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Thinning increases drought tolerance of European beech: a case study on two forested slopes on opposite sides of a valley

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Abstract European beech (Fagus sylvatica L.) is one of the economically most important broadleaved tree species in Central Europe. However, beech shows high drought sensitivity and calls for profound research to test its ability to cope with limited water resources. Here, we investigated the drought tolerance of beech to the 2003 drought as influenced by Kraft class, aspect and thinning intensity. Annual basal area increment data of 126 sample trees from southwest Germany were used to assess the variability of drought tolerance indices, by comparing three social classes (predominant, dominant and co-dominant), two contrasting sites [a dry southwest (SW) aspect and a moist northeast (NE) aspect], and three treatments [control, strong thinning (stand basal area 15 m² ha⁻¹) and very strong thinning (stand basal area 10 m² ha⁻¹)] in mature beech stands. Our results show that the co-dominant and dominant trees had lower growth recovery and lower growth resilience after the drought, compared to the predominant trees. The differences between aspects pointed to a growth-drought tolerance trade-off, in which trees on the

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¹ Chair of Forest Growth and Dendroecology, Albert-Ludwigs-University Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany SW aspect displayed lower growth rates but higher resilience indices than trees on the moist NE aspect. Furthermore, our results suggest that the resistance to and resilience after the 2003 drought significantly increased for the thinned trees. Our results provide novel insights into the linkage between the forest stand management and drought tolerance of beech under contrasting sites. We conclude that thinning can partially alleviate effects of severe drought on European beech forests in southwest Germany and can be applied as an adaptive measure to increase the mitigation potential of beech stands.

Keywords Fagus sylvatica · Adaptive management · Resistance · Recovery · Resilience · Kraft class

Introduction

Extreme climatic events, such as the dry summers of 2003, 2011 and 2015 in Central Europe are considered warning signals of climate change. The observed and projected changes in climate for Central Europe indicate longer, more frequent and more intense summer droughts (Christensen et al. 2007; Teskey et al. 2015). Development of new management guidelines for European forests is crucial in the process of increasing the adaptive capacity of current forests to the predicted changes in climate. Silvicultural treatments such as thinning were suggested in many studies as tools which not only could accelerate growth, but also improve tolerance of individual trees towards drought (Cescatti and Piutti 1998; Kohler et al. 2010).

European beech is one of the most important forest tree species in Central Europe (Bohn et al. 2003; Ellenberg 1996), and its climate sensitivity has been assessed by many authors. Several studies provide evidence for low tolerance of European beech to drought (Fotelli et al. 2002; Dittmar et al. 2003; Geßler et al. 2007). Similarly, the growth-stimulating effects of thinning on European beech stands are well acknowledged. Cescatti and Piutti (1998) demonstrated that sensitivity of beech to climate and drought is strongly determined by intraspecific competition. At high intensity of competition, trees are more sensitive to increased temperature and reduced water availability, whereas at low competition level, trees benefit from warm temperature. Le Goff and Ottorini (1993) and van der Maaten (2012b) confirmed that thinning stimulates growth independently of site conditions and during wet as well as dry seasons. Nevertheless, the capacity of European beech to cope with the anticipated warmer climate is still controversially discussed (Rennenberg et al. 2004; Ammer et al. 2005). This imminent lack of knowledge demands for profound research at different scales of analysis.

The concept for the assessment of tree growth responses to drought introduced by Lloret et al. (2011) is based on four indices: resistance (Rt), recovery (Rc), resilience (Rs) and relative resilience. In this way, the drought tolerance of different tree species and for different drought events can be assessed, evaluated and compared in a uniform way.

Previous studies concerning the tolerance of different tree species to drought have focused on the effect of weather and climate, species mixture or individual tree characteristics on Rt, Rc and Rs (Pretzsch et al. 2013; Montwé et al. 2015a; Zang et al. 2014; Metz et al. 2015). In this case study, we analyse the effect of thinning, aspect, tree social class and tree size on drought tolerance of European beech. Specifically, we address the following research questions (RQ):

- RQ 1: What is the effect of basal area increment, tree social class and aspect on drought tolerance indices Rt, Rc and Rs to the 2003 summer drought?
- RQ 2: Is the effect of tree size, i.e. tree basal area, and tree social class on drought tolerance modified by aspect?
- RQ 3: What is the effect of the thinning treatments on the drought tolerance indices referring to the 2003 summer drought?
- RQ 4: Is the effect of the thinning treatments on drought tolerance indices modified by tree social class and aspect?

With this study, we provide experimental evidence for considering thinning as a potential silvicultural tool to increase the adaptive capacity of beech stands to a more extreme climate. Our overall hypothesis is that in a warmer climate, the effects of drought can be reduced by allocating more growing space to individual (crop) trees and that in this way the resilience and stability of beech on the tree and stand level can be increased.

Materials and methods

Study site and experimental design

The study site is located in a beech-dominated forest area in southwest Germany (longitude 8°40'E; latitude 48°00'N). The study plots are situated on two contrasting slopes: north-eastern (NE) and south-western (SW) aspects of a narrow valley close to the city of Tuttlingen. The climate in the study region is semi-continental, with a mean annual air temperature of 7.0 °C, and an annual precipitation sum of 900 mm (referring to the period 1961–1990). Rainfall does not vary significantly across the valley (Gessler et al. 2001). Limestone-derived soil types can be found on both aspects, whereas the soil on the SW aspect is shallower and particularly rocky with lower water holding capacity (Hildebrand et al. 1998; Geßler et al. 2005) (Table 1).

