	Height in m				DBH in cm			
			Douglas-fir		European beech		Douglas-fir		European beech	
			pure	mixed	pure	mixed	pure	mixed	pure	mixed
Walkertshofen	1 2 3	2013	23.8	22.4	18.9	16.3	26.2	24.7	13.9	13.5
	4 5 6	2013	32.3	35.7	22.3	22.0	45.1	53.1	23.3	19.3
	7 8 9	2013	44.9	39.4	28.1	27.7	74.0	62.0	38.3	25.8
Würzburg	1 2 3	2013	20.3	16.5	14.3	16.9	18.2	14.0	8.7	10.7
	4 5 6	2013	27.3	29.9	22.3	21.2	28.3	36.2	15.2	17.0
	7 8 9	2013	43.4	46.8	39.3	35.2	58.0	75.4	53.6	36.2
Spessart	1 2 3	2013	29.2	27.3	19.8	17.3	32.9	34.2	15.4	15.1
	10 11 12	2013	49.2	44.7	35.6	35.8	63.9	80.8	42.4	36.4
	4 5 6	2013	41.2	38.2	31.8	29.9	64.1	63.1	35.6	29.7
	7 8 9	2013	41.8	43.5	29.1	30.2	55.2	78.6	30.9	29.9
Eberberger Forst	4 5 6	2013	26.2	25.0	22.6	23.2	27.6	29.9	21.3	15.6
Daun	1 2 3	2014	31.4	31.2	17.7	18.0	36.7	45.7	16.4	15.2
	4 5 6	2014	36.4	38.7	24.8	21.5	46.4	73.7	28.1	22.1
	7 8 9	2014	49.0	40.9	29.9	22.0	70.3	83.2	37.0	23.2
Hirschwald	1 2 3	2013	24.9	24.7	19.0	19.7	26.6	30.2	17.9	17.2
Pfälzerwald	1 2 3	2012	13.0	10.0	11.4	9.0	11.5	9.1	9.0	7.8
	4 5 6	2012	29.8	24.1	17.7	21.0	26.4	23.0	16.6	17.9
	7 8 9	2012	43.4	46.2	33.1	32.9	62.5	69.8	38.2	33.6
Mean		2013	33.8	32.5	24.3	23.3	43.0	49.3	25.7	21.5
Species-specific mean			33.1		23.8		46.1		23.6	

Experimental location	Triplet	Sampling year	Age					Stand density				
			Douglas-fir		European beech		Mixed stand	Douglas-fir		European beech		Mixed stand
			pure	mixed	pure	mixed		pure	mixed	pure	mixed	
Walkertshofen	1 2 3	2013	30	30	36	36	33	821	739	1115	451	622
	4 5 6	2013	56	56	64	64	61	1147	1280	713	786	1043
	7 8 9	2013	89	82	82	82	82	1585	1142	580	702	1036
Würzburg	1 2 3	2013	29	29	29	29	29	1065	739	610	452	562
	4 5 6	2013	42	46	54	54	51	763	900	1061	550	667
	7 8 9	2013	98	98	102	102	100	961	861	586	525	697
Spessart	1 2 3	2013	40	40	42	42	41	1079	1158	1243	708	951
	10 11 12	2013	99	99	103	103	103	978	1208	492	736	918
	4 5 6	2013	82	84	84	84	84	825	1053	620	642	773
	7 8 9	2013	91	91	94	94	93	1704	993	549	627	711
Eberberger Forst	4 5 6	2013	54	48	51	51	50	921	1075	627	662	811
Daun	1 2 3	2014	43	43	45	45	44	1116	1060	891	649	840
	4 5 6	2014	70	78	89	82	80	703	788	717	482	625
	7 8 9	2014	125	110	125	120	115	1407	1082	568	664	842
Hirschwald	1 2 3	2013	37	37	37	37	36	981	938	690	574	802
Pfälzerwald	1 2 3	2012	32	32	28	28	28	617	714	244	437	581
	4 5 6	2012	47	43	57	52	47	1203	1753	1143	1070	1343
	7 8 9	2012	88	91	90	90	90	703	919	594	561	697
Mean		2013	64	63	67	66	65	1032	1022	725	627	807
Species-specific mean			64		67			1027		676		

Experimental location	Triplet	Sampling year	PAIV m^3 ha^{-1} yr^{-1}					Growing stock m^3 ha^{-1}				
			Douglas-fir		European beech		Mixed stand	Douglas-fir		European beech		Mixed stand
			pure	mixed	pure	mixed		pure	mixed	pure	mixed	
Walkertshofen	1 2 3	2013	20.5	22.8	15.0	7.2	16.5	435.5	362.4	386.1	145.9	274.6
	4 5 6	2013	39.1	61.6	11.7	10.4	37.1	969.3	1242.1	415.3	408.0	842.8
	7 8 9	2013	39.2	39.2	11.4	11.7	32.6	2001.0	1270.0	506.6	507.4	1085.9
Würzburg	1 2 3	2013	18.6	14.8	16.9	7.7	10.4	424.2	209.0	120.6	117.1	152.3
	4 5 6	2013	16.1	39.0	17.5	8.0	18.4	482.2	665.8	491.7	245.5	385.9
	7 8 9	2013	22.9	27.5	13.5	13.0	20.4	1171.8	1176.8	812.5	576.6	884.3
Spessart	1 2 3	2013	45.0	37.8	21.4	12.9	26.3	755.1	769.5	509.8	245.3	528.6
	10 11 12	2013	26.5	48.2	13.4	21.7	31.9	1351.0	1592.4	566.9	821.6	1119.3
	4 5 6	2013	19.3	26.0	15.8	17.0	19.9	953.5	1139.7	589.4	548.9	737.2
	7 8 9	2013	34.4	39.0	11.9	12.6	18.6	1955.3	1263.4	453.3	534.9	701.8
Eberberger Forst	4 5 6	2013	27.6	36.3	19.2	18.2	24.7	542.6	606.8	331.6	311.6	418.0
Daun	1 2 3	2014	31.3	38.5	9.0	6.4	21.3	872.7	870.6	331.7	228.7	526.6
	4 5 6	2014	25.1	28.2	11.2	9.5	18.2	683.0	884.1	505.1	255.3	549.3
	7 8 9	2014	27.3	15.1	12.0	9.1	11.6	2005.1	1309.2	538.9	381.6	777.4
Hirschwald	1 2 3	2013	28.6	33.9	20.3	13.2	26.2	539.0	536.5	277.7	230.5	422.4
Pfälzerwald	1 2 3	2012	12.6	15.2	5.1	6.9	11.2	127.6	93.9	38.2	48.9	72.3
	4 5 6	2012	31.7	67.4	14.3	21.6	39.9	822.3	948.7	430.4	503.8	681.4
	7 8 9	2012	15.1	33.5	11.5	10.0	18.9	635.2	1224.6	612.7	541.8	800.2
Mean		2013	26.7	34.7	13.9	12.0	22.4	929.2	898.1	439.9	369.6	608.9
Species-specific mean			30.7		13.0			913.7		404.8		

Online resource 2 Principal component analysis (PCA) of site conditions for the 54 plots (colored dots). The circles indicate correlation and contribution of site conditions for the first two axes. 95% confidence intervals for average coordinates of experimental locations (top left) and the single triplets (top right) was depicted by ellipses. On the one hand the PCA is intended to show the equality of the whole conditions inside an experimental location and a triplet. On the other hand it should show how experimental location and the triplets differ from each other. The variables factor map (bottom) shows the factors which included into the PCA and show their orientation.

The number codes for the experimental location are: Walkertshofen – 1001; Würzburg – 1002; Spessart – 1003, Ebersberger Forst – 1004; Daun – 1005; Hirschwald – 1006; Pfälzerwald – 1007.



Online Resource 3 Overview about the measured and cored trees, separated by Douglas-fir, European beech and other tree species. Depending if needle or leaf tree, the other trees species added to Douglas-fir or European beech in calculation.

Experimental location	Triplet	Plot	Number of trees				Number of cored trees			
			Total	Douglas-fir	E. beech	others	Total	Douglas-fir	E. beech	others
Walkertshofen	1 2 3	1	20	20	0	0	19	19	0	0
		2	26	0	26	0	26	0	26	0
		3	47	23	21	3	40	22	17	1
	4 5 6	4	21	20	0	1	21	20	0	1
		5	37	0	37	0	37	0	37	0
		6	64	16	47	1	32	14	18	0
	7 8 9	7	30	18	1	11	18	18	0	0
		8	20	0	20	0	20	0	20	0
		9	36	17	14	5	35	17	13	5
Würzburg	1 2 3	1	22	22	0	0	22	22	0	0
		2	20	0	20	0	19	0	19	0
		3	41	16	23	2	40	16	23	1
	4 5 6	4	24	24	0	0	24	24	0	0
		5	38	0	38	0	19	0	19	0
		6	92	18	74	0	47	17	30	0
	7 8 9	7	17	17	0	0	17	17	0	0
		8	15	0	15	0	14	0	14	0
		9	26	9	17	0	26	9	17	0
Spessart	1 2 3	1	20	20	0	0	19	19	0	0
		2	51	0	51	0	24	0	24	0
		3	50	17	33	0	43	16	27	0
	4 5 6	4	12	12	0	0	8	8	0	0
		5	17	0	16	1	17	0	16	1
		6	27	5	21	1	26	5	20	1
	7 8 9	7	15	14	0	1	11	10	0	1
		8	26	0	25	1	17	0	17	0
		9	57	5	51	1	24	5	19	0
	10 11 12	10	13	13	0	0	13	13	0	0
		11	19	0	19	0	17	0	17	0
		12	18	4	14	0	15	4	11	0
Eberberger Forst	4 5 6	4	52	52	0	0	18	18	0	0
		5	67	0	66	1	21	0	21	0
		6	96	27	65	4	32	14	18	0
Daun	1 2 3	1	28	28	0	0	28	28	0	0
		2	41	0	41	0	21	0	21	0
		3	79	15	64	0	39	14	25	0
	4 5 6	4	16	16	0	0	16	16	0	0
		5	25	0	25	0	25	0	25	0
		6	71	12	59	0	28	5	23	0
	7 8 9	7	12	12	0	0	12	12	0	0
		8	19	0	19	0	18	0	18	0
		9	37	5	32	0	20	4	16	0
Hirschwald	1 2 3	1	25	25	0	0	25	25	0	0
		2	33	0	33	0	22	0	22	0
		3	60	32	28	0	31	23	8	0
Pfälzerwald	1 2 3	1	22	22	0	0	22	22	0	0
		2	22	0	22	0	20	0	20	0
		3	43	17	18	8	33	15	15	3
	4 5 6	4	27	27	0	0	20	20	0	0
		5	49	0	49	0	23	0	23	0
		6	48	18	29	1	34	16	18	0
	7 8 9	7	97	97	0	0	20	20	0	0
		8	29	0	29	0	20	0	20	0
		9	68	16	52	0	35	15	20	0
Total	**18**	**54**	**1987**	**731**	**1214**	**42**	**1293**	**562**	**717**	**14**

Online Resource 4 Descriptive statistics for the pure stands of Douglas-fir (Df) and European beech (Eb), the mixed stands and the mixing effects on growth. Listed are stand age of pure stands (Age_{Df}, Age_{Eb}), dominant height of pure stands at age 100 (ho), mixing proportion of Douglas-fir and beech (m_{Df},m_{Eb}); periodic mean annual volume increment (PAIV) , mixing effect of the volume increment absolute (MEAV) and relative(MERW); the same for the periodic mean annual aboveground biomass increment (PAIW).

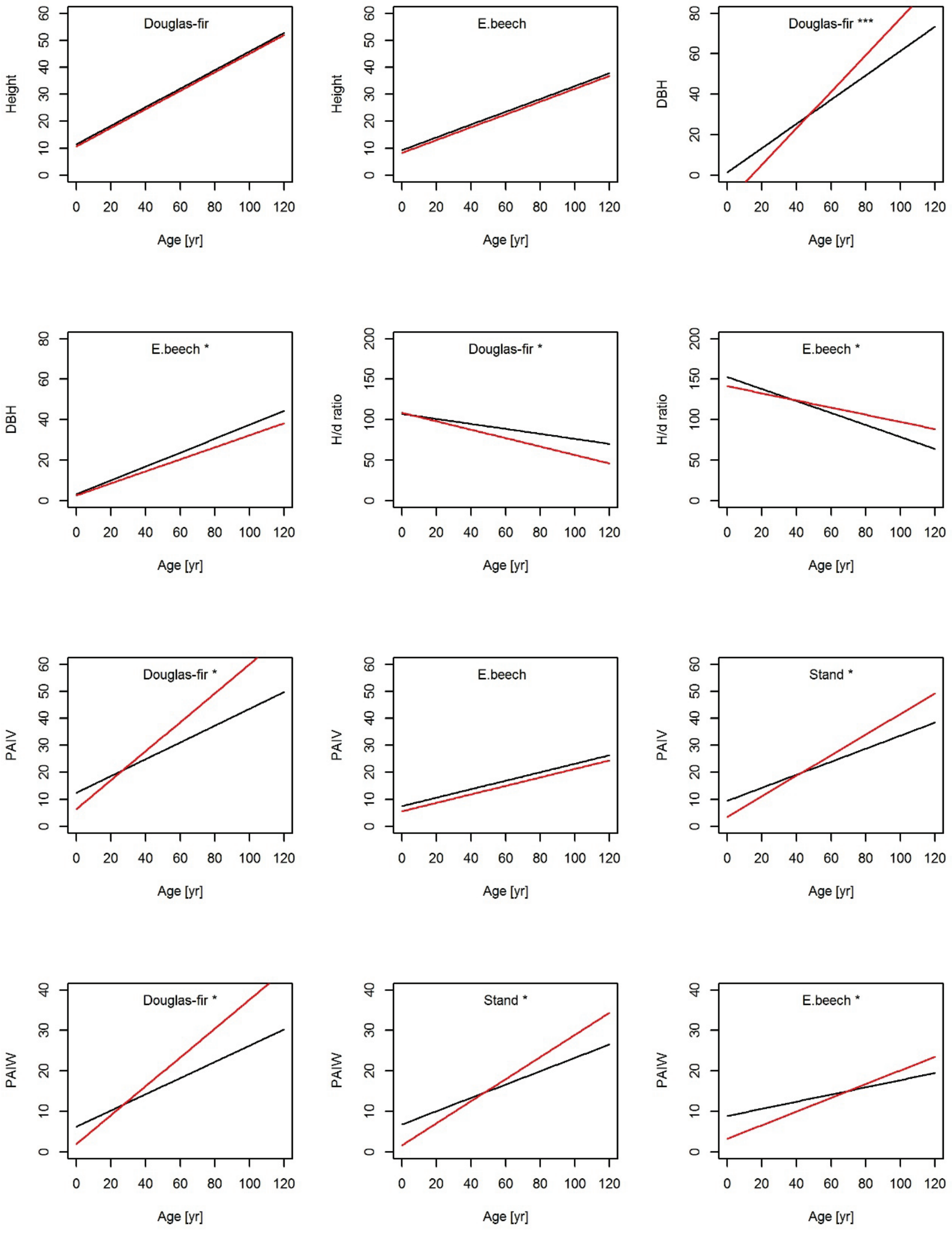
Variable	Unit	Sample size n	Mean	Standard deviation	Minimum	Maximum
Age_{Df}	years	66	61	27.59	22	125
Age_{Eb}	years	66	66	24.62	27	125
ho_{Df} at age 100	m	66	47.2	2.68	43.07	53.25
ho_{be} at age 100	m	66	36.9	3.26	31.13	43.36
m_{Df}	-	66	0.47	0.12	0.22	0.76
m_{Eb}	-	66	0.53	0.12	0.24	0.78
$PAIV_{Df}$	$m^3\ ha^{-1}\ yr^{-1}$	66	26.12	7.67	8.83	44.96
$PAIV_{Eb}$	$m^3\ ha^{-1}\ yr^{-1}$	66	13.59	3.88	2.28	21.5
$PAIV_{Df,\ Eb}$	$m^3\ ha^{-1}\ yr^{-1}$	66	21.08	6.69	2.62	39.88
$PAIV_{Df}$: $PAIV_{Eb}$	-	66	2.09	0.85	0.71	4.27
$PAIV_{Df,(Eb)}$: $PAIV_{(Df),\ Eb}$	-	66	2.69	0.97	1.25	5.85
$MEAV_{Df,Eb}$	$m^3\ ha^{-1}\ yr^{-1}$	66	1.63	5.19	-7.79	16.73
$MERV_{Df,Eb}$	-	66	1.08	0.28	0.45	1.73
$MERV_{Df,(Eb)}$	-	66	1.20	0.42	0.35	2.65
$MERV_{(Df),Eb}$	-	66	0.91	0.35	0.37	1.99
$PAIW_{Df}$	$t\ ha^{-1}\ yr^{-1}$	66	15.62	4.09	7.33	24.77
$PAIW_{Eb}$	$t\ ha^{-1}\ yr^{-1}$	66	12.44	4.27	3.11	23.8
$PAIW_{Df,Eb}$	$t\ ha^{-1}\ yr^{-1}$	66	14.73	4.74	4.27	31.08
$PAIW_{Df}$: $PAIW_{Eb}$	-	66	1.39	0.56	0.46	2.78
$PAIW_{Df,(Eb)}$: $PAIW_{(Df),Eb}$	-	66	1.59	0.43	0.7	2.73
$MEAW_{Df,Eb}$	$t\ ha^{-1}\ yr^{-1}$	66	0.81	4.02	-6.52	13.24
$MERW_{Df,Eb}$	-	66	1.06	0.28	0.54	1.87
$MERW_{Df,(Eb)}$	-	66	1.17	0.33	0.54	2.21
$MERW_{(Df),Eb}$	-	66	1.03	0.42	0.39	2.52

Online resource 5a Supplementary statistic to the linear mixed models for structure (height, DBH and h/d ratio) in Fig. 3, productivity (periodic mean annual increment of volume and aboveground biomass) in Fig. 5.

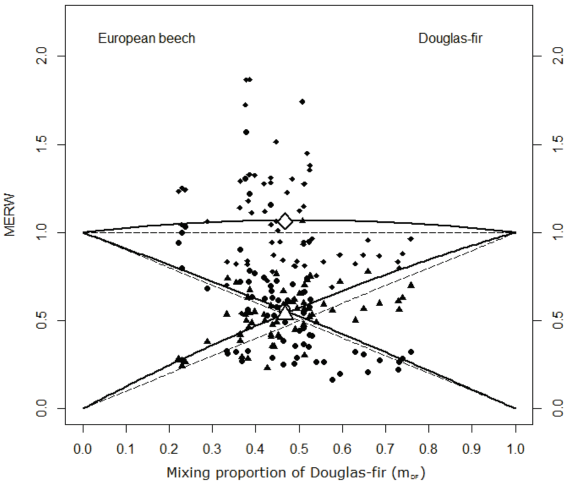
		Dependent variables	Explanatory variables	Estimate	StdError	Df	p-value	
Structure								
	Douglas-fir	Height	Intercept	5.75	2.48	5.52	0.06	.
			Mixture (pure)	1.96	1.31	28.17	0.15	
			Age	0.44	0.04	4.67	0.00	***
		DBH	Intercept	-12.92	3.34	10.93	0.00	**
			Mixture (pure)	14.32	3.18	15.17	0.00	***
			Age	0.90	0.07	9.21	0.00	***
			Mixture*Age	-0.30	0.06	17.25	0.00	***
		H/d ratio	Intercept	104.02	6.47	13.22	0.00	***
			Mixture (pure)	8.89	2.45	9.24	0.01	**
			Age	-0.37	0.22	6.28	0.14	
	European beech	Height	Intercept	5.98	2.14	2.16	0.10	.
			Mixture (pure)	1.93	0.61	15.95	0.01	**
			Age	0.31	0.06	3.09	0.01	*
		DBH	Intercept	2.63	1.04	24.00	0.02	*
			Mixture (pure)	0.55	0.95	15.16	0.57	
			Age	0.30	0.02	6.49	0.00	***
			Mixture*Age	0.05	0.02	17.33	0.05	*
		H/d ratio	Intercept	128.90	13.47	3.31	0.00	**
			Mixture (pure)	-5.01	4.47	17.15	0.28	
			Age	-0.22	0.31	3.59	0.53	
Productivity								
	Stand	PAIV	Intercept	3.55	3.39	7.51	0.33	
			Mixture (pure)	5.92	1.90	35.77	0.00	**
			Age	0.38	0.09	9.89	0.00	**
			Mixture*Age	-0.14	0.05	10.11	0.02	*
		PAIW	Intercept	1.65	1.81	7.81	0.39	
			Mixture (pure)	5.14	1.52	34.67	0.00	**
			Age	0.27	0.05	11.23	0.00	***
			Mixture*Age	-0.11	0.04	9.65	0.03	*
	Douglas-fir	PAIV	Intercept	6.42	5.28	6.49	0.27	
			Mixture (pure)	6.02	3.17	29.01	0.07	.
			Age	0.54	0.12	11.61	0.00	***
			Mixture*Age	-0.22	0.09	8.30	0.03	*
		PAIW	Intercept	1.97	3.02	6.53	0.54	
			Mixture (pure)	4.27	2.29	13.90	0.08	.
			Age	0.36	0.08	10.27	0.00	**
			Mixture*Age	-0.16	0.07	9.00	0.04	*
	European beech	PAIV	Intercept	5.61	2.60	6.15	0.07	.
			Mixture (pure)	1.92	1.15	17.13	0.11	
			Age	0.16	0.08	3.81	0.11	
		PAIW	Intercept	3.23	1.80	28.36	0.08	.
			Mixture (pure)	5.66	2.01	21.59	0.01	*
			Age	0.17	0.04	16.50	0.00	***
			Mixture*Age	-0.08	0.03	22.69	0.02	*

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Online resource 5b Comparison between pure (black line) and mixed stands (red line) based on the linear mixed models of Online resource 5a. Asterisks represent the decisive significance level of mixture or the interaction of mixture and age. Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.



Online Resource 6 Cross diagrams according to Harper (1977)and Kelty (1992) for display the mixing effect on productivity of Douglas-fir and European beech for aboveground biomass increment. The left (European beech) and right (Douglas-fir) ordinates in the cross diagrams, represent the relative productivity. The abscissa shows the mixing portion of Douglas-fir (mDf). Broken lines represent the productivity expected for neutral mixing effects on the level of the stand as a whole (horizontal 1.0-line) and on the level of the two contributing species (decreasing with respect to increasing lines). The solid lines show the observed productivity from whole stand (upper bold curve) and species-specific (lower thin curves), respectively. Black symbols represent the single observation of whole stand (diamond), Douglas-fir (triangle) and European beech (circle). The means were printed by white symbols



Online resource 7 Supplementary statistic to Fig. 5, statistic summary for Chapman-Richard growth models of tree height and position of crown for Douglas-fir and European beech in mixed stands fitted by non-linear least squares

Species	Model	Parameter	Estimate	Standard error	P-value	
Douglas-fir	Height	a	53.249	3.717	0.000	***
		k	0.027	0.006	0.000	***
		p	1.573	0.321	0.000	***
	Crown	a	19.275	0.877	0.000	***
		k	0.086	0.021	0.000	***
		p	8.981	5.789	0.129	
European beech	Height	a	49.439	8.411	0.000	***
		k	0.013	0.006	0.033	*
		p	1.000	0.212	0.000	***
	Crown	a	15.132	0.551	0.000	***
		k	0.083	0.019	0.000	***
		p	10.000	6.635	0.134	

*Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

Article -II-

Mixture reduces climate sensitivity of Douglas-fir stem growth

in ***Forest Ecology and Management (2016)***

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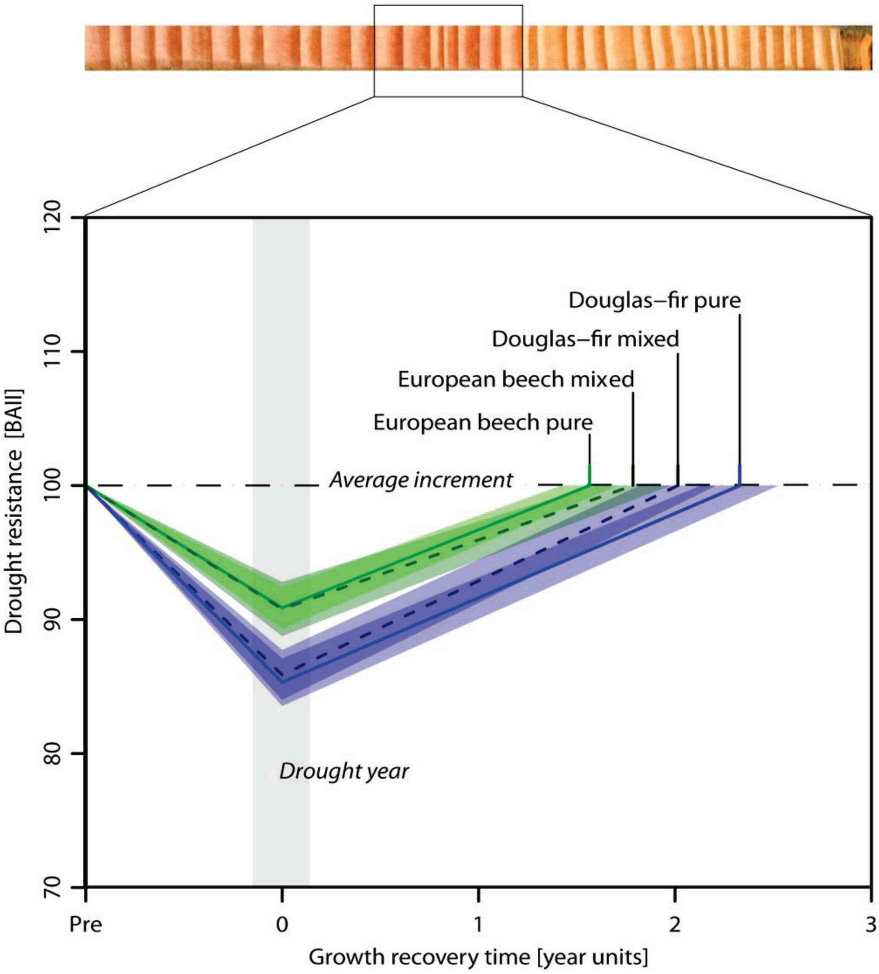


Abstract

Due to possible positive and compensatory interaction between species, mixed stands are a commonly accepted silvicultural response to reduce risks arising from climate change. Nonetheless, only a few species combinations have been studied more detailed so far revealing variable mixing effects. Here, we analyze the effect of the mixture of Douglas fir and European beech with regard to the species-specific climate sensitivity of growth. We focus on three hypotheses: i) Species-specific long term growing performance and climate sensitivity do not differ between monocultures and mixed stands, (ii) species-specific growth reactions to severe drought events do not differ between monocultures and mixed species stands and (iii) species-specific growth reactions on severe drought events are not influenced by differing ecological growing conditions.

To scrutinize the hypothesis we analyzed tree cores from both species taken from pure and mixed stands covering different site conditions and age classes. Tree ring characteristics were used to analyze the differences in climate related long-term growth responses in pure and mixed stands. Short-term responses were investigated by growth reaction indices on individual tree and stand level involving drought events during the years 1950 to 2010. Linear mixed models were applied to detect effects of ecological co-variables on the indices.

Results reveal that Douglas-fir in mixed stands exhibit a significant improved growing performance compared to pure stands. European beech seems to react indifferently concerning its performance in mixture compared to pure stands.Differences in drought stress resistance and growth recovery time mainly arose between the species. Douglas-fir showed a significantly lower resistance and required more time to reach again its initial growth level compared to European beech. In mixture we found a trend that Douglas-fir growth recovery time is shortened and extended for European beech.

The analysis along the ecological gradients showed that base-limited soils systems are more drought-tolerant during drought events. Lower basal area as a proxy for reduced stand competition decreased the relative growth loss by drought.We hypothesize that mainly spatial differentiation in height trigger enhanced diameter growth of Douglas-fir in mixture. Temporal differentiation expressed by deferred phenology attenuates climate sensitivity of this conifer. We conclude that in mixed Douglas-fir and European beech stands the former species is stabilized against climatic impacts. On the contrary, climate sensitivity of European beech is increased.

Keywords: Drought stress; European beech; Resistance; Growth recovery time; Overyielding; Stabilization

1. Introduction

1.1. *Risk distribution by mixing species*

An increase in frequency and intensity of ecosystem disturbances such as severe drought events have been observed in many regions of the world (IPCC, 2014) challenging forest management to deal with adaptation issues. In this context species mixing seems to be an effective way to stabilize forests against such impacts (Kelty, 1992; Knoke et al., 2008; Lüpke, 2004). Previous studies focusing on productivity (Forrester, 2014; Toïgo et al., 2014; Vallet and Pérot, 2011) provide evidence, that mixing species modifies resource utilization within a stand. Generally, interactions between combined species seem to be responsible for a change in resource partitioning. Larocque et al. (2013) separate these into interactions resulting in positive (through facilitation and complementarity) or negative (through competition) outcomes. Mainly processes of facilitation and niche differentiation improve the utilization of available resources in mixed stands. Mixing effects are not a constant phenomenon but depend on developmental stage of a stand (Binkley and Greene, 1983; Zhang et al., 2012) and on site conditions (Toïgo et al., 2014). According to the stress gradient hypothesis the effect of facilitation is more pronounced on sites with stressful growing conditions whereas under benign conditions competition dominates (Bertness and Callaway, 1994; Callaway and Walker, 1997).

When considering drought events as temporal setbacks of growing conditions it is assumable that in mixed stands comprised by species exhibiting different functional traits and resistance behavior negative growth reactions may also be attenuated. Growth loss or dramatic drop out of one species by a disturbance may be mitigated or even compensated by the second species (Kelty, 1992). Some studies provide evidence that mixture has a positive effect during drought events for at least one species (Lebourgeois et al., 2013; Pretzsch et al., 2013).

