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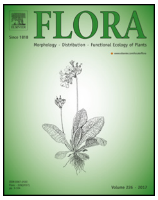

Influence of multiple biotic and abiotic factors on the crown die-back of European beech trees at their drought limit

Tamalika Chakraborty[a,*], Somidh Saha[b,c], Andreas Matzarakis[d], Albert Reif[a]

[a] Chair of Site Classification and Vegetation Science, Institute of Forest Sciences, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacherstr. 4, D-79106 Freiburg, Germany
[b] Institute for Technology Assessment and Systems Analysis, Karlsruhe Institute of Technology, Karlstr. 11, D-76133, Karlsruhe, Germany
[c] Chair of Silviculture, Institute of Forest Sciences, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacherstr. 4, D-79106 Freiburg, Germany
[d] Research Centre Human Biometeorology, German Weather Service, Stefan-Meier-str. 4, D-79104 Freiburg, Germany

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ABSTRACT

Owing to the growing sensitivity of forests to drought under the warming climate, more attention should be paid to the role of soil drought, plant–plant interactions, tree species and structural diversity, and other abiotic factors on the crown die-back of trees. We studied how permanent soil water stress had impacted on crown die-back of beech trees (*Fagus sylvatica* L.) at their drought limit in near-natural temperate forests of Germany and Switzerland. Crown die-back was quantified by the proportion of dead above-ground biomass to total biomass for the individual beech tree. We quantified the available soil water storage capacity as a measure of soil drought stress in combination with other biotic (e.g., plant–plant interactions, tree species diversity, stand structural diversity, plant height and proportion of oak trees) and abiotic (e.g., light availability, soil pH, soil bulk density, potential evapotranspiration) factors to determine the influence of those stressors on crown die-back. We found increases in soil water storage capacity, neighbourhood interactions, plant height and light decreased crown die-back of the beech trees. These stressors differently influenced the die-back among different parts of tree crown. Soil water storage capacity, light availability, intra- and interspecific interactions, plant height and tree species diversity had the strongest influence on die-back in the upper part of the crown. Permanent death of beech trees occurred when the amount of dead above-ground biomass exceeded a 58% mortality threshold. We conclude that vitality of beech trees in drought stressed forests is related to soil water storage capacity, light availability, neighbourhood interactions and tree species diversity.

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1. Introduction

European beech (*Fagus sylvatica* L.) is one of the most important economic tree species in central Europe, with a wide range of distribution (Ellenberg and Leuschner, 2010). However, species distribution modelling scenarios under changing climate forecasted that beech trees will be outcompeted by more drought-tolerant species such as oaks in drought prone regions (Gessler et al., 2007), particularly at the edges of the distribution (Jump et al., 2007; Rasztovits et al., 2014). In contrast, some studies demonstrated that beech trees could overcome drought stress due to having a competitive advantage over other co-occurring tree species (Metz et al., 2016; Pretzsch et al., 2013; Rose et al., 2009). Bolte et al. (2007) discussed about the probable ecophysiological reasons behind the drought driven distribution contraction of beech, but also mentioned that this macro-climatic reason alone could not be responsible for restricting the distribution of beech; and recommended to consider the phenotypic plasticity and the adaptation processes in further studies.

In this context, one important morphological parameter to study the drought stress is biomass as trees can alter their biomass to tune the root–shoot ratio under the environmental fluctuation like irregular water supply on dry sites (Schulze et al., 2005). The drought response of beech trees in respect to biomass has been studied by several authors mainly under controlled environmental conditions (Fotelli et al., 2001; Lof et al., 2005; vanHees, 1997). However, field studies on beech trees in forest sites by considering the capacity of forest soil to store water were rarely done (but see Meier and Leuschner, 2010; Peiffer et al., 2014).

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* Corresponding author.
E-mail addresses: tamalika.chakraborty@waldbau.uni-freiburg.de, chakraborty.tamalika@gmail.com (T. Chakraborty).

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Forest soil can act as an environmental stabiliser for mitigating drought stress (Breda et al., 2006), particularly in case of beech due to its sensitivity to drought (Granier et al., 2007; Sitková et al., 2014). Nevertheless, it is not well understood how and to what extent beech trees can adapt, including physiological reactions and morphological modifications, to mitigate the effect of drought on plant growth. The modification of biomass, e.g. by partial crown die-back, impacts the vitality of the trees and could lead to tree die-back in case of severe stress from drought, which should be accounted for in drought related research (Dobbertin, 2005; McDowell, 2011).

Drought-induced die-back of forest trees seems to be an increasing global phenomenon under climate warming conditions (Allen et al., 2010, 2015; McDowell et al., 2011). In Europe, multiple cases of tree die-back have been reported (Allen et al., 2015). However, quantitative evaluations of crown die-back in forest trees and the relationship between crown die-back and the growth environment in natural forests are rare for many tree species including beech. Assessments on the pattern, magnitude, and causes of drought induced tree death in temperate natural forests are scarce because of the difficulties in measuring tree's growing environment and damage with high precision (but see Anderegg et al., 2012, 2015). Therefore, observational field studies are needed to understand the responses of trees to their growing environment at the drought limits of their distribution, where climatic patterns and soil properties interact as physical stressors (Breda and Badeau, 2008; Granier et al., 2007; Peiffer et al., 2014), particularly in beech trees where elastic tissue reservoirs play a minor role in the total water budget of the trees under severe soil drought conditions compared to the soil water storage capacity (Betsch et al., 2011). Some studies reported that biomass and growth in beech trees could be impacted by edaphic drought (Chakraborty et al., 2013; Weber et al., 2013), and limits distribution of beech trees under a soil water gradient (Gärtner et al., 2008). Edaphic factors like soil bulk density, texture, skeleton content, and soil depth are important in water retention of the soil (Teepe et al., 2003) that regulates the availability of water to the plants' roots and influences the growth of roots under drought condition (Breda et al., 2006; Meier and Leuschner, 2008). Furthermore, the pH values of forest soils can indicate availability of soil nutrients. Seynave et al. (2008) had shown that soil pH is a growth limiting factor for European beech trees in many forest sites in France. Therefore, soil water storage capacity together with other soil properties like bulk density and pH as a measure of edaphic stress should be included to study the influence of drought on crown die-back of beech trees.