The experiment was established in winter 1998–1999. The experimental design was defined by three treatments of varying thinning intensity established on each aspect: a very strong thinning (VT) which reduced stand basal area (BA) to $10 \text{ m}^2 \text{ ha}^{-1}$ and a strong thinning (ST) which reduced BA to 15 m² ha⁻¹ and no thinning (control, CT, BA ~24.5 m² ha⁻¹). The reduction in BA was slightly different between aspects: for the strong thinning regime, the reduction in BA to 15 m² ha⁻¹ corresponded to $\sim 41\%$ for the NE and 31% for the SW aspect, while for the very strong thinning regime, the reduction in BA to $10 \text{ m}^2 \text{ ha}^{-1}$ was $\sim 60\%$ on the NE and 57% on the SW aspect. Each treatment (plot area 0.5–0.7 ha) was replicated three times on the NE and two times on the SW aspect in a randomised block design. The thinning treatment was applied once, at the beginning of the experiment in 1999. The criteria of the

Table 1 Characteristics of the research site (mean annual volumeincrement (MAI_{100}) refers to the 2012 assessment)

Parameter	Aspect		
	NE	SW	
Elevation (m a.s.l.)	820	760	
Inclination (°)	23	30	
Aspect (°)	60	240	
Soil profile (% of rocks) < 0.2 m	15	20-45	
Soil profile (% of rocks) > 0.5 m	30	80	
Stand age (years)	90	110	
MAI ₁₀₀ (m ³ /ha/year)	6.0	4.2	

applied thinning regime were to reduce the stand basal area to 15 and 10 m² ha⁻¹ by maintaining the shape of the diameter distribution. The measured stand-level parameters—height of the tree with mean basal area, height of dominant trees, diameter of the tree with mean basal area, diameter of dominant trees, stand basal area and stand volume—were described and comparatively analysed in a previous study done in the same research area by Diaconu et al. (2015).

Sampling and measurements of tree-ring characteristics

The material consisted of 216 increment cores (2 cores per tree) sampled in November 2015 from six trees per social class, treatment, aspect and block (treatment replication) plus 36 increment cores (2 cores per tree) sampled in February 2014, and therefore, the number of analysed trees totalled 126 (7 trees per social class, treatment and aspect, 21 trees per treatment and 63 trees per aspect). The social class indicating vitality and competitive status of individual trees was assessed according to the crown classification system of Kraft (Kraft 1884): 1—predominant, 2—dominant, 3—co-dominant.

The sample trees were cored at 1.3 m stem height using a 5.15 mm Haglöf increment borer, perpendicular to the slope in order to avoid tension wood. The samples were mounted on plastic supports and glass plates and their surface was prepared with an ultra-precise diamond fly cutter (Kugler F500, Kugler GmbH, Salem, Germany) as described by Spiecker et al. (2000). Tree-ring width (TRW) was measured using an image analysis software developed at the Chair of Forest Growth and Dendroecology, Freiburg. Individual tree-ring series were cross-dated using the software PAST4 (Personal Analysis System for Tree-Ring Research, SCIEM, version 4.3.1014) by grouping them according to social class, block, treatment and aspect.

Assessment of drought tolerance

In this study, we focus on the period 1999–2007, which encompasses the 4-year period before and after the extreme drought event of summer 2003. The 4-year period 1999– 2002 was chosen as a reference period, which immediately follows the thinning (winter 1998–1999). We calculated the drought tolerance indices resistance, recovery and resilience according to Lloret et al. (2011). Drought resistance (Rt) is the inverse of the growth reduction to the drought year (DrY) relative to the mean growth in the years prior to the drought year (PreDrY). Drought recovery (Rc) specifies the ability of a tree to recover after the drought stress and is estimated as the ratio of mean growth in the years after the drought (PostDrY) relative to DrY. Drought resilience (Rs) characterizes the capacity of a tree to absorb stress, and it is estimated as the ratio of mean growth PostDrY relative to PreDrY:

$$Rt = DrY/PreDrY$$
(1)

$$Rc = PostDrY/DrY$$
(2)

$$Rs = PostDrY/PreDrY$$
(3)

The statistical analyses were carried out in the R programming environment (R Development Core Team 2016). Drought tolerance indices were calculated from the annual basal area increments (BAI) of individual trees. Tree-ring width measurements were transformed into BAI using the *bai.out* function of the *dplr* package (Bunn et al. 2015). We did not detrend the data, as the BAI of the sample trees, which were over 90–110 years old at the time of the extreme drought event, did not show any age-related trend. The packages used in the analysis were: *ggplot2* (Wickham 2009), *reshape* (Wickham 2007), *tydr* (Wickham 2016), *plyr* (Wickham 2011), *multcomp* (Hothorn et al. 2008) and *lsmeans* (Lenth and Herve 2015).