1.2. *The mixture of Douglas-fir and European beech*

In Central Europe forest managers aim at reducing the share of conifer monocultures, mainly dominated by the highly vulnerable Norway spruce (*Picea abies* (L.) H. Karst.) by establishing mixed stands of conifers and broadleafed species (Klimo et al., 2000; Zerbe, 2002). In this context, mixed stands of Douglas fir (*Pseudotsuga menziesii* (Mirb.)Franco) and European beech (*Fagus sylvatica* L.) receive increasing attention (Reyer et al., 2010). European beech is one of the most competitive species and would dominate the potential natural vegetation in Central Europe (Bolte et al., 2007; Ellenberg and Leuschner, 2010). Douglas-fir as a non-indigenous species in Europe provides the advantages of having high growth rates and good wood quality and being very adaptable to various site conditions (Kleinschmit and Bastien, 1992). Its growth rates outperform Scots pine (*Pinus sylvestris* L.) and Norway spruce (Hermann and Lavender, 1999; Pretzsch, 2005). Additionally, its drought tolerance seems to be more accomplished compared to other European conifers (Bréda et al., 2006; Eilmann and Rigling, 2012). Complementary characteristics of both species have been described by Hendriks and Bianchi (1995) concerning below ground space occupation and by Thomas et al. (2015) concerning crown stratification.

1.3. Research objective

To enhance knowledge about the effect of mixing Douglas-fir and European beech concerning their resistance against drought, the study analyzed the respective past growth responses of both species. We tested three null hypotheses: i) Species-specific long term growing performance and climate sensitivity do not differ between monocultures and mixed stands, (ii) species-specific growth reactions to severe drought events do not differ between monocultures and mixed species stands and (iii) species-specific growth reactions on severe drought events are not influenced by differing ecological growing conditions.

Our analyses of the tree growth performance make use of the comparison of two stand types (pure and mixed) growing on similar site conditions. This enables to detect possible mixing effects on tree chronology characteristics by contrasting intra- and interspecific competition situations.

In a first step, we use tree ring characteristics to analyze the long term climate response of the trees. Fritts (1976) described the changes of tree chronology characteristics under a gradient from forest interior to semiarid forest border. Trees under harsher conditions built *sensitive* tree rings, with higher mean sensitivity, lower autocorrelation and smaller ring width. In contrast, trees under benign conditions built *complacent* year rings with opposite characteristics. Additionally, Biondi and Qeadan (2008b) showed that tree ring variability computed by the Gini-coefficient varied between different species and between different time periods.

Tree ring chronologies are further used to analyses the short term growth reaction of the species during past droughts event. Pretzsch et al. (2013) could show that resistance of trees is modified in mixture compared to pure stands. We introduce growth recovery time and loss of increment as measure of growth reaction due to drought, whereas the pre drought growth level serves as reference. Several studies suggest that subsequent years with unfavorable water supply have to be considered when looking at growth recovery time (Eilmann and Rigling, 2012; Hartmann, 2011; McDowell et al., 2008). Therefore, we also take a look at the climate condition after a drought year and link it with the growth recovery time.

We look at both, growth reaction on individual tree and stand level. As growth reaction to drought may be dependent on tree size individual reaction do not allow to scale up to stand level without considering tree size distribution (Mérian and Lebourgeois, 2011). This is even more relevant when comparing pure and mixed stands as tree size distribution may differ between stand types (Pretzsch and Schütze, 2016). By providing relative reaction values, it is possible to explain the biological response patterns of the trees during drought. Absolute growth values on stand level enable a link to forest management.

2. Materials and methods

2.1. Study site and plot set-up

The study was conducted in Central Europe and covered a range of 430 km. Seven different ecological regions were included from “Osteifel” (N 6°44'36.33'', O 50°10'23.86'') in the north west to “Schwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaft” (N 11°51'09.88'',E 48°07'16.78'') in the south east (Fig. 1). The study made use of a triplet experimental setup. Each triplet is composed of a mono-specific stands of Douglas-fir and European beech, respectively and a mixed stand of both species, growing on identical site conditions and exhibiting similar stand age. The plots of a triplet were selected in direct proximity, mostly in the same compartment, to minimize residual effects like soil, tree genetic and management effects. When the plots were not in inside the same compartment, the similarity of the soil was visually checked by a sample with a boring rod. All triplets represented more or less fully stocked and mono-layered forest stands (see Supplementary material 1). General differences in stand density resulted from species-specific, tree size related space occupation (Reineke, 1933) and from mixing effect (Pretzsch and Biber, 2016). By this, comparisons of growth reactions in pure stands of Douglas-fir and European beech as well as in mixed stands of both species under similar growing conditions are enabled. The climate response of the species in mono-specific stands is used to reference possibly deviating response of the species in mixed stands.

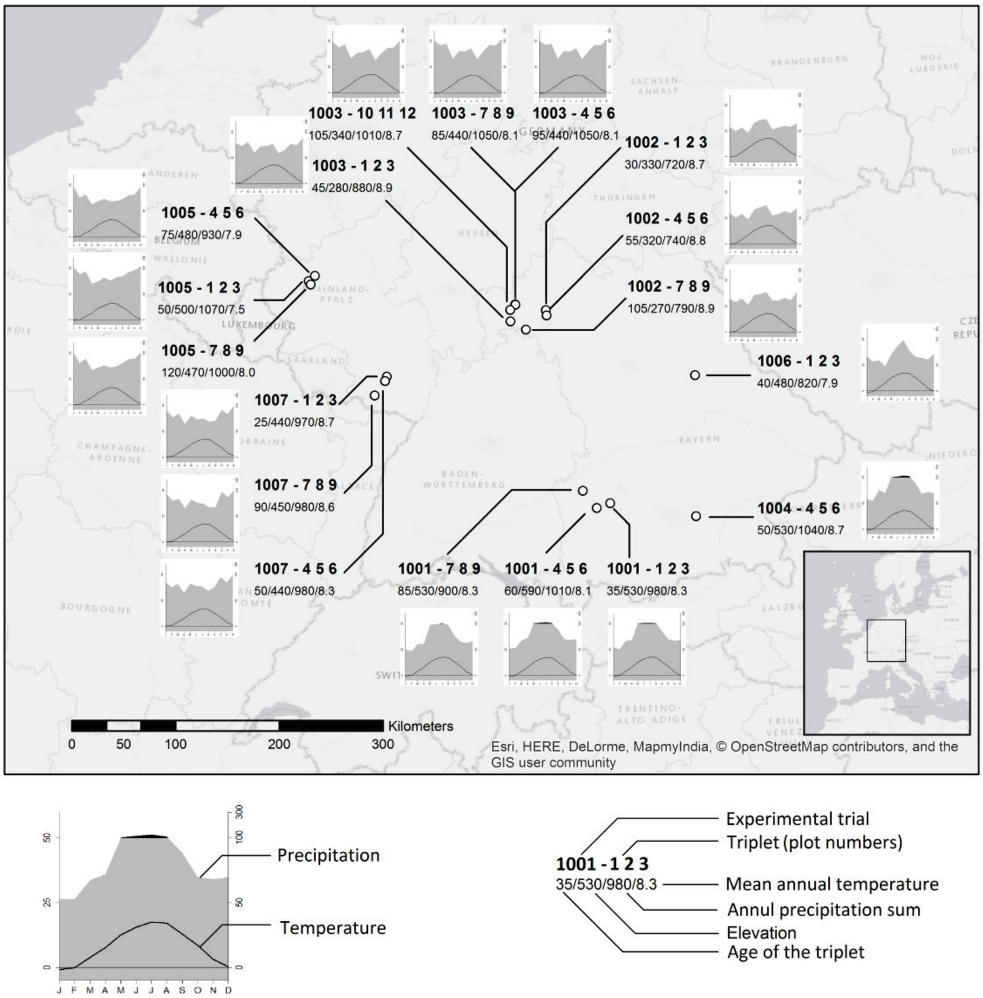


Fig. 1 Location of the 18 triplets in Central Europe (dots) with the associated climate charts according to Walter and Lieth (1967). The experimental trial number results from a four-digit experimental number and a three-digit triplet number. Beneath the experimental trial number, plot information concerning stand age of the triplet, elevation above sea level, annual precipitation sum and mean annual temperature is given.

Abb. 1 *Standorte der 18 Triplets in Mitteleuropa (Punkte) mit den dazugehörigen Klimadiagrammen nach Walter und Lieth (1967). Die Nummer an den Triplets bestehen aus den vierstelligen Nummer der Versuchsanlagen und den drei Ziffern der Versuchsflächen auf dem Triplet. Unterhalb der Versuchsnummer befinden sich Informationen über das Alter, die Meereshöhe, die Jahresniederschlagssumme und die mittlere Jahrestemperatur.*

The mean annual temperatures between the triplets range from 7.0 to 9.5 °C and from 13.7 to 15.7 °C during the growing period. The mean annual precipitations range from 733 to 1066 mm, and to 322 - 576 mm in the growing period, respectively (multi annual values from 1981 to 2010) (Deutscher Wetterdienst, 2015). The soil water supply of the triplets, described by a combination of water holding capacity, precipitation and transpiration, ranged from dry to very fresh. The base equipment of the soils ranged from base-poor to base-rich. The age gradient covers three classes: young (approx. 30 years), mature (approx.60 years) and old stands (approx. 90 to 120 years). Table 1 gives an overview of the triplet's site conditions and stand parameters. Sampling and standardization of tree rings

Table 1 Stand and site characteristics of the 18 triplets sampled between 2012 and 2014 (Survey) indicating ecoregions (Gauer and Kroiher, 2012) and climate data (Temp - mean annual temperature, Prcp - mean annual precipitation sum) (Deutscher Wetterdienst, 2015), base-richness (Base), water supply (Water) and plant available water capacity (PAWC) (Landesforst Rheinland-Pfalz, 2014a; Taegger and Kölling, 2016), diameter at breast height (DBH) and tree height (Height) refer to the quadratic mean diameter tree. Number of cored trees (Cored trees); Base-richness is ranked from very base-poor (1) to very base-rich (5) and water supply is ranked from very dry (1) to very fresh (7).

***Tabelle 1** Bestandes- und Standortsinformationen der 18 Triplets die im Zeitraum 2012-2014 aufgenommen wurden; eingeteilt in Ökoregionen nach Gauer und Kroiher 2012, Klimadaten (Temp – Jahresmitteltemperatur, Prcp - Jahresniederschlagssummer) (Deutscher Wetterdienst, 2015), Basensättigung (Base), Wasserversorgung (Water) und pflanzenverfügbare Wasserkapazität (Landesforst Rheinland-Pfalz, 2014a; Taegger und Kölling, 2016), Brusthöhendurchmesser (DBH), und Baumhöhe (Height) gemessen am Grundflächenmittelstamm. Anzahl an Bäumen mit Bohrkern (Cored trees). Basensättigung ist gegliedert von basenarm (1) bis sehr basenreich (5); die Wasserversorgung ist gegliedert nach sehr trocken (1) bis sehr frisch (7).*

Experimental trial	Triplet	Ecoregion	Temp [C°]	Prcp [mm]	Base	Water	PAWC [mm]	Stand age [year]	Survey	Douglas-fir						European beech					
										Pure			Mixed			Pure			Mixed		
										DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees
1001	1 2 3	Tertiäres Hügelland	8.3	977	3	7	192	33	2013	26.2	23.8	19	24.7	22.4	22	13.9	18.9	26	13.5	16.3	17
	4 5 6	Tertiäres Hügelland	8.1	1011	3	7	130	60	2013	45.1	32.3	20	53.1	35.7	14	23.3	22.3	37	19.3	22.0	18
	7 8 9	Tertiäres Hügelland	8.3	898	3	7	214	85	2013	74.0	44.9	18	62.0	39.4	17	38.3	28.1	20	25.8	27.7	13
1002	1 2 3	Fränkische Platte	8.7	718	4	3	210	29	2013	18.2	20.3	22	14.0	16.5	16	8.7	14.3	19	10.7	16.9	23
	4 5 6	Fränkische Platte	8.8	740	4	3	200	54	2013	28.3	27.3	24	36.2	29.9	17	15.2	22.3	19	17.0	21.2	30
	7 8 9	Fränkische Platte	8.9	792	4	3	210	103	2013	58.0	43.4	17	75.4	46.8	9	53.6	39.3	14	36.2	35.2	17
1003	1 2 3	Spessart	9	878	2	7	144	43	2013	32.9	29.2	19	34.2	27.3	16	15.4	19.8	24	15.1	17.3	27
	4 5 6	Spessart	8.1	1054	3	4	154	95	2013	64.1	49.2	8	63.1	44.7	5	35.6	35.6	16	29.7	35.8	20
	7 8 9	Spessart	8.1	1054	3	4	154	85	2013	55.2	41.2	10	78.6	38.2	5	30.9	31.8	17	29.9	29.9	19
	10 11 12	Spessart	8.7	1012	2	6	144	105	2013	63.9	41.8	13	80.8	43.5	4	42.4	29.1	17	36.4	30.2	11
1004	4 5 6	Schwäbisch-Bayerische Schotterplatten und Altmoränenlandschaft	8.5	1044	4	7	132	49	2013	27.6	26.2	18	29.9	25.0	14	21.3	22.6	21	15.6	23.2	18
1005	1 2 3	Osteifel	7.5	1066	3	6	171	49	2014	36.7	31.4	28	45.7	31.2	14	16.4	17.7	21	15.2	18.0	25
	4 5 6	Osteifel	7.9	926	3	6	155	75	2014	46.4	36.4	16	73.7	38.7	5	28.1	24.8	25	22.1	21.5	23
	7 8 9	Osteifel	8	1000	3	6	155	119	2014	70.3	49.0	12	83.2	40.9	4	37.0	29.9	18	23.2	22.0	16
1006	1 2 3	Frankenalb und Oberpfälzer Jura	7.9	821	3	5	156	37	2013	26.6	24.9	25	30.2	24.7	23	17.9	19.0	22	17.2	19.7	8
1007	1 2 3	Pfälzerwald	8.7	974	2	5	146	26	2012	11.5	13.0	22	9.1	10.0	15	9.0	11.4	20	7.8	9.0	15
	4 5 6	Pfälzerwald	8.3	980	2	5	193	51	2012	26.4	29.8	20	23.0	24.1	16	16.6	17.7	23	17.9	21.0	18
	7 8 9	Pfälzerwald	8.6	981	2	5	172	92	2012	62.5	43.4	20	69.8	46.2	15	38.2	33.1	20	33.6	32.9	20
		total	8.4	940				66		41.2	33.3	331	49.3	32.5	231	25.7	24.3	379	21.5	23.3	338
		(min - max)	(7.5 - 9.0)	(718 - 1066)				(25.7 - 119.0)		(11.5 - 74.0)	(13.0 - 49.2)	(8.0 - 28.0)	(9.1 - 83.2)	(10.0 - 46.8)	(4.0 - 23.0)	(8.7 - 53.6)	(11.4 - 39.3)	(14.0 - 37.0)	(7.8 - 36.4)	(9.0 - 35.8)	(8.0 - 30.0)

During the years 2012 to 2014, in total 1279 trees were sampled by extracting two increment cores from northern and eastern direction from each tree at breast height (1.30 m). Ring widths were measured with digital positiometer (Biritz GmbH, Gerasdorf bei Wien, Austria) with an accuracy of 0.01 mm. Cross-dating and synchronization of the tree chronologies were conducted using the software platform TSAP-Win (Rinntech, Heidelberg, Germany). We measured diameter at breast height (DBH) and tree height from all cored tree and from the remaining trees of each plot (n = 1987, see Table 1).

In order to extract the climate related growth reaction from the chronologies the individual tree core series were standardized. Here, we use basal area increment (BAI) series instead of ring width series for detrending and statistical analyses, because the BAI as a two-dimensional measurement, better reflects three-dimensional growth of the whole tree (volume) than the one-dimensional growth of tree ring width (Biondi and Qeadan, 2008a; LeBlanc, 1990). The BAI for each individual tree was calculated using the mean radial increment of both cores. A double detrending procedure was applied to standardize BAI time series (Holmes et al., 1986). This two-stage curve fitting (see example in Appendix A) was used to eliminate the deterministic age trend at first. Due to the nature of BAI age trend we applied a Hugershoff function (1936) instead of a negative exponential function or linear regression, usually used for detrending. For the second detrending procedure, a cubic spline was applied because residual growth trends from forest trees strongly depend on competition and release of competition through thinning. The wavelength of the cubic spline was fixed by 15 years with a frequency response of 0.5. A 15 year window was used as it covers a usual time interval of thinning activities.

To quantify the long-term growth behavior of both species in pure and in mixed stands, we used five standard tree ring characteristics (Biondi and Qeadan, 2008b; Fritts, 1976; Speer, 2010). The mean basal area increment (Mean), calculated as mean value for each tree chronology, provides a measure of the general growth potential. The Gleichlaeufigkeit (GLK) describes the intra-specific conformity of the tree chronologies within a sample stand. The first-order autocorrelation (AC) indicates to what extent the increment of year n correlated with year n-1. In terms of sensitivity we calculated mean sensitivity (MS), which quantifies the year-to-year variability. AC indicates the existence of low frequency variability in tree ring chronologies which is triggered for instance by physiological processes leading to a lag in response to climate conditions. MS is a measure of high frequency variability and is regulated by short term shifts in climate related growing conditions (Fritts 1976). Lastly, the Gini coefficient (GINI) represents a quantitative measure of the heterogeneity of increment in tree ring chronologies. GINI, MS and GLK where calculated based on index values, whereas AC were calculated based on measured raw ring width.

The basal area of the stands was calculated by summing up the basal area of all individual trees per plot and afterwards scaled up to 1 hectare. Missing basal area increments of not drilled trees were calculated by fitting a function that relates DBH and previous growth rates of drilled trees ($\ln(i_{\mathrm{d}}) = \mathrm{a} + b \cdot \ln(DBH)$). All in all, not drilled trees represented less than 15 percent of the whole basal area.

By the calculation for the drought response of the whole stands, the stand increment was detrended by a Hugershoff function.

For the descriptive core statistics and the calculation of the cubic spline we used the package *dplR* (Bunn, 2008; Bunn, 2010).

2.2. Weather data

The climatic characterization of the sites and the calculation of the drought indices are based on 1*1 km grid of multi annual and monthly precipitation and temperature data (Deutscher Wetterdienst, 2015). The plots of a triplet were mostly located closer than 200 m together, so that climate data were aggregated only for the mixed stand but also used for the whole triplet (for a more detailed view of experimental setup see Thurm and Pretzsch, in review). The standardized precipitation-evapotranspiration index (SPEI) was used to identify drought years (Vicente-Serrano et al., 2010). The SPEI was calculated for a time scale of 5 month using a Gaussian kernel function. The length of the timescale was deduced from a comparison of drought events and BAI response. Thereafter, the mean SPEI of the growth period from May to September was calculated. As drought years, the seven years (10^{th} percentile) with lowest SPEI during 1950 to 2010 per triplet were selected (see Supplementary material 2). Thereby, we investigated tree response during extreme drought years as well as during moderate drought years.

To consider different drought stress behaviors of Doulas-fir and European beech, e.g. isohydric or anisohydric traits (Hartmann, 2011; Tardieu and Simonneau, 1998), drought years were classified into three groups. The classification depended on the climate conditions after a drought year. If after a drought year a year with above average dry climate conditions was following, it was classified as *good post-year*. Respectively average conditions after a drought year were classified as *average post-year* and below-average conditions as *adverse post-year*. The selection was done individually for every triplet. Classification concerning a specific drought year may thus vary between sites.

2.3. Drought year analyses

The *drought year analyses* focused on short-term individual trees' response to drought weather events. Secondly, the drought year analysis was performed for the whole stand. Lloret et al. (2011) introduced three indices (resistance, resilience and recovery) describing the performance of trees under drought stress. Here, beside resistance, we used two new indices characterizing the growth reactions (growth recovery time, increment loss due to drought) of individual trees and stands to drought.

The *resistance* (Rt) quantifies the ability of plants to withstand a disturbance. Lloret et al. (2011) defined Rt as the ratio between growth during the drought event and a mean growth level of a reference period prior to the drought event.

For the resilience (Rs), we found different definitions in the literature. Lloret et al. (2011) described the resilience as the ratio of post-disturbance growth level to pre-disturbance growth level. Pimm (1984) refers to resilience as the time a system needs to return to an equilibrium following disturbance. Here, we used resilience in terms of the duration starting in the drought year until reaching the pre-drought growth level again (Fig. 2). To avoid confusion of ideas the index is named *growth recovery time* (GRT). The index's unit is year units, as possible decimal figures do not represent ratios of a full year.

The index *increment loss due to drought* (Loss) describes the loss of stand growth due to drought in relation to the pre-drought growth level. It is the cumulated loss during the time of recovery.

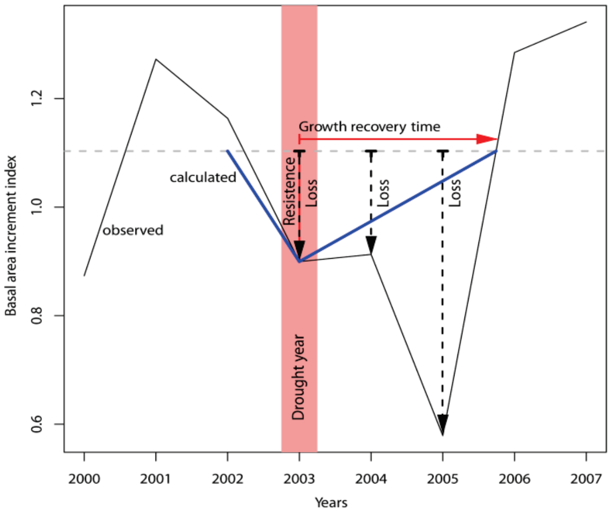


Fig. 2 Schematic illustration of the growth reaction indices used in the analyses (resistance, growth recovery time and increment loss due to drought). The solid black line represents the detrended basal area increment. The bold solid blue line shows the drought response calculated by resistance and growth recovery time, also used in Fig. 5 and Fig. 6.

Abb. 2 *Schematische Darstellung des verwendeten Trockenheitsindizes (Resistenz, Erholungsreaktion und dem Zuwachsverlust durch das Trockenjahr). Die dicken schwarzen Linien repräsentieren die trendeleminierten Grundflächenzuwächse. Die dicken blauen Linien stellen die Trockenreaktion dar, berechnet nach Resistenz und Erholungszeit. Dieses Indizes wurde ebenfalls in Abb. 5 und Abb. 6 genutzt.*

To provide a value more common in forest practice, basal area increment loss due to drought was transformed into volume loss. Therefore, we fitted a stand volume function (Eq. 1) for each mixture (m, Douglas-fir pure stand, mixed stand, European beech pure stand) at survey point (p) with basal area and stand age as independent variables, including their interaction. The coefficients $a_0 \dots a_3$ of the fixed effect from the single models are shown in Appendix B.

$$\ln(Volume_{mp}) = a_0 + a_1 \cdot \ln(Basal\ area_{mp}) + a_2 \cdot \ln(Stand\ age_{mp}) + a_3 \cdot \ln(Basal\ area_{mp} \cdot Stand\ age_{mp}). \qquad (1)$$

As mentioned in chapter 2.2, deterministic age trend that may influence pre- and post-drought growth rates can be removed by double detrending procedures. Additionally, specific weather conditions prior and after drought events, may also affect the index values. To cope with this problem, all indices for drought event identified along the chronologies were pooled assuming to average possible differences in pre- and post-drought weather conditions.

2.4. Statistics

2.4.1. Tree chronology characteristics

Species-specific chronologies characteristics were used to test for differences of long-term growth behavior between Douglas-fir and European beech in mixed and in pure stands. Therefore, we applied a linear mixed model (Eq.2), *lmer* from the R-package *lme4* (Bates et al., 2015). Y_{ij} refers to the mean tree chronology characteristics per plot and species. The mixing types (mixed Douglas-fir, pure European beech and mixed European beech) were included as fixed effects and coded as binary variables, which switch between 1 and 0, depending on which mixing type is fitted.

$$Y_{ij} = a_0 + a_1 \cdot mixed\ Douglas\text{-}fir_{ij} + a_2 \cdot pure\ E.beech_{ij} + a_3 \cdot mixed\ E.beech_{ij} + \ b_i + b_{ij} + \varepsilon_{ij} \qquad (2)$$

The indexes i and j represent experimental location and the triplet. a_0 and a_1 represent the coefficients of fixed effects. Random effects are considered with *b* on experimental location and plot level. The symbol ε represents the independent and identically distributed random error. Results were checked for homoscedasticity and normal distribution. A generalized linear hypothesis test was used for contrasting all mixing type effects, as obtained by the linear mixed model, against each other. We applied the R-package “multcomp” (Hothorn et al., 2008).

In a second step a multivariate analysis of tree chronology characteristics was performed by a Principal Component Analysis (PCA) using the packages “FactomineR” (Husson et al., 2015). It was applied to identify patterns in tree characteristics which are linked to the species, mixing types, age and experimental trial. The four mixing types (pure and mixed Douglas-fir, pure and mixed European beech) of each triplet were addressed individually within the analysis. Mean tree characteristics (mean basal area increment, autocorrelation, mean sensitivity, Gini coefficient and Gleichlaeufigkeit) were included as quantitative variables. Ellipses corresponding to 95% confidence intervals were calculated, based on the coordinates of mixing types, species, age and experimental location.

2.4.2. Drought year analyses

A linear mixed model approach was applied to analyze possible effectors on resistance and growth recovery time and increment loss due to drought on individual tree and stand level. The effectors were separated into two types: plot specific (species, mixing type, post-year conditions) and overarching ecological factors.

With Eq. 3, we tested the effect of plot specific variables at the individual tree level for the resistance and the growth recovery time (YI).

$$YI_{ijkt} = a_0 + a_1 \cdot species_{ij} + a_2 \cdot mixture_{ij} + a_3 \cdot species_{ij} \cdot mixture_{ij} + a_4 \cdot post\text{-}years_{ij} + a_4 \cdot species_{ij} \cdot post\text{-}years_{ij} + a_4 \cdot mixture_{ij} \cdot post\text{-}years_{ij} + a_4 \cdot species_{ij} \cdot mixture_{ij} \cdot post\text{-}years_{ij} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \quad (3)$$

In addition to equation 2, the indexes k and t represent individual tree and drought event, respectively. Additionally, the tree number was considered as random effect. In case of resistance, the dependent effect of post-year and its respective interactions were omitted.

To test the resistance, the growth recovery time and the increment loss due to drought at stand level (YS) we used Eq. 4. The two stand types, European beech pure stand and the mixed stand, are considered as binary variables like in Eq. 2. The Douglas-fir pure stand is represented by the intercept. The post-year factor was omitted on this level completely, because in most cases the weather conditions in 2004 were below average.

$$YS_{ijt} = a_0 + a_1 \cdot pure\ E.beech\ stand_{ij} + a_1 \cdot mixed\ stand_{ij} + b_i + b_{ij} + \varepsilon_{ijt} \quad (4)$$

To verify the influence of the ecological factors on resistance and growth recovery time, the following independent variables were taken into account: age, DBH (in case of stand level model the basal area per hectare), relative DBH (ratio of DBH to DBH of the quadratic mean diameter tree per plot), water supply, base-richness, mean annual temperature, annual precipitation sum and in case of stand level model the proportion of European beech ($proportion_{(Eb)}$)(Table 1).

Individual tree level:

$$YI_{ijkt} = a_0 + a_1 \cdot age_{ijkt} + a_2 \cdot DBH_{ijkt} + a_3 \cdot age_{ijkt} \cdot DBH_{ijkt} + a_4 \cdot relative\ DBH_{ijkt} + a_5 \cdot base\text{-}richness_{ij} + a_6 \cdot temperature_{ij} + a_7 \cdot precipitation_{ij} + a_8 \cdot water\ supply_{ij} + a_9 \cdot precipitation_{ij} \cdot water\ supply_{ij} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijt} \quad (5)$$

Stand level:

$$YS_{ijt} = a_0 + a_1 \cdot age_{ijt} + a_2 \cdot proportion_{(\mathrm{Eb})ijt} + a_3 \cdot basal\ area_{ijt} + a_4 \cdot base\text{-}richness_{ij} + a_5 \cdot temperature_{ij} + a_6 \cdot precipitation_{ij} + a_7 \cdot water\ supply_{ij} + a_8 \cdot precipitation_{ij} \cdot water\ supply_{ij} + b_i + b_{ij} + \varepsilon_{ijt} \quad (6)$$

Model selection was based on the Akaike Information Criterion (Burnham and Anderson, 1998) and biological plausibility of the results. The selection was made with additionally help of automated model selection (*dredge*) from the R package *MuMln* (Barton, 2015), which consider all possible variable combinations.

All statistical analyses were performed in the statistical environment R version 3.2.2 (R Core Team 2015).

3. Results

3.1. Tree chronology characteristics

The analysis of the tree characteristics revealed considerable differences between the mixing types (Fig. 3). In general, the mean basal area increment of Douglas-fir (29.0 cm2 a-1) was significantly larger than European beech (9.6 cm2 a-1). Douglas-fir in mixed stands (33.5 cm2 a-1) showed a significantly higher increment than in pure stands (26.0 cm2 a-1). Between the increments of European beech in mixture (8.7 cm2 a-1) and pure stands (10.5 cm2 a-1) no significant differences were observed. The autocorrelation of tree ring chronologies of Douglas-fir in pure stands (0.68) was highest compared to Douglas-fir in mixed stands as well as to European beech in both stands types. The autocorrelation of European beech in pure stand (0.60) did not differ significantly from Douglas-fir (0.58) or European beech in mixture (0.61).

The patterns of the mixed stands concerning mean sensitivity and Gini coefficient were similar. European beech in mixed stands showed the highest sensitivity (MS = 0.28, Gini = 0.14) whereas Douglas-fir in mixture (MS = 0.24, Gini = 0.12) showed the lowest sensitivity. Douglas-fir in pure (MS = 0.25, Gini = 0.13) and in mixed stands did not differ significantly. The sensitivity of European beech in pure stands (MS = 0.26, Gini = 0.13) did not differ from any mixing type. Concerning Gleichlaeufigkeit a significant interspecific variation was found; Douglas-fir having a higher Gleichlaeufigkeit (pure = 0.63, mixed = 0.64) than European beech (pure = 0.58, mixed = 0.57).