Crown die-back of trees indicates worsening health conditions and decreasing tree vitality as the crown is the most important functional part of the tree (Innes, 1993; Manion, 1991; Pedersen, 1998). When a crown die-back starts from the upper part of the stem, then it is most likely related to stressors such as drought because of hydraulic failure (Allen et al., 2015; Breda and Badeau, 2008; McDowell, 2011). Kohler et al. (2006) found severe upper crown die-back in beech trees after the event of 2003 summer drought in Germany. Therefore, it is important to partition die-back based on crown length and position, which necessitates morphometric quantification of die-back in the tree crowns (Dobbertin, 2005). In this context, height of the tree is also crucial as taller trees would be subjected to higher risk of hydraulic stress, higher radiation stress and evaporative demand (Bennett et al., 2015). According to the tree vitality model proposed by Dobbertin (2005), after crossing a certain tipping point of decreasing vitality, a tree could reach a point of no return at which it has incurred irreparable damage leading to death. To our knowledge, research on survival thresholds of forest tree species in relation to drought induced crown die-back at multiple sites has not yet been undertaken but has utmost importance (see the case study by Chakraborty et al., 2013).

Recent studies (Dale et al., 2010; Fauset et al., 2012; Peters et al., 2015) proposed that forest compositional diversity may buffer drought-related stress in forests through multiple ecological feedbacks (Hantsch et al., 2014). However, in a recent synthesis, Allen et al. (2015) postulated that tree species diversity can ameliorate but not prevent mortality from "much hotter droughts" because of fundamental thresholds of physiological stress and mortality of species; this proposition warrants more proof from field ecological research. A synthesis of biodiversity experiments on grassland ecosystems showed high species richness can increase the stability, resistance and resilience of ecosystem productivity to drought (Isbell et al., 2015). In contrast to grasslands, Martinez-Vilalta et al. (2012) showed that greater tree species richness sometimes can exacerbate drought stress through interspecific competition in forests. Therefore, it is important to test whether an increase in tree species diversity would reduce die-back of beech trees in forests, particularly in areas with high susceptibility to drought, or not. The proportion of one species in a forest stand can influence performance of another species through multiple feedback loops of ecosystem functions. In this context, one hypothesis from Pretzsch and co-authors was that deep rooting trees such as oaks can facilitate the growth of beech trees by hydraulically lifting water in oak–beech mixed forests (Pretzsch et al., 2013).

In this context, due to facilitating effects of species mixture whether drought induced die-back would be reduced or not needs to be tested. Furthermore, structural diversity of living trees plays a "foundational role" in regulating ecosystem processes, including nutrient cycling rates, patterns of resource availability, and understorey plant community dynamics (D'Amato et al., 2011; Ellison et al., 2005). Grote et al. (2016) reported that structural diversity of forest canopy can change the micro-environment of the forests by altering vapour pressure deficit, solar radiation and temperature. These changes in micro-environment can influence the water demand of the trees, thus creating or reducing a local drought stress. In this case, a site specific radiation based potential evapotranspiration model could assess the probable water demand of the specific forest in respect to climatic drought situation. Therefore, while assessing relationships between drought induced mortality and the growth environment of the trees, it is important to consider the neighbourhood interactions as biotic factor together with site specific potential evapotranspiration as abiotic factor.

According to the 'decline spiral model' (Manion, 1991), competitive interactions of neighbouring trees could act as long-term stressors or predisposing factors that could result in tree damage when coupled with acute stressors such as drought. Trees that are already weakened by competition and drought may lose vigour and eventually die (Manion, 1991; Pedersen, 1998). However, in harsh forest ecosystems, competition can result in positive interactions by ameliorating local environments in a resource-limited ecosystem and create a positive feedback for maintaining plant health (Bertness and Callaway, 1994). Nevertheless, in their recent review Holmgren and Scheffer (2010) discussed that not only under harsh condition, but also in moderately stressed environment, facilitation could cancel out competition. Furthermore, such beneficial effects of plant–plant interactions could depend on plant density and the nature of the interaction, i.e., inter- or intraspecific (Metz et al., 2016; Pretzsch et al., 2013). Yet in a recent review, St. Clair et al. (2013) discussed on the positive and antagonistic plant–plant interactions that could be modified by the environmental fluctuations like drought and temperature; and also suggested to identify the environmental conditions to balance between competition and facilitation. Nakagawa et al. (2016) showed that a plant can be facilitated by indirect positive effects resulting from the interactions between two other plants in a forest neighbourhood. Whether the potential beneficial effects of plant interactions described above would increase along with higher diversity in forest structure and

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