



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



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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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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, Martínez-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



**Fig. 1.** Figure showing location of the study sites in Germany and Switzerland (Yellow pins). Map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Source: Google Earth®.

composition in respect of reducing crown die-back in beech trees needs to be ascertained.

To what degree a tree can respond elastically, i.e., by allowing partial crown die-back, and at what point the stress response becomes plastic, i.e., losing the ability to recover after stress leading to complete die-back, depends on the physiological adaptability of the species of interest and the degree of stress experienced (Manion, 1991; Schulze et al., 2005). However, at what severity or exposure (e.g. a threshold of crown die-back) a tree would lose its resilience by shifting the strain from an elastic to plastic response is still unclear. A recent study by Grossiord et al. (2014) showed that drought exposure in the forests can be diminished with increasing tree species diversity in dry sites but not in moist sites. It warrants more research to find out the threshold of crown die-back in dry sites where distribution of trees is regulated by water scarcity (e.g. transitions between forest types).

Here, we investigated tree response in a near-natural forest ecosystem, in this case, drought stressed beech forest at its ecotone to oak (i.e., *Quercus pubescens* Willd., *Q. petraea* (Mattuschka) Liebl., and their hybrids) forest in Germany and Switzerland where seed-born beech trees are growing close to their drought limit under the canopy of oaks (Gärtner et al., 2008). Our goal was to quantify beech tree vitality and the influences of different abiotic and biotic factors on the vitality of beech trees. We hypothesized that available soil water storage capacity (as water availability) and other abiotic and biotic factors would influence crown die-back in beech trees; and death of trees would occur after crossing a threshold of crown die-back. Under this hypothesis, we addressed four research questions: (a) How do abiotic factors such as available soil water storage capacity, soil bulk density, soil pH, potential evapotranspiration, and light availability influence crown die-back of beech trees? (b) Would plant–plant interactions (intra- vs. interspecific), plant height, tree species and structural diversity reduce crown die-back of beech trees with decreasing soil water availability? (c) Would these biotic and abiotic factors influence die-back in different compartments within a tree crown? (d) Do beech trees die after crossing a certain threshold of crown die-back?

## 2. Materials and methods

### 2.1. Study area description and sampling design

Five forest stands, formed on Jurassic limestone (rendzina soil) from three locations in Southern Germany and Northern Switzerland, were selected for this study (Fig. 1). These forest stands are situated on south-facing hill slopes and have low capacity to store water (Tables 1 and 2). Forests in the study locations were

**Table 1**  
Topographic and climatic characteristics of five oak–beech stands on Jurassic limestone in Germany and Switzerland. m a.s.l.: metres above sea level, ha: hectare, MAT: mean annual temperature, MTAP: mean total annual precipitation, MTAPET: mean total annual potential evapotranspiration, °: degree; <sup>1</sup> = after Gauer and Aldinger (2005); <sup>2</sup> = Average and sums were calculated from the climatic data collected from German (DWD, 2015) and Swiss (MeteoSwiss, 2015) weather services for the period of 65 years (1947–2011); <sup>3</sup> = after Turc (Turc, 1961).

Stands	Country	Locality	Region (Growing zone / Growing district) <sup>1</sup>	Geographic location (Long. °E, Lat. °N)	Altitude (m a.s.l.)	Size (ha)	MAT (°C) <sup>2</sup>	MTAP (mm) <sup>2</sup>	Days > 10 °C <sup>3</sup>	MTAPET (mm) <sup>23</sup>	Slope angle (°)	Aspect (°)
Innerberg	Germany	Badenweiler	Oberrhinesisches Tiefland und Rhein-/Markgräflerland	7.67, 47.81	524	0.9	9.2	1000	177	1085	23	155–180
Schönberg	Germany	Swabian Alps	Schwäbische Alb/Traufzone der Mittleren Alb	9.12, 48.42	781	0.8	5.3	831	143	912	31	205–243
Kätzler	Germany	Klettgau	Südwestdeutsches Alpenvorland/Klettgau	8.43, 47.62	566	0.3	7.7	966	164	1006	30	185–228
Steimüri	Switzerland	Canton Schaffhausen	Südwestdeutsches Alpenvorland/Klettgau	8.50, 47.65	584	0.5	7.7	966	164	992	24	251–280
Steinbruch	Switzerland	Canton Schaffhausen	Südwestdeutsches Alpenvorland/Klettgau	8.50, 47.67	643	0.4	7.7	966	164	1004	16	210–220

**Table 2**

Description of some stand level attributes. AWC: available soil water storage capacity, N = number of plots, for TSF (Total Site Factor) it was number of tree specific hemispherical photographs.

Stands		AWC (mm)	Bulk Density (g/cm <sup>3</sup> )	pH of Ah horizon	pH of B horizon	Availability of light (TSF)	Stand basal area (m <sup>2</sup> /ha)	Proportion of Oak basal area (%)	Tree species diversity <sup>a</sup>	Tree structural diversity <sup>b</sup>
Innerberg	Mean	59.17	1.29	6.23	6.71	0.19	46.94	88.29	1.10	1.69
	S.E.	2.36	0.03	0.03	0.06	0.01	1.40	1.16	0.04	0.03
	N	20	20	20	20	54	20	20	20	20
Schönberg	Mean	71.91	1.45	6.62	7.01	0.12	30.18	36.16	1.64	1.50
	S.E.	4.74	0.02	0.02	0.02	0.01	1.53	3.78	0.03	0.02
	N	18	18	18	18	66	18	18	18	18
Kätzler	Mean	52.60	1.44	6.28	6.35	0.07	53.39	68.45	0.98	1.39
	S.E.	5.18	0.09	0.04	0.11	0.01	3.44	5.17	0.08	0.06
	N	6	6	6	6	22	6	6	6	6
Steimüri	Mean	50.39	1.07	6.35	6.31	0.11	39.39	30.24	1.25	1.50
	S.E.	2.09	0.03	0.09	0.13	0.01	1.61	4.38	0.08	0.02
	N	14	14	14	14	38	14	14	14	14
Steinbruch	Mean	48.39	1.98	6.82	7.12	0.14	38.25	28.98	1.19	1.71
	S.E.	1.72	0.05	0.03	0.02	0.01	1.15	4.50	0.05	0.02
	N	9	9	9	9	44	9	9	9	9

<sup>a</sup> Shannon diversity index.