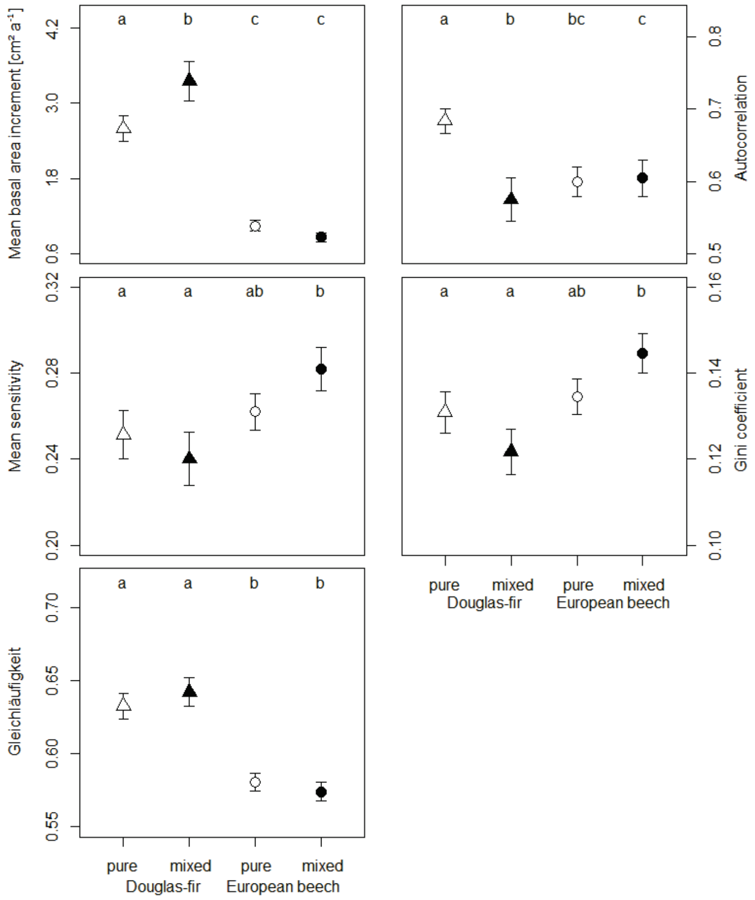


Fig. 3 Statistics of growth series of Douglas-fir (triangle) and European beech (circle) in pure (white) and mixed stand (black) based on 1279 cored trees. Autocorrelation was calulated on ring width. Mean sensitivity, Gini coefficient and Gleichläufigkeit calculated on double detrended basal area increment indices. Significant differnences between the mixing types are indicated by different upper case letters.

Abb 3. *Auswertungsstatistik der Wachstumsreihen von Douglasie (Dreieck) und Rotbuche (Kreis) in Rein- (weiß) und Mischbestand (schwarz) basierend auf 1279 beprobte Bäume. Die Autokorrelation wurde auf Basis der Jahrringbreite berechnet. Mittlere Sensitivität, Gini-Koeffizient und Gleichläufigkeit wurden mit den doppelt-trendeliminierten Grundflächenzuwächsen berechnet. Signifikanzunterschiede sind erkennbar an den unterschiedlichen Buchstaben in den jeweiligen Abbildungen.*

The principal component analyses (Fig. 4) showed, that the two axes (PC1 and PC2) performed on tree chronology characteristics explained 53.0% and 23.5%, respectively of the total variance. The descriptive statistic of the PCA can be seen in Supplementary material 3. The similar trend of mean sensitivity (MS) and Gini coefficient (Gini) is evident by the correlation of first dimension (Fig. 4a). Autocorrelation (AC1) was negative correlated to sensitivity. Mean basal area increment (Mean) and Gleichlaeufigkeit showed same correlation on both dimensions. Each of the five tree chronology characteristics were significant correlated to the first dimension and to the second dimension, except for the Gini coefficient.

Each qualitative variables (species Fig.4d) explained significant differences in tree chronology characteristics, mainly concerning experimental location (R^2= 0.57, p <0.001) and mixing type (R^2= 0.35, p <0.001). The qualitative variables species (Fig. 4b) and mixing type (Fig. 4c) mainly differ by mean basal area increment and Gleichlaeufigkeit. Fig. 4b shows that Douglas-fir and European beech differ significantly in their characteristics. Douglas-fir offered higher mean basal area increment, Gleichlaeufigkeit and autocorrelation; whereas European beech is characterized by lower mean basal area increment, higher sensitivity (MS), and heterogeneity (GINI). Same can be seen in mixing types (Fig. 4c). It is remarkable, that Douglas-fir and European beech differ significantly more in their characteristics in mixed than in pure stands. Young stands differ significantly in their tree chronology characteristics from mature and old stands (R^2=0.08, p<0.05). They exhibited higher sensitivity, heterogeneity and lower mean basal area increment (Fig. 4d). The PCA showed that younger stands revealed a higher sensitivity. The experimental location was strongly determined by the shift from high autocorrelation to high sensitivity (Fig. 4e).

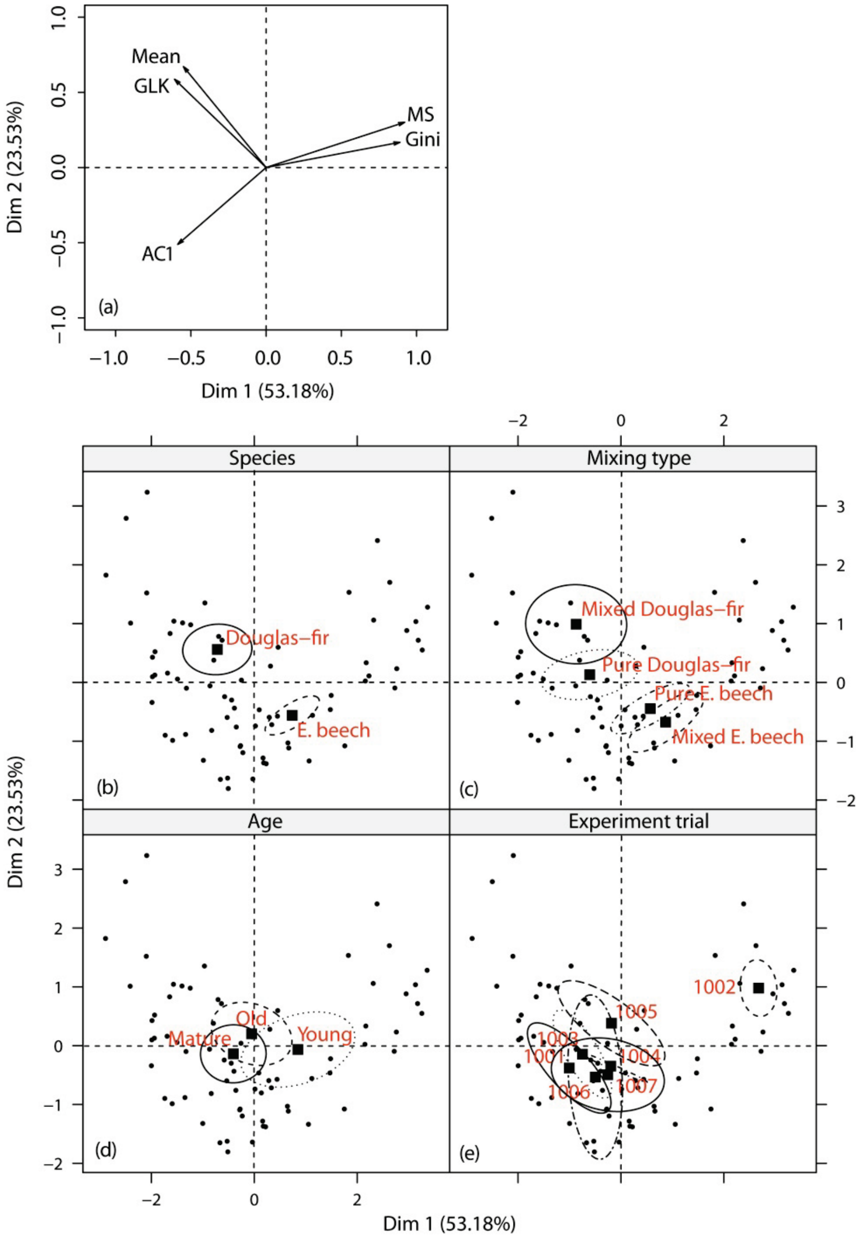


Fig. 4 Principal component analysis (PCA) applied on tree chronologies characteristics (n = 72) for mixing types (Douglas-fir pure and mixed, European beech pure and mixed). (a) The variables factor map indicates correlation and contribution of tree chronology characteristics on the first two axes. (b…e) 95% confidence intervals for average coordinates of species, mixing type, age and experimental trial was depicted by ellipses.

Abb. 4 *Hauptkomponentenanalyse (PCA) angewandt auf die Eigenschaften der Jahrringchronologien (n = 72) getrennt nach den unterschiedlichen Mischungstypen (Douglasie in Rein- und Mischbestand, Rotbuche in Rein- und Mischbestand). (a) Das Ladungsdiagramm der Hauptkomponenten stellt die Zusammenhänge zwischen den Eigenschaften der Jahrringchronologien dar. (b… e) Projizierung der einzelnen Chronologien innerhalb der ersten beiden Dimensionen und Darstellung der 95% Konfidenzintervalle anhand von Ellipsen von den Variablen: Art, Mischungstyp, Alter und Versuchsanlage.*

3.2. Drought year analyses

3.2.1. Individual tree level

The general response of the Douglas-fir and European beech to drought years is illustrated in Fig. 5. The appendant results from the multi comparisons of the linear mixed models are summarized in Table 2. The increment of European beech (resistance = 90.8 %) during the drought years dropped significantly less than of Douglas-fir (Rt =85.5 %, $p<0.001$). No significant mixing effect was existent for both Douglas-fir and European beech. The resistance of both species either in pure or in mixed stands was nearly equal (European beech pure = 90.9, mixed = 90.8, $p>0.05$; Douglas-fir pure = 85.3, mixed = 85.9, $p>0.05$). The analysis of plot specific and overarching factors on growth reaction due to drought indicated that the resistance of Douglas-fir was negatively influenced by the DBH and positive by the age (Table 3). This contradiction is solved by the fact that smaller DBH at same age showed a higher resistance for Douglas-fir. The resistance of European beech seemed to be influenced by the social position. Trees with smaller DBH than the basal area tree per plot tended to have a better resistance. Higher base-richness of soils seemed to reduce resistance of both species.

Concerning growth recovery time the analysis showed that European beech (GRT = 1.67) recovered significantly faster than Douglas-fir (GRT = 2.21, $p<0.01$) (Fig. 5, Table 2). Mixing species affected the growth recovery time but not significantly. The growth recovery time in mixed stands was shortened for Douglas-fir (pure = 2.33, mixed = 2.01, $p>0.05$) and extended for European beech (pure = 1.57, mixed = 1.79, $p>0.05$). The growth recovery times of European beech and Douglas-fir in mixed stand range between growth recovery times of both species in pure stand.

The condition of the post-years showed a clear signal for both species; improved weather situation one year after drought, lead to a significant reduction of the growth recovery time (Rs; good = 1.48, average = 2.01, adverse = 2.25, $p<0.01$). In case of adverse post-years the differences of the growth recovery time between European beech (GRT = 1.94) and Douglas-fir (GRT = 2.67) increased ($p<0.001$). European beech needed significantly more time to return to its initial yield in mixed stands (GRT = 2.33) than in pure stands (GRT = 1.64, $p<0.05$) if dry weather conditions followed a drought event.

Concerning the ecological co-variables only tree age showed a significant effect on growth recovery time for Douglas-fir. Progressive tree age extended growth recovery time (Table 3).

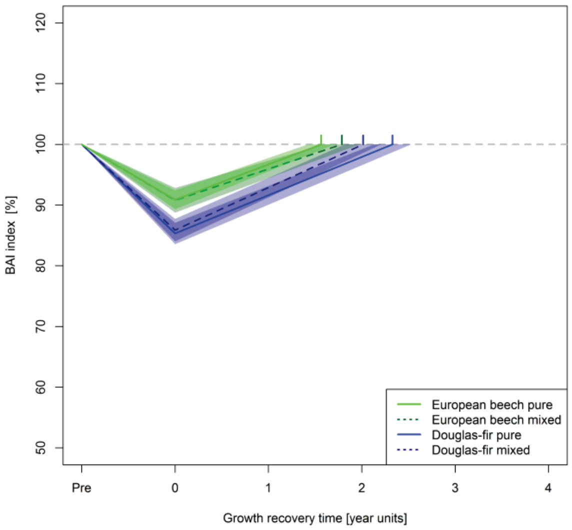


Fig. 5 Mean drought response on individual tree level for all drought events represented by the indices resistance and growth recovery time for European beech (green) and Douglas-fir (blue) in pure (solid) and mixed stands (dashed). The colored bands behind the lines show the respective 95% confidence interval.

Abb. 5 *Durchschnittliches Trockenstressverhalten (zusammengefasst alle Trockenjahre zwischen 1950 - 2010) auf Einzelbaumebene, dargestellt anhand von den Indizes Resistenz und Erholungszeiten für Rotbuche (grün) und Douglasie (blau) in Rein-(durchgezogene Linie) und Mischbeständen (gestrichelte Linie). Die farbigen, transparenten Bänder stellen die 95% Konfidenzintervalle dar.*

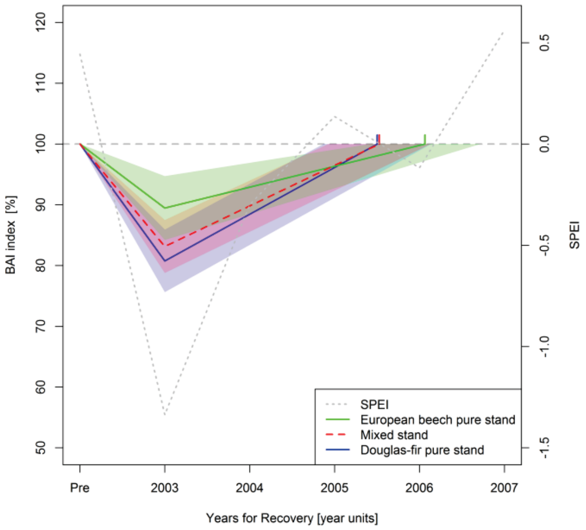


Fig. 6 Mean drought response on stand level to drought event 2003. The response is represent by the indices resistance and growth recovery time for European beech (green solid line) and Douglas-fir (blue solid line) pure stands and for the mixed stands (red dashed line).The grey dashed line represents the average standardized precipitation-evapotranspiration index (SPEI) for all triplets. The colored bands behind the lines show the respective 95% confidence interval.

Abb. 5 *Durchschnittliches Trockenstressverhalten des Trockenjahres 2003 auf Bestandesebene, dargestellt anhand von den Indizes Resistenz und Erholungszeiten für die Rotbuchen-Reinbestände (grün) und Douglasien-Reinbestände (blau) und die Mischbestände (gestrichelte, rote Linie). Die farbigen, transparenten Bänder stellen die 95% Konfidenzintervalle dar. Grau, gepunktet hinterlegt der Klimaindex SPEI, mit einem deutlichen Einbruch 2003 und dem unterdurchschnittlich trockenen Jahr 2004.*

Table 2 Mean values, estimates and significance levels of the multiple comparison of the parameters used in the models (Eq.3 and Eq.4) to estimate resistance and growth recovery time. As independent variable we used species, mixture and post-year (effect of the weather condition on year after drought year). Minor differences between the measured and estimated data arose, because of the random effects. Significant pairs are printed in bold.

Tabelle 2 *Mittelwert, Modelschätzer und Signifikanzen aus den Modellen (Formel 3 und 4) für die Resistenz und die Erholungszeit. Als unabhängige Variablen dienten Baumart, Mischung und das Nachjahr (Wetterkonditionen des Folgejahres eines Trockenjahres im Vergleich zum durchschnittlichen Klima). Kleinere Unterschiede zwischen gemessenen Mittelwerten (Mean) und der Differenz welche aus den Modellen geschätzt (Estimate) wurden, kommen durch die zufälligen Effekte zustande, welche in den Modellen integriert sind. Signifikante Unterschiede zwischen den Paaren sind dick gedruckt.*

	Individual tree level (1950 - 2010)						
			Mean		**Multiple comparison**		
	Variables	**Pairs (A - B)**	**A**	**B**	**Estimate**	**P-value**	
Resistance	**Species**	**Douglas-fir - E. beech**	**85.5**	**90.8**	**-5.27**	**0.00**	***
	Mixture	mixed - pure	89.0	88.4	-0.30	0.88	
	Species:Mixture	Douglas-fir mixed - Douglas-fir pure	85.9	85.3	-0.66	0.79	
	Species:Mixture	E. beech mixed - E. beech pure	90.8	90.9	0.07	0.98	
Growth recovery time	**Species**	**Douglas-fir - E. beech**	**2.2**	**1.7**	**0.41**	**0.00**	**
	Mixture	mixed - pure	1.9	1.9	-0.05	0.80	
	Post-years	**average - adverse**	**2.0**	**2.2**	**-0.38**	**0.01**	**
	Post-years	**average - good**	**2.0**	**1.5**	**0.46**	**0.00**	***
	Post-years	**adverse - good**	**2.2**	**1.5**	**0.85**	**0.00**	***
	Species:Mixture	Douglas-fir mixed - Douglas-fir pure	2.0	2.3	-0.22	0.37	
	Species:Mixture	E. beech mixed - E. beech pure	1.8	1.6	0.12	0.60	
	Species:Post-years	Douglas-fir good - E. beech good	1.8	1.3	0.30	0.11	
	Species:Post-years	Douglas-fir average - E. beech average	2.2	1.9	0.31	0.14	
	Species:Post-years	**Douglas-fir adverse - E. beech adverse**	**2.7**	**1.9**	**0.63**	**0.00**	***
	Mixture:Post-years	mixed good - pure good	1.5	1.5	0.05	0.85	
	Mixture:Post-years	mixed average - pure average	1.8	2.2	-0.32	0.24	
	Mixture:Post-years	mixed adverse - pure adverse	2.3	2.2	0.12	0.61	
	Species:Mixture:Post-years	Douglas-fir mixed good - Douglas-fir pure good	1.7	1.8	0.10	0.75	
	Species:Mixture:Post-years	E. beech mixed good - E. beech pure good	1.4	1.3	-0.01	0.97	
	Species:Mixture:Post-years	Douglas-fir mixed average - Douglas-fir pure average	1.9	2.4	-0.41	0.24	
	Species:Mixture:Post-years	E. beech mixed average - E. beech pure average	1.8	2.0	-0.22	0.50	
	Species:Mixture:Post-years	Douglas-fir mixed adverse - Douglas-fir pure adverse	2.4	2.9	-0.35	0.27	
	Species:Mixture:Post-years	**E. beech mixed adverse - E. beech pure adverse**	**2.3**	**1.6**	**0.60**	**0.04**	*
	Stand level (2003)						
Resistance	Species:Mixture	Douglas-fir pure stand - Mixed stand	80.8	83.1	-2.40	0.45	
		Douglas-fir pure stand - E. beech pure stand	**80.8**	**89.5**	**-8.70**	**0.00**	**
		Mixed stand - E. beech pure stand	**83.1**	**89.5**	**-6.30**	**0.05**	*
G. recovery	Species:Mixture	Douglas-fir pure stand - Mixed stand	2.5	2.5	0	0.9	
		Douglas-fir pure stand - E. beech pure stand	2.5	3.1	-0.6	0.1	
		Mixed stand - E. beech pure stand	2.5	3.1	-0.5	0.2	

*Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

Table 3 Estimates for ecological parameters with effect on resistance, growth recovery time and increment loss due to drought separated for individual tree level and stand level. Hyphens indicate that the respective independent variable was neglected in the model (Eq.5 and Eq.6). The lower part of the table provides information about the quality of the model.

Tabelle 3 *Geschätzte Koeffizienten der Umweltvariablen für die Indizes Resistenz, Erholungszeit und Zuwachsverlust durch das Trockenjahr auf Einzelbaum- und Bestandesebene. Bindestrichen zeigen, dass die Variable nicht in der Modellformel (Formel 5 und 6) berücksichtigt wurden. Der untere Teil der Table enthält Informationen über die Modellgüte.*

Independent variables:	Dependent variables: **Individual tree level (1950 - 2010)**				**Stand level (2003)**		
	Resistance (%)		***Growth recovery time (year units)***		***Resistance (%)***	***Growth recovery time (year units)***	***Loss due to drought (%)***
	Douglas-fir	***E. beech***	***Douglas-fir***	***E. beech***			
DBH	**-0.415***** *(0.064)*				-	-	-
Rel DBH		**-0.131***** *(0.019)*			-	-	-
Basal area per hectare							**0.004*** *(0.002)*
Mixing proportion of E. beech	-	-	-	-	**8.150*** (3.016)		
Age	**0.164**** *(0.054)*		**0.017***** *(0.004)*		**0.135*** *(0.056)*	**0.022**** *(0.007)*	
Base-richness	**-4.407*** *(0.203)*	**-4.016 .** *(1.775)*			**-4.225 .** *(2.196)*		0.012 *(0.007)*
Water supply						**0.378*** *(0.135)*	
Precipitation							**0.001*** *(0.001)*
Temperature							0.132 *(0.124)*
Intercept	**106.288***** *(6.494)*	**114. 199***** *(5.728)*	**1.579***** *(0.198)*	**1.658***** *(0.144)*	**85.394***** *(7.545)*	-0.18 *(0.755)*	-2.241 *(1.444)*
Observations	1556	2242	1556	2242	54	54	54
Log Likelihood	-7237.847	-10805.140	-3827.272	-5502.645	-195.076	-90.51	-21.146
Akaike Inf. Crit.	14491.690	21624.280	7666.543	11015.290	404.152	193.019	58.293
Bayesian Inf. Crit.	14534.490	21664.280	7698.642	11043.860	418.075	204.953	74.204

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

3.2.2. Stand level

Analysis of the stand level reaction showed that the resistance of the European beech pure stands (Rt = 89.5) on drought event were significantly greater than in mixed stands (Rt = 83.1, $p<0.05$) and that of Douglas-fir in pure stands (Rt = 80.8, $p<0.01$) (Table 2, see also Fig. 6). The mixed stands range between the European beech and the Douglas-fir pure stands. The analysis of the effect of co-variables indicated an increasing resistance with increasing age and with decreasing proportion of European beech (Table 3). Also base-poorer sites appeared to bear higher resistance.

The climate specification of 2003 represented an extreme drought year for all triplets and an adverse post-year in 2004 for most of the triplets. Only in case of four triplets a year with good or average weather conditions followed 2003. Concerning the drought year 2003 growth recovery time did not differ significantly between the stands. Douglas-fir pure (GRT = 2.50) and mixed stands (GRT = 2.53) tended to recover relatively faster, whereas European beech pure stands (GRT = 3.06) needed more time to return to their initial level. In contrast to the positive influence of age on resistance, a higher age extended the growth recovery time. Also improved water supply characteristics of soils extended growth recovery time.

The loss of increment caused by the drought year 2003 was on average 50% of the long-term growth level, independent of species or mixture (Table 4). But reflecting the general growth levels absolute basal area increment loss due to drought was highest in Douglas-fir pure stands. The loss increased in plots with higher stand density (basal area per hectare) (Table 3). Additionally, base-poverty, higher precipitation and warmer temperatures led to a lower increment loss due to drought.

Table 4 Absolute and relative loss of increment at stand level for the drought year 2003. SD represents the standard deviation. The significant differences were tested by a multiple comparison of the linear mixed models and are indicated by letters. The loss of volume increment was calculated on the independent variables basal area increment, age and their interaction (Eq. 1).

Tabelle 4 *Absoluter und relative Zuwachsverlust durch das Trockenjahr 2003 auf Bestandesebene. SD steht für die Standardabweichung. Die signifikanten Unterschiede, gekennzeichnet durch die Buchstaben, wurden durch einen Post-hoc-Test überprüft und basieren auf der Grundlage der linearen gemischten Modelle. Der Volumenzuwachsverlust basiert auf einer Hochrechnung von Grundflächenzuwachs, Alter und deren Wechselwirkung (Form).*

Mixing type	**Loss of basal area increment (m2 ha-1)**	**SD**		**Relative loss of basal area increment (%)**	**SD**		**Loss of volume increment (m3 ha-1)**	**SD**
Douglas-fir pure stand (1.60 m2 ha-1 a-1)	0.82	0.49	a	0.52	0.29	A	15.13	11.11
Mixed stand (1.29 m2 ha-1 a-1)	0.65	0.35	ab	0.50	0.25	A	11.12	6.10
E. beech pure stand (0.91 m2 ha-1 a-1)	0.45	0.44	b	0.50	0.32	A	6.54	5.48
Total	0.64	0.45		0.50	0.28		10.93	7.56

4. Discussion

4.1. Tree chronology characteristics

As expected, mean basal area increment of Douglas-fir was higher than for European beech. Individual growth of Douglas-fir in mixture overtopped the increment of Douglas-fir in pure stands. This is conform with the results of a previous study, based on the same sample plots (Thurm and Pretzsch, in review). The authors reported that overyielding in Douglas-fir – European beech stands is realized mainly by Douglas-fir. They assumed that higher productivity of Douglas-fir in mixture results from an improved growth on individual tree level. Niche complementarity, fostered by improved resource utilization, may lead to accelerated growth of species in mixture (Vandermeer, 1989). Structural diversification, through dominant Douglas-fir and inferior European beech, as observed here in mixed stands (Thurm and Pretzsch, in review), enables an increasing utilization of incoming light (Thomas et al., 2015). Studies of Hendriks and Bianchi (1995) and Thomas et al. (2015) supposed that roots of Douglas-fir dominate in the top soil, whereas those of European beech spread into deeper soil layers. This may promote Douglas-fir by better access to nutrient because the uppermost soil layer is the dominant area of decomposition and mineralization of organic matter (Thomas et al., 2015). Species-specific basal area increment varied stronger between European beeches in pure mixed stands than for Douglas-firs, as indicated by the pattern of Gleichlaeufigkeit. This may result from a higher variation in diameter and tree heights for European beech compared to Douglas-fir (Pretzsch and Schütze, 2016).

Growth responses of large trees, who dominated the stand, are less influenced by competition. Their growing performance is stronger connected with the weather conditions than the suppressed trees (Chhin et al., 2008; Piutti and Cescatti, 1997). The calculation of the Gleichlaeufigkeit with a conglomeration of large and small trees results in a declined Gleichlaeufigkeit.

Autocorrelation is assumed to indicate the existence of low frequency variation in tree chronologies and a higher persistency of growth level from year to year. Here, Douglas fir in pure stands showed highest values of autocorrelation but contrasting low values in mixed stands. LaMarche and Stockton (1974) analyzed the link between autocorrelation in tree ring growth series and needle growth. They showed that needle growth by bristlecone pines (*Pinus longaeva* D.K. Bailey and *P. aristata* Engelm.) decreased under negative weather conditions. Consequently, the photosynthetic potential of a tree with perennial needles declined resulting in declined current year ring growth. The influence of the previous year's needles still increase by the fact that the photosynthetic rate of previous year needles can be greater than current year needles (Clark, 1961; Hébert et al., 2011; Hom and Oechel, 1983). In summary, autocorrelation in growth series of conifers having perennial needles should be higher than that of broadleaved species. This can also be seen in a study of silver fir (*Abies alba* Miller) and European beech by Lebourgeois et al. (2014). The low autocorrelation of Douglas-fir which we found in mixed stands might be related to improved resource supply. Douglas-fir seems to be less influenced by the resource store of previous years. Annual variation of the photosynthetic leaf area may be stabilized by higher resource use efficiency in mixed stands.

Sensitivity, here measured by the mean sensitivity and the Gini-coefficient tend to be greater on sites with harsher conditions (Fritts et al., 1965). We observed that European beech showed an increased sensitivity in mixed stands compared to pure stands whereas for Douglas-fir an opposing trend was revealed. This positive mixing effect on sensitivity was also observed by silver fir which growing together with European beech (Lebourgeois et al., 2013). In contrast, the same study could not detect similar effects in a mixture of silver fir and Norway spruce. It might be that the partitioning of water resources varies between pure stands and mixed stands of coniferous and broad-leave trees. Douglas-fir as a coniferous species transpires nearly throughout the whole year (Waring and Running, 1978). The transpiration time of European beech is restricted to the growing period, where the trees carry leaves. During spring times, Douglas-fir in mixed stands profits from higher water availability in spring due to less intra-specific competition than in pure stands. When European beech starts to transpire, water supply is already reduced by Douglas-fir. Moore et al. (2011) observed this temporal partitioning of water utilization by Douglas-fir and red alder. We assume that this is a main reason for the differences in sensitivity between Douglas-fir and European beech in mixed stands. This is also in accordance with the hypothesis that the lower autocorrelation of Douglas-fir in mixed stands is related to a higher independency of previous year resources, which would reflect a facilitation effect by European beech.

4.2. Drought year analyses

4.2.1. Individual tree level

Resistance to drought events of Douglas-fir was generally lower than that of European beech. This is in line with the results of Weigt et al. (2015), who also examined the resistance of European beech and Douglas-fir. But the species-specific differences must be reflected in the context of generally higher absolute increment rates of Douglas-fir, especially in mixed stands. An analysis with the absolute increment values was not appropriate here, because tree age and residual trends may obscure possible responses (also mentioned in chapter 2.4). Resistance in our study did not differentiate between the mixing types. This consists with findings of resistance for European beech admixed to other species (Metz et al., 2016).