To reveal the effect of BAI, aspect, tree social class, and treatment on drought tolerance indices, parameters of mixed-effects models were determined with *lme4* (Bates 2010) and *lmerTest* (Kuznetsova et al. 2014) packages. Eight different mixed-effects model formulations were used to answer our research questions. The effect of BAI, Kraft class and aspect on drought tolerance indices (RQ 1) were tested using models M1–M3, the interacting effects of BAI and Kraft class with aspect (RQ 2) were tested using model M4 and M5, and the effect of treatment on the drought tolerance indices (RQ 3) were tested in model M6. Accordingly, the interacting effects of aspect and Kraft class with treatment on the drought tolerance indices (RQ 4) were tested in model M7 and M8. The formalized models are as following:

- M1: Rt, Rc, Rs ~ BAI
- M2: Rt, Rc, Rs ~ Kraft class
 M3: Rt, Rc, Rs ~ Aspect
 M4: Rt, Rc, Rs ~ BAI * Aspect
 M5: Rt, Rc, Rs ~ Kraft class * Aspect
 M6: Rt, Rc, Rs ~ Treatment
 M7: Rt, Rc, Rs ~ Treatment * Aspect
 M8: Rt, Rc, Rs ~ Treatment * Kraft class

All models were formulated as linear mixed-effects models with the drought tolerance indices used as response variables. In the models, the variables BAI, Kraft class, aspect, treatment and their interactions were tested as fixed effects, while the variable plot (treatment replications) was used as random effect. BAI in M1 and M4 represented the mean over all respective years for each individual tree. For the first five models (M1–M5), only data from the control plots were included in the analysis in order to test the effects of BAI, of Kraft class and aspect on drought tolerance indices, effects which should not be confounded by changes in competition intensity due to thinning. For the models M6–M8, data from all plots were included in the analysis.

Results

Results of models M1 to M5 are presented in Table 2. The output of the analysis of variance indicates that the recovery and resilience after the 2003 drought event were influenced by tree basal area increment (BAI), by Kraft class and by aspect. The tested variables did not show any significant effect on the resistance index of the sample trees to the 2003 summer drought.

The larger BAI in the pre-drought period, the faster its recovery after the drought (p < 0.01) (Table S1). Besides BAI, the recovery index was significantly influenced by the tree social class (Table 2). The Kraft class was significant (p < 0.01) in the single-variable model (M2) but also when combining it with aspect (M5). This indicates that trees with a lower social position within a stand need longer time to recover after a severe drought. Furthermore, the analysis shows that Kraft class and aspect significantly affected the resilience of trees after the 2003 drought. The effect of Kraft class on the resilience index indicates that the lower the ranking of the tree within the stand is, the lower its resilience (p < 0.001) after the 2003 summer drought (Fig. 1). Aspect does not modify the effect of Kraft class on drought resilience.

Table 2 Analysis of variance output for the mixed-effects models M1–M5 with resistance (Rt), recovery (Rc) and resilience (Rs) as response variable and basal area increment (BAI), Kraft class and aspect as independent variables

Model	Independent variable	Rt p value	Rc p value	Rs p value
M1	BAI	0.1635	0.0092**	0.3436
M2	Kraft class	0.1459	0.0059**	0.0008***
M3	Aspect	0.0946	0.6434	0.0302*
M4	BAI	0.5100	0.0152*	0.1692
	Aspect	0.6707	0.2534	0.2029
	$BAI \times Aspect$	0.8183	0.6586	0.9816
M5	Kraft class	0.1157	0.0057**	0.0003***
	Aspect	0.0741	0.6003	0.0081**
	Kraft class × Aspect	0.4522	0.9389	0.2753

Sample size n: 42 trees

Asterisk indicate the level of significance (* p < 0.05; ** p < 0.01; *** p < 0.001)

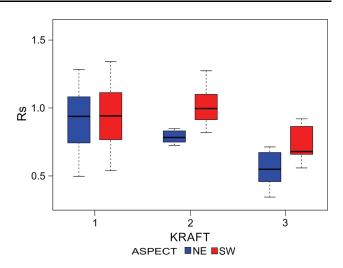


Fig. 1 Box plots of resilience index (Rs) of trees from different Kraft classes (1— predominant, 2—dominant, 3—co-dominant) and from both aspects (*NE* northeast, *SW* southwest). Sample size n = 42 trees

Concerning the effect of aspect, the analysis based on data of the control trees indicates that the resilience of trees growing on the SW aspect was significantly higher than that of trees growing on the opposite NE aspect (Table S2). When the Kraft class variable was included in the model (M5), the effect of aspect on Rs remained significant. The difference between aspects was significant only for Kraft class 2 and 3 (Fig. 1). The decrease in drought resilience for trees with lower social position within stands was more pronounced on the NE aspect compared to the SW aspect. In contrast to this finding, there was no significant effect of aspect on either resistance or recovery index.

The effect of treatment on drought tolerance indices was tested in models M6–M8 (Table 3). Thinning had a significant positive effect on the resistance and resilience to the 2003 drought, as trees in thinned stands showed a

Table 3 Analysis of variance output for the mixed-effects models M6–M8 with the drought tolerance indices resistance (Rt), recovery (Rc) and resilience (Rs) as response variables and treatment, Kraft class and aspect as independent variables

Model	Independent variable	Rt p value	Rc <i>p</i> value	Rs <i>p</i> -value
M6	Treatment	0.0212*	0.3535	0.0024**
M7	Treatment	0.0175*	0.3142	0.0013**
	Kraft	0.4821	0.0782	0.0249*
	Treatment × Kraft	0.2908	0.0622	0.1827
M8	Treatment	0.0191*	0.3499	0.0019**
	Aspect	0.1724	0.6158	0.2477
	Treatment × Aspect	0.4340	0.5990	0.1621

Sample size n: 126 trees

Asterisk indicate the level of significance (* p < 0.05; ** p < 0.01; *** p < 0.001)

significantly higher resistance and resilience than unthinned ones (Tables S3, S4). The increase in drought resistance and resilience was directly proportional to the thinning intensity: the higher the thinning intensity, the larger the increase in drought tolerance. Thinning did not have a significant effect on the recovery of growth following the drought of 2003.