<sup>b</sup> Shannon index for 5 cm DBH classes.

**Table 3**

Dendrometric information of sampled beech trees from the five study locations. a) Height and diameter of living beech saplings and trees (N = 224), b) diameter of snags or standing dead plants (N = 59); DRC = diameter at root collar.

(a)							
Stand	N	Mean DRC (cm)	Minimum DRC (cm)	Maximum DRC (cm)	Mean height (m)	Minimum height (m)	Maximum height (m)
Innerberg	54	7.9	1.2	21.0	5.9	0.5	15.0
Schönberg	66	8.2	1.6	20.4	6.2	1.3	9.5
Kätzler	22	9.6	1.8	19.0	7.1	2.0	16.0
Steimüri	38	8.1	1.1	21.0	5.2	0.5	15.0
Steinbruch	44	4.7	1.1	17.0	2.9	0.5	14.0

(b)				
Stand	N	Mean DRC (cm)	Minimum DRC (cm)	Maximum DRC (cm)
Innerberg	22	5.2	1.8	22.0
Schönberg	11	9.5	3.3	30.6
Kätzler	4	11.0	1.4	27.5
Steimüri	16	8.7	4.5	14.0
Steinbruch	6	10.2	3.4	15.0

used as oak coppice forest but have been unmanaged since the end of the Second World War. Old oak trees dominate the canopy layer, mixed with other broadleaf tree species (see Table 2 for the proportion of oak basal area and the basal area of other species). In these forest stands, beech trees have regenerated naturally under the canopy of oaks (Fig. 2). Past studies from these forest sites showed that beech-dominated mixed forests in adjacent sites form a transitional zone with oak-dominated forests where occurrence and establishment of beech trees is limited by water availability (Sayer, 2000; Gärtner et al., 2008; Kohler et al., 2006). The beech trees found in those transition areas generally belong to the intermediate, and co-dominant layers in terms of vertical height cohort (Fig. 2). Detail dendrometric information of the sampled beech trees are given in Table 3.

The field data were collected from these five forest stands during the months of May to October in the years of 2012 and 2013. In each stand, we laid at least 3 transects starting from beech-dominated forest and ending in oak-dominated forest to account for changes in soil water storage capacity, beech tree vitality and forest composition and structure (Mueller-Dombois and Ellenberg, 1974) (see Fig. 3 for a schematic representation of the sampling design). Nineteen transects were laid in total, and each of these was 10 m in width and up to a maximum of 50 m in length; transect length was set so as to capture the transition zone between beech and oak



**Fig. 2.** Pictures from different forest stands situated in southern Germany and northern Switzerland. (A) Old coppiced oaks at the canopy layer with beech trees in the secondary layer at Innerberg; (B) Intermediate and co-dominant beech trees with other broadleaf trees at Schönberg.

forest. Each transect was subdivided into continuous quadrats of 10 m × 10 m plots, totaling 67 quadrats or plots.

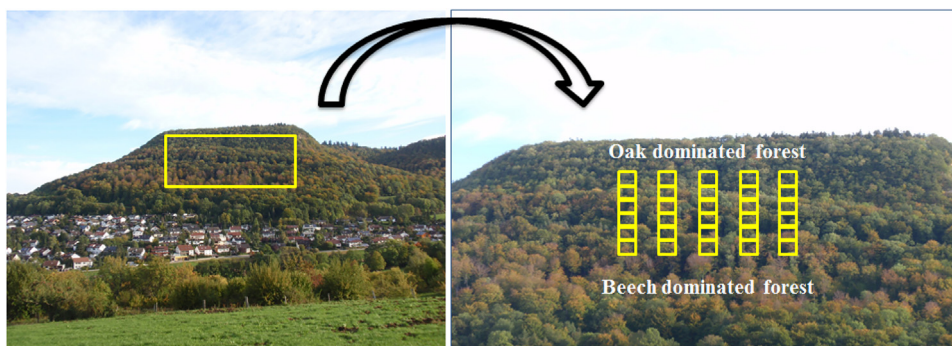


Fig. 3. Schematic diagram of laying sampling plots in study sites (the study site Schönberg is shown in this figure).



Fig. 4. Sampled beech trees from the study sites and sampling design; (A) example of a standing beech tree with upper crown die-back in Innerberg, (B) example of partial stem die-back that was observed and marked on sampled beech tree at Schönberg, (C) example of a standing dead beech tree in Innerberg.

## 2.2. Field inventory and soil analysis

Across all 67 plots, each beech tree with a minimum height of 0.5 m and diameter at root collar of 1 cm was permanently marked (see Fig. 4A–C for a description of sampled beech trees). For every beech tree, we recorded the following: stem diameter at root collar or 5 cm above-ground (DRC), stem diameter at 1.3-m height (DBH), height, living status of main stem (i.e., healthy or partially dead stem), height from the ground to the beginning of stem die-back, and height to green crown base from ground. In addition, we measured the diameters of all living and dead branches (>0.5 cm) for each beech tree using a 10-m-tall telescopic pole assisted with a TruPulse professional laser rangefinder. The crown length was derived in the field as the distance from the beginning of green crown to the tip of the tallest living stem or branch. The crown was divided equally into three compartments: upper, middle and lower. The position of each living and dead branch in respective crown compartments was noted during the morphometric inventory. DRC was recorded for each standing dead beech sapling and tree (see Table 3 for dendrometric information of living and dead beech trees). In addition to these detailed measurements, we also measured height, DBH and species identity of all living plants of more than 1.3-m height across all 67 plots to quantify species and structural diversity applying Shannon indices (cf. Section 2.4). The proportion of oak basal area to total plot basal area was quantified for each plot from the inventory data (see Table 2 for the stand level description).