Concerning growth recovery time there was also a significant species-specific difference, with longer growth recovery time for Douglas-fir. The growth recovery time was reduced for Douglas-fir in mixed stands compared to pure stands and extended for European beech, but not on a significant level. These trends are in line with the findings for autocorrelation and mean sensitivity. We assume that trees in pure stands start simultaneously to grow in the subsequent year. In mixed stands Douglas-fir may have an advantage by starting to grow earlier than European beech, providing the chance to replenish its reserves more quickly. Douglas-fir in mixed stands starts to deplete water resources earlier during the growing season and this better access to water may shorten the growth recovery time in the years after drought. In cases where a year with below average water supply follows a dry year the effect of growth recovery time extension for European beech becomes more pronounced and significant. This supports the hypothesis that in mixed stands water resources are temporally more partitioned to Douglas-fir. This would lead to a stabilization effect for this coniferous species. As mentioned in chapter 4.1, a spatially different utilization of water resource by diverging rooting patterns between both species is also possible, but current studies do not enable general statements.

Anderegg et al. (2015) examined the recovery of stem growth after drought on a huge amount of forest sites across the globe and several genera. They found a general recovery time between 1 to 4 years after drought. During the drought year 2003, comparable to the stress conditions considered by Anderegg et al. (2015) the reaction of the trees examined here showed an average growth recovery time of 2.7 years and lies within the reported range.

Our data reveal, that the inter-specific differences of the growth recovery time between single drought event and extended drought periods (adverse post-year) increase. This would lead to the conclusion that Douglas-fir is disadvantaged by extended dryer weather conditions, whereas European beech is better capable to compensate this situation. We suggest, that growth recovery time is a good measure to distinguish between iso- or anisohydric traits of tree species.

Anderegg et al. (2015) drew the conclusion that species with lower safety margin of leaf water potential (isohydric species) tend to slower growth recovery after drought. Similar features were hypothesized by McDowell et al. (2002) stating greater suffering for isohydric species during extended drought periods. From this, Douglas-fir tends to have a more isohydric character than European beech.

Klein and Niu (2014) recommended to differ iso- and anisohydric characteristics by the stomatal conductance of leaf water potential at 50% of the maximum ($\Psi g_s 50$). According to Woodruff et al. (2008), $\Psi g_s 50$ for Douglas-fir provinces from Wind River Basin of southwestern Washington (USA) range between from -0.75 to -1.25. Stout and Sala (2003) measured a $\Psi g_s 50$ of –4.83 for Douglas-fir var. *glauca.* In the current paper we investigated Douglas-fir var. *viridis*. European beech had a $\Psi g_s 50$ from -2.12 to -3.17 (Aranda et al., 2000; Köcher, 2013). This would strengthen the assumption that Douglas-fir has isohydric and European beech anisohydric traits. The anisohydric strategy and the greater cross section of xylem predisposed European beech for hydraulic failure (McDowell et al., 2008). Nevertheless, several additional factors influenced the risk of hydraulic failure, like tree height, crown disposition and root system which were not all measured here.

The hydric characteristics might also be a reason for the unchanged resistance in mixed stands versus pure stands. In drought years, Douglas-fir stomatal safety margin leads to an earlier stop of water consumption than that of European beech. This enables European beech to use free water resources and prevent a more drastic drop of increment compared to pure stands (Pretzsch et al., 2013).

4.2.2. Stand level

During the drought year 2003 the stand level resistance concerning basal area increment followed the species specific single tree pattern being higher in European beech than in Douglas-fir stands. Mixed stands showed an intermediate response, being only significantly different from European beech stands. Due to the high proportion of Douglas-fir in mixed stands, the value for resistance was closer to the reaction of Douglas-fir pure stands. When comparing the measured resistance in mixed stands with the expected value from pure stands, weighted by the mixing proportion no deviation occurred (Appendix C). Because of the responses of both species (Jucker et al., 2014) no compensatory mixing effect concerning resistance was detectable.

In contrast to the general pattern of the growth recovery time for European beech, in 2003 European beech needed much longer to recover. In this case initial growth level was reached even later than for Douglas-fir. This might be a consequence of the subsequent year 2004 when European beech had a high fructification rate (Konnert et al., 2014; Landesforst Rheinland-Pfalz, 2014b). Eichhorn et al. (2008) observed a decreased stem wood production for European beech in 2004 in North Germany. They detected a shift of biomass production from stem wood to fruits. Heavy 'mast'-years generally lead to a high consumption of reserve stores (Burschel, 1966). This might be a reason for the extended growth recovery time for European beech.

Nevertheless, the relative loss due to drought amounted to around 50% for both species and mixing types. The variation in loss of absolute basal area increment was a result of the diverging levels of increment rates between Douglas-fir and European beech. When reflecting stand volume growth a loss due to drought of 15.1 m3 ha-1 was found for Douglas-fir pure stands, 11.1 m3 ha-1 for mixed stands and 6.5 m3 ha-1 for European beech stands (Table 4). Concerning the loss of volume increment, the absolute differences between mixing types is more pronounced compared to the loss of basal area increment. This bias might be induced by the applied volume estimation function (Appendix B), but is presented here to provide a dimension for the forest management. The presentation of relative and absolute drought responses is a major issue of our study. Relative values provide a biological understanding, whereas absolute values take differences in productivity of tree species into account.

4.3. Changing patters along ecological gradients

The applied statistical models revealed that several ecological variables influence drought response of trees. The response of ecological system to ecological conditions is inherently nonlinear (Burkett et al., 2005). Therefore, we additionally checked the courses of independent variables with generalized additive mixed models. Because crucial variables showed linear or almost linear courses we decided to use linear mixed models for better interpretation.

The observed linear course may result because our study covering as well the current planting area of Douglas-fir and European beech pure and mixed stands in Germany but the potential growing area would be greater. So a greater gradient may show a nonlinear course.

It seems that on fertile sites drought has a more severe impact on growth. Higher base richness reduces resistance of Douglas-fir and European beech at individual tree and at stand level. It is assumed that base limited systems are less influenced by short-term water restriction than water limited systems (Mitscherlich, 1909). On sites with higher water supply the impact of drought events also seems to have a more severe impact in terms of growth recovery time and relative growth loss at stand level. Sergent et al. (2014b) investigated Douglas-fir on different fertile sites and found a better recovery on the more fertile ones. The influence of nutrients can have variable effects (Rennenberg et al., 2006)and is less well understood. Additionally, different proveniences response variable on drought stress (Eilmann et al., 2013; García-Plazaola and Becerril, 2000; Sergent et al., 2014a) and may compensate drought stress an different ways.

Tree age was also a significant co-variable in most models. It seems to trigger a twofold pathway of reaction concerning Douglas-fir. On the one hand resistance is higher with progressive tree age on the other hand growth recovery time is extended. An age-related increase of drought stress sensitivity was found for European larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) by Carrer and Urbinati (2004). They supposed that hydraulic constraints increase with tree age and tree height. The assumption is that the gravitation potential in the hydraulic pathways of plants increases with the height (Matyssek et al., 2010; McDowell et al., 2008). The height growth dynamic of Douglas-fir and its huge hydraulic path length may explain such age-dependent drought sensitivity. We additionally performed a drought year analysis on a small collective of sample trees for which we reconstructed tree heights (not shown in the method and result section). The results reveal a significant interaction between increasing height and decreasing resistance and increasing growth recovery time. We assume that the tree height is a major driver of drought response. This interaction of increasing size and increasing sensitivity could also observed for European beech and silver fir (Mérian and Lebourgeois, 2011) and for Scots pine(Merlin et al., 2015). For Douglas-fir in our study, tree age correlates very closely with tree height. This is not the case for European beech. Because of their shade-tolerant traits, European beech forms a wider range of tree heights at similar age (Pretzsch and Schütze, 2016). Therefore, no correlation of tree age with resistance was found for European beech. The negative correlation of the relative DBH with resistance indicates that trees in lower social classes with lower heights and smaller tree rings have a better resistance. This is conform to the findings concerning size dependent patterns of resistance.

The mentioned contradiction of the age effect of Douglas-fir at individual tree level is explained when considering the DBH effect. We suggest that the older trees with smaller DBH had higher wood density and form stronger hydraulic pathways bearing better resistance against hydraulic pressure under drought (Hacke et al., 2001).

The PCA indicated a general higher climate sensitivity of younger compared to older stands. As tree chronologies have been analyzed throughout the entire tree age this may reveal a climate change effect on trees' sensitivity. Young stands have faced a greater share of time under recent climate change conditions than older ones. Biondi and Qeadan (2008b) also reported from a species-unspecific change in sensitivity over a time period of 400 years.

Increment loss to drought was linked with stand density. With increasing basal area the stand level loss also increased. This outcome is in line with the findings of Rais et al. (2014), who found higher resistance in Douglas-fir plantation with lower stand density. Lebourgeois et al. (2014) confirmed a negative impact on sensitivity with increasing stand density for European beech and silver fir, as well. Rais et al. (2014) concluded that lower stand density is associated with better availability of soil space and a larger root system of the individual tree.

5. Conclusions

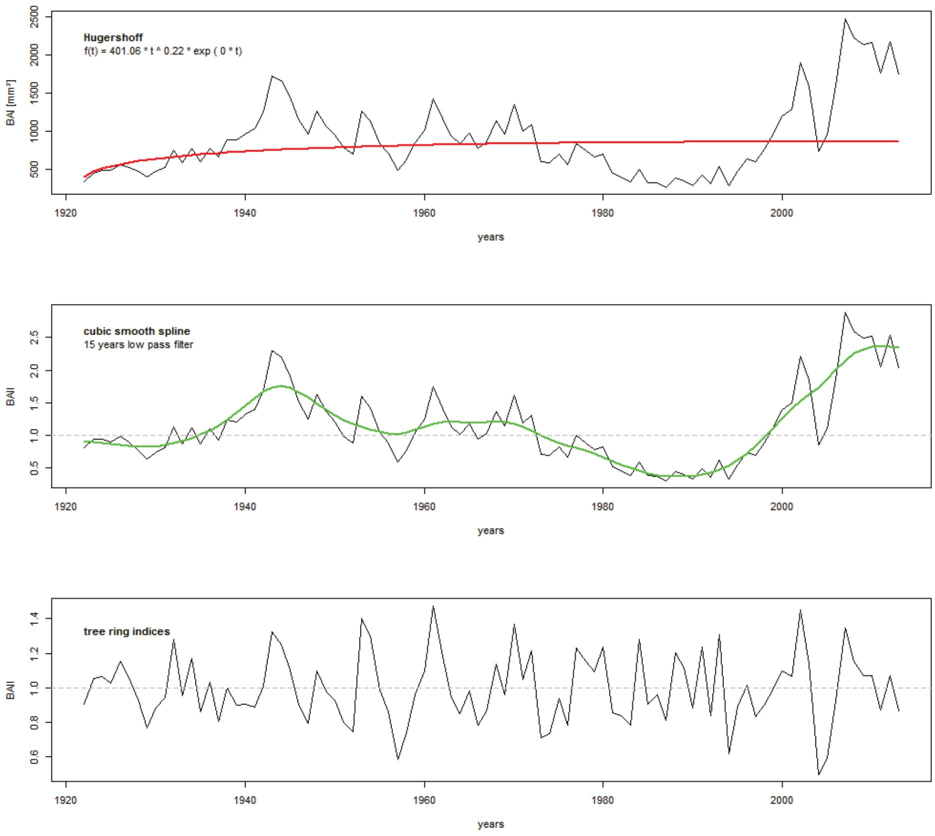
Our study of mixing effects between Douglas-fir and European beech on individual tree and stand level comprised a wide range of site conditions, stand ages, and mixing proportions in Central Europe. The results give evidence that Douglas-fir profits from being mixed with European beech in terms of productivity, drought stress release, and time of growth recovery. The stabilized growth of Douglas-fir seems to be on the expense of European beech. Nevertheless, mixed stands with European beech contribute to risk mitigation for the high productive coniferous Douglas-fir.

The study indicate that base limited systems are less affected by drought events and that taller trees have less resistance, both facts are independent from species and mixing type.

The study focused on tree ring information at DBH height. Although the trunk represents a major share of total tree biomass (Pretzsch et al., 2014), resource allocation pattern between above and below ground organs (Nikolova et al., 2011; Pretzsch et al., 2012) or wood density (Toïgo et al., 2015) may also change during drought periods. Considering these aspects in future analyses may refine the picture of mixing effect between Douglas-fir and European beech.

Appendix

Appendix A Exemplary illustration of the double detrending method for a single European beech tree chronology



The figures show the individual European beech No. 1003_11_1 and the steps of double detrending applied to all series of the study. A) Original basal area increment course (BAI) calculated on the mean of two cores per tree (black line) Growth trend estimated according to Hugershoff equation (red line). B) Index Series (BAII) (black line) as basal area increment index (BAII) and trend estimated by cubic spline of 15-year wavelength (green line). C) Resulting basal area increment indices after two step detrending (black line)

Appendix B Estimates of the regression coefficients (Eq.1) and model quality for calculating volume area loss due to drought.

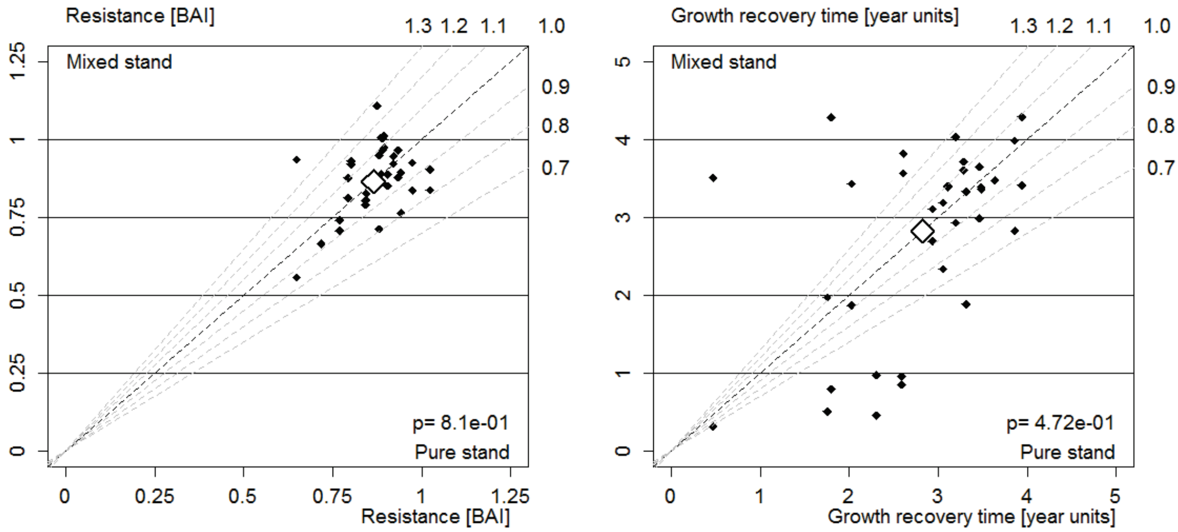
The table contains the coefficients a1...a3 of the fixed effects from the model which estimated volume by basal area increment loss. The last row represents the coefficient of determination (R²).

Mixing type	a0	a1	a2	a3	R^2
Douglas-fir pure stand	0.50	1.78	0.57**	-0.16	0.81
Mixed stand	0.75	-2.58 .	0.50**	0.89*	0.80
European beech pure stand	-0.75	1.31	0.86***	-0.04	0.82

*Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

Appendix C Comparison of pure and mixed stands resistance and growth recovery time

This figure shows the comparison of the observed parameter value for mixed stand ($p1.2$ – y-axis) and expected value derived from pure stands ($\hat{p}1.2$ –x.axis). The resistance and growth recovery time of the expected mixed stand was calculated by summarizing the species-specific values of pure stands (p_1 ,p_2) weighted by the species-specific mixing proportion in mixed stand (m_1, m_2); $\hat{p}1.2 = p_1 * m_1 + p_2 * m_2$ (for a more detailed view see Pretzsch et al. (2010)).



Supplementary material

See “Supplementary material 1.pdf”, “Supplementary material 2.pdf” and “Supplementary material 3.pdf”

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References

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M. et al, 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, pp. 528–532.

Aranda, I., Gil, L., Pardos, J.A., 2000. Water relations and gas exchange in Fagus sylvatica L. and Quercus petraea (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. Trees 14, pp. 344–352.

Barton, K., 2015. MuMIn: Multi-model inference.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4.

Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. Trends in Ecology & Evolution 9, pp. 191–193.

Binkley, D., Greene, S., 1983. Production in mixtures of conifers and red alder: the importance of site fertility and stand age., in: Ballard, R., Gessel., S. (Eds.), International Union of Forestry Research Organizations Symposium on Forest Site and Continuous Productivity, pp. 112–117.

Biondi, F., Qeadan, F., 2008a. A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Research 64, pp. 81–96.

Biondi, F., Qeadan, F., 2008b. Inequality in paleorecords. Ecology 89, pp. 1056–1067.

Bolte, A., Czajkowski, T., Kompa, T., 2007. The north-eastern distribution range of European beech a review. Forestry 80, pp. 413–429.

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science 63, pp. 625–644.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, pp. 115–124.

Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, pp. 251–258.

Burkett, V.R., Wilcox, D.A., Stottlemyer, R., Barrow, W., Fagre, D., Baron, J. et al, 2005. Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. Ecological complexity 2, pp. 357–394.

Burnham, K.P., Anderson, D.R., 1998. Model selection and inference: A practical information-theoretic approach. Springer, New York.

Burschel, P., 1966. Untersuchungen in Buchenmastjahren. Forstw Cbl 85, pp. 204–219.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, pp. 1958–1965.

Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. Ecology 85, pp. 730–740.

Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2008. Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. Forest Ecology and Management 256, pp. 1692–1703.

Clark, J., 1961. Photosynthesis and respiration in white spruce and balsam fir. State University College of Forestry, Syracuse, N.Y. State University College of Forestry at Syracuse University. Technical publication no. 85.

Deutscher Wetterdienst, 2015. Grids germany-monthly: mean temperature and precipitation. ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/monthly/, 18 March 2016.

Eichhorn, J., Dammann, I., Schönfelder, E., Albrecht, M., Beck, W., Paar, U., 2008. Untersuchungen zur Trockenheitstoleranz der Buche am Beispiel des witterungsextremen Jahres 2003. Assessment of the drought resistance of beech exemplified by the 2003 extreme weather conditions. Ergebnisse angewandter Forschung zur Buche 3, pp. 109–134.

Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species' drought tolerance. Tree Physiology 32, pp. 178–187.

Eilmann, B., Vries, S.M.G. de, den Ouden, J., Mohren, G.M.J., Sauren, P., Sass-Klaassen, U., 2013. Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (Pseudotsuga menziesii (Mirb.)) provenances. Forest Ecology and Management 302, pp. 133–143.

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht: 203 Tabellen, 6., vollst. neu bearb. und stark erw. Aufl. Ulmer, Stuttgart. UTB 8104.

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, pp. 282–292.

Fritts, H.C., 1976. Tree rings and climate. Acad. Pr, London.

Fritts, H.C., Smith, D.G., Cardis, J.W., Budelsky, C.A., 1965. Tree-Ring Characteristics Along a Vegetation Gradient in Northern Arizona. Ecology 46, pp. 394–401.

García-Plazaola, J.I., Becerril, J.M., 2000. Effects of drought on photoprotective mechanisms in European beech (Fagus sylvatica L.) seedlings from different provenances. Trees 14, pp. 485–490.

Gauer, J., Kroiher, F. (Eds.), 2012. Waldokologische Naturraume Deutschlands: Forstliche Wuchsgebiete und Wuchsbezirke – Digitale Topographische Grundlagen – Neubearbeitung Stand 2011. Landbauforschung vTI Agriculture and Forestry Research Sonderheft Nr. 359.

Hacke, G.U., Sperry, S.J., Pockman, T.W., Davis, D.S., McCulloh, A.K., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126, pp. 457–461.

Hartmann, H., 2011. Will a 385 million year-struggle for light become a struggle for water and for carbon? - How trees may cope with more frequent climate change-type drought events. Global Change Biology 17, pp. 642–655.

Hébert, F., Thiffault, N., Munson, Alison D., 2011. Field Photosynthesis Measurements on Black Spruce (Picea mariana): Does Needle Age Matter? Communications in Soil Science and Plant Analysis 42, pp. 2738–2750.

Hendriks, C., Bianchi, F., 1995. Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. Netherlands Journal of Agricultural Science 1995, pp. 321–331.

Hermann, R., Lavender, D., 1999. Douglas-fir planted forests. New Forests 17, pp. 53–70.

Holmes, R.L., Adams, R.K., Fritts, H.C., 1986. Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin with procedures used in the chronology development work including users manuals for computer programs COFECHA and ARSTAN.

Hom, J.L., Oechel, W.C., 1983. The photosynthetic capacity, nutrient content, and nutrient use efficiency of different needle age-classes of black spruce (Piceamariana) found in interior Alaska. Can. J. For. Res. 13, pp. 834–839.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. Biom. J. 50, pp. 346–363.

Hugershoff, R., 1936. Die mathematischen Hilfsmittel der Kulturingenieurs und Biologen: Herleitung von gesetzmäßigen Zusammenhängen als Manuskript veröffentlicht, Dresden.

Husson, F., Josse, J., Le, S., Mazet, J., 2015. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining.

IPCC, 2014. Climate Change 2014: Synthesis Report.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., Knops, J., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. Ecol Lett 17, pp. 1560–1569.

Kelty, M., 1992. Comparative productivity of monocultures and mixed-species stands, in: Kelty, M., Larson, B., Oliver, C. (Eds.), The Ecology and Silviculture of Mixed-Species Forests. Springer Netherlands. Forestry Sciences, pp. 125–141.

Klein, T., Niu, S., 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct Ecol 28, pp. 1313–1320.

Kleinschmit, J., Bastien, J.C., 1992. IUFRO's role in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco.) tree improvement. Silvae genetica 41, pp. 161–173.

Klimo, E., Hager, H., Kulhavý, J. (Eds.), 2000. Spruce Monocultures in Central Europe: Problems and Prospects. European Forest Institute.

Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. Eur J Forest Res 127, pp. 89–101.

Köcher, P., 2013. Hydraulic traits and their relevance for water use strategies in five broad-leaved tree species of a temperate mixed forest. Niedersächsische Staats- und Universitätsbibliothek Göttingen, Göttingen.

Konnert, M., Schneck, D., Zollner, A., 2014. Blühen und Fruktifizieren unserer Waldbäume in den letzten 60 Jahren. LWF Wissen, pp. 37–45.

LaMarche, V.C.J., Stockton, C.W., 1974. Chronologies from Termperature-Sensitive Bristlecone Pines at Upper Treeline in Western United States. Tree-Ring Bulletin 1974, pp. 21–45.

Landesforst Rheinland-Pfalz, 2014a. Forsteinrichtung Rheinland-Pfalz: Basenaustattung, Wasserhaushalt.

Landesforst Rheinland-Pfalz, 2014b. Waldzustandsbericht 2014, Mainz.

LeBlanc, D.C., 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Can. J. For. Res. 20, pp. 1399–1407.

Lebourgeois, F., Eberlé, P., Mérian, P., Seynave, I., 2014. Social status-mediated tree-ring responses to climate of Abies alba and Fagus sylvatica shift in importance with increasing stand basal area. Forest Ecology and Management 328, pp. 209–218.

Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. Forest Ecology and Management 303, pp. 61–71.

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, pp. 1909–1920.

Lüpke, B.v., 2004. Risikominderung durch Mischwälder und naturnaher Waldbau-ein Spannungsfeld. forstarchiv 75, pp. 43–50.

Matyssek, R., Fromm, J., Rennenberg, H., Roloff, A., 2010. Biologie der Bäume: Von der Zelle zur globalen Ebene ; 32 Tabellen. Ulmer, Stuttgart. UTB Biologie, Agrar- und Forstwissenschaften, Landschaftsplanung 8450.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T. et al, 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologist 178, pp. 719–739.

McDowell, N.G., Phillips, N., Lunch, C., Bond, B.J., Ryan, M.G., 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiology 22, pp. 763–774.

Mérian, P., Lebourgeois, F., 2011. Size-mediated climate–growth relationships in temperate forests: A multi-species analysis. Forest Ecology and Management 261, pp. 1382–1391.

Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. Forest Ecology and Management 339, pp. 22–33.

Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.-D. et al, 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. Glob Change Biol 22, pp. 903–920.

Mitscherlich, E.A., 1909. Das Gesetz des Minimums und das Gesetz des abnehmenden Bodenertrages, Landwirtschaftliche Jahrbücher. Parey, Berlin 38, pp. 537–552.

Moore, G.W., Bond, B.J., Jones, J.A., 2011. A comparison of annual transpiration and productivity in monoculture and mixed-species Douglas-fir and red alder stands. Forest Ecology and Management 262, pp. 2263–2270.

Nikolova, P.S., Zang, C., Pretzsch, H., 2011. Combining tree-ring analyses on stems and coarse roots to study the growth dynamics of forest trees: a case study on Norway spruce (Picea abies [L.] H. Karst). Trees 25, pp. 859–872.

Phipps, R.L., 2005. Some Geometric Constraints on Ring-Width Trend. Tree-Ring Research 61, pp. 73–76.

Piutti, E., Cescatti, A., 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can. J. For. Res. 27, pp. 277–284.

Pretzsch, H., 2005. Diversity and Productivity in Forests: Evidence from Long-Term Experimental Plots, in: Scherer-Lorenzen, M., Körner, C., Schulze, E.-D. (Eds.), Forest Diversity and Function. Springer Berlin Heidelberg. Ecological Studies, pp. 41–64.

Pretzsch, H., Biber, P., 2016. Tree species mixing can increase maximum stand density. Can. J. For. Res., pp. 1–15.

Pretzsch, H., Biber, P., Uhl, E., Hense, P., 2012. Coarse root–shoot allometry of Pinus radiata modified by site conditions in the Western Cape province of South Africa. Southern Forests: a Journal of Forest Science 74, pp. 237–246.

Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J. et al, 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Annals of Forest Science 67, p. 712.

Pretzsch, H., Block, J., Dieler, J., Gauer, J., Göttlein, A., Moshammer, R. et al, 2014. Nährstoffentzüge durch die Holz- und Biomassenutzung in Wäldern. Teil 1: Schätz-funktionen für Biomasse und Nährelemente und ihre Anwendung in Szenariorechnungen. Allg. Forst Jagdztg 185, pp. 261–285.

Pretzsch, H., Schütze, G., 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur J Forest Res 135, pp. 1–22.

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

Rais, A., van de Kuilen, Jan-Willem G., Pretzsch, H., 2014. Growth reaction patterns of tree height, diameter, and volume of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) under acute drought stress in Southern Germany. Eur J Forest Res 133, pp. 1043–1056.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res 46, pp. 627–638.

Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R.S. et al, 2006. Physiological responses of forest trees to heat and drought. Plant biology (Stuttgart, Germany) 8, pp. 556–571.

Reyer, C., Lasch, P., Mohren, G.J., Sterck, F., 2010. Inter-specific competition in mixed forests of Douglas-fir (Pseudotsuga menziesii) and common beech (Fagus sylvatica) under climate change — a model-based analysis. Annals of Forest Science 67, p. 805.

Sergent, A.-S., Bréda, N., Sanchez, L., Bastein, J.C., Rozenberg, P., 2014a. Coastal and interior Douglas-fir provenances differ in growth performance and response to drought episodes at adult age. Annals of Forest Science 71, pp. 709–720.

Sergent, A.-S., Rozenberg, P., Bréda, N., 2014b. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. Annals of Forest Science 71, pp. 697–708.

Speer, J.H., 2010. Fundamentals of tree-ring research. University of Arizona Press.

Stout, D.L., Sala, A., 2003. Xylem vulnerability to cavitation in Pseudotsuga menziesii and Pinus ponderosa from contrasting habitats. Tree Physiology 23, pp. 43–50.

Taegger, S., Kölling, C., 2016. Standortinformationssystem BaSIS. AFZ-DerWald, pp. 10–13.

Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. Journal of experimental botany 49, pp. 419–432.

Thomas, F.M., Bögelein, R., Werner, W., 2015. Interaction between Douglas fir and European beech: Investigations in pure and mixed stands = Wechselwirkungen zwischen Douglasie und Rotbuche : Untersucheungen an Rein- und Mischbeständen. Forstarchiv : forstwissenschaftliche Fachzeitschrift 86, pp. 83–91.

Thurm, E.A., Pretzsch, H., in review. Productivity and structural properties of mixed versus pure stands of European beech (Fagus sylvatica L.) and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) depends on environmental conditions. Ann. For. Sci.

Toïgo, M., Vallet, P., Perot, T., Bontemps, J.D., Piedallu, C., Courbaud, B., 2014. Over-yielding in mixed forests decreases with site productivity. J Ecol, pp. n/a.

Toïgo, M., Vallet, P., Tuilleras, V., Lebourgeois, F., Rozenberg, P., Perret, S. et al, 2015. Species mixture increases the effect of drought on tree ring density, but not on ring width, in Quercus petraea–Pinus sylvestris stands. Forest Ecology and Management 345, pp. 73–82.

Vallet, P., Pérot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway spruce: Evidence based on large-scale inventory data and a generic modelling approach. Journal of Vegetation Science 22, pp. 932–942.

Vandermeer, J.H., 1989. The ecology of intercropping. Cambridge University Press, Cambridge [England], New York.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Climate 23, pp. 1696–1718.

Walter, H., Lieth, H., 1967. Klimadiagramm-Weltatlas: Von Heinrich Walter und Helmut Lieth. G. Fischer, Jena.

Waring, R.H., Running, S.W., 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant Cell Environ 1, pp. 131–140.

Weigt, R.B., Bräunlich, S., Zimmermann, L., Saurer, M., Grams, T.E.E., Dietrich, H.-P. et al, 2015. Comparison of δ(18) O and δ(13) C values between tree-ring whole wood and cellulose in five species growing under two different site conditions. Rapid communications in mass spectrometry : RCM 29, pp. 2233–2244.

Woodruff, D.R., Meinzer, F.C., Lachenbruch, B., 2008. Height-related trends in leaf xylem anatomy and shoot hydraulic characteristics in a tall conifer: safety versus efficiency in water transport. New Phytologist 180, pp. 90–99.

Zerbe, S., 2002. Restoration of natural broad-leaved woodland in Central Europe on sites with coniferous forest plantations. Forest Ecology and Management 167, pp. 27–42.

