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Mixture reduces climate sensitivity of Douglas-fir stem growth

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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 1950–2010. 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.

1. Introduction

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

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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).

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.

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 "S chwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaf t" (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.

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. 90–120 years). Table 1 gives an overview of the triplet's site conditions and stand parameters.

2.2. Sampling and standardization of tree rings

During the years 2012–2014, 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