Slope, aspect, GPS coordinates and elevation were recorded for each plot. Soil profiles were taken at the centre of each 10 m × 10 m plot to determine soil physical and chemical properties (Fig. 5). Bulk density ( $\text{g}/\text{cm}^3$ ) (Rowell, 2014) and available soil water storage capacity (mm) were calculated using soil texture, humus content, soil depth, horizon thickness and skeleton content for each plot

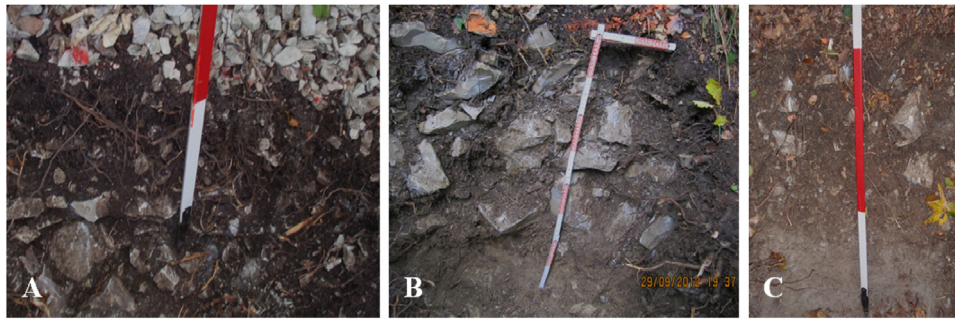
following the method developed by the German Soil Classification Working Group (Arbeitskreis Standortskartierung, 2016) and Food and Agriculture Organization of the United Nations (FAO, 2006) (see Appendix A1 for detailed calculation of bulk density and available soil water storage capacity). Available soil water storage capacity ranged from 24 to 168 mm. These values should be regarded as minimum values because on limestone the roots can penetrate deep cracks in the bedrock and contribute to the water supply. Soil pH was calculated after laboratory analysis for each soil horizon by  $\text{CaCl}_2$  and distilled water. Ah and B horizons were slightly acidic to neutral, with pH ranging from 6.3 to 7.1. Soil pH from these two horizons were used as interacting terms during statistical modelling to find the combined effect of pH from two horizons on crown die-back of beech trees.

## 2.3. Measurement of light and assessment of tree neighbourhood interactions

We used hemispherical photography to indirectly measure the light supply of all understory beech trees as the total site factor (see Appendix A2 for details of the sampling method used to determine the light measurement). The hemispherical photographs were taken in September of 2012 and 2013 before the starting of leaf shedding in deciduous trees. Total site factor is the relative amount of incident diffuse radiation plus the incident direct radiation that penetrates below the canopy for one growing season (April to September) which reaches the upper part of the tree crown of the sampled beech trees. Analysis of the hemispherical photographs was conducted using the software program WinSCANOPY (Regent Instrument Incorporation, 2008). In addition, neighbourhood interactions were assessed for each target beech tree because plant–plant interactions can be altered by size (i.e., size asymmetric interaction) and thereby influence the resource and space utilization between trees in mixed forests of diverse age (Coomes and Allen, 2007). Neighbourhood interactions were quantified using Hegyi's competition index (Hegyi, 1974); this index is independent of stand age and size, and depends only on the relative spatial pattern of the trees. Intra- and inter-specific interactions were calculated, and competitors were selected applying the searching cone method described by Pretzsch et al. (2010).

## 2.4. Assessment of stand compositional and structural diversity

We preferred to focus on simple and readily available measures of compositional and structural diversity, such as those used by D'Amato et al. (2011). We used our plot level inventory data for this purpose. Compositional diversity refers to the relative abundance and diversity of tree species within each plot. For each plot at each



**Fig. 5.** Example of three soil profiles out of total 67 profiles dug in this study depicting contrast in soil depth and skeleton content. Soil profile at: (A) Steinbruch site, Canton Schaffhausen, Switzerland, soil depth: 41 cm, available soil water storage capacity = 30 mm; (B) Schönberg site, Swabian Alps, Germany, soil depth: 84 cm, available soil water storage capacity = 54 mm; (C) Schönberg site, Swabian Alps, Germany, soil depth: 101 cm, available soil water storage capacity = 146 mm.

measurement, the Shannon diversity index was used to estimate species diversity in terms of stem density.

$$H_{\text{species}} = - \sum_{i=1}^S \frac{d_i}{D} \ln \left( \frac{d_i}{D} \right)$$

where  $S$  is the total number of species in the plot,  $D$  is the density of the plot, and  $d_i$  is the density of species  $i$ .