Significant differences in drought resistance between thinning intensities indicate that the 2003 drought was associated with a reduction in growth compared to the reference period 1999–2002 by 21% for the control, and by ca. 5% for both thinning treatments at the NE aspect (Rt = 0.79, 0.95, and 0.93, respectively). At the SW aspect, the reduction in growth was slightly less, with 11% for the control, 6% for the strong, and 3% for the very strong thinning treatment (Rt = 0.89, 0.94, and 0.97 respectively). Regarding the resilience index, in the 4-year period after the 2003 drought, trees on the control plots on the NE aspect, had a lower drought resilience compared to the released trees (Rs = 0.74, 0.98, and 0.97). In contrast, on the SW aspect, both the released as well as the control trees reached a growth level similar to the pre-drought period (Rs = 0.90, 0.96, and 0.98).

When Kraft class was included in the model (M7), the effect of treatment on resistance and resilience remained significant (Table 3). Thinning significantly affected the drought tolerance indices of trees in different social classes (Fig. 2). Thinning affected resistance to and resilience after the 2003 summer drought of dominant and co-dominant (Kraft class 2 and 3) but not of predominant trees. Particularly, the resistance of dominant trees under very strong thinning was significantly higher (p < 0.05) than that of the control trees (Table S5). A similar effect was observed for the resilience index (Table S6), as growth of the released dominant and co-dominant trees in the post-drought period was close to the growth in the pre-drought period whereas growth of the control trees remained reduced. Therefore, differences in drought resistance and resilience between trees of different social classes that existed on the control plots disappeared under the thinning treatment.

In the final model (M8), we tested whether the effect of treatment was modified by aspect. The released trees on both aspects exhibited significantly higher drought resistance and resilience than the control trees (Fig. 3). The recovery index points to a slight increase for the released trees although this effect was not significant (Table 3).

For the control trees, all three drought tolerance indices were higher on the SW compared to the NE aspect (Fig. 3). Although no significant interaction between treatment and aspect was found, the effect of thinning on resistance, recovery and resilience was larger on the NE than on the SW aspect (Fig. 3). The increase in drought tolerance

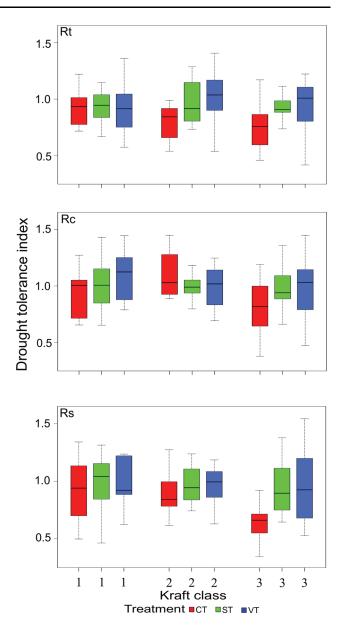


Fig. 2 Box plots of the drought tolerance indices resistance (Rt), recovery (Rc) and resilience (Rs) of trees from different thinning treatments (*CT* control, *ST* strong thinning, *VT* very strong thinning) and social classes (1—predominant, 2—dominant, 3—co-dominant). Sample size n = 126 trees

values (Rt and Rs) was approximately 20–30% at the NE aspect and only 5–10% at the SW aspect.

Discussion

Tree stem growth and Kraft class determine drought tolerance

The social ranking of trees within a stand according to tree height and crown dimension provides a proxy for the

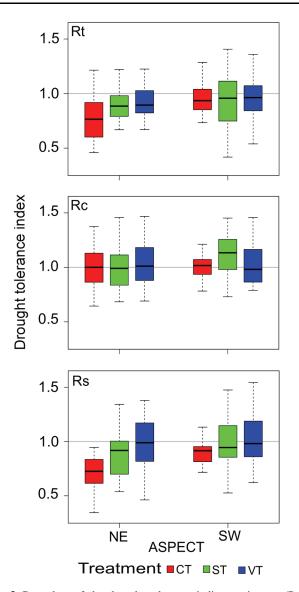


Fig. 3 Box plots of the drought tolerance indices resistance (Rt), recovery (Rc) and resilience (Rs) of trees from different thinning treatments (*CT* control, *ST* strong thinning, *VT* very strong thinning) and from both aspects (*NE* northeast, *SW* southwest). Sample size n = 126 trees

distribution of growth among individual trees within a stand (Assmann 1970; Pretzsch 2010), which affects the yield development over time (Spiecker 1991). Our results confirm the close link between tree stem growth and tree social status. The results of the mixed-effects models (M1 and M4) indicated that the higher the basal area increment, the faster the growth recovery after the extreme 2003 drought event. This implies that fast-growing trees recover faster. In even-aged stands, fast-growing trees are those with higher social position within stand (Kraft class 1 and 2). Similarly, our results showed that tree social class has a significant effect on drought sensitivity of beech trees, so that trees with a lower social position within stand (e.g. Kraft class 3 trees) are less resilient towards drought