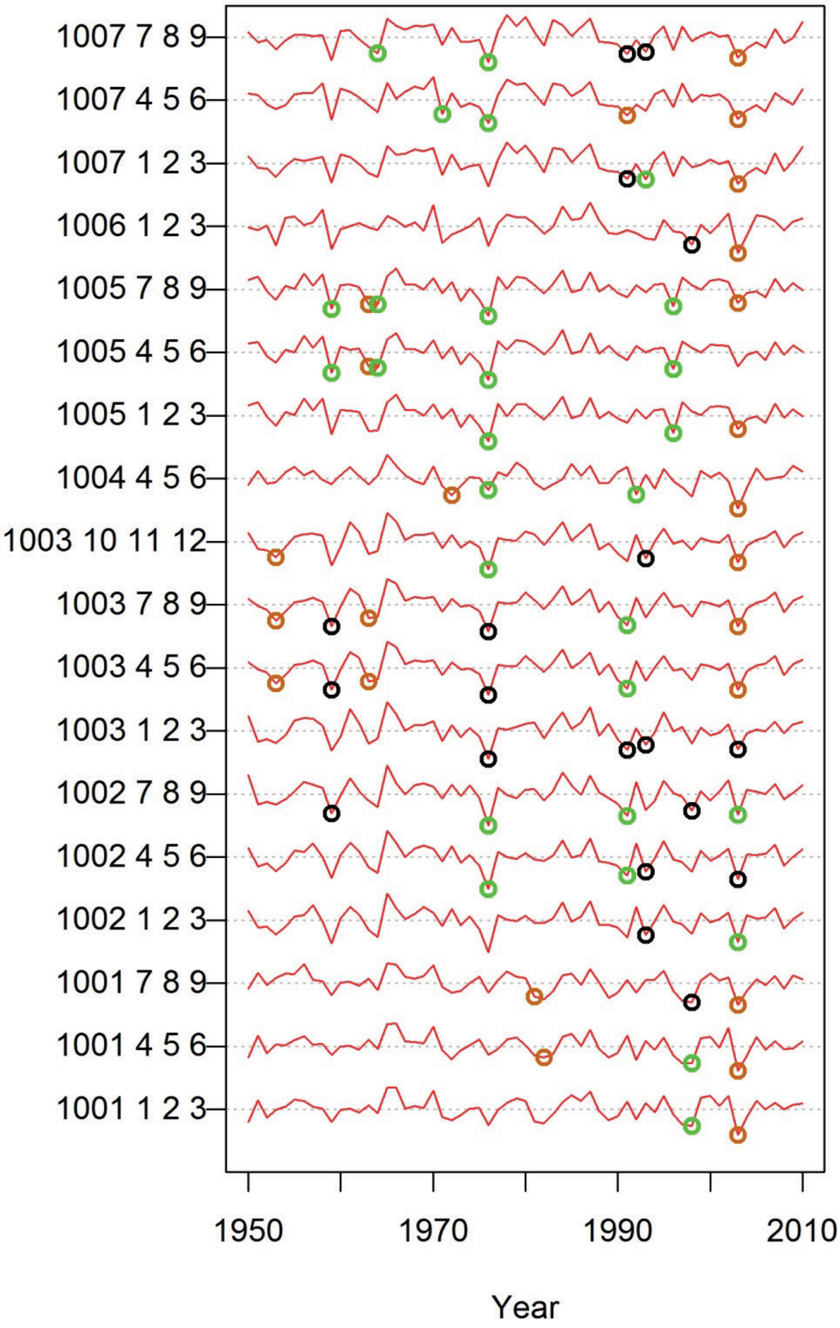
Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. Journal of Ecology 100, pp. 742–749.

Supplementary material

Supplementary material 1 Mean values of the stands of the 18 triplets at the 7 experimental locations. Growing stock, stand density index and Stand basal area based on the last five years before measurement. The growing stock, stand density and basal area of the species in mixed are scaled up to a hectare by mixing proportion.

		Sampling year	**Growing stock m^3 ha^{-1}**					**Reineke's Stand Density Index (1933)**					**Stand basal area m^2 ha^{-1}**				
			Douglas-fir		**European beech**		Mixed	**Douglas-fir**		**European beech**		Mixed	**Douglas-fir**		**European beech**		Mixed stand
experimental location	triplet		pure	mixed	pure	mixed	stand	pure	mixed	pure	mixed	stand	pure	mixed	pure	mixed	
Walkertshofen	1 2 3	2013	435.5	362.4	386.1	145.9	274.6	821	739	1115	451	622	41.0	36.1	43.4	17.6	28.6
	4 5 6	2013	969.3	1242.1	415.3	408.0	842.8	1147	1280	713	786	1043	70.8	84.3	34.0	34.9	60.6
	7 8 9	2013	2001.0	1270.0	506.6	507.4	1085.9	1585	1142	580	702	1036	116.6	80.0	33.6	34.6	69.0
Würzburg	1 2 3	2013	424.2	209.0	120.6	117.1	152.3	1065	739	610	452	562	46.1	28.9	19.7	15.8	20.8
	4 5 6	2013	482.2	665.8	491.7	245.5	385.9	763	900	1061	550	667	39.3	51.0	42.8	23.2	32.5
	7 8 9	2013	1171.8	1176.8	812.5	576.6	884.3	961	861	586	525	697	65.6	65.2	39.0	29.9	48.0
Spessart	1 2 3	2013	755.1	769.5	509.8	245.3	528.6	1079	1158	1243	708	951	59.1	64.3	50.3	28.5	47.8
	10 11 12	2013	1351.0	1592.4	566.9	821.6	1119.3	978	1208	492	736	918	69.4	93.6	29.8	41.9	61.9
	4 5 6	2013	953.5	1139.7	589.4	548.9	737.2	825	1053	620	642	773	58.7	74.2	34.9	33.8	46.7
	7 8 9	2013	1955.3	1263.4	453.3	534.9	701.8	1704	993	549	627	711	113.7	76.7	29.2	33.0	43.0
Eberberger Forst	4 5 6	2013	542.6	606.8	331.6	311.6	418.0	921	1075	627	662	811	47.1	55.7	28.9	27.0	37.3
Daun	1 2 3	2014	872.7	870.6	331.7	228.7	526.6	1116	1060	891	649	840	63.7	66.0	37.0	26.2	44.7
	4 5 6	2014	683.0	884.1	505.1	255.3	549.3	703	788	717	482	625	44.1	59.2	36.9	22.5	39.7
	7 8 9	2014	2005.1	1309.2	538.9	381.6	777.4	1407	1082	568	664	842	103.9	85.6	32.5	31.6	54.7
Hirschwald	1 2 3	2013	539.0	536.5	277.7	230.5	422.4	981	938	690	574	802	49.3	49.6	29.7	24.3	40.1
Pfälzerwald	1 2 3	2012	127.6	93.9	38.2	48.9	72.3	617	714	244	437	581	22.3	23.5	8.0	13.6	18.7
	4 5 6	2012	822.3	948.7	430.4	503.8	681.4	1203	1753	1143	1070	1343	60.4	83.3	47.7	46.6	61.2
	7 8 9	2012	635.2	1224.6	612.7	541.8	800.2	703	919	594	561	697	37.7	67.3	34.5	30.9	44.7
Mean		2013	**929.2**	**898.1**	**439.9**	**369.6**	**608.9**	**1032**	**1022**	**725**	**627**	**807**	**61.6**	**63.6**	**34.0**	**28.6**	**44.4**
Species-specific mean			**913.7**		**404.8**			**1027**		**676**			**62.6**		**31.3**		

Supplementary material 2 A compilation of the drought events, separated by triplets (y - axis). The red lines represented the triplet specific standardized precipitation evapotranspiration index. The dots marked the drought events. The colors of the dots show if after a drought year follows a year with average (black), good (green) or adverse (darkorange) conditions in growing period. Drought years are only selected if there is an existent tree chronology to the event.



Supplementary material 3 Descriptive statistics of the PCA for the first and second dimension. It was used to identify patterns in tree characteristics which are linked to the species, mixing types, age and experimental trial. Age was classified as qualitative variable (young, mature, old). Only significant variables and characteristics are shown.

Statistic of Principal Component analyses for tree characteristics

	Dim.1			**Dim.2**		
Quantitative supplementary variables						
		Correlation	P-value		Correlation	P-value
	MS	0.92	0.00	Mean	0.67	0.00
	Gini	0.89	0.00	GLK	0.59	0.00
	Mean	-0.55	0.00	MS	0.30	0.01
	AC1	-0.59	0.00	AC1	-0.51	0.00
	GLK	-0.61	0.00			
Qualitative supplementary variables						
		R^2	P-value		R^2	P-value
	Experimental trial	0.57	0.00	Mixing type	0.35	0.00
	Species	0.20	0.00	Species	0.27	0.00
	Mixing type	0.21	0.00	Experimental trial	0.23	0.01
	Age	0.09	0.04			
Categorical variables						
		Estimate	P-value		Estimate	P-value
	European beech	0.73	0.00	Mixed Douglas-fir	0.99	0.00
	Mixed European beech	0.88	0.01	Douglas-fir	0.56	0.00
	Young	0.72	0.02	Pure European beech	-0.45	0.04
	Mixed Douglas-fir	-0.86	0.01	Mixed European beech	-0.67	0.00
	Douglas-fir	-0.73	0.00	European beech	-0.56	0.00

Article -III-

Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir *(Pseudotsuga menziesii)* and European beech *(Fagus sylvatica)*

in ***Trees (2016)***

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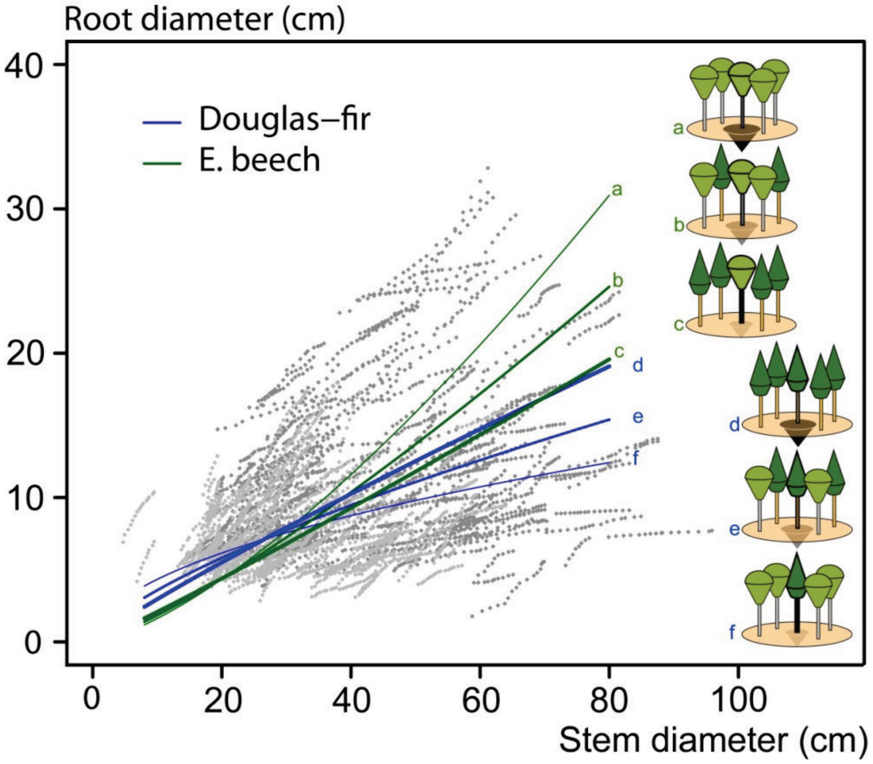

Key message

The study found an increased investment into stem growth (compared to root growth) if trees were surrounded by a complementary species. This response is consistent with known patterns about root-stem allometry under favorable conditions (humidity, stand density).

Abstract

The study investigated partitioning of resources between roots and stems in mono-species and mixed-species stands of Douglas-fir and European beech at four different sites. We combined tree ring analyses of stems and coarse roots in order to scrutinize root-stem allometry with a focus on how it is influenced by species mixture and humidity. The results show that allometry in mixed stands changed in favor of stem growth for both species. Greatest relative allocation into stem growth was observed for individual trees which were completely surrounded by trees of the other species. The data indicate that a decrease of stand density, which was used as a proxy for tree competition, has the same effect on allocation.

To analyze the influence of humidity we used a long and a short-term- index. Based on these we can show that allocation changes with general site conditions and annual humidity variations. We found that on both time scales both species increase resource investment into stem growth if conditions are more humid. Under harsher conditions, allocation shifts into root growth.

The findings contribute to understanding the overyielding in mixed stands. Mixing Douglas-fir and European beech leads to the same allocation patterns as an improvement of site conditions. We suggest that for both species mixture is equivalent to growing on a better site.

Keywords: Mixed stands, Root-stem allometry, Density, Site gradient, Complementarity

Introduction

Since long, species mixture is deemed to be a standard measure for improving productivity and stability of forest stands in the practice of silviculture (Liang et al. 2016). The underlying mechanisms behind such mixing effects and the conditions, under which they occur, however, are only partly understood so far. Many studies were conducted to analyze the aboveground overyielding (Binkley and Greene 1983; Bartelink 1998; Amoroso and Turnblom 2006) and the reduced climate sensitivity of stem growth in mixed stands (Pretzsch et al. 2013; Lebourgeois et al. 2013; Jucker et al. 2014). But for a holistic understanding of the mixing effect, it is essential to investigate the whole system, the aboveground as well as the belowground production.

Several studies could show that an increased resource uptake of the involved species is responsible for the higher productivity often found in mixed stands (Binkley 2003; Forrester et al. 2006b; Thomas et al. 2015). Two mechanisms lead to this increasing uptake, facilitation and species complementary (Larocque et al. 2013). Facilitation may, i.a., modify resource availability, whereas complementarity means a more efficient use of resources which result from niche differentiations.

Changes of resource uptake in mixed stands imply shifts of resource allocation among tree compartments (Dieler and Pretzsch 2013). This can be observed by measuring the size of tree compartments or investigating tree allometry (Amoroso and Turnblom 2006; Erickson et al. 2009; Radosevich et al. 2006). The allometry between root and stem size is of particular interest and has been repeatedly examined (Nikolova et al. 2011; Shainsky et al. 1992). Nevertheless, the results about the influence of intraspecific competition show diverse patterns (Poorter et al. 2012) and species specific analyses, especially for woody plants, seems to be advisable.

In our context of interest, two theories have been advanced to describe the allocation in plants. The first one is the allometric biomass partitioning theory (APT). It describes how organismal attributes change with plant size according to the allometric equation (Peters 1983):

$$\log Y_1 = \log\beta + \alpha \log Y_2. \qquad \text{(Eq. 1)}$$

The variables Y_1 and Y_2 in the equation represent the sizes of two interdependent tree compartments, in our case (coarse) root and stem diameter. The parameter α represents the allometric exponent, while β is a scaling parameter. The constancy of α is the major statement of APT. The second theory differs in this assumption. The optimal partitioning theory (OPT) states that plants allocate additional biomass to the organ that takes up the most limiting resource (Bloom et al. 1985; Thornley 1972). Thereby, the allometric exponent α must be variable. Several studies could show plastic responses of tree compartments beyond the predetermined allometric development (Schall et al. 2012; Meier and Leuschner 2008; Nikolova et al. 2011).

From a methodological point of view, the allocation between belowground and aboveground tree compartments can be scrutinized in different ways. The destructive approach excavates whole trees and weighs aboveground and belowground biomass. Especially for mature trees, this method is extremely laborious and difficult to realize at a large number of trees, which is required for statistical evidence as only one observation per tree is possible. For this reason we applied a method which compares coarse root and stem diameter growth based on increment borings. The method has already been successfully applied in studies about relationships of site and tree allometry (Nikolova et al. 2011; Pretzsch et al. 2012a; Pretzsch et al. 2012b). It allows for sampling a larger number of trees and to obtain retrospective time series per tree.

In the study at hand, the species mixing effect on root-stem allometry is investigated for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and European beech (*Fagus sylvatica* L.) under mixed and monospecific settings. Previous studies identified an overyielding in mixed stands of both species compared to mono-species stands (Bartelink 1998; Thurm and Pretzsch 2016). Notwithstanding, while complementarity of both species in the crown layer was considered a major effect, there was evidence for additional effects in the root zone. Thurm and Pretzsch (2016) supposed that under harsher conditions species complementary shifts from the crown stratum into the soil stratum. Drought year analyses, which could show a complementary water use between Douglas-fir and European beech, confirm this assumption (Thurm et al. 2016). In this context, the study at hand intends to supplement the understanding of mixing effects by investigating root-stem allometry and its possible differences due to species mixing.

Based on the existing knowledge, we start from the hypothesis that (1) Douglas-fir and European beech have different root-stem allometry and (2) that mixing both species modifies their allocation into coarse roots and stems compared to their growth in monospecific environments. In this context we also scrutinize the impact of stand density on allometry. Additionally, we formulated the hypotheses that (3) unfavorable general site conditions (low humidity) influence the allocation in favor of root growth, and that (4) short-term droughts have an analogous effect.

Material and methods

Study area and experimental setup

The study was conducted in spring 2014 on several locations in Southern Germany, which belongs to the warm temperate climate zone. We made use of a triplet experimental setup which has meanwhile turned out an effective method for detecting the mixed stands effects in many studies (e.g. Dirnberger and Sterba 2014; Pretzsch et al. 2015). Each triplet is composed of a pure Douglas-fir stand, a pure European beech stand and a mixed stand of both species (Table 1). The plots consisted of around 20 individuals in pure stand and 20 individual per species in mixed stands (mean plot size 660 m²). Each triplet is characterized by homogenous site conditions, and both species have the same age in the respective pure and the mixed stand. Beside these two requirements, the proximity of the plots was a crucial factor. The distance of the plots inside a triplet is on median 90 meters (maximum 570 m). Another requirement of the triplet was the structural comparability. The proximity of the plots should ensure the same management regime. Selected were fully stocked stands with very low thinning intensity as confirmed by stump counting. The sampling was made in a managed forest, so totally unthinned situations could not be found. However, we deemed thinning intensity of the selected stands close to self-thinning, maximum stand density conditions (for a more detailed description of the setup and stand level growth parameter see Thurm and Pretzsch, 2016).

In total, four triplets comprising twelve plots altogether were established. The four triplets were set up in three different ecological regions which range from drier, warmer sites in the ecological region of *Fränkische Platte* to moister, colder sites in the ecoregion *Schwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaft* (see Gauer and Kroiher (2012) for an overview of the German forest ecoregions). The long-term mean annual temperature covers a span of 8.1 to 8.9 C° with an annual mean precipitation between 727 mm and 1054 mm. Multiannual and monthly temperature and precipitation data were obtained along a 1 x 1 km grid of the German Weather Service (Deutscher Wetterdienst 2015). The profundity of soil was always deeper than 1 m (for the skeleton section in soil depth 60 – 90 cm and the soil type see Table 1).

Table 1 Site characteristics of the 4 triplets indicating ecoregions (Gauer and Kroiher 2012), climate data (Deutscher Wetterdienst 2015), soil data (Taegger and Kölling 2016) and age

Tabelle 1 *Standorteigenschaften der 4 untersuchten Triplets mit Information über die Ökoregion (Gauer und Kroiher 2012), Klimadaten (Deutscher Wetterdienst 2015), Bodendaten (Taegger und Kölling 2016) und das Alter*

Experimental number	**Plot**	**Ecological region**	**Geographic position**		**Elevation**	**Mean annual Temperature (1981 - 2014)**	**Mean annual Precipitation (1981 - 2014)**	**Base-richness from base-poor (1) to base-rich (5)**	**Water supply from very dry (1) to very fresh (7)**	**Sand**	**Clay**	**Silt**	**Soil types by LUFA**	**Age**	**Skeleton section between 60 – 90 cm**
			N-longitude	E-latitude	m above sea level	[°C]	[yr mm-1]			[%]	[%]	[%]		[years]	[%]
1001	4	Tertiäres Hügelland	4393914.11	5343070.81	597	8.1	1011	3	7	55	22	22	sandy loam	56	48.1
	5	Tertiäres Hügelland	4393968.08	5343012.33	597	8.1	1011	3	7	55	22	22	sandy loam	64	48.1
	6	Tertiäres Hügelland	4393923.63	5342981.38	588	8.1	1011	3	7	55	22	22	sandy loam	61	48.1
1002	4	Fränkische Platte	4352612.71	5529925.84	312	8.9	727	4	3	16	59	24	clay	51	0.6
	5	Fränkische Platte	4352830.72	5530457.12	319	8.8	740	4	3	16	59	24	clay	54	0.6
	6	Fränkische Platte	4352743.94	5530469.82	319	8.8	740	4	3	16	59	24	clay	51	0.6
	7	Fränkische Platte	4332272.39	5517554.27	293	8.9	792	4	3	12	56	32	clay	98	1.8
	8	Fränkische Platte	4332385.63	5517503.25	285	8.9	792	4	3	12	56	32	clay	102	1.8
	9	Fränkische Platte	4332372.5	5517593.21	272	8.9	792	4	3	12	56	32	clay	100	1.8
1003	4	Spessart	4323073.04	5541828.39	439	8.1	1054	3	4	31	36	34	clay loam	85	8.3
	5	Spessart	4322988.25	5542160.09	447	8.1	1054	3	4	31	36	34	clay loam	88	8.3
	6	Spessart	4323072.25	5542183.9	449	8.1	1054	3	4	31	36	34	clay loam	87	8.3
Total					**410**	**9**	**895**	**4**	**4**	**29**	**43**	**28**		**75**	

Long and short-term humidity indices

For scrutinizing short-term weather effects on root-stem allometry, we used the standardized precipitation-evapotranspiration index SPEI (Vicente-Serrano et al. 2010). It was summarized as an annual value based on the average of monthly SPEI values in the growing period (May to September). The SPEI uses the monthly differences between precipitation and the climatic water balance after Thornthwaite (1948). The input variables of the climatic water balance are monthly mean temperature and geographic latitude. We calculated the climatic water balance at a time scale of 5 months using a Gaussian kernel function, respective for every triplet. The SPEI indexed a time period from 1950 to 2010, whereas the mean weather conditions in this period represent by the index zero and dry conditions represent by negative indices.

As a measure of long-term climate-induced site productivity, the CVP index by Paterson (1956) was brought to bear (Eq.2).

$$CVP = \frac{Tv \cdot P \cdot G \cdot E}{Ta \cdot 12} \tag{Eq. 2}$$

The CVP index is designed to indicate the growth potential of plants just by climate parameters. Greater CVP indices mean better growing conditions. We calculated it for a time span of 30 years

(1980-2010). The variable Tv is the mean monthly temperature of the warmest month (°C); P is the sum of the annual rainfall (mm a^{-1}); G represents the length of the growing period (number of months). Growing season length in Central Europe is mainly determined by temperature (Vitasse et al. 2009). According to Paterson (1956), we attributed months with an average temperature equal to or higher than 3°C to the growing period. Ta is the difference between the mean maximum temperature of the warmest month and the mean minimum temperature of the coolest month (°C). The variable E is the so-called evapotranspiration reducer, which Paterson (1956) suggested to calculate by relating the solar radiation at the poles to the radiation at the site of interest. While this is meaningful for differentiating potential plant productivity on a global scale as originally intended by Paterson, we used a modification E' introduced by Gandullo and Serrada (1977) which better reflects the comparably small spatial scope of our study. E' considers the real insolation at the plots by using the local annual sunshine hours per year n_{sun} (Eq.3):

$$E' = \frac{2500}{n_{sun}+1000} \qquad \text{(Eq.3)}$$

The sunshine hours were derived from 1 x 1 km grid data from the German Weather Service (Deutscher Wetterdienst 2016). In this study the values of E' fluctuated around 0.97, which represents an average sunshine duration of 1583 hours per year.

Sampling and measurement

For this study, we sampled approximately 10 dominant trees per species at each plot. At these trees, we measured tree height, DBH and diameter of the cored root at the position of coring (see below). In order to quantify the competitive situation of such a tree we determined the basal area (m²/ha) in the tree’s vicinity with an angle count sampling using a relascope (Bitterlich 1952) with the tree of interest in the center of the sampling spot. The local basal area (local BA) was used as a tree individual competition index. For the counted trees we recorded also their affiliation to the groups of coniferous (Douglas-fir) and broadleaved trees (European beech). This enabled us to tell whether competition for a given tree of interest was more inter- or intraspecific (cf. Pretzsch 2009) and we get and individual tree mixing proportion (mixing proportion doug, based on proportion of surrounding Douglas-firs). Finally, we adjusted the mixing proportion of European beech with an equivalence coefficient (1.6). Douglas-fir and European beech have different patterns of spatial occupation. Douglas-fir reached greater stand densities, European beech lower. To avoid a spatial overestimation of one species, it was applied the mentioned coefficient. The equivalence coefficient results from the ratio of stand density index from pure Douglas-fir and a pure European beech stand. It was detected in a mixed study of 18 triplets which also used the triplets of the study at hand (for further information see Thurm and Pretzsch, 2016).

Table 2 Characteristics of the sampled trees separated by species and mixture

Tabelle 2 *Eigenschaften der beprobten Einzelbäume differenziert nach Baumart und Mischung*

Species	**Mixture**	**Number**	**DBH [cm]**			**Height [m]**			**H/d ratio**			**Root diameter [cm]**			**Age [years]**			**LocalBA [$m^2\ ha^{-1}$]**		
			Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Douglas-fir	**Pure**	49	47.4	19.6	87.5	35.4	23.0	46.8	72	50	100	12.2	5.7	29.8	56	24	89	52.9	27.6	90.8
	Mixed	41	52.3	28.5	95.9	35.8	26.5	49.2	96	66	181	14.0	5.1	33.6	54	28	96	49.8	28.8	86.4
European beech	**Pure**	40	38.3	17.0	63.9	31.0	23.9	43.7	81	50	127	9.3	4.9	18.4	65	35	110	44.2	10.4	74.0
	Mixed	45	30.8	9.5	55.4	28.0	17.2	43.2	87	52	148	8.4	5.0	17.5	61	23	108	52.8	36.0	92.2
Total		**175**	**42.2**			**32.6**			**72**			**11.0**			**59**			**52.9**		

For taking stem cores, we applied long term standard procedures (Pretzsch 2002; Cook and Kairiūkštis 1990). For the selection and the drilling of the roots, we were geared to a pilot study from Nikolova et al. (2011) which has been successfully applied in several other studies later (Pretzsch et al. 2012a; Pretzsch et al. 2012b). All cores were sampled with a Haglöf increment borer. The stem was cored twice at breast height in North and East direction. The root cores were taken at two tall, lateral structural roots which were excavated. The root coring position was about 60-80 cm from their offset at the trunk. This distance range was chosen a compromise between having the lowest number of missing or discontinuous root growth rings (Krause and Morin 1995) and avoiding strongly eccentric cross sectional-shapes which result from root growth response to wind load (Nicoll and Ray 1996).

Nevertheless, many sampled roots show elliptic shapes with the largest radius from the upper edge to the downmost edge and smallest parallel to the soil surface. In order to obtain the mean annual growth of the roots, one core was taken from the root’s top edge to the center (largest radius) and another one perpendicularly from one lateral root edge to the center (smallest radius). This method also minimizes the amount of year rings which are not hit perpendicularly with the borer. This procedure provided six cores for every tree (two from the stem, two from the first root and two from the second root). All in all, the dataset comprises 175 trees (see Table 2, Fig. 1).

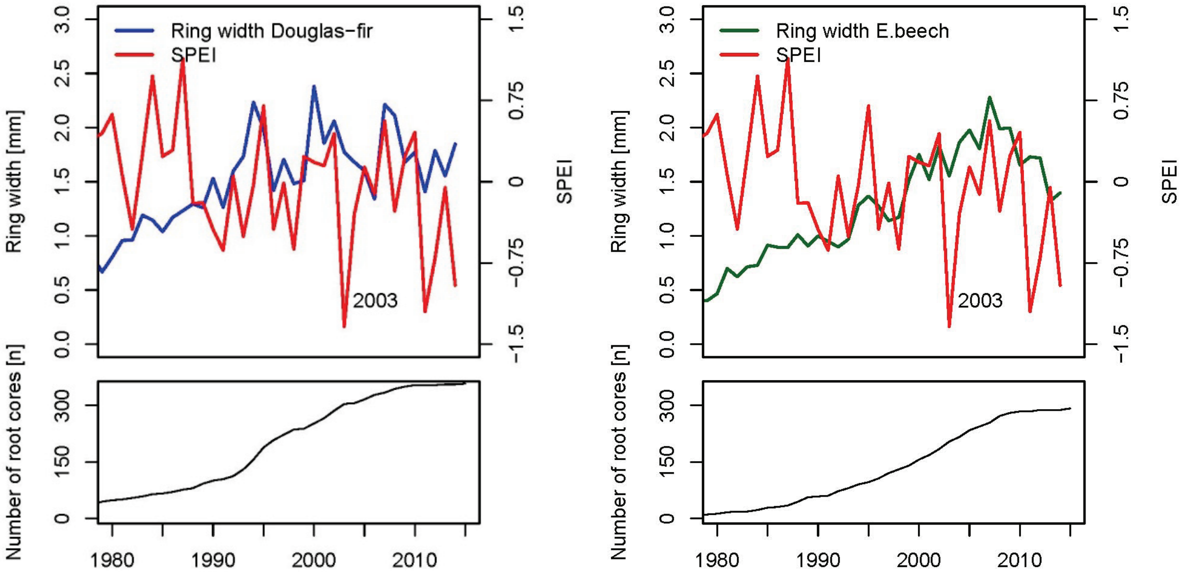

Fig. 1 Ring width master chronologies of the lateral roots for Douglas-fir (blue line, left) and European beech (green line, right) and the standardized precipitation-evapotranspiration index SPEI (red line). Labeled is the extreme drought year 2003. The black line shows the number of available cores in the respective year.