Structural diversity within each plot was based on the diversity of tree diameters (DBH) within a given plot. Tree size diversity was quantified using the Shannon index, which was applied to tree diameters and calculated with 5 cm DBH classes (Staudhammer and LeMay, 2001).

$$H_{\text{DBH}} = - \sum_{i=1}^S \frac{n_i}{N} \ln \left( \frac{n_i}{N} \right)$$

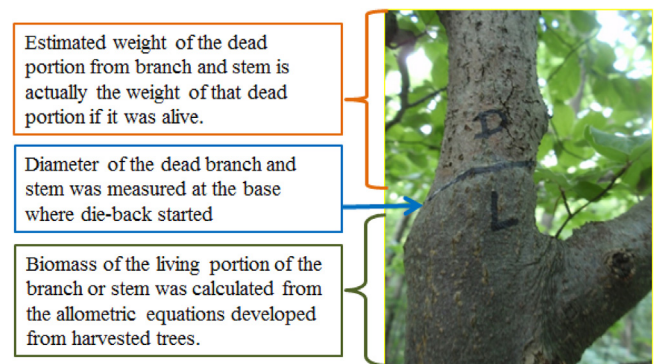
where  $S$  is the total number of size classes in the plot,  $N$  is the total number of trees in the plot, and  $n_i$  is the number of trees in size class  $i$ , with values generally increasing with greater numbers of size classes within a stand.

## 2.5. Calculation of potential evapotranspiration as site factor

The daily climate data were obtained from the German and Swiss Weather stations (DWD, 2015; MeteoSwiss, 2015) to quantify potential evapotranspiration (PET) for each study location. Weather variables that included daily mean temperature and relative humidity were used in combination with daily solar radiation data to calculate PET. Daily solar radiation was calculated in RayMan software (Matzarakis et al., 2007) by using topographic information (i.e., slope, aspect, latitude, longitude, and elevation) gathered during the field survey and climate data (daily mean temperature, cloud cover and relative humidity) obtained from the climate stations. Radiation based PET formula coined by Turc (1961) was calculated for each study location for the last 65 years by the period of 1947–2011. Finally, the daily PET data were averaged to a single value for three locations of Badenweiler, Swabian Alps and Klettgau (consisting with Kätzler, Steimürli and Steinbruch).

## 2.6. Quantification of crown die-back

We quantified the above-ground biomass (including main stem with bark without branches and branches with leaves) of each inventoried beech tree using an allometric biomass equation that was built for this study based on harvested beech trees from the five stands. We prepared these biomass equations to simulate crown die-back of a tree as described previously (Chakraborty, 2010; Chakraborty et al., 2013, 2016) (see Appendix A3 for a detailed description). Crown die-back for each tree was calculated as the



**Fig. 6.** Figure showing living (L) and dead (D) portions of a standing beech tree, with the base demarcation indicating the location for the diameter measurement of the dead portion. Diameters of all living and dead branches and stems were recorded during the field inventory. Allometric equations were developed based on data from living branches and stems. Weight of the dead portion was simulated based on living portions.

proportion of living and dead biomass components as a percentage (Fig. 6), after calculating the total simulated dead above-ground biomass and actual living biomass of each tree:

$$\% \text{of dead above-ground biomass} = (D/AB) * 100$$

where  $D$  = dead simulated biomass of a tree and  $AB$  = total above-ground biomass of the tree. In addition, crown die-back for each crown compartment was also calculated as per the recorded information of living and dead branch status of each compartment during the inventory. An increase in percentage values indicates a decrease in vitality of that respective tree because the proportion of dead above-ground biomass had increased. For a tree with no mortality or dead biomass, this proportion would be zero, and for a totally dead but standing tree (snag), the proportion would be 100 (see Appendix A3, Tables A1 and A2 for detailed calculations).

## 2.7. Statistical analysis to quantify influences of biotic and abiotic factors on crown die-back of beech trees

We wanted to find out the relation among the crown die-back with various biotic and abiotic factors. The aim was also to look on the relation of the individual crown compartment-wise die-back. For that reason, the dependent variables were chosen as: crown die-back for the whole tree and the compartment-wise die-back quantified for upper, middle and lower crown. The biotic and abiotic factors chosen as independent variables were: available soil water storage capacity, bulk density, height of the sampled beech tree, total site factor (as availability of light), intra-specific interaction, inter-specific interaction, tree species diversity, tree