events. Therefore, (pre-)dominant trees are more likely to successfully compete for water and nutrient resources during drought. These findings are consistent with results achieved by Zang et al. (2014) on Norway spruce, silver fir and common beech, who found a positive effect of tree size on all drought tolerance indices. The study by van der Maaten (2012a) on the climate sensitivity of beech radial growth, carried out in the same study area, showed that dominant and co-dominant trees are particularly more sensitive to dry conditions from June to August, compared to intermediate trees, and that trees on the SW aspect are more drought-prone compared to the NE aspect. In contrast, our results show that drought resilience decreased for trees with lower social position, and that the resilience of dominant and co-dominant trees on the SW aspect was higher than on the NE aspect (M5, Fig. 1). This inconsistency could be related to the difference in the study approach, as in our study the drought sensitivity was assessed only for the 2003 drought event whereas in the study of van der Maaten (2012a) the drought sensitivity of beech was assessed based on long-term tree-ring analyses.

Effect of aspect and the trade-off between rate of growth and drought tolerance

Previous work done in the same study area demonstrated that tree growth rates (in height and diameter) are significantly higher on the NE than on the SW aspect (Hauser 2003; van der Maaten 2012b; Diaconu et al. 2015). Our results reveal that the higher radial growth rates of the trees on the NE aspect are at the cost of their drought tolerance, as the resilience index of these trees was significantly lower than on the SW aspect (Table S2). The lower average growth level of the control trees growing under the warmer and drier conditions on the SW aspect coupled with their higher average drought tolerance indices suggests a tradeoff between stand-level tree growth and stand-level tree tolerance to drought. This trade-off highlights the species plasticity regarding its inter-annual growth response and is indicative of the adaptive strategy of beech with respect to differing site conditions. The faster growth of the trees on the NE aspect confounds the parameter estimation since the intensity of competition between trees as well increases faster on the NE aspect, which particularly affects the control plots. The higher intensity of competition on the NE aspect is due to higher resource availability on the one hand, and to the higher average stand density compared to the SW aspect on the other hand, as trees on the NE aspect reach larger size within the same period of time. Accordingly, growth of Kraft class 3 trees was reduced more on the NE aspect, and therefore their drought tolerance indices are lower than at the SW aspect. Our results are confirmed

by Zang et al. (2014) who found an increase in Rs values from favourable to less favourable sites.

The difference in tree tolerance to drought between aspects can also be attributed to differences in competition modes. For example Pretzsch and Biber (2010) found a significant distinction in competition modes between sites: an asymmetric competition mode on mesic sites where growth is limited by light and a symmetric competition mode on dry sites where tree growth is limited by belowground resources. Correspondingly, in our study, soil moisture availability is rather high on the NE aspect and trees face high levels of competition mainly for light, while on the SW aspect, trees face higher levels of competition for soil water and nutrients than for light. Consequently, trees on the NE aspect face less competition for soil resources, and are not as well adapted to drought conditions as the trees on the SW, resulting in lower drought tolerance indices related to the 2003 drought event.

Thinning to mitigate drought impact

The differing mesoclimates expressed by contrasting aspect and the differing stand densities according to the thinning treatments led to significant disparities in tree resistance to and resilience after the 2003 summer drought event. We hypothesized that thinning will increase the drought tolerance of beech trees on both aspects independent of crown class. The drought tolerance indices were indeed higher for the trees under the thinning treatments than for the trees in the unthinned control plots, and the positive thinning effect was pronounced more on the NE aspect compared to the SW aspect. The thinning effect, that was significant for Rt and Rs, highlights the importance of growing space, i.e. lower competitive stress, for improving tree growth and for alleviating drought stress. Differences between treatments were not significant for Rc; however, the recovery tended to be higher for the thinned trees. Similar results regarding the effect of thinning on drought tolerance indices have been presented by Sohn et al. (2016) who found that for broadleaves, thinning improved drought resistance, most likely through an increase in soil water availability.

The trees released by thinning experience lower competitive stress for soil resources and light, and therefore, become more vigorous. At the same time, a negative response to thinning could be expected due to the anticipated increase in transpiration levels of the remaining trees (Whitehead et al. 1984). However, our results are in agreement with Breda et al. (1995) who demonstrated that with more growing space for the individual tree and reduced stand-level leaf area, the average soil water content is higher, mainly due to less precipitation interception losses at the canopy layer. Our results confirm that the crown release of mature beech trees (stand age at the time of thinning 76 and 90 years on the NE and SW aspect, respectively) leads to higher tree vitality. Additionally, after thinning the remaining trees may also respond to the crown release by developing a more extensive root system, a factor that may be beneficial during future drought events. With a deep rooting system, trees are capable to extract larger amounts of water from the soil during dry events especially from deeper soil layers. This might actually explain why trees on the NE aspect, where soil available to root extensions is deeper compared to shallow soils at the SW aspect, benefit more from thinning. Thus, access to water during a drought event may last longer and discharge of water reserves occurs later (this affecting the resistance to drought), and possibly are more quickly replenished by precipitation after a drought as more water is retained in the soil (affecting the resilience after drought).