Abb. 1 *Dargestellt sind die mittleren Jahrringchronologien der Hauptwurzeln von Douglasie (blaue Line, links) und Rotbuche (grüne Linie, rechts) und der standartisierte Niederschlags-Evapotranspirationsindex SPEI (rote Linie). Beschriftet ist das Trockenjahr 2003. Die schwarzen Linien in den unteren Abbildungen zeigen die jeweilige Belegung von Jahrringchronoligen der Masterchronolgie.*

Ring width measurements were made using a digital positiometer after Johann (1977) (Biritz GmbH, Gerasdorf bei Wien, Austria) with an accuracy of 0.01 mm. Measurements of cores stops when tree rings run non-perpendicular. For cross-dating and synchronization of the tree chronologies we used the software platform TSAP-Win (Rinntech, Heidelberg, Germany). The analyses of root-stem allometry base on relating diameter changes between roots and stem. Diameters were calculated backwards by subtracting the measured increments from the diameter at survey time. This annual backward diameter calculation was only done for the time span which was covered by both increment cores per sampling point.

In order to extract the climate signal in root and stem growth, we detrended the basal area increment of the tree compartments in two steps as described in detail Thurm et al. 2016). In a nutshell, the first detrending step relied on fitting a Hugershoff increment function (1936). For the second step, we fitted a cubic spline with a wavelength of 15 years.

Statistical analyses

The basic allometric model (cf. Eq. 1) we used for relating root and stem diameter (droot, dstem) can be written as follows.

$$\ln(droot) = a_0 + a_1 \cdot \ln(dstem) \qquad \text{(Eq. 4)}$$

The coefficient a_0 represents the scaling parameter, and a_1 is the allometric exponent.

In order to answer our research questions, this model was extended to incorporate several explanatory variables of interest (see below) and fitted to the data. For taking into account the nested data structure (triplet, plot, tree, root), we applied linear mixed models. Model selection was based on the Akaike Information Criterion (Burnham and Anderson 1998; Burnham and Anderson 2004) and biological plausibility of the results.

At first we tested for a general difference in the root-stem allometries of Douglas-fir and European beech. To this end, the fixed effect $species$ coded as binary variable (1: European beech, 0: Douglas fir) was introduced:

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot species + a_3 \cdot \ln(dstem_{ijklt}) \cdot species + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt} \qquad \text{(Eq. 5)}$$

$a_0 \dots a_n$ represent the coefficients of the fixed effects. Random effects *b* are considered triplet i, plot j, tree k and root level l. The index t stands for the year a measurement belongs to. The symbol ε represents i.i.d. errors. If the estimate of a_2 differs significantly from zero, this suggests species-specific allometric scaling factors. If, however a_3 differs significantly from zero, we have to assume species-specific allometric slopes.

Further models were fitted separately for Douglas-fir and European beech. Related to the second research question, the influence of the mixture on allometry, we applied the Eq. 6. The fixed effect $mixture$ was included as a binary variable (0: pure stand, 1: mixed stand).

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot mixture_{ij} + a_3 \cdot \ln(dstem_{ijklt}) \cdot mixture_{ij} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt} \qquad \text{(Eq. 6)}$$

Similar as the binary variable species in Eq. 5, the parameters a_2 and a_3 indicate mixture effects on the scaling factor and the allometric slope, respectively.

Additionally, in order to refine the view on species mixing effects, we investigate the shift of allocation by introducing the individual $mixing\ proportion\ doug$ as a continuous variable. The proportion ranged between 0 and 1. The value 0 means the individual tree is completely surrounded by European beech and 1 surrounded by Douglas-fir.

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot mixing\ proportion\ doug_{ijk} + a_3 \cdot \ln(dstem_{ijklt}) \cdot mixing\ proportion(df)doug_{ijk} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt} \quad \text{(Eq. 7)}$$

To investigate, whether there is also a pattern of stand density, we fitted a model with the $local\ BA$.

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot local\ BA_{ijk} + a_3 \cdot \ln(dstem_{ijklt}) \cdot local\ BA_{ijk} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt} \quad \text{(Eq. 8)}$$

The short and long-term climatic influences on root-stem allometry were analyzed based on Eq. 9 and Eq. 10. Fixed effects are the standardized precipitation-evapotranspiration index $SPEI$, and the Paterson index CVP, respectively. Because the influence of mixture turned out non-significant on long-term scale, we omitted it in Eq. 10.

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot SPEI_{ijt} + a_3 \cdot mixture_{ij} + a_4 \cdot \ln(dstem_{ijklt}) \cdot SPEI_{ijt} + a_5 \cdot \ln(dstem_{ijklt}) \cdot mixture_{ij} + a_6 \cdot SPEI_{ijt} \cdot mixture_{ij} + a_7 \cdot \ln(dstem_{ijklt}) \cdot SPEI_{ijt} \cdot mixture_{ij} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt} \quad \text{(Eq. 9)}$$

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot CVP_{ij} + a_3 \cdot \ln(dstem_{ijklt}) \cdot CVP_{ij} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt} \quad \text{(Eq. 10)}$$

All statistical analyses and graphics were conducted with the statistical environment R version 3.2.2 (R Core Team 2015). Linear mixed models were fitted with *lmer* from the R package *lme4* (Bates et al. 2015). The significances of the coefficients were tested with an F-Test with Satterthwaite's approximation (Kuznetsova et al. 2015) from the R-package *lmerTest*.

Results

Species-specific root-stem allometry

The average age of the sampled trees was approximately 59 years (Table 2). However, Douglas-fir was on average 7 years younger, it was 4.4 meters higher in pure stands than European beech in pure stands. In mixed stands, the height difference was amounted to even 7.9 meters between Douglas-fir and European beech. Douglas-fir had a 9.2 cm greater diameter in pure stands and a 21.5 cm greater diameter in mixed stands than European beech. Overall, the DBH ranged from 19.6 to 95.9 cm and from 9.5 to 63.9 cm for Douglas-fir and European beech, respectively. We found the same pattern of size differences for the root diameters. The average coarse root diameter of Douglas-fir was 13.1 cm (pure = 12.2 cm; mixed =14.0 cm) and 8.9 cm for European beech (pure = 9.3 cm; mixed =8.4 cm).

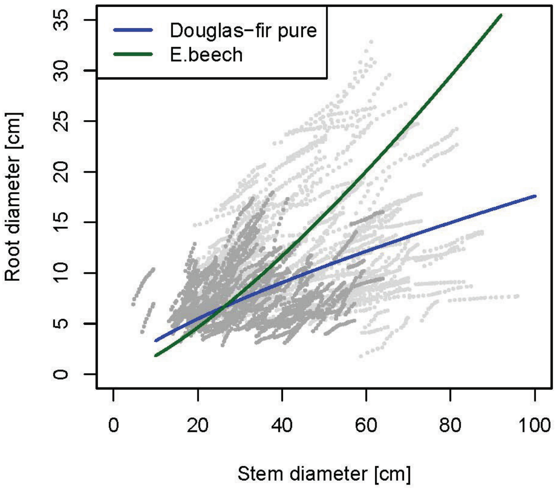

Fig. 2 Root-stem allometry from fitted models according to Eq. 5,and the related, measured and reconstruced diameter for Douglas-fir (grey) and European beech (dark grey). Model coefficents can be seen in Table 3.

Abb. 2 *Stamm-Wurzel Allometrien anhand des Modelles Formel 5 und die dazugehörigen gemessenen und rekonsturierten Durchmesser von Douglasie (grau) und Rotbuche (dunkelgrau). Die Modelkoeffizienten sind in Tabelle 3 abgebildet.*

The fit results of all linear mixed models shown above are summarized in Table 3. The species-specific model (Eq. 5) indicates that Douglas-fir and European beech significantly differ in their root-stem allocation. European beech has a significantly lower allometric scaling factor but a significantly steeper slope than Douglas fir. We illustrate this result in Fig. 2; up to a DBH of about 26, cm, a typical Douglas-fir invested more resources into coarse roots growth than European beech, at greater diameters, European beech shows a greater root growth. The inclusion of stand level mixing (dichotomous variable *mixture*) into the allometric model (Eq. 6, Fig. 3) indicates that Douglas-fir in pure stand has a significant smaller scaling factor than in mixed stands, but a significant greater slope. Same effect can be seen for European beech but much it is more pronounced. Both species in pure stands allocate higher biomass portions to the roots if they have DBH beyond about 30 cm (Douglas fir) and 45 cm (European beech), respectively.

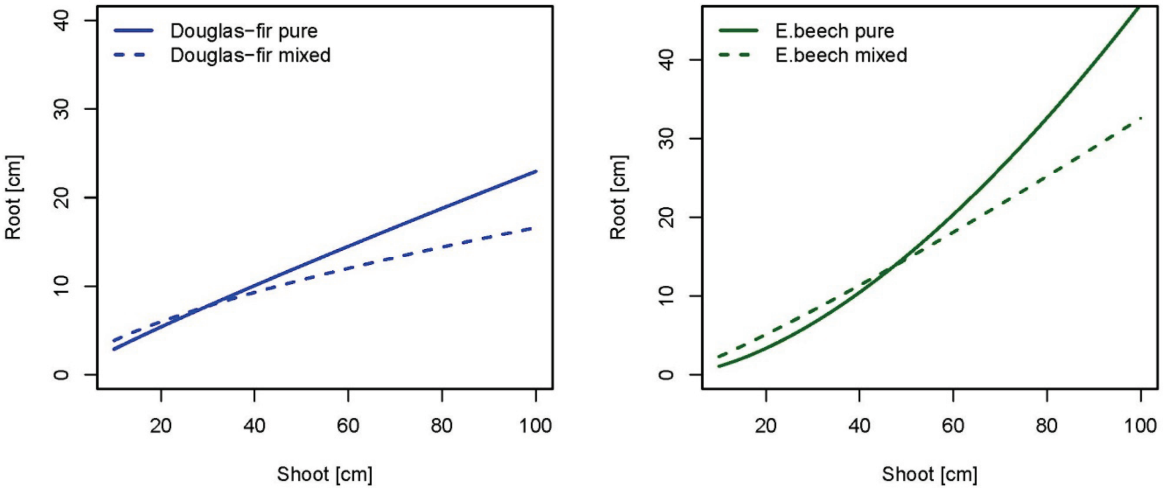

Fig. 3 Root-stem allometry in dependence of stand level mixing type for Douglas-fir (left) and European beech (right). Model coefficents can be seen in Table 3 Eq. 6.

Abb. 3 *Stamm-Wurzel Allometrien in Abhängigkeit vom Mischungstyp für Douglasie (blau) und Rotbuche (grün). Die Modelkoeffizienten sind in Tabelle 3 (Formel 6) abgebildet.*

Including mixing proportion at individual tree level, gives a clearer view on the shift between root and stem allocation (Table 3, Eq. 7). As shown in the methods section, the proportion of Douglas-fir in the local BA is the variable which was used to this end in the models for both species. Therefore, the highest interspecific competition presented in Fig. 4 is 0.8 for European beech and 0.2 for Douglas-fir. Both species exhibit a significantly higher allocation to stem growth compared to root growth if they compete more against the other species than against their own.

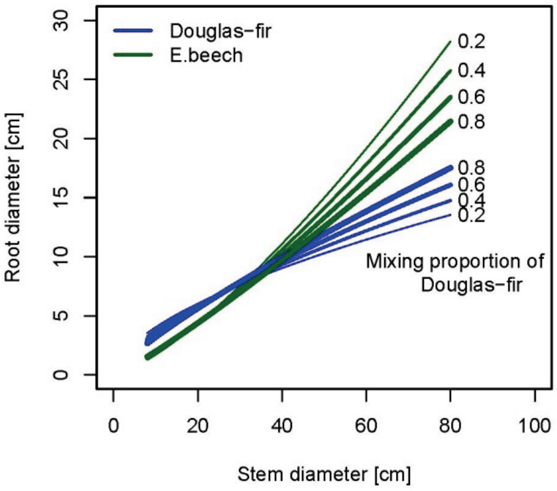

Fig 4. Root-stem allometry in dependence of interspecific competition represented by mixing proportion of the own species for Douglas-fir (blue) and European beech (green) related to Eq. 7. Mixing proportions are to be understood as shares of Douglas fir in the local BA. Model coefficent are shown in Table 3.

***Abb. 4** Stamm-Wurzel Allometrien für Douglasie (blau) und Rotbuche (grün) in Abhängigkeit von der interspezifischen Konkurrenz repräsentiert durch den Mischungsanteil. Der Mischungsanteil berechnet sich aus dem relativen Anteil von Douglasie an der Stammgrundfläche welcher den jeweiligen Probebaum umgibt. Die Modelkoeffizienten sind in Tabelle 3 (Formel 7) abgebildet.*

Influence of competition

The 95% of the local BA’s arranged between 26.0 m²/ha and 82.6 m²/ha. Fig. 5 shows by means of the fitted Eq. 8, how the trees partitioned resource between root and stem under increasing stand density. The analyses aggregate all trees, independent if mixed or not. The sampled trees in mixed stands shows a little bit higher local BA (50.8 m²/ha) than pure stands (49.1 m²/ha) but the difference was not significant. The data exhibited that with increasing competition allocation favors root growth relative to stem growth. This pattern was significant for both species but more pronounced for Douglas-fir.

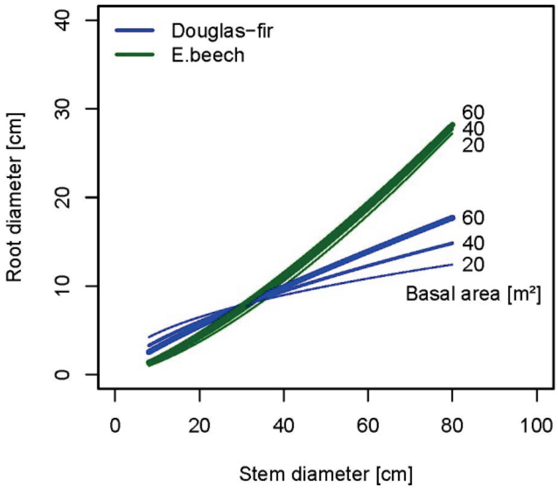

Fig 5. Root-stem allometry in dependence of local stand density for Douglas-fir (blue) and European beech (green) according to Eq. 8. Density is represented by local BA which is defined as surrounding basal area of a individual tree. Model coefficents are shown in Table 3.

Abb. 5 *Stamm-Wurzel Allometrien für Douglasie (blau) und Rotbuche (grün) in Abhängigkeit von der lokalen Stammgrundfläche. Die lokale Stammgrundfläche beschreibt die Grundfläche, die den jeweiligen Probebaum umgibt und ergibt sich aus einer Winkelzählprobe an dem entsprechenden Baum. Die Modelkoeffizienten sind in Tabelle 3 (Formel 8) abgebildet.*

Influence of short-term humidity variation

As shown in the methods section, the short-term variation of humidity was represented by the SPEI. In the measuring period, the SPEI ranged between -1.58, which was reached in the drought year 2003, and 1.14, which was reached 2002. The SPEI index for all triplets existed from 1998 to 2010 which results in a lower observation account in Table 3. As mentioned in the methods section, the triplet specific SPEI enables to calculate site-specific minimum and maximum SPEI values. Fig. 6 illustrates the allocation pattern of Douglas-fir and European beech in pure and mixed stand. Under humid weather conditions, both species allocate resources in favor of stem growth compared to root growth (Eq. 9). This reaction could be found in pure as well as in mixed stands. The response of Douglas-fir to SPEI in Fig. 6 is almost invisible but this is a problem of scale. However small, the model shows a significant relationship between SPEI and root stem allometry. Obviously the reaction to short –term humidity fluctuations is very small, but existent. It is all the more surprising that one can separate the reaction to short-term humidity from other effects.

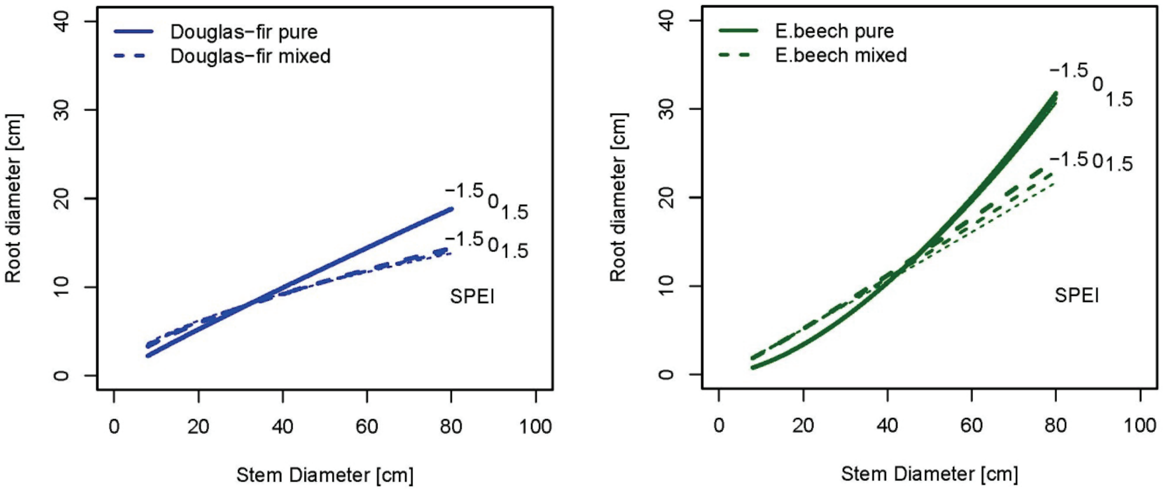

Fig 6. Root-stem allometry in dependence of humidity in growing period for Douglas-fir (left, blue) and European beech (right, green) according to the fitted Eq. 9 Humidity is represented by standardized precipitation-evapotranspiration index SPEI (model predictions shown for SPEI = -1.5, 0, 1.5, corresponding SPEI values at the ends of the lines), although the SPEI-effects are very small they turned out significant nevertheless. Model coefficients are shown in Table 3.

Abb. 5 *Stamm-Wurzel Allometrien für Douglasie (links, blau) und Rotbuche (rechts, grün) in Abhängigkeit von den Wetterbedingungen in der Vegetationsperiode. Die Wetterbedingungen werden dabei durch den standartisierten Niederschlags-Evapotranspirationsindex SPEI beschrieben. Die Enden der Modellkurven sind mit den jeweilgen SPEI beschriftet. Ein SPEI von -1,5 repräsentiert einen sehr trockenen Sommer wie beispielsweise 2003. Ein SPEI von + 1,5 repräsentiert eine sehr feuchte Vegetationsperiode. Obwohl der Effekt des Wetters auf die Stamm-Wurzel Allometrie sehr schmal aussieht, ist er dennoch signifikant. Die Modelkoeffizienten sind in Tabelle 3 (Formel 9) abgebildet.*

The linear mixed models of the short-term humidity variation (Eq. 9) were significant as well as the models of mixture and local BA (Eq. 7 and 8). Nevertheless, it can be seen that mixture and local BA had a stronger influence on allocation than the SPEI. Only for European beech in mixed stands, a variation of humidity seems to have a large effect.

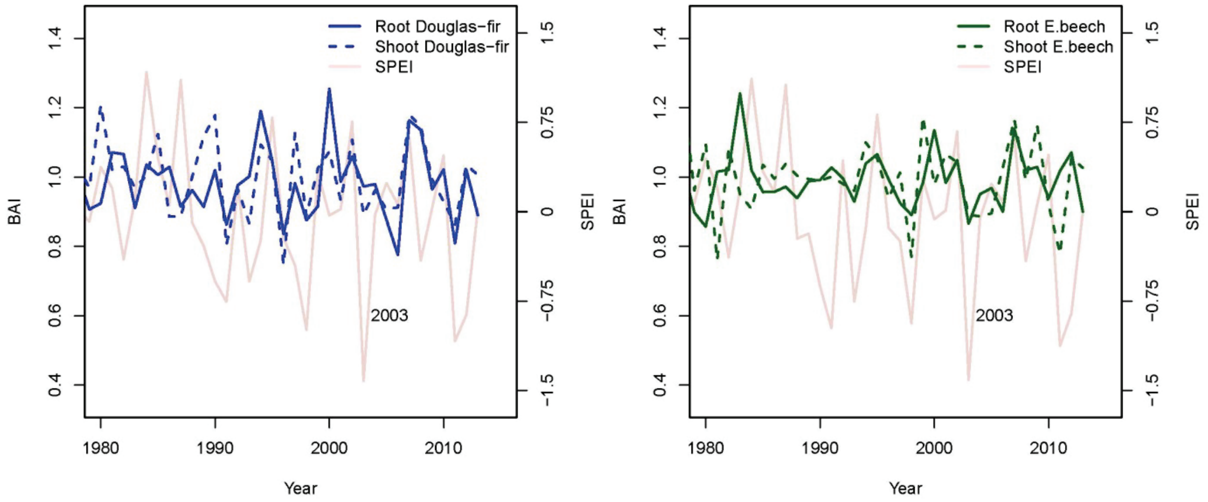

Fig. 7 Detrended root and stem chronologies for Douglas-fir (blue line, left) and European beech (green line, right). The standardized precipitation-evapotranspiration index SPEI is added as red line. Labeled is the extreme drought year 2003.

Abb. 7 *Trendelleminierte Wurzel- und Stammjahrringchronologien für Douglasie (links, blau) und Rotbuche (rechts, grün). Der standartisierten Niederschlags-Evapotranspirationsindex SPEI ist als rote Linie dargestellt. Das Trockenjahr 2003 ist in den Abbildungen beschriftet.*

To clarify, if drought causes contrary responses in root and stem growth or if the allocation of resource is more reduced for one than for the other, we pictured the course of detrended root and stem growth (Fig. 7). A dendrochronological parameter which compared the course of two chronologies against each other is the 'Gleichläufigkeit' (Eckstein and Bauch 1969). The Gleichläufigkeit respects the direction of index (ups and downs) and not the strength of deflection. The Gleichläufigkeit for the mean root and stem growth index was 0.76 between 1990 and 2013. This means 76 % of the ups and downs are equal. The year-to-year agreement of root and stem reduced with 1990 because of the decreased number of root chronologies (see also Fig. 1). The 'Gleichläufigkeit' let us suggest that root and stem growth do not have a contrary course.

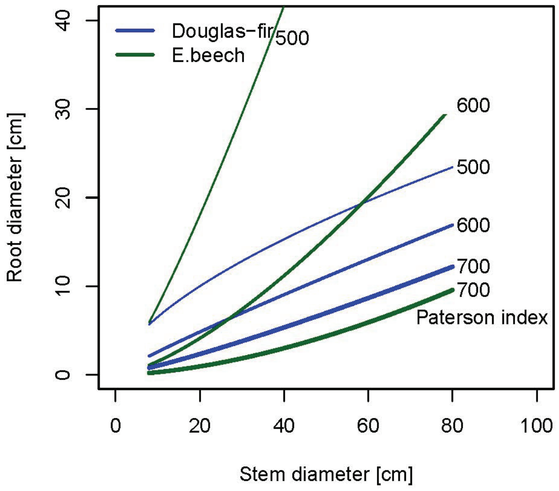

Fig 8. Root-stem allometry in dependence of long-term site-specific humidity for Douglas-fir and European beech, according to the fitted model after Eq. 10. Humidity at the site is represented by the CVP index by Paterson (1956).

Abb. 8 *Stamm-Wurzel Allometrien für Douglasie (blau) und Rotbuche (grün) in Abhängigkeit von den Klimabedingungen des Wuchsstandortes. Die Klimabedingungen wurden mit Hilfe des Klima-Vegetationsindex nach Paterson (1956) berechnet. Hohe Index-Werte zeigen dabei günstige bzw. feuchte Standortsbedingungen an. Die Modelkoeffizienten sind in Tabelle 3 (Formel 10) abgebildet.*

Influence of long-term humidity variation

In comparison to the influence of short-term humidity, the effect of site conditions, expressed through the CVP index, on tree allometry was much more pronounced. The CVP index at the driest site was 497 (ecoregion 'Fränkische Platte'). The site with the most favorable growing conditions (ecoregion 'Spessart') had a CVP index of 676. The models of both species indicate that the allometry of trees is strongly determined by the site specific growth conditions (Fig. 8, Eq. 10).

Douglas-fir as well as European beech invests in root growth under harsher conditions at the expense of stem growth compared to more favorable sites. This response was especially pronounced for European beech.

Table 3 Estimated fixed effects for the extended root–stem allometry models (Equations 5-10). The numbers in brackets represented the standard deviation of the independent variables (EB – E. beech, DF – Douglas-fir, SPEI - Standardized precipitation-evapotranspiration index, Local BA – Local basal area, CVP – Paterson index)

***Tabelle 3** Die Koeffizienten aus den Stamm-Wurzel-Allometrie Modellen (Formel 5 - 10). In Klammern befinden sich die Standardabweichungen der unabhängigen Variablen (EB Rotbuche, DF – Douglasie, SPEI - standartisierten Niederschlags-Evapotranspirationsindex, Local BA – lokale Stammgrundfläche, CVP – Paterson Index)*

	Dependent variable:										
	log(droot)										
	Tree allometry pattern			Competition/ Density / Mixing proportion				Humidity response			
Equation:	*5*	*6*	*6*	*7*	*7*	*8*	*8*	*9*	*9*	*10*	*10*
Independent Variable:	**EB - DF**	**Douglas-fir**	**E.beech**	**Douglas-fir**	**E.beech**	**Douglas-fir**	**E.beech**	**Douglas-fir**	**E.beech**	**Douglas-fir**	**E.beech**
log(dstem)	0.726*** *(0.013)*	0.633 *(0.015)*	1.149*** *(0.028)*	0.506*** *(0.027)*	1.416*** *(0.033)*	0.282*** *(0.04)*	1.501*** *(0.087)*	0.608*** *(0.018)*	1.078*** *(0.032)*	-0.825*** *(0.114)*	0.058 *(0.176)*
Species E.beech	-1.990*** *(0.109)*										
log(dstem)*Species E.beech	0.608*** *(0.024)*										
SPEI								-0.075** *(0.028)*	-0.074* *(0.031)*		
Mixture(Pure)		-0.904*** *(0.194)*	-1.889*** *(0.378)*					-1.096*** *(0.205)*	-1.979*** *(0.38)*		
log(dstem)*SPEI								0.020** *(0.007)*	0.025** *(0.01)*		
log(dstem)*Mixture(Pure)		0.267*** *(0.025)*	0.490*** *(0.045)*					0.315*** *(0.031)*	0.522*** *(0.052)*		
Mixing Proportion doug				-1.279*** *(0.247)*	1.025 . *(0.549)*						
log(dstem)*Mixing Proportion doug				0.390*** *(0.043)*	-0.338** *(0.108)*						
Local BA						-0.032*** *(0.004)*	0.014* *(0.007)*				
log(dstem)*Local BA						0.009*** *(0.001)*	-0.003 . *(0.002)*				
SPEI*Mixture(Pure)								0.072* *(0.036)*	0.045 *(0.045)*		
log(dstem)*SPEI*Mixture(Pure)								-0.019* *(0.01)*	-0.016 *(0.013)*		
CVP										-0.016*** *(0.002)*	-0.022*** *(0.003)*
log(dstem)*CVP										0.003*** *(0.0002)*	0.002*** *(0.0003)*
Constant	-0.471 . *(0.144)*	-0.104 *(0.253)*	-1.809*** *(0.26)*	0.300 *(0.277)*	-2.773*** *(0.215)*	1.105*** *(0.288)*	-3.290*** *(0.384)*	-0.019 *(0.264)*	-1.590*** *(0.259)*	8.403*** *(1.259)*	10.091** *(2.000)*
Number of Observations	4 433	2 512	1 921	2 512	1 929	2 512	1 929	1 994	1 482	2 512	1 929

*Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

Discussion

Patterns in root-stem allometry

The study investigated the allometric relationship of root and stem growth. We could show that the allometric exponent was influenced by tree species mixture, mixture proportion, stand density, short term humidity variation, and long term site-specific humidity. Thereby, the strength of the influence differed strongly among these variables. The finding of a general variability of the allometric exponent supports the optimal partitioning theory (OPT). This is consistent with results for root-stem allometry from several other studies (Nikolova et al. 2011; Pretzsch et al. 2012b; McConnaughay and Coleman 1999).

The pattern of allocation between root and stem were similar for mixture, density and humidity. More favorable conditions lead to a pronounced growth of stem, whereas unfavorable conditions increase growth of roots (see Fig. 9).

Methodological restrictions

Basis of the study is the comparison of stem diameter in breast height and two prominent coarse roots per tree. This method has several advantages to total tree excavation (non-destructive, less resource-demanding, allows sampling mature trees). Nonetheless, the results are diameter comparisons. They cannot be equated with the measured biomasses of above and belowground tree compartments, because in contrast to biomass they describe resource allocation only indirectly. Another related problem is that we do not know the total number of roots. So it might be that some of the observed effects are only shifts from individual root increment to a number of roots. This would however presuppose that trees changed the structure of their root system. Studies about Douglas-fir where entire root systems were excavated, found out that for this species the number of coarse roots per tree is nearly equal (Mauer and Palátová 2012), going along with a uniform structure of the root system (McMinn 1963). It seems plausible that trees can modify their structural composition within certain limits only. Therefore, we assume that tree species mixing does not lead to significantly different of root numbers.

Several authors found a species-specific, vertical stratification of root systems in mixed stands (Kelty 2006; Forrester et al. 2006a; Bolte and Villanueva 2005). The stratification could be seen in a displacement of fine roots. Two options for this displacement of fine roots in deeper soils are possible: (a) A displacement, realized by sinker roots which branch from the horizontal roots. We should have observed such a reaction when sampling horizontal roots in this study. (b) A greater stratification, in which one species displaces their nutrient uptake into deeper soil layers. This displacement would be generated by an increased growth in heart or tap roots. Douglas-fir as well as European beech feature a heart-root system (Matyssek et al. 2010). So both species are potentially capable to form a secondary root layer by increase heart root growth and decrease the growth of the horizontal roots. This would mean, that the results we obtained with horizontal roots have to be interpreted in another way, namely that the mixing effect is not an allocation between roots and stems, but an allocation inside the root system. The retreating species would shift the nutrient transport respectively fine root production on these types of roots. Root growth is preferentially favored near the soil surface because nutrients, soil strength, aeration and temperature are more favorable there than at depth (Sands and Mulligan 1990). Therefore, stratification without a struggle seems to be not expedient.