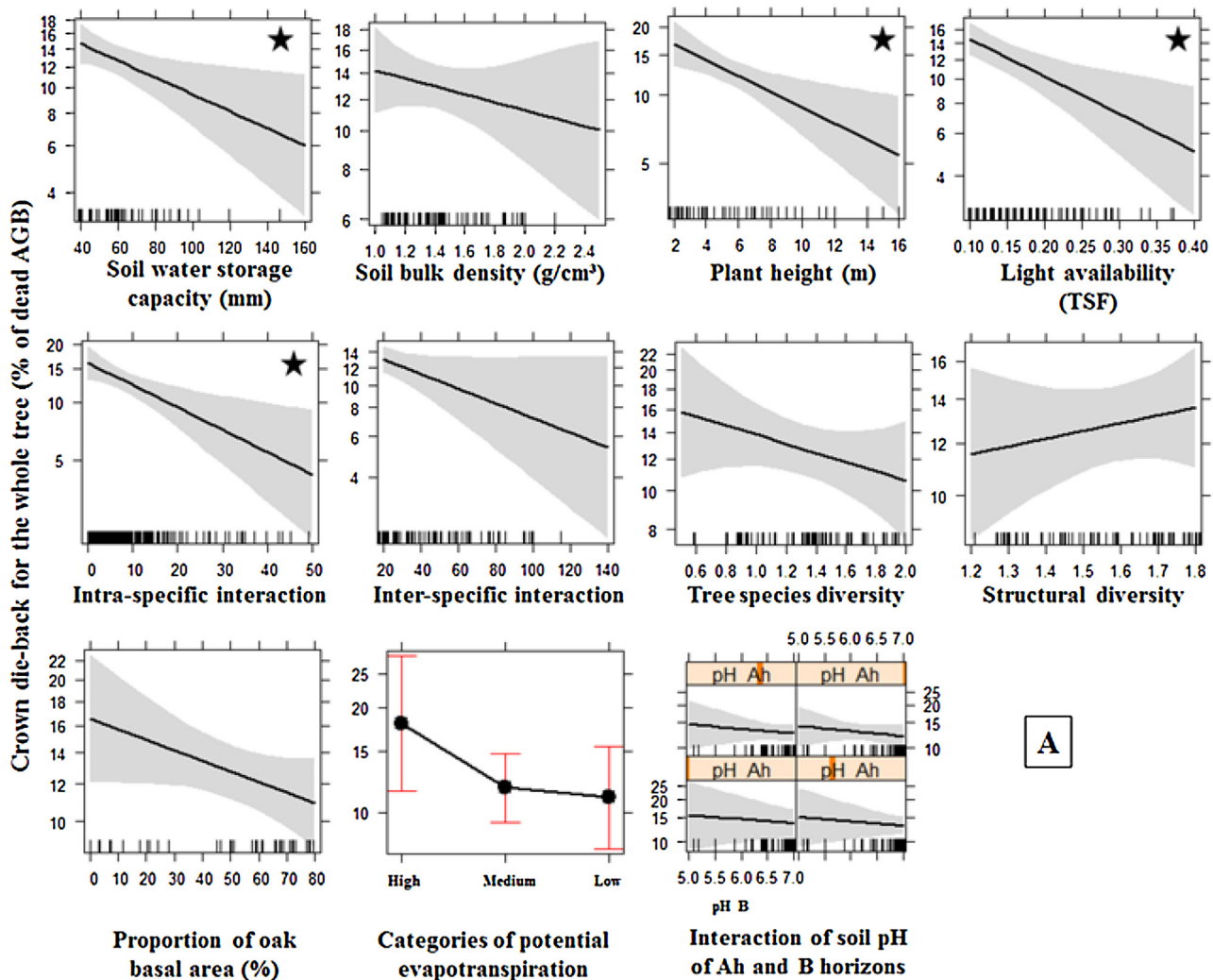
structural diversity, proportion of oak basal area in plots, potential evapotranspiration and soil pH. First of all, the distribution of both dependent and independent variables were checked by the Shapiro-Wilk test. Data did not follow the Gaussian distribution. The independent variables were not auto-correlated, as collinearity between independent variables was checked by auto-correlation analysis as suggested in Dormann et al. (2013). The dependent variables were nearly following the gamma distribution. Therefore, we chose the generalised linear model (GLM) by fitting Gamma with log link function to look upon the relation among the various factors and the crown die-back. The GLM permits fitting of linear models to any distribution function included in the exponential family by performing maximum likelihood analysis. GLM directly fits the expected mean of the dependent variable, thus avoiding biases for transformed (e.g., log transformed) linear models (McCullagh and Nelder, 1989). All variables were included as continuous variables excluding potential evapotranspiration. This was included as ordinal variable by ranking low, medium and high depending on the value of the potential evapotranspiration as it was calculated for

each of the three study locations. The data of soil pH of Ah and B horizons were included as interaction as the target was to look on the combined influence of the pH of both horizons. The statistical analyses were done in SPSS software version 20.0 (IBM, 2011) and R software (R Development Core Team, 2016). The GLM analysis was performed using “glm” function in R and results were plotted by the “effects” package of R (Fox, 2003; Fox and Hong, 2009).

### 3. Results

#### 3.1. Total crown die-back

For the investigated beech trees near their drought limit available soil water storage capacity had a significant negative effect on crown die-back (Fig. 7A). As water availability increased, crown mortality decreased while tree vitality improved. With increasing height, die-back in beech trees was reduced. Greater availability of light was negatively related to crown die-back which means with increasing available light, die-back was decreasing. Intraspe-



**Fig. 7.** Results from the Generalized Linear Models, showing the relationships among crown die-back and various explanatory factors (Soil water storage capacity, soil bulk density, plant height, light availability (TSF: total site factor), intra-specific interaction, inter-specific interaction, tree species diversity, structural diversity, oak basal area, potential evapotranspiration and soil pH). (A) Relationship of the crown die-back for the whole crown with the independent variables; (B) relationship of the crown die-back for the upper crown with the independent variables; (C) relationship of the crown die-back for the middle crown with the independent variables, and (D) relationship of the crown die-back for the lower crown with the independent variables. The black line denotes the trend of mean values of crown die-back and the grey colour represents the range of confidence intervals of standard errors (represented by the width of the slopes) at 95%. Mean (black dots) and confidence interval of the standard error at 95% (red line bars) for potential evapotranspiration (ordinal independent variable) are presented. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