When thinning is applied, differences in drought tolerance indices between tree social classes diminish or even disappear (Fig. 2), an effect which can be explained by stand density. In the thinned plots, especially in the very strongly thinned plots, a large number of trees were able to improve its position in the canopy, so that the trees at the time of sampling in 2015 have more or less similar social position within the stands. In fact, this also made the selection of sample trees (7 trees per social class, treatment and aspect) sometimes difficult to assess. In such cases, we used the diameter at breast height as a third proxy for tree class, beside tree height and crown dimension.

The growth acceleration caused by thinning (see Fig. S1 in Diaconu et al. 2016a) was most pronounced in trees which otherwise would experience increasing competition, which in our case, are the Kraft class 3 trees. Therefore, it is not surprising that in the control plots their growth rate was decreasing while in the thinned plots the impact of competition on growth was reduced drastically, particularly for these trees. Hence, the "drought tolerance indices" not only capture the effect of drought but as well the effect of different trends in the level of competition, and, because of that, the effect of thinning on the drought tolerance of released trees may be overestimated. For overcoming this drawback, we recommend to include analyses of climategrowth relationships in further studies. Such relationships could help to disentangle the effects of competitive release on drought response and general growth trend.

Cescatti and Piutti (1998) demonstrated that climate and drought sensitivity of beech is strongly influenced by intraspecific competition: when the intensity of competition is high, trees are more sensitive to high temperature and low water availability, whereas at low competition level trees are positively influenced by warm temperature. In a recent study describing short- and long-term thinning efficacy to mitigate impacts of extreme drought in

mountain forests in the European Alps, Elkin et al. (2015) indicated that thinning can be seen as a temporary measure to reduce impacts of severe drought. Nevertheless, the authors state that the magnitude of the thinning effect depends on many factors such as drought intensity, site conditions, tree age, timing and the intensity of thinning. Likewise, work carried out by Bosela et al. (2016) revealed that BAI increased in European beech forests managed by free crown thinning, while it decreased in forests managed by heavy thinning from below. Thus the authors conclude that the effects of a warmer climate on growth of beech forests in Eastern Europe depend on site productivity and thinning strategy. Similarly, previous research conducted in the same study area as ours indicated that thinning stimulates tree growth in a warmer and drier climate (SW aspect), however, to a smaller extent than on more favourable site (NE aspect) (Diaconu et al. 2015).

Our results are consistent with other research done within the same experiment regarding the xylem plasticity of European beech in response to thinning and aspect (Diaconu et al. 2016a). In this study it was demonstrated that trees growing on the NE aspect have significantly larger vessels compared to trees growing on the SW exposed slope. Additionally, it has been proven that by thinning the waterconducting system of European beech trees becomes more robust against hydraulic failure. Larger vessels are more efficient for water transport, but wood tissue with a large vessel area percentage also is at higher risk of cavitation (Hacke and Sperry 2001). Hence, the lower values of Rt and Rs for the control trees on the NE aspect as compared to the SW aspect can be explained by the larger xylem conduits that are more vulnerable to cavitation during dry events. The hydraulic architecture, especially hydraulic changes observable during dry events play a critical role in tree responses to drought events and hence have been reported to underlie the wide spread of drought-induced mortality (Anderegg et al. 2013).

Diaconu et al. (2016a) found that thinning reduces the risk of embolism especially for the more drought vulnerable trees on the NE aspect. Therefore, higher wood density values after thinning are expected. Previous work showed that with increasing tree-ring width, the mean wood density of the trees growing on the warm and dry SW aspect was higher than on the cold and moist NE site (Diaconu et al. 2016b). Trees with denser wood are more resistant to drought-induced cavitation (Hacke et al. 2001; Poorter et al. 2010; Montwé et al. 2015b). Therefore, beech trees growing on more drought-prone sites such as the ones on the SW aspect can cope better with water shortages as it was also described by Eilmann et al. (2014) in a study regarding wood structural differences between northern and southern beech provenances. Accordingly, trees on more favourable sites such as the ones on the NE aspect are more vulnerable to drought stress but their drought tolerance can be increased by thinning. Therefore, thinning can help to achieve not only higher productivity rates on the tree-level, but also to mitigate drought-related inter-annual growth depressions. Nevertheless, our results are derived from a single case study from one valley and concerns only one drought event, and therefore one should be careful in extrapolating these findings to other sites and summer drought events.

Conclusions

This study established a link between forest management measures and their effects on the growth response and drought tolerance of beech under contrasting site conditions, contributing evidence-based knowledge relevant for the future management of beech forests. We could show that the co-dominant and dominant trees, which face higher competitive pressure for light and water, need longer to reach pre-drought growth levels compared to the predominant trees. Further, climatic and edaphic differences between the two aspects revealed a trade-off between growth and drought tolerance: lower growth levels of trees growing on the warm and dry SW aspect were coupled with higher drought resilience, and vice versa. By reducing stand density through thinning, growth resistance to and resilience after drought increased, especially for the more drought vulnerable trees on the NE aspect. Furthermore, when trees were strongly released differences between aspects and tree social classes were either reduced or no longer significant. Therefore, we can conclude that thinning represents a forest management tool, which can at least temporarily mitigate climate change effects in southwest Germany. However, these conclusions are drawn from a single case study, and the effects of thinning are analysed based on a 9-year post-treatment period (1999-2007). Our results do not provide information on how long the positive effect of thinning on drought tolerance indices lasts beyond this period. We studied the growth response of beech to the summer drought in the year 2003 in a 4-year post-drought period as influenced by Kraft class, aspect and thinning, but other characteristics like tree age and microsite or the effect of genetics which could also be relevant for growth and drought tolerance were not considered. Hence, for further studies, we strongly recommend to consider these factors in order to facilitate generalization of the findings.