A study which was made on a part of our plots found out that out that mixing effects on soil organic carbon and nitrogen concentrations were restricted to the forest floor and the uppermost mineral soil (Cremer et al. 2016). A mixture-induced stratification into deeper soil horizons would cause a change of carbon and nitrogen concentrations in these soil layers compared to pure stands. Hendriks and Bianchi (1995) measured root density and biomasses in pure and mixed stands of Douglas-fir and European beech. Their data indicate that both species did not extend their fine root growth pattern in a soil layer but they have lower root density in mixed stands in the uppermost soil layer (down to 30 cm) compared to pure stands. This would strengthen the assumption of reduced struggle for resources. The data of Hendriks and Bianchi (1995) show a considerable drop of belowground biomass in the mixed stands (25 – 50 %) below what would have been expected from pure stands. This is consistent with our findings of reduced investment into root growth in mixed stands.

Bolte and Villanueva (2005) bring evidence for a root stratification of mixed stands from European beech and Norway spruce. In contrast to our species of interest, European beech and Norway spruce have different root systems which may trigger the stratification. Nevertheless, they also found a reduced fine root biomass in mixed stands.

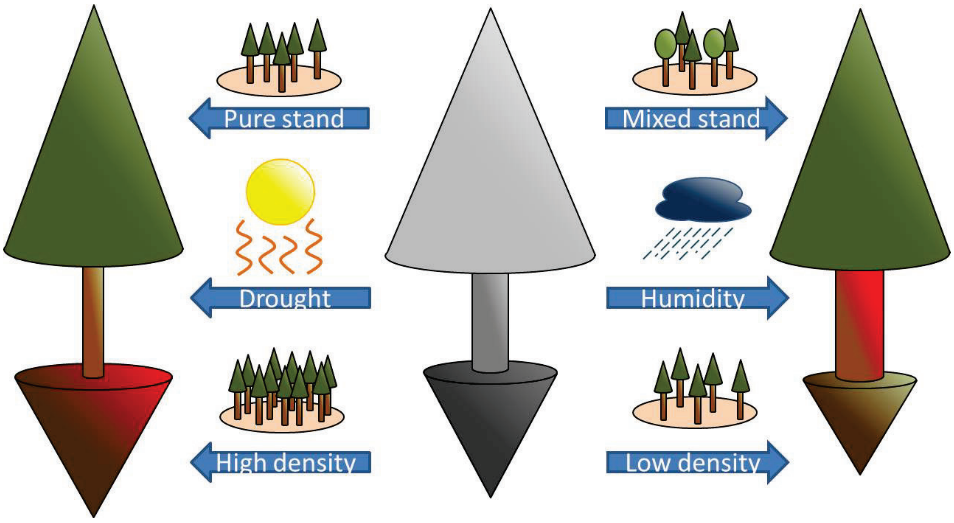

Fig. 9 Comparsion of the factors mixing type, humidity and stand density and their influence on root-stem allometry in schematic representation. A gradient from unfavorable conditions to favorable conditions went from left to right and shift growth allocation from root to stem. The schematic trees represents Douglas-fir as well as European beech.

Abb. 9 *Schematische Darstellung der Einflussfaktoren Mischungstyp, Feucht- und Bestandesdichte und deren Wirkung auf die Wurzel-Stamm-Allometrie. Links sind die Einflussfaktoren als negative Ausprägung dargestellt und rechts mit positiver Ausprägung. Dabei soll gezeigt werden, wie sich die Allomtrie von der Wurzel (links) zum Stamm (rechts) verschiebt. Der schematische Baum repräsentiert sowohl eine Douglasie als auch ein Rotbuche.*

Humidity

The sensitivity of root-stem allometry to site conditions was pointed out for lodgepole pine *Pinus contorta* (Dougl. ex. Loud) and Douglas-fir by Comeau and Kimmins (1989), and Keyes and Grier (1981). These studies provided evidence, that conifers increase stem growth at the expense of root growth under favorable soil moisture conditions. This is a tree individual adaption to site conditions which develops over decades and may explain the great pronounced influence of humidity on root-stem allometry in our results.

The influence of short-term humidity fluctuations was much weaker but also significant in our data. Plants under short-term water-stress may proliferate roots into unexplored regions of soil to unlock water resources and avoid rapid water depletion (Lavelle and Spain 2005). The short allometry response in the current study accords with results from Pretzsch et al. (2012b) for lodgepole pine. They found a more pronounced root growth in a climatically unfavorable period. Nevertheless, growth potential is not excessive in such short periods. Therefore, the reaction cannot compare with a long-term adaptation of allometry (Fig. 8, Eq. 10) to site conditions. Additionally, the possibility for unexplored root space in existing stands is not boundless. Easy accessible and favorable root strata are just occupied. The individual trees are restricted in their ability to respond by hardly variable neighbor constellations. That is another reason why there is only a small possibility to root extension. In this context it is interesting that this effect was most pronounced in European beech mixed stands. In a previous study on the same plots it was found that European beech had limited access only to the soil water storage (Thurm et al. 2016).

Nevertheless, the general patterns of improved root growth in dryer growing periods do not mean that lateral roots get a growth spurt. Stem increment and root increment show a contrary course. Under unfavorable weather conditions both tree compartments exhibited a loss of growth but absorbed resources will mainly be invested into root growth. This is conform with the findings of Nikolova et al. (2011) who worked with Norway spruce (*Picea abies* [L.] Karst.).

Mixture and Density

Our data showed that an increasing proportion of the admixed species comes with a higher investment in stem growth. Pretzsch and Biber (2016) provide evidence that maximum tree density is higher in mixed stands. Such a more intense crowding might be possible because of a better or complementary nutrient utilization. Pretzsch et al. (2014) showed significant differences in the nutrient content of Douglas-fir and European beech on the whole-tree level. European beech accumulate more potassium and Douglas-fir more phosphor. The combination of different, species-specific nutrient requirements per hectare enables greater supply for the individual. The mixing of complementary species like Douglas-fir and European beech can likely be seen as an improved resource availability (Bartelink 1998; Thurm and Pretzsch 2016; Thomas et al. 2015). However, an increasing density increased the root-stem ratio in general as also highlighted by Pearson et al. (1984). Species mixing seems to attenuate the competition situation (Piotto 2008).

Our data indicate that increasing age augmented the mixing effect on root-stem allometry. The finding that the mixing effect takes time to appear was also confirmed in other studies (Zhang et al. 2012; Cavard et al. 2011). An increased investment into stem growth with increasing shares of interspecific competition were well pronounced for both species. However, the general comparison of European beech in pure and mixed stands (Eq. 6, Fig. 3) shows that the allocation of stem growth in smaller DBH classes is more pronounced in pure stands than in mixed stand. This allometry first differs when stem size of European beech pass the mean DBH in our plots. Interestingly, we could observe an analogous response in a previous investigation on the same plots, which deals with above ground biomass productivity (Thurm and Pretzsch 2016). Overyielding of European beech likewise begins when the species reach greater DBH values, in other words, with some delay. Although these responses do not directly match with this study because the study at hand deals with individual tree level data whereas the previous study deals with stand level data, this analogy remains remarkable.

When comparing tree allometry in pure and mixed stands, it should be taken into account that DBH distributions in pure and mixed stands might be different(Pretzsch and Schütze 2016).

A previous study about Douglas-fir and European beech in mixture (Thurm and Pretzsch 2016) and studies about mixing other species (Pretzsch et al. 2016) could show that overyielding and aboveground structural diversity enhanced soil water availability. Due to partitioning of water resources (Jonard et al. 2011; Forrester et al. 2010), mixed stands may not reach a limit of sufficient water supply while mono-species stands already do. Therefore, the limiting factor, which drives the overyielding respectively the height stratification, shifts from soil to light (Forrester 2014; Pretzsch et al. 2016) and root growth can be reduced in mixed stands.

Seemingly, there is a connection between increasingly differing allometry in pure and mixed stands and overyielding in mixed stands with increasing age. Keyes and Grier (1981) found out that total stand net biomass production (above plus belowground) did not change significantly under a varying site condition gradient but only the partitioning between above and belowground biomass. Maybe the measured overyielding in mixed stands is partly a partitioning of growth into aboveground biomass with comparable total biomass to pure stands. This is of particular interest because carbon-balance based forest models might overestimate the overyielding in mixed stands.

A physiological adaption against drought is likely to shift allocation in favor of the roots (Bréda et al. 2006). This was clearly confirmed in our study. But this fact alone would also suggest a declined drought tolerance of mixed stands where we found a decreased root-stem ratio. However, it was found in several studies that mixing tree species can improve their drought tolerance (Lebourgeois et al. 2013; Thurm et al. 2016; Pretzsch et al. 2013). Maybe, the complementary water partitioning between the species in mixed stands (Jonard et al. 2011; Forrester et al. 2010; Thurm et al. 2016) or water pumping property of trees (Aranda et al. 2012) improved the drought sensitivity of mixed species by enhancing the general water supply. But these mechanisms in mixed stands are not well understood so far. In addition, the role of mycorrhizae in the water uptake of trees keeps our interpretation open. Lehto and Zwiazek (2011) mentioned that this could also have an effect on water uptake under stress.

We are aware that there might be complex interactions of stand density, mixture and humidity that influence root stem allometry (Elkin et al. 2015; Guillemot et al. 2015). However, this was not the main focus of the study and we refrained from including them in order to avoid over-complex statistical models.

Wind load and root-stem allometry

Wind stability is another reason for trees to change their root-stem ratio (Coutand et al. 2008; Reubens et al. 2009; Gardiner et al. 2016). In general, stronger wind loads result in a shift in favor of the roots. The decreased investment in roots in mixed stands could suggest a higher risk of windthrow in mixed stands. However, a positive influence of species mixture on wind stability of trees was confirmed by several studies (Mayer et al. 2005; Schütz et al. 2006; Schelhaas 2008). Schelhaas (2008), who investigated the influence of wind on European beech and Douglas-fir found out that a lower height-stem diameter ratio (h/d) of Douglas-fir in mixed stands decreased the risk of wind damage. This different h/d ratio results from a changed competition situation in mixed compared to pure stands (Schelhaas 2008; Thurm and Pretzsch 2016). Abetz (1976) concluded that the predominant species in mixture decreased their h/d ratio whereas suppressed species increased their h/d ratio. Reason is the necessity to grow to light. Thurm and Pretzsch (2016) also observed this pattern of predominant Douglas-fir and suppressed beech with modified h/d ratios in mixed stands. Nevertheless, there seems to be no direct link between h/d ratio and root stem allometry because the response in h/d went contrary whereas the allometry pattern based on root stem diameters in mixed stands for both species is similar.

A contrasting point should not go unmentioned in this context: e.g. Röhrig et al. (2006) point out, stand canopy roughness strengthens wind turbulences and increases the risk of wind damages. In mixed stands as covered by our plots, the great tree height difference between Douglas-fir and European beech would thus predispose Douglas-fir.

Conclusions

The morphological plasticity and adaptability of tree stems and crowns to a given competitive status is rather easy to measure and well known. It affects, among others, growth resilience of the stand, stand stability, and wood quality. Compared with this, the plasticity of the stem in relation to roots is much more difficult to access and therefore rather unknown. But of course it is also highly relevant, for, many important tree and stand traits, e.g. tree and stand stability against wind, below and above-ground carbon storage, resource use, and tree and stand productivity. Although based on rather rough sampling we could show a high plasticity and adaptability of the root-stem relationship. Further detailed analyses seem desirable, as they might show to what extent this partitioning affects overyielding in mixed stands, as well as their susceptibility to windthrow or drought compared to pure stands.

Acknowledgements

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References

Abetz P (1976) Beiträge zum Baumwachstum. Der h/d-Wert - mehr als ein Schlankheitsgrad. Forst- u. Holzwirt 31:389–393

Amoroso MM, Turnblom EC (2006) Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Can. J. For. Res. 36(6):1484–1496. doi: 10.1139/X06-042

Aranda I, Forner A, Cuesta B, Valladares F (2012) Species-specific water use by forest tree species: From the tree to the stand. Agricultural Water Management 114:67–77. doi: 10.1016/j.agwat.2012.06.024

Bartelink HH (1998) Simulation of growth and competition in mixed stands of Douglas-fir and beech. Landbouwuniversiteit Wageningen, Wageningen

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: Linear mixed-effects models using Eigen and S4

Binkley D (2003) Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Can. J. For. Res. 33(11):2274–2279. doi: 10.1139/x03-158

Binkley D, Greene S (1983) Production in mixtures of conifers and red alder: the importance of site fertility and stand age. In: Ballard R, Gessel. S (eds) International Union of Forestry Research Organizations Symposium on Forest Site and Continuous Productivity, pp 112–117

Bitterlich W (1952) Die Winkelzählprobe. Forstwissenschaftliches Centralblatt 71:215–225

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants—an economic analogy. Annual review of Ecology and Systematics:363–392

Bolte A, Villanueva I (2005) Interspecific competition impacts on the morphology and distribution of fine roots in European beech (Fagus sylvatica L.) and Norway spruce (Picea abies (L.) Karst.). European Journal of Forest Research 125(1):15–26. doi: 10.1007/s10342-005-0075-5

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science 63(6):625–644. doi: 10.1051/forest:2006042

Burnham KP, Anderson DR (1998) Model selection and inference: A practical information-theoretic approach. Springer, New York

Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. Sociological methods & research 33(2):261–304

Cavard X, Bergeron Y, Chen HYH, Paré D, Laganière J, Brassard B (2011) Competition and facilitation between tree species change with stand development. Oikos 120(11):1683–1695. doi: 10.1111/j.1600-0706.2011.19294.x

Comeau PG, Kimmins JP (1989) Above-and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. Canadian Journal of Forest Research 19(4):447–454

Cook E, Kairiūkštis L (1990) Methods of dendrochronology: Applications in the environmental science. Kluwer Academic Publishers; International Institute for Applied Systems Analysis, Dordrecht, Netherlands, Boston, [Place of publication not identified]

Coutand C, Dupraz C, Jaouen G, Ploquin S, Adam B (2008) Mechanical stimuli regulate the allocation of biomass in trees: demonstration with young Prunus avium trees. Annals of Botany 101(9):1421–1432. doi: 10.1093/aob/mcn054.

Cremer M, Kern NV, Prietzel J (2016) Soil organic carbon and nitrogen stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce. Forest Ecology and Management 367:30–40. doi: 10.1016/j.foreco.2016.02.020

Deutscher Wetterdienst (2015) Grids germany-monthly: mean temperature and precipitation. ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/monthly/. Accessed 18 March 2016

Deutscher Wetterdienst (2016) Grids germany-annual: sunshine duration 1951-2016. ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/annual/sunshine_duration/. Accessed 18 March 2016

Dieler J, Pretzsch H (2013) Morphological plasticity of European beech (Fagus sylvatica L.) in pure and mixed-species stands. Forest Ecology and Management 295:97–108. doi: 10.1016/j.foreco.2012.12.049

Dirnberger GF, Sterba H (2014) A comparison of different methods to estimate species proportions by area in mixed stands. Forest Syst 23(3):534. doi: 10.5424/fs/2014233-06027

Eckstein D, Bauch J (1969) Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstw Cbl 88(1):230–250. doi: 10.1007/BF02741777

Elkin C, Giuggiola A, Rigling A, Bugmann H (2015) Short- and long-term efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. Ecological Applications 25(4):1083–1098. doi: 10.1890/14-0690.1

Erickson HE, Harrington CA, Marshall DD (2009) Tree growth at stand and individual scales in two dual-species mixture experiments in southern Washington State, USA. Can. J. For. Res. 39(6):1119–1132. doi: 10.1139/X09-040

Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. Forest Ecology and Management 312:282–292. doi: 10.1016/j.foreco.2013.10.003

Forrester DI, Bauhus J, Cowie AL, Vanclay JK (2006a) Mixed-species plantations of Eucalyptus with nitrogen-fixing trees: A review. Forest Ecology and Management 233(2-3):211–230. doi: 10.1016/j.foreco.2006.05.012

Forrester DI, Cowie AL, Bauhus J, Wood JT, Forrester RI (2006b) Effects of Changing the Supply of Nitrogen and Phosphorus on Growth and Interactions between Eucalyptus globulus and Acacia mearnsiiin a Pot trial. Plant Soil 280(1-2):267–277. doi: 10.1007/s11104-005-3228-x

Forrester DI, Theiveyanathan S, Collopy JJ, Marcar NE (2010) Enhanced water use efficiency in a mixed Eucalyptus globulus and Acacia mearnsii plantation. Productivity in Tropical Plantations 259(9):1761–1770. doi: 10.1016/j.foreco.2009.07.036

Gandullo JM, Serrada R (1977) Mapa de productividad potencial forestal de la España peninsular. Monografias INIA (Spain). no. 16.

Gardiner B, Berry P, Moulia B (2016) Review: Wind impacts on plant growth, mechanics and damage. Plant Science 245:94–118. doi: 10.1016/j.plantsci.2016.01.006

Gauer J, Kroiher F (eds) (2012) Waldokologische Naturraume Deutschlands: Forstliche Wuchsgebiete und Wuchsbezirke – Digitale Topographische Grundlagen – Neubearbeitung Stand 2011, Sonderheft Nr. 359. Landbauforschung vTI Agriculture and Forestry Research

Guillemot J, Klein EK, Davi H, Courbet F (2015) The effects of thinning intensity and tree size on the growth response to annual climate in Cedrus atlantica: A linear mixed modeling approach. Annals of Forest Science 72(5):651–663. doi: 10.1007/s13595-015-0464-y

Hendriks C, Bianchi F (1995) Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. Netherlands Journal of Agricultural Science 1995(43):321–331

Hugershoff R (1936) Die mathematischen Hilfsmittel der Kulturingenieurs und Biologen: Herleitung von gesetzmäßigen Zusammenhängen als Manuskript veröffentlicht, Dresden

Johann K (1977) Eine neue Jahrringmeßanlage fuer Bohrkerne und Stammscheiben. forstarchiv 48:24–26

Jonard F, André F, Ponette Q, Vincke C, Jonard M (2011) Sap flux density and stomatal conductance of European beech and common oak trees in pure and mixed stands during the summer drought of 2003. Journal of Hydrology 409(1-2):371–381. doi: 10.1016/j.jhydrol.2011.08.032

Jucker T, Bouriaud O, Avacaritei D, Coomes DA, Knops J (2014) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. Ecol Lett 17(12):1560–1569. doi: 10.1111/ele.12382

Kelty MJ (2006) The role of species mixtures in plantation forestry. Improving Productivity in Mixed-Species Plantations 233(2–3):195–204. doi: 10.1016/j.foreco.2006.05.011

Keyes MR, Grier CC (1981) Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11(3):599–605. doi: 10.1139/x81-082

Krause C, Morin H (1995) Changes in radial increment in stems and roots of balsam fir [Abies balsamea (L.) Mill.] after defoliation spruce budworm. The Forestry Chronicle 71(6):747–754. doi: 10.5558/tfc71747-6

Kuznetsova A, Brockhoff B, Christensen HB (2015) lmerTest: Tests in Linear Mixed Effects Models

Larocque GR, Luckai N, Adhikary SN, Groot A, Bell FW, Sharma M (2013) Competition theory — science and application in mixed forest stands: review of experimental and modelling methods and suggestions for future research. Environ. Rev. 21(2):71–84. doi: 10.1139/er-2012-0033

Lavelle P, Spain AV (2005) Soil Ecology, 2. print with corr. Springer, Dordrecht

Lebourgeois F, Gomez N, Pinto P, Mérian P (2013) Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. Forest Ecology and Management 303:61–71. doi: 10.1016/j.foreco.2013.04.003

Lehto T, Zwiazek JJ (2011) Ectomycorrhizas and water relations of trees: a review. Mycorrhiza 21(2):71–90. doi: 10.1007/s00572-010-0348-9

Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, McGuire AD, Bozzato F, Pretzsch H, Miguel S de, Paquette A, Hérault B, Scherer-Lorenzen M, Barrett CB, Glick H, Hengeveld GM, Nabuurs G-J, Pfautsch S, Viana H, Vibrans AC, Ammer C, Schall P, Verbyla D, Tchebakova N, Fischer M, Watsan JV, Chen H, Lei X, Schelhaas M-J, Lu H, Gianelle D, Parfenova EI, Eljatib CS, Lee E, Lee B, Kim, H.-A-, Bruelheide, H., Coomes DA, Piotto D, Sunderland T, Schmid B, Rautiainen M, Gourlet-Fleury S, Sonké B, Tavani R, Zhu J, Brandl S, Vayreda J, Kitahara F, Searle EB, Neldner VJ, Ngugi MR, Baraloto C, Frizzera L, Balazy R, Oleksyn J, Zawila-Niedzwiecki T, Bouriaud O, Bussotti F, Finér L, Jaroszewicz B, Jucker T, Valladares F, Jagodzinski AM, Luis PP, Gonmadje C, Marthy W, O'Brien T, Martin EH, Marshall A, Rovero F, Bitariho R, Niklaus PA, Alvarez-Loayza P, Chamuya N, Valencia R, Mortier F, Wortel V, Obiang NE, Ferreira LV, Odeke DE, Vasquez RM, Reich PB (2016) Positive Biodiversity-Productivity Relationship predominant in global forests. Science

Matyssek R, Fromm J, Rennenberg H, Roloff A (2010) Biologie der Bäume: Von der Zelle zur globalen Ebene ; 32 Tabellen. UTB Biologie, Agrar- und Forstwissenschaften, Landschaftsplanung, vol 8450. Ulmer, Stuttgart

Mauer O, Palátová E (2012) Root system development in Douglas fir (Pseudotsuga menziesii [Mirb.] Franco) on fertile sites. Journal of Forest Science 58(9):400–409

Mayer P, Brang P, Dobbertin M, Hallenbarter D, Renaud J-P, Walthert L, Zimmermann S (2005) Forest storm damage is more frequent on acidic soils. Ann. For. Sci. 62(4):303–311. doi: 10.1051/forest:2005025

McConnaughay KDM, Coleman JS (1999) Biomass allocation in plants: Ontogeny or optimality? A test along three resource gradients. Ecology 80(8):2581–2593. doi: 10.1890/0012-9658(1999)080[2581:BAIPOO]2.0.CO;2

McMinn RG (1963) Characteristics of Douglas-fir root systems. Canadian Journal of Botany 41(1):105–122

Meier IC, Leuschner C (2008) Belowground drought response of European beech: Fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Global Change Biology 14(9):2081–2095. doi: 10.1111/j.1365-2486.2008.01634.x

Nicoll BC, Ray D (1996) Adaptive growth of tree root systems in response to wind action and site conditions. Tree Physiology 16(11-12):891–898. doi: 10.1093/treephys/16.11-12.891

Nikolova PS, Zang C, Pretzsch H (2011) Combining tree-ring analyses on stems and coarse roots to study the growth dynamics of forest trees: a case study on Norway spruce (Picea abies [L.] H. Karst). Trees 25(5):859–872. doi: 10.1007/s00468-011-0561-y

Paterson SS (1956) Forest area of the world and its potential productivity, Göteborg

Pearson JA, Fahey TJ, Knight DH (1984) Biomass and leaf area in contrasting lodgepole pine forests. Can. J. For. Res. 14(2):259–265. doi: 10.1139/x84-050

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Piotto D (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecology and Management 255(3-4):781–786. doi: 10.1016/j.foreco.2007.09.065

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. New Phytologist 193(1):30–50. doi: 10.1111/j.1469-8137.2011.03952.x

Pretzsch H (2002) Grundlagen der Waldwachstumsforschung. Parey, Berlin

Pretzsch H (2009) Forest dynamics, growth and yield: From measurement to model. Springer, Berlin, London

Pretzsch H, Biber P (2016) Tree species mixing can increase maximum stand density. Can. J. For. Res.:1–15. doi: 10.1139/cjfr-2015-0413

Pretzsch H, Biber P, Uhl E, Hense P (2012a) Coarse root–shoot allometry of Pinus radiata modified by site conditions in the Western Cape province of South Africa. Southern Forests: a Journal of Forest Science 74(4):237–246. doi: 10.2989/20702620.2012.741794

Pretzsch H, Block J, Dieler J, Gauer J, Göttlein A, Moshammer R, Schuck J, Weis W (2014) Nährstoffentzüge durch die Holz- und Biomassenutzung in Wäldern. Teil 1: Schätz-funktionen für Biomasse und Nährelemente und ihre Anwendung in Szenariorechnungen. Allg. Forst Jagdztg 185(11/12):261–285

Pretzsch H, del Río M, Ammer C, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Dirnberger G, Drössler L, Fabrika M, Forrester DI, Godvod K, Heym M, Hurt V, Kurylyak V, Löf M, Lombardi F, Matović B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Schütze G, Schweig J, Skrzyszewski J, Sramek V, Sterba H, Stojanović D, Svoboda M, Vanhellemont M, Verheyen K, Wellhausen K, Zlatanov T, Bravo-Oviedo A (2015) Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe. Eur J Forest Res. doi: 10.1007/s10342-015-0900-4

Pretzsch H, del Río M, Schütze G, Ammer C, Annighöfer P, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Drössler L, Fabrika M, Forrester DI, Kurylyak V, Löf M, Lombardi F, Matović B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Skrzyszewski J, Sramek V, Sterba H, Svoboda M, Verheyen K, Zlatanov T, Bravo-Oviedo A (2016) Mixing of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) enhances structural heterogeneity, and the effect increases with water availability. Forest Ecology and Management 373:149–166. doi: 10.1016/j.foreco.2016.04.043

Pretzsch H, Schütze G (2016) Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur J Forest Res 135(1):1–22. doi: 10.1007/s10342-015-0913-z

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

Pretzsch H, Uhl E, Biber P, Schütze G, Coates KD (2012b) Change of allometry between coarse root and shoot of Lodgepole pine (Pinus contorta DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia. Scandinavian Journal of Forest Research 27(6):532–544. doi: 10.1080/02827581.2012.672583

R Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Radosevich SR, Hibbs DE, Ghersa CM (2006) Effects of species mixtures on growth and stand development of Douglas-fir and red alder. Can. J. For. Res. 36(3):768–782. doi: 10.1139/x05-280

Reubens B, Pannemans B, Danjon F, Proft M de, Baets S de, Baerdemaeker J de, Poesen J, Muys B (2009) The effect of mechanical stimulation on root and shoot development of young containerised Quercus robur and Robinia pseudoacacia trees. Trees 23(6):1213–1228. doi: 10.1007/s00468-009-0360-x

Röhrig E, Bartsch N, Lüpke B von, Dengler A (2006) Waldbau auf ökologischer Grundlage: 91 Tabellen, 7., vollst. aktual. Aufl. UTB Forst- und Agrarwissenschaften, Ökologie, Biologie, vol 8310. UTB, Stuttgart

Sands R, Mulligan DR (1990) Water and nutrient dynamics and tree growth. Forest Ecology and Management 30(1-4):91–111. doi: 10.1016/0378-1127(90)90129-Y

Schall P, Lödige C, Beck M, Ammer C (2012) Biomass allocation to roots and shoots is more sensitive to shade and drought in European beech than in Norway spruce seedlings. Forest Ecology and Management 266:246–253. doi: 10.1016/j.foreco.2011.11.017

Schelhaas MJ (2008) The wind stability of different silvicultural systems for Douglas-fir in the Netherlands: A model-based approach. Forestry 81(3):399–414. doi: 10.1093/forestry/cpn028

Schütz J-P, Götz M, Schmid W, Mandallaz D (2006) Vulnerability of spruce (Picea abies) and beech (Fagus sylvatica) forest stands to storms and consequences for silviculture. European Journal of Forest Research 125(3):291–302. doi: 10.1007/s10342-006-0111-0

Shainsky LJ, Newton M, Radosevich SR (1992) Effects of intra- and inter-specific competition on root and shoot biomass of young Douglas-fir and red alder. Can. J. For. Res. 22(1):101–110. doi: 10.1139/x92-014

Taegger S, Kölling C (2016) Standortinformationssystem BaSIS. AFZ-DerWald(4):10–13

Thomas FM, Bögelein R, Werner W (2015) Interaction between Douglas fir and European beech: Investigations in pure and mixed stands = Wechselwirkungen zwischen Douglasie und Rotbuche :

Untersuchungen an Rein- und Mischbeständen. Forstarchiv : forstwissenschaftliche Fachzeitschrift 86(4):83–91

Thornley JH (1972) A balanced quantitative model for root: shoot ratios in vegetative plants. Annals of Botany 36(2):431–441

Thornthwaite CW (1948) An Approach toward a Rational Classification of Climate. Geographical Review 38(1):55–94. doi: 10.2307/210739

Thurm EA, Pretzsch H (2016) Improved productivity and modified tree morphology of mixed versus pure stands of European beech (Fagus sylvatica) and Douglas-fir (Pseudotsuga menziesii) with increasing precipitation and age. Ann. For. Sci.:1–15. doi: 10.1007/s13595-016-0588-8

Thurm EA, Uhl E, Pretzsch H (2016) Mixture reduces climate sensitivity of Douglas-fir stem growth. Forest Ecology and Management(376):205–220. doi: 10.1016/j.foreco.2016.06.020

Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Climate 23(7):1696–1718. doi: 10.1175/2009JCLI2909.1

Vitasse Y, Delzon S, Dufrêne E, Pontailler J-Y, Louvet J-M, Kremer A, Michalet R (2009) Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? Agricultural and Forest Meteorology 149(5):735–744. doi: 10.1016/j.agrformet.2008.10.019

Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. Journal of Ecology 100(3):742–749. doi: 10.1111/j.1365-2745.2011.01944.x

Article -IV-

Douglasie: Wie die Mischung den Zuwachs und die Stabilität steigert

Der Einfluss der Rotbuche auf das Wachstum der Douglasie

in ***LWF aktuell (2017)***

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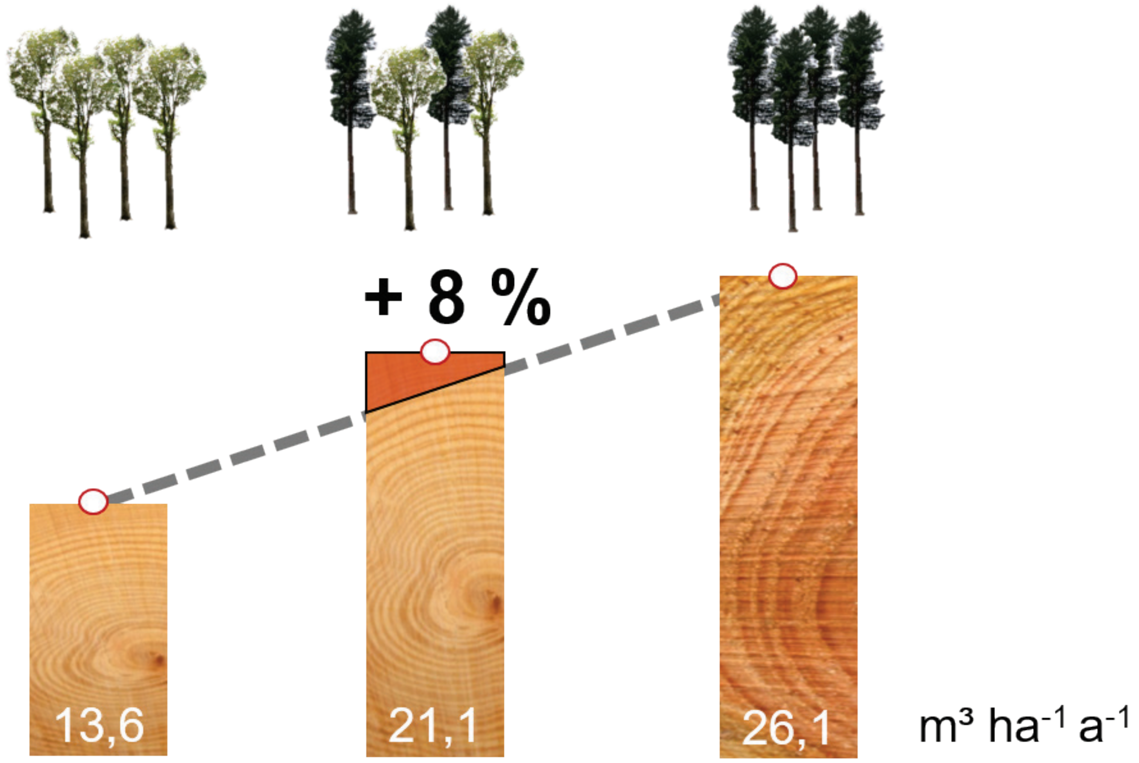

Der Umgang mit der Douglasie als nichtheimische Art wird seit geraumer Zeit kontrovers diskutiert. So wird sie beispielsweise vom Bundesamt für Naturschutz (BfN) aufgrund eines möglichen Invasionspotenzials auf der Schwarzen Liste geführt. Der Deutsche Verband Forstlicher Forschungsanstalten (DVFFA) hat sich hingegen bewusst für einen Anbau der Douglasie ausgesprochen, denn sie zeichnet sich durch ihre hohe Zuwachsleistung und ihre höhere Trockenheitstoleranz im Vergleich zur Fichte aus.