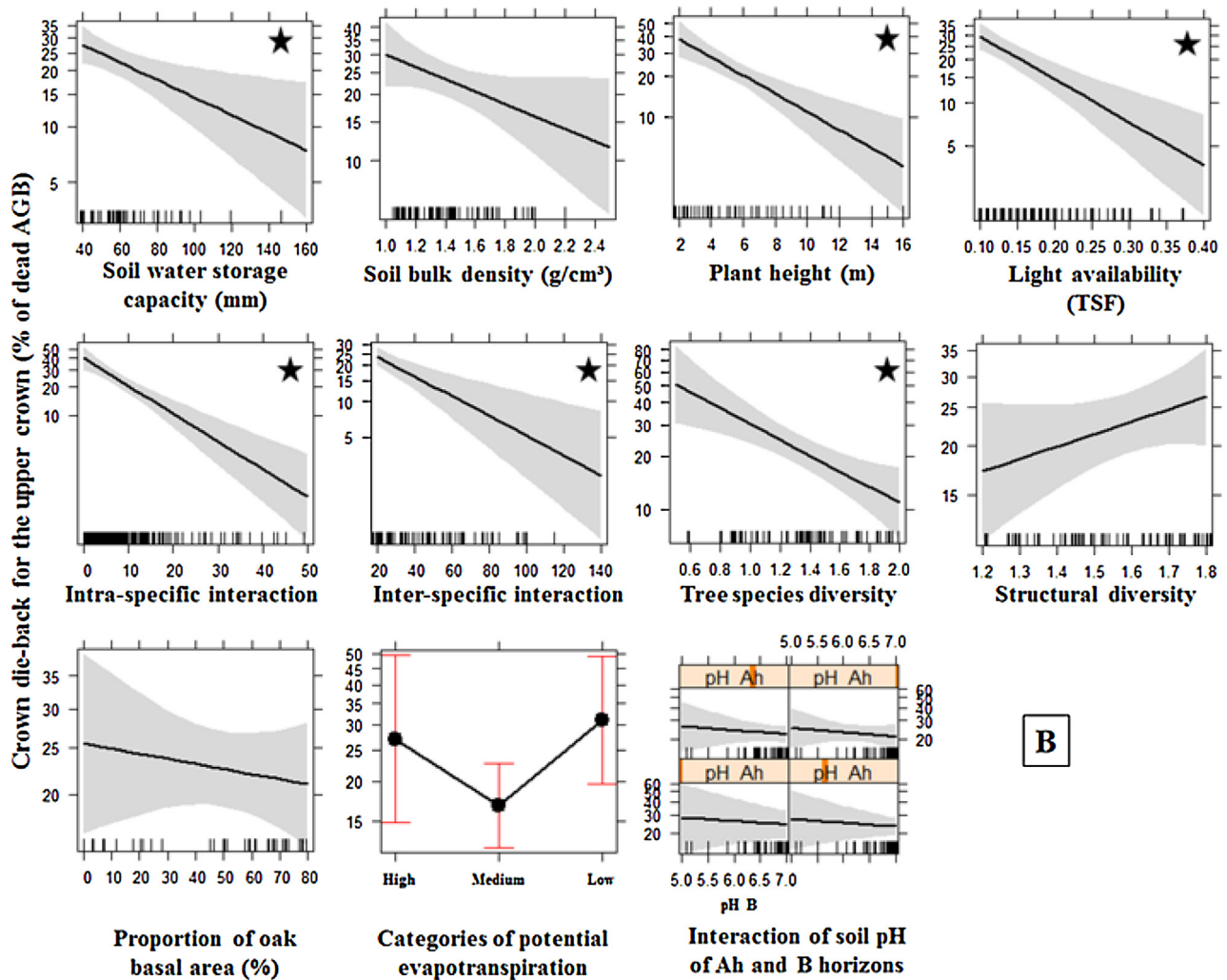


Fig. 7. (Continued)

cific interaction positively influenced vitality of beech trees, i.e. beech–beech or intraspecific neighbourhood may have reduced crown die-back of the beech trees. A similar trend was found in relation with inter-specific interaction and proportion of oak basal area, but those relations were not significant at the level of  $p=0.05$  (Table in Appendix A4). Soil bulk density, tree species diversity, structural diversity, potential evapotranspiration and soil pH did not show any significant relation with the crown die-back of the whole tree (Fig. 7A and Table in Appendix A4).

### 3.2. Compartment-wise crown die-back

Increasing soil water storage capacity significantly reduced crown die-back in the upper part of the crown (Fig. 7B and Table in Appendix A4). Like for whole crown die-back, increase in height, light availability, intra- and inter-specific interactions reduced the magnitude of upper crown die-back in beech trees. Along with that, we showed that the increasing level of tree species diversity significantly reduced crown die-back in upper crown. In the middle crown (Fig. 7C and Table in Appendix A4), increase in total site factor (light availability), intra- and inter-specific interaction reduced die-back. In the lower crown, no significant relations were found between the investigated independent variables and die-back (Fig. 7D and Table in Appendix A4).

### 3.3. Crown die-back threshold

The greatest amount of crown die-back, in terms of biomass, was found to be 58% with data from all five stands taken together. Stand-specific values were as follows: Innerberg, 58%; Schönberg, 52%; Kätzler, 56%; Steimürli, 53%; and Steinbruch, 58%. When crown die-back exceeds this percentage, trees die. These results were based on 283 (224 living and 59 standing dead trees or snags) beech trees in five stands (Fig. 8).

## 4. Discussion

This study shows the response of European beech at its drought limit under temperate climate. Due to the extreme site conditions the sampled beech individuals were intermediate to co-dominant, whereas oaks dominated the main canopy. For these situations, we show that increasing soil water storage capacity, plant height, tree species diversity and interactions between trees are related with reduced partial crown die-back of beech trees. Death became inevitable in beech trees when the proportion of die-back exceeded a threshold of 58% with respect to the tree's above-ground biomass. These findings allow us to accept our hypothesis that water availability, interacting with other abiotic and biotic factors, influences crown die-back in beech trees, and finally death of trees.