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Compliance with ethical standards

Conflict of interest None.

References

- Ammer C, Albrecht L, Borchert H, Brosinger F, Dittmar C, Elling W, Ewald J, Felbermeier B, gilsa H von, Huss J, kenk G, Kölling C, Kohnle U, Meyer P, Mosandl R, Moosmayer HU, Palmer S, Reif A, Rehfuess KE, Stimm B (2005) Zur Zukunft der Buche (*Fagus* sylvatica L.) in Mitteleuropa: Kritische Anmerkungen zu einem Beitrag von RENNENBERG et al. (2004). Allgemeine Forstund Jagd Zeitung 176:60–67
- Anderegg WRL, Plavcova L, Anderegg LDL, Hacke UG, Berry JA, Field CB (2013) Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. Glob Change Biol 19(4):1188–1196. doi:10.1111/gcb.12100
- Assmann E (1970) The principles of forest yield study. Pergamon Press, Oxford
- Bates DM (2010) lme4: Mixed-effects modeling with R. Springer, Madison
- Bohn U, Gollub G, Hettwer C, Weber H, Neuhäuslová Z, Raus T, Schlüter H (2003) Map of the natural vegetation of Europe—Scale 1:2 500 000, map and explanatory text. Landwirtschaftsverlag, Münster
- Bosela M, Štefančík I, Petráš R, Vacek S (2016) The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. Agric For Meteorol 222:21–31. doi:10.1016/j.agrformet.2016. 03.005
- Breda N, Granier A, Aussenac G (1995) Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiol 15:295–306
- Bunn A, Korpela M, Biondi F, Campelo F, Mérian P, Qeadan F, Zang C (2015) dplR: dendrochronology program library in R. R package version 1.6.3
- Cescatti A, Piutti E (1998) Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. For Ecol Manage 102(2–3):213–223. doi:10.1016/S0378-1127(97) 00163-1
- Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon WT, Laprise R, Magaña Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P (eds) (2007) The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, New York
- Diaconu D, Kahle H-P, Spiecker H (2015) Tree- and stand-level thinning effects on growth of European beech (*Fagus sylvatica* L.) on a northeast- and a southwest-facing slope in southwest Germany. Forests 6(9):3256–3277. doi:10.3390/f6093256
- Diaconu D, Stangler DF, Kahle H-P, Spiecker H (2016a) Vessel plasticity of European beech in response to thinning and aspect. Tree Physiol. doi:10.1093/treephys/tpw053
- Diaconu D, Wassenberg M, Spiecker H (2016b) Variability of European beech wood density as influenced by interactions

between tree-ring growth and aspect. For Ecosyst 3(6):1–9. doi:10.1186/s40663-016-0065-8

- Dittmar C, Zech W, Elling W (2003) Growth variations of Common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe—a dendroecological study. For Ecol Manage 173(1–3):63–78. doi:10.1016/S0378-1127(01)008 16-7
- Eilmann B, Sterck F, Wegner L, de Vries SMG, von Arx G, Mohren GMJ, den Ouden J, Sass-Klaassen U (2014) Wood structural differences between northern and southern beech provenances growing at a moderate site. Tree Physiol 34(8):882–893. doi:10. 1093/treephys/tpu069
- Elkin C, Giuggiola A, Rigling A, Bugmann H (2015) Short and longterm efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. Ecol Appl 25(4): 1083–1098
- Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht: 170 Tabellen, 5., stark veränd. und verb. Aufl. UTB, vol 8104. Ulmer, Stuttgart
- Fotelli MN, Rennenberg H, Geßler A (2002) Effects of drought on the competitive interference of an early successional species (Rubus fruticosus) on *Fagus sylvatica* L. seedlings: 15 N uptake and partitioning, responses of amino acids and other N compounds. Plant Biol 4(3):311–320. doi:10.1055/s-2002-32334
- Gessler A, Schrempp S, Matzarakis A, Mayer H, Rennenberg H, Adams MA (2001) Radiation modifies the effect of water availability on the carbon isotope composition of beech (*Fagus sylvatica*). New Phytol 150(3):653–664. doi:10.1046/j.1469-8137.2001.00136.x
- Geßler A, Jung K, Gasche R, Papen H, Heidenfelder A, Börner E, Metzler B, Augustin S, Hildebrand E, Rennenberg H (2005) Climate and forest management influence nitrogen balance of European beech forests: microbial N transformations and inorganic N net uptake capacity of mycorrhizal roots. Eur J Forest Res 124(2):95–111. doi:10.1007/s10342-005-0055-9
- Geßler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees 21(1):1–11. doi:10. 1007/s00468-006-0107-x
- Hacke U, Sperry J (2001) Functional and ecological xylem anatomy. Perspect Plant Ecol Evol Syst 4(2):97–115. doi:10.1078/1433-8319-00017
- Hacke U, Sperry JS, Pockman WT, Davis SD, McCulloh KA (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
- Hauser S (2003) Dynamik hochaufgelöster radialer Schaftveränderungen und des Dickenwachstums bei Buchen (*Fagus sylvatica* L.) der Schwäbischen Alb unter dem Einfluss von Witterung und Bewirtschaftung, Albert-Ludwigs-Universität Freiburg
- Hildebrand E, Augustin S, Schack-Kirchner H (1998) Bodenkundliche Charakterisierung der Kernflächen. In: Rennenberg H (ed) Buchendominierte Laubwälder unter dem Einfluß von Klima und Bewirtschaftung: Ökologische, waldbauliche und sozialwissenschaftliche Analysen—Vorcharakterisierung der Untersuchungsflächen. Eigenverlag der Universität Freiburg, Freiburg, pp 7–12
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50(3):346–363
- Kohler M, Sohn J, Nägele G, Bauhus J (2010) Can drought tolerance of *Norway spruce (Picea abies* (L.) Karst.) be increased through thinning? Eur J Forest Res 129(6):1109–1118. doi:10.1007/ s10342-010-0397-9
- Kraft G (1884) Beiträge zur Lehre von den Durchforstungen. Schlagstellungen und Lichtungshieben. Klindworth's Verlag, Hannover