Die Empfehlung des Deutschen Verbands Forstlicher Forschungsanstalten DVFFA richtet sich auf die Beteiligung der Douglasie in Mischung mit anderen Baumarten, insbesondere mit der Buche. Die Baumartenmischung Buche-Douglasie ist zwar schon seit einiger Zeit in geringem Anteil in den deutschen Wäldern zu finden, dennoch ist bisher wenig über das Zuwachsverhalten der beiden Baumarten in Mischung veröffentlicht worden. In den vergangenen drei Jahren hat sich der Lehrstuhl für Waldwachstumskunde im Rahmen eines von der Bayerischen Forstverwaltung geförderten Projekts intensiv mit Mischbeständen aus Buche und Douglasie auseinandergesetzt. Ziel dieser Forschungsarbeit war es, die Wechselwirkungen zwischen Douglasie und Rotbuche und ihre Effekte auf Zuwachsverhalten und Resilienz zu beleuchten, die Ergebnisse zu interpretieren und Möglichkeiten für waldbauliche Behandlungsprogramme aufzuzeigen.

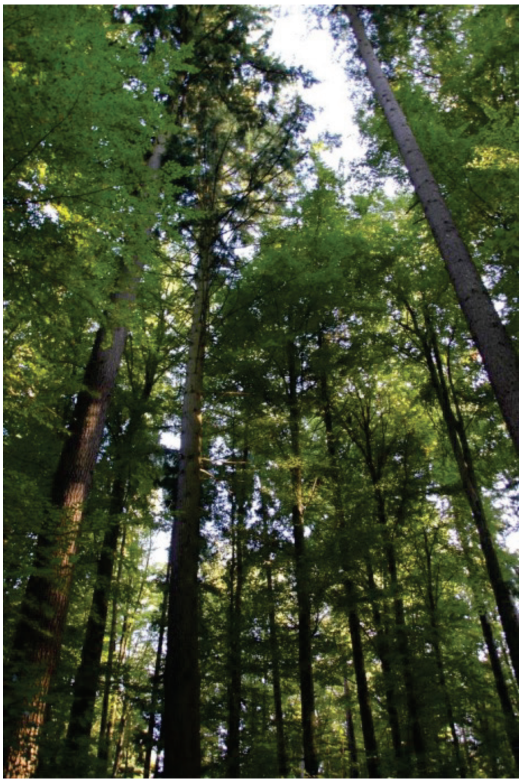

Fig. 1 Douglas-fir crowns overtop the European beech crowns obviously. This enables Douglas-fir to apply their great light use efficiency, whereas European beech, as shade tolerant species is still able to use the diffuse light.

***Abb. 1** Deutlich überragt die Douglasienkrone die Buchen. So kann die Douglasie ihre hohe Lichtnutzungseffizienz voll ausspielen. Die Buche als Schattenbaumart hingegen kann immer noch das einfallende Streulicht in spürbares Wachstum umsetzen.*

Nachdem sich für einige Baumarten gezeigt hat, dass in Mischbeständen (z. B. Buche-Fichte oder Buche-Eiche) ein höherer Zuwachs als in Reinbeständen zu erwarten ist (Pretzsch et al. 2013; Pretzsch et al. 2010), wurde dies zunächst auch für die Mischung aus Buche und Douglasie angenommen. Um dies zu verifizieren, legte der Lehrstuhl für Waldwachstumskunde an verschiedenen Standorten in Bayern und Rheinland-Pfalz temporäre Versuchsflächen an und analysierte den Zuwachs von Buchen und Douglasien in Rein- und Mischbeständen. Auch bei dieser Baumartenkombination stellte sich ein höherer Volumenertrag von rund 8 % ein (Thurm und

Pretzsch 2016). Abbildung 2 zeigt den Verlauf des Zuwachses in Abhängigkeit des Mischungsanteils der Douglasie. Der Douglasien-Anteil von 0 % spiegelt den Buchen-Reinbestand mit 13,6 Vorratsfestmetern (Vfm) Zuwachs pro Jahr wider, 100 % Douglasien Anteil steht für den Douglasie-Reinbestand mit 26,1 Vfm Zuwachs. Der Mischbestand (dickere, obere Linie) in der aktuellen Untersuchung besaß einen durchschnittlichen Mischungsanteil von 47 % Douglasien und produzierte 21,1 Vfm, was einem Mehrzuwachs von 8 % bzw. 1,63 Vfm entspricht. Die gestrichelten Linien zeigen die rechnerische Produktivität, welche sich aus den Reinbeständen ergeben würden. Die dünneren Linien stellen die Leistung von Buche und Douglasie am Mischbestandszuwachs dar.

Beim Zustandekommen des Mehrzuwachses zeigte die Mischung beider Baumarten jedoch einige Besonderheiten.

Zuwachssteigerung durch Mischung

Ausgangspunkt der Untersuchung waren sogenannte Tripletts. Diese bestehen aus Untersuchungseinheiten mit jeweils einem Douglasien-Reinbestand, einem Buchen-Reinbestand und einem Mischbestand beider Arten. Die Bestände standen in unmittelbarer Nähe zueinander (rund 200 m Entfernung) und waren dem Bestandsalter und dem Standort nach identisch. Somit konnte für jedes Triplett verglichen werden, wie sich die jeweilige Baumart im Rein- und im Mischbestand verhält.

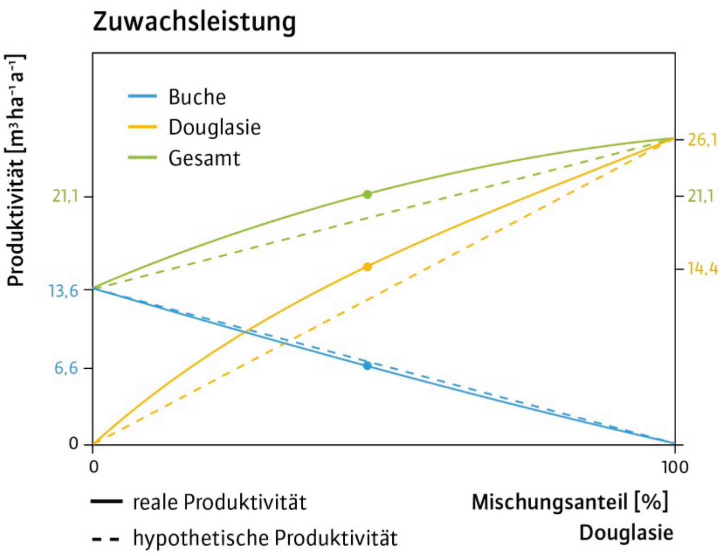

Fig. 2 Response of the overyielding depending on mixing proportion of Douglas-fir.

Abb. 2 *Verlauf des Zuwachses anhand des Mischungsanteils der Douglasie.*

Die Anlage dieser Tripletts erfolgte auf unterschiedlichen Standorten und in verschiedenen Altersklassen. Es spannten sich so ein Standortsgradient vom Feuchten zum Trocknen und ein Altersgradient von 30 bis 120 Jahre auf. Mit Hilfe der Gradienten konnte neben dem generellen

Mehrzuwachs im Mischbestand aufgezeigt werden, dass der Mehrzuwachs insbesondere auf Standorten mit höherem Niederschlag und bei höherem Bestandsalter auftritt (Abbildung 3). Diese Zuwachssteigerung wird dabei im Wesentlichen durch ein stärkeres Dickenwachstum der Douglasie getragen. Die Buche zeigte ein verhältnismäßig gleiches Wachstumsverhalten im Rein- und im Mischbestand. Sie trägt erst im hohen Alter zum Mehrzuwachs im Mischbestand bei.

Die Struktur macht den Unterschied

Warum verbessert aber nun die Mischung der Baumarten den Zuwachs? Hierzu bestehen unterschiedliche Theorien, wie die einzelnen Baumarten von der Mischung profitieren: Ist es eine Verbesserung (Faszilitation) des Nährstoffangebots wie bei Douglasie und Roterle (Alnus rubra)? Oder ist es eine bessere Ausnutzung von Licht oder Wasser wie bei Buche und Kiefer (Pinus sylvestris) (Komplementarität)?

Grundsätzlich zeigt sich in der aktuellen Mischbestandsforschung, dass es einen einzigen Mischungseffekt, der für alle Baumartenkombinationen zutrifft, nicht gibt. Die Eigenschaften der jeweils gemischten Baumarten führen zu unterschiedlichen Mischungseffekten und verbessern bzw. verschlechtern die Ressourcenaufnahme der Baumindividuen. Die limitierend wirkende Ressource bestimmt letztlich auch die Abhängigkeit des Mehrzuwachses vom Standort.

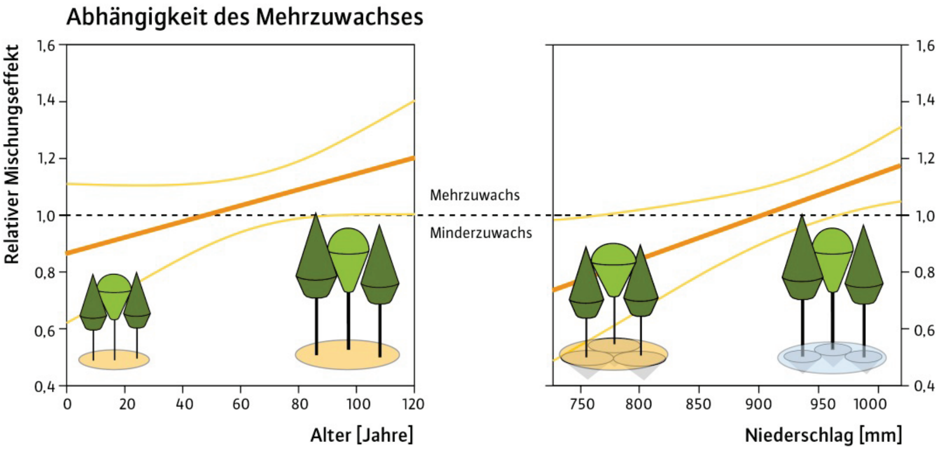

Fig. 3 Overyielding of Douglas-fir – European beech mixed stands compared to pure stands depending on a) stand age (left) and b) annual precipitation sum (right).

Abb. 3 Verlauf des Mehrzuwachses in Douglasien- Buchen-Mischbeständen gegenüber Reinbeständen in Abhängigkeit a) Bestandsalter (li.) und b) Jahresniederschlag (re.).

Douglasie gewinnt im Licht, Buche ist im Schatten stark

Bei der Mischung von Buche und Douglasie hat sich gezeigt, dass besonders die Höhenstrukturierung den Mischungseffekt bestimmt (Thurm und Pretzsch 2016). So finden sich im Alter von 100 Jahren problemlos Bestände, in denen die Douglasie (h = 46 m) die Buche (h = 36 m) um 10 m überragt. Die Douglasie als Baumart mit einer sehr hohen Lichtnutzungseffizienz kann diese »Freistellung« des oberen Kronenbereiches effektiv nutzen. Die Buche mit ihrem niedrigen Lichtkompensationspunkt ist dennoch in der Lage, auch das einfallende Streulicht noch effizient umzusetzen. Das Licht ist bei dieser Mischung offenbar der limitierende Faktor beider Baumarten. Damit erklärt sich, dass mit höherem Alter und größerer Höhenstrukturierung der Mischungseffekt zunimmt. Der Standort hat einen ähnlichen Effekt: Auf einem besseren Standort gewinnt die Douglasie an Wuchsvorsprung und durch die somit stärkere Strukturierung stellt sich ein höherer Mehrzuwachs ein.

Die biologisch getriebene Strukturierung bietet neben der besseren Lichtausnutzung einen weiteren Vorteil: Die in Mischbeständen auftretende horizontale Struktur führt zu einer Qualifizierung der Stämme, die in Reinbeständen nur durch aufwendige Pflegemaßnahmen zu erreichen ist (Pretzsch und Rais 2016).

Wenn das Licht im Mischbestand limitierend wirkt, stellt sich die Frage, wie die beiden Baumarten im Boden interagieren. Allgemein wird gelehrt, dass sich die Streu verbessert, wenn ein Nadelbaum mit einem Laubbaum gemischt wird. Fakt ist, dass die Douglasie keine so ungünstige Streu hat (Edmonds 1980; Augusto et al. 2002). Auch der positive Effekt der höheren Struktur der gemischten Nadel-Laub-Streu ist bei weitem nicht so ausgeprägt, wie es häufig vermutet wird. Es sind vielmehr die veränderten Umweltbedingungen und die faunistische Zusammensetzung, die im Mischbestand für eine schnellere Umsetzung sorgen (Berger und Berger 2014).

Mehr Stamm-, weniger Wurzelwachstum

Ein wichtiger Aspekt bei Buche und Douglasie ist vielmehr, dass sich beide Baumarten in der Nährstoffaufnahme ergänzen, weil unterschiedliche Nährstoffe für ihre Versorgung wichtig sind (Pretzsch et al. 2014). Diese Konkurrenzminderung im Boden ermöglicht es, dass die Bäume verstärkt in das oberirdische Wachstum investieren können.

Bei unseren Untersuchungen an Wurzel und Stamm der Bäume (Abbildung 4) konnten wir feststellen, dass im Vergleich zum Reinbestand Bäume im Mischbestand eher in das Dickenwachstum des Stammes und weniger in das Dickenwachstum der Grobwurzeln investieren (Thurm et al. 2017). Im Reinbestand, wo die intraspezifische Konkurrenz 100 % beträgt, ist der Wurzeldurchmesser im Verhältnis zum Stammdurchmesser stets größer als in Mischungssituationen, wo der untersuchte Baum von Individuen der eigenen und der anderen Art umgeben ist (50 % intraspezifische Konkurrenz). Am geringsten ist jeweils der Wurzeldurchmesser, wenn der untersuchte Baum ausschließlich von der anderen Art (100 % interspezifische Konkurrenz) umgeben ist. Demnach zeigt ein höherer Mischungsanteil bei beiden Baumarten eine Verschiebung der Kurve zugunsten des Stammwachstums.

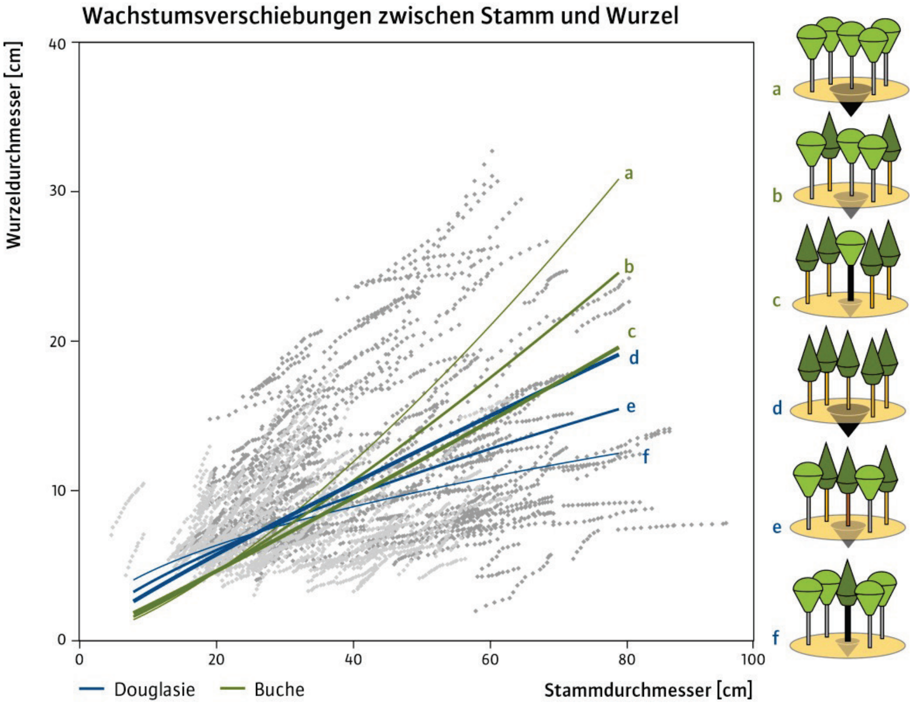

Fig. 4 Partitioning of growth between stem diameter and root diameter depending on mixture of surrounding trees. *(a,d) 100 % intraspecific competition for the tree – pure stand, (b,e) 50 % intraspecific competition for the tree – measured tree is surrounded by individuals of its own species and by the other species, (c,f) 100 % interspecific competition for the tree.*

***Abb. 4** Verschiebung des Wachstums zwischen Stammdurchmesser und Wurzeldurchmesser in Abhängigkeit der umgebenden Mischung von Buche und Douglasie; (a,d) 100 % intraspezifische Konkurrenz für den Baum - Reinbestand, (b,e) 50 % intraspezifische Konkurrenz für den Baum – der Messbaum ist von Bäumen der eigenen Art und Bäumen der anderen Art umgeben, (c,f) 100 % interspezifische Konkurrenz für den Baum.*

Dieses veränderte Spross-Wurzel-Verhältnis zugunsten des Stammwachstums war auch im Hinblick auf andere Einflussfaktoren festzustellen. So zeigen Douglasien auf besseren Standorten ein geringeres Wurzelwachstum als auf schlechteren Standorten. Eine geringere Bestandsdichte beeinflusst die Stamm-Wurzel-Relation ähnlich zu Gunsten des Stammes. Dass die Mischung den gleichen positiven Einfluss auf das Stammwachstum hat, konnte mit der aktuellen Studie jedoch zum ersten Mal festgestellt werden. Der Vergleich von Standortgüte und Bestandsdichte zeigt jedoch, welche positive Wirkung die Mischung von Buche und Douglasie auf die Bäume ausübt.

Mischung verkürzt die Erholungszeit

Ein weiterer Teil unserer Arbeit befasste sich mit dem Einfluss von Trockenstress auf das Zuwachsverhalten (Thurm et al. 2016). Dazu untersuchten wir die Jahrringzuwächse der Stämme mit Hilfe von Bohrkernen. Betrachtet wurden die stärksten Trockenereignisse zwischen 1950 und 2010 und dahingehend analysiert, wie stark der Grundflächenzuwachs des Einzelbaumes im Trockenjahr einbricht und wie viel Zeit die Baumarten benötigen, um sich wieder auf ihr Niveau vor dem Trockenereignis einzufinden.

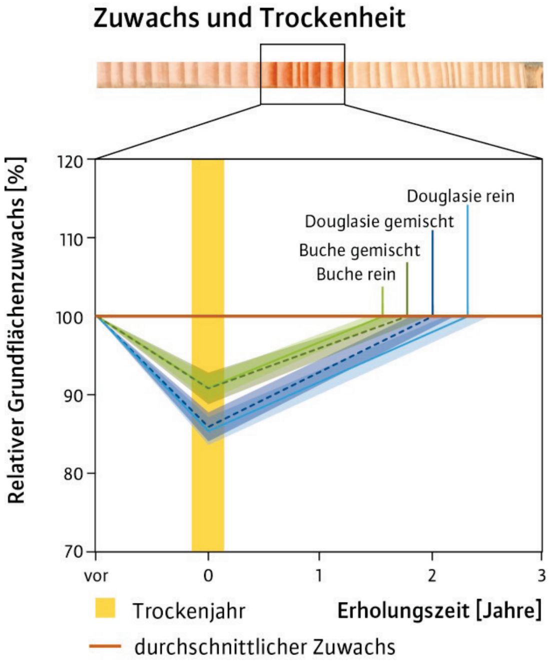

Fig. 5 Relative drop of the year ring growth from European beech and Douglas-fir separated into pure and mixed stands.

Abb. 5 *Relativer Zuwachseinbruch innerhalb der Jahrringe von Buche und Douglasie im Rein- und Mischbestand in Trockenjahren.*

Dabei stellte sich heraus, dass die Mischung keinen Einfluss auf den Zuwachseinbruch im Trockenjahr hat. Abbildung 5 beschreibt den relativen Zuwachseinbruch innerhalb der Jahrringe von Buche und Douglasie im Rein- und Mischbestand in Trockenjahren und die anschließende Erholungsphase. Der Einbruch zeigt den Zuwachsverlust gegenüber dem durchschnittlichen Zuwachs an (orange Linie). Die aufstrebenden Linien stellen dar, wann sich die Bäume wieder von einem Trockenjahr erholt haben und sich auf dem Wachstumsniveau vor dem Trockenstress befinden. Die Douglasien brechen im Reinbestand prozentual etwas mehr ein, besitzen aber auch ein generell höheres Wachstumsniveau als die Buchen. In der Erholungsphase regenerierten sich die Douglasien im Mischbestand jedoch etwas schneller als die Douglasien im Reinbestand. Die Buchen benötigten im Mischbestand eine längere Erholungszeit. Wir vermuten, dass eine zeitlich verzögerte Wassernutzung im Folgejahr die Ursache ist. Die Douglasie als immergrüne Baumart fängt mit der Transpiration an, sobald es die Witterungsbedingungen erlauben. Die Buche beginnt erst wieder mit der Transpiration ab Laubaustrieb. Das bedeutet: Im Mischbestand kann die Douglasie bei günstigen Bedingungen im Frühjahr frühzeitig ihre Reserven wieder auffüllen, das jedoch ohne Konkurrenz der noch nicht ausgetriebenen Buche. In den jeweiligen Reinbeständen beginnen die beiden Baumarten jeweils gleichzeitig zu transpirieren. Die Douglasie, die im Vergleich zur Fichte generell eine bessere Trockenheitsresistenz hat, profitiert also zusätzlich von der Buchenmischung nach Trockenphasen.

Schlussfolgerungen für die Bewirtschaftung

Unsere Studie hat gezeigt, dass die Mischung von Buche und Douglasie positive Effekte nach sich zieht. Das Wachstum der Douglasie wird gesteigert und das Wachstum der Buche bleibt mindestens konstant. Einen durchschnittlichen Bestandszuwachs von 21 Vorratsfestmetern je Hektar und Jahr (Vfm ha-1 a-1) im Alter von 60 Jahren auf guten Standorten erreichen sicherlich nur wenige Bestandstypen in Mitteleuropa. Im Hinblick auf eine prognostizierte Nadelholzverknappung stellt die Douglasie damit eine sinnvolle Alternative zur Fichte dar. Hohe Niederschläge fördern dabei den Mischungseffekt zusätzlich. Im besonderen Maße ist es das Alter, das zu einem Mehrzuwachs von Mischbeständen gegenüber Rein- beständen führt. Die Mischung braucht Zeit, um einen Mischbestandseffekt auszubilden (unabhängig davon, wie der Mischungseffekt zustande kommt).

Eine weitere waldbauliche Konsequenz ist, dass Buchen-Douglasien-Mischbestände aufgrund der besseren Lichtausnutzung in höheren Bestandsdichten gehalten werden können, ohne dass dadurch Zuwachsverluste verursacht werden. Diese höheren Dichten erlauben auch im späteren Bestandsalter zusätzliche waldbauliche Spielräume. Aufgrund der starken Dominanz der Buche im Jugendalter empfiehlt es sich, die Douglasie truppweise in die Buche einzubringen. Somit erhält man im Altbestand die gewünschte Durchmischung von ein bis maximal drei starken Douglasien, die von Buchen umfasst werden.

Mit Blick auf künftige klimatische Veränderungen zeigt sich die Douglasie ohnehin resistenter als die wichtige einheimische Nadelbaumart Fichte. Die Mischung mit der Buche verschafft ihr noch einen weiteren Stabilitätsvorteil für die Zukunft.

Zusammenfassung

In Rein- und Mischbeständen von Douglasie und Buche wurden die Wechselwirkungen zwischen diesen beiden Baumarten hinsichtlich Zuwachsverhalten und Resilienz untersucht. Vor allem das Wachstum der Douglasie ist im Mischbestand deutlich höher als im Reinbestand. Der Zuwachs der Buche bleibt in Rein- und Mischbeständen weitgehend gleich. Wegen der besseren Lichtausnutzung sind in Mischbeständen höhere Bestandsdichten möglich, ohne dass es zu Zuwachsverlusten kommt. Nach Zuwachseinbrüchen in Trockenjahren erholen sich Douglasien in Mischbeständen schneller als in Reinbeständen.

Projekt

Das Projekt »Zuwachs- und Wertleistung von Buchen - Douglasien - Mischbeständen in Abhängigkeit von den Standortbedingungen« (W 44) wurde vom Bayerischen Staatsministerium für Ernährung, Landwirtschaft und Forsten finanziert.

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Literatur

Augusto, L.; Ranger, J.; Binkley, D.; Rothe, A. (2002): Impact of several common tree species of European temperate forests on soil fertility. In: Ann. For. Sci. 59 (3), S. 233–253. DOI: 10.1051/forest:2002020

Berger, T. W.; Berger, P. (2014): Does mixing of beech (Fagus sylvatica) and spruce (Picea abies) litter hasten decomposition? In: Plant and Soil 377 (1-2), S. 217–234. DOI: 10.1007/s11104-013-2001-9

Edmonds, R. L. (1980): Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver fir eco- systems in western Washington. In: Can. J. For. Res. 10 (3), S. 327– 337. DOI: 10.1139/x80-056

Pretzsch, H.; Bielak, K.; Block, J.; Bruchwald, A.; Dieler, J.; Ehrhart, H.-P. et al. (2013): 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: Eur J Forest Res 132 (2), S. 263–280. DOI: 10.1007/s10342-012-0673-y

Pretzsch, H.; Block, J.; Dieler, J.; Gauer, J.; Göttlein, A.; Moshammer, R. et al. (2014): Nährstoffentzüge durch die Holz- und Biomassenutzung in Wäldern. Teil 1: Schätz-funktionen für Biomasse und Nährelemente und ihre Anwendung in Szenariorechnungen. In: Allg. Forst Jagdztg 185 (11/12), S. 261–285

Pretzsch, H.; Block, J.; Dieler, J.; Dong, P. H.; Kohnle, U.; Nagel, J. 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), S. 712. DOI: 10.1051/forest/2010037

Pretzsch, H.; Rais, A. (2016): Wood quality in complex forests versus even-aged monocultures. Review and perspectives. In: Wood Sci Technol 50 (4), S. 845–880. DOI: 10.1007/s00226-016-0827-z

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

Thurm, E. A.; Biber, P.; Pretzsch, H. (2017): Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir (Pseudotsuga menziesii) and European beech (Fagus sylvatica). In: Trees 31 (1), S. 349–365. DOI: 10.1007/s00468- 016-1512-4

Thurm, E. A.; Pretzsch, H. (2016): Improved productivity and modified tree morphology of mixed versus pure stands of European beech (Fagus sylvatica) and Douglas-fir (Pseudotsuga menziesii) with increasing precipitation and age. In: Ann. For. Sci. 73 (4), S. 1047–1061. DOI: 10.1007/s13595-016-0588-8

Thurm, E. A.; Uhl, E.; Pretzsch, H. (2016): Mixture reduces climate sensitivity of Douglas-fir stem growth. In: Forest Ecology and Management (376), S. 205–220. DOI: 10.1016/j.foreco.2016.06.020