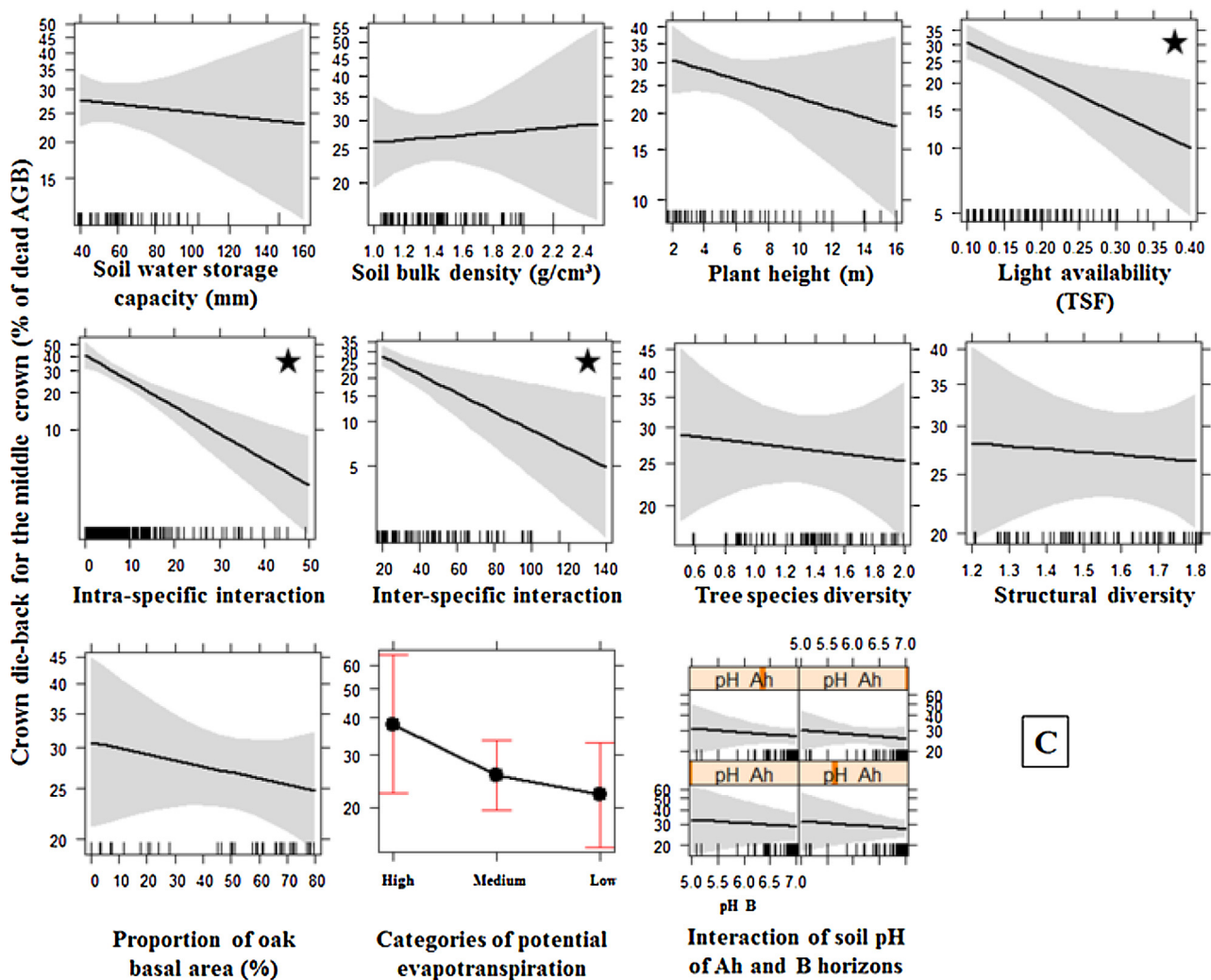


Fig. 7. (Continued)

Under the increasing frequency of climate change induced drought events, trees growing in areas with greater soil water storage capacity have an advantage over trees growing in areas with shallow soil in terms of the ability to take up water (Peiffer et al., 2014). Tree vitality depends on the ability to absorb water at a rate that prevents an internal water deficit during transpiration (Breda et al., 2006; Dobbertin, 2005). As soil dries, fine roots die, thus gradually failing to supply soil water (Leuschner et al., 2004). One of the most important functions of stomatal control of transpiration is the maintenance of the tree water status within a secure range of water potential to avoid xylem cavitation (Cochard et al., 1999; Rust and Roloff, 2002). Gessler et al. (2007) discussed beech as a species which is more susceptible to drought-induced xylem embolism because stomata do not respond adequately to prevent loss of hydraulic conductivity compared to other species such as oaks (but see Hentschel et al., 2016; Peiffer et al., 2014).

Kohler et al. (2006) found severe crown die-back primarily in the upper crown of trees in the study location Badenweiler just one year after the 2003 Europe-wide summer drought. Drought-induced xylem cavitation and subsequent upper crown mortality decreased the overall leaf area and increased the mortality risk of beech. The dependency of crown die-back in the upper part of the stem on soil water storage capacity might support our claim that die-back beginning in the upper crown was indeed due to a scarcity of soil water and was thus induced by drought. In contrast, die-back

in middle and lower crown was not regulated by the available soil water probably due to lower stress from xylem embolism in middle and lower crown than upper crown of the trees. European beech trees show increasing stomatal conductance from the base to the top of the crown (Aranda et al., 2000; Cochard et al., 1999; Lemoine et al., 2002) which might cause higher upper crown die-back during drought. Severe drought events (e.g., the regional drought during 1976 and the 2003 nationwide summer drought) might have aggravated the high incidence of crown die-back (Kohler et al., 2006).

In addition, drought could result in carbon shortage in shoots in dry sites because of increased carbon allocations to fine root biomass after droughts in response to fine root death during droughts (Meier and Leuschner, 2010). The strategy of beech is to allocate higher amounts of assimilates to roots under drought to maintain root osmotic potential and prioritize root functioning (Hommel et al., 2016). Partial die-back of crown and variation between the crown compartments can be seen as a stress tolerance mechanism of beech trees to keep their intrinsic physiological processes elastic or flexible which supports the hypothesis postulated by Schulze et al. (2005) based on 'physical stress concept' (Levitt, 1980). Such elasticity essentially describes a reversible deformation of strain after stress release. A recent study by Andregg et al. (2015) on aspen die-back quantified the threshold of lethal drought stress for xylem cavitation leading to permanent tree death, which indirectly supports our finding of a threshold in crown die-back