- Kuznetsova A, Brockhoff PB, Christensen R (2014) ImerTest: Tests in Linear Mixed Effects Models. R package version 2.0-29
- Le Goff N, Ottorini J-M (1993) Thinning and climate effects on growth of beech (*Fagus sylvatica* L.) in experimental stands. For Ecol Manage 62:1–14
- Lenth R, Herve M (2015) lsmeans: least-squares means. R package version 2.18
- 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
- Metz J, Annighöfer P, Schall P, Zimmermann J, Kahl T, Schulze E-D, Ammer C (2015) Site adapted admixed tree species reduce drought susceptibility of mature European beech. Glob Change Biol. doi:10.1111/gcb.13113
- Montwé D, Isaac-Renton M, Hamann A, Spiecker H (2015a) Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. Glob Change Biol. doi:10.1111/gcb.13123
- Montwé D, Spiecker H, Hamann A (2015b) Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. Tree Genet Genomes 11(2):1–11. doi:10.1007/s11295-015-0854-1
- Poorter L, McDonald I, Alarcón A, Fichtler E, Licona J-C, Peña-Claros M, Sterck F, Villegas Z, Sass-Klaassen U (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol 185(2):481–492. doi:10.1111/j.1469-8137. 2009.03092.x

Pretzsch H (2010) Forest dynamics, growth and yield. Springer, Berlin

- Pretzsch H, Biber P (2010) Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Can J For Res 40(2):370–384. doi:10.1139/X09-195
- 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 Biol 15(3):483–495. doi:10.1111/j.1438-8677.2012.00670.x
- R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

- Rennenberg H, Seiler W, Matyssek R, Geßler A, Kreuzwieser J (2004) Die Buche (*Fagus sylvatica* L.) ein Waldbaum ohne Zukunft im südlichen Mitteleuropa? AFJZ 175:210–244
- Sohn JA, Saha S, Bauhus J (2016) Potential of forest thinning to mitigate drought stress: a meta-analysis. For Ecol Manage 380:261–273. doi:10.1016/j.foreco.2016.07.046
- Spiecker H (1991) Controlling the diameter growth and the natural pruning of Sessile and Pedunculate oaks. Habilitation. Selbstverlag der Landesforstverwaltung Baden-Württemberg, Stuttgart
- Spiecker H, Tilman E, Park Y, Hansen J, Schinker MG, Döll W (2000) Cell structure in tree rings: novel methods for preparation and image analysis of large cross sections. IAWA J 21(3):361–373. doi:10.1163/22941932-90000253
- Teskey R, Wertin T, Bauweraerts I, Ameye M, McGuire MA, Steppe K (2015) Responses of tree species to heat waves and extreme heat events. Plant, Cell Environ 38(9):1699–1712. doi:10.1111/pce.12417
- van der Maaten E (2012a) Climate sensitivity of radial growth in European beech (*Fagus sylvatica* L.) at different aspects in southwestern Germany. Trees 26(3):777–788. doi:10.1007/ s00468-011-0645-8
- van der Maaten E (2012b) Intra- and interannual growth responses of European beech (*Fagus sylvativa* L.) to climate, aspect and thinning in the Swabian Alb - southwestern Germany. Dissertation, Albert-Ludwigs-Universität Freiburg
- Whitehead D, Jarvis PG, Waring RH (1984) Stomatal conductance, transpiration, and resistance to water uptake in a Pinussylvestris spacing experiment. Can J For Res 14(5):692–700
- Wickham H (2007) Reshaping data with the reshape package. J Stat Softw 21:1–20
- Wickham H (2009) Ggplot2. Elegant graphics for data analysis. Use R!. Springer, Dordrecht
- Wickham H (2011) The split-apply-combine strategy for data analysis. J Stat Softw 40(1):1–29
- Wickham H (2016) Tidyr: easily tidy data with 'spread()' and 'gather()' functions. R package version 0.4.1. https://CRAN.R-project.org/package=tidyr
- Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A (2014) Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. Glob Change Biol 20(12):3767–3779. doi:10.1111/gcb.12637