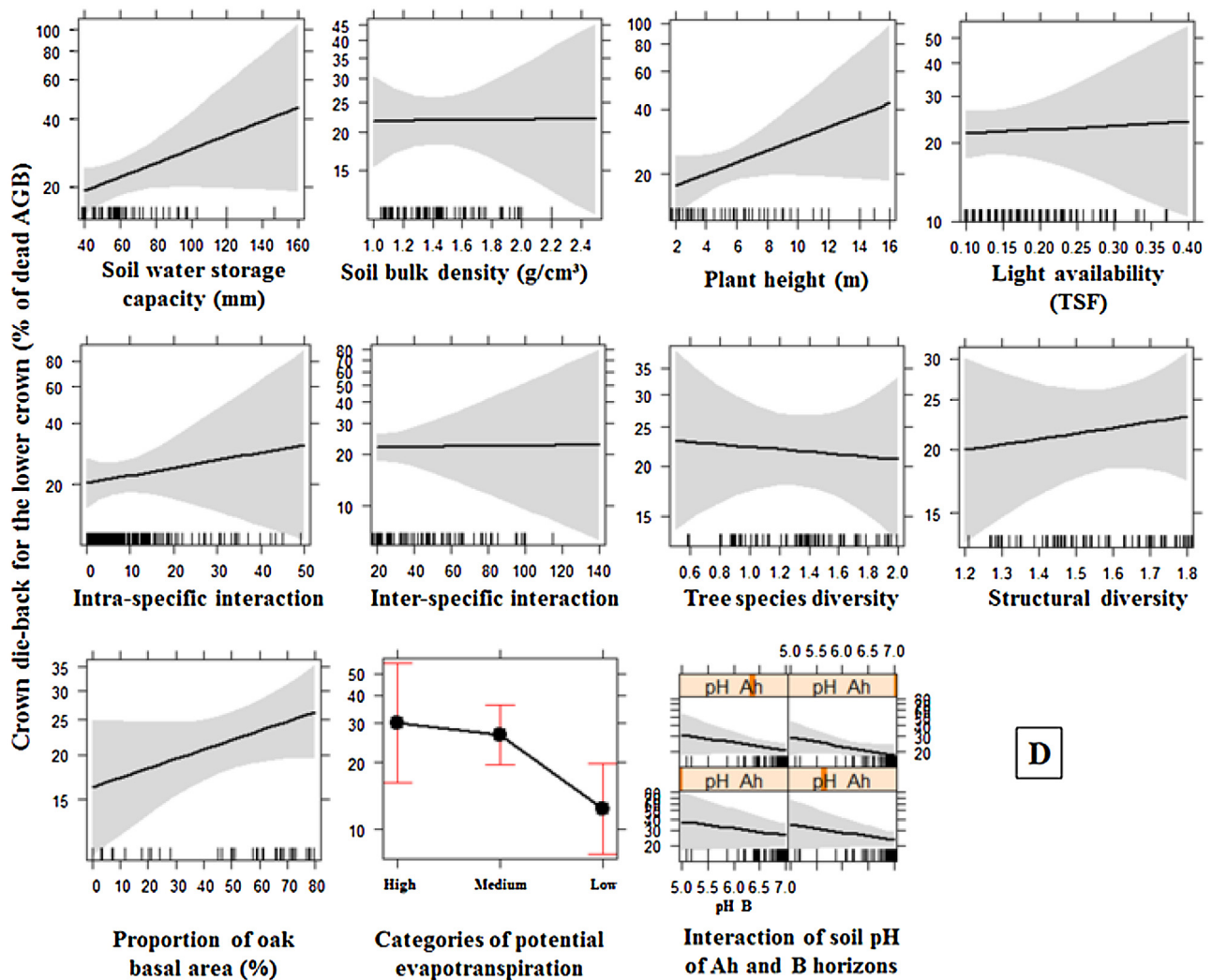


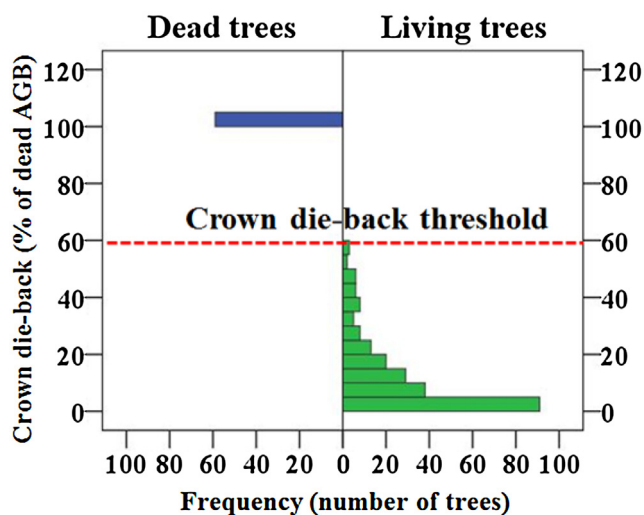
Fig. 7. (Continued)

relative to the proportion of above-ground biomass. Likewise, our finding on tree death after exceeding a tipping point supports Manion's 'decline spiral model' (1991) of tree death with the presence of inciting and predisposing factors, such as permanent soil water stress and periodic climatic drought.

As beech trees struggle to survive from drought, processes at the community level become important. Tree species diversity might buffer the impacts of water scarcity on the vitality of beech trees. As forests become more diverse, beech trees benefit in their fight for survival across a gradient of increasing water scarcity (Grossiord et al., 2014). Furthermore, higher tree species diversity could increase available solar radiation for photosynthesis and light use efficiency of beech trees as a complementarity effect (Forrester and Albrecht, 2014). This claim was evidenced by the positive effect of light availability on reducing crown die-back in the upper and middle crown.

In contrast, tree structural diversity did not show any influence on crown die-back in this study. One explanation might be that the canopy layer was dominated mostly by the even aged oaks which might facilitate vitality of beech trees discussed below. The positive effect of interspecific interactions on reducing crown die-back supports results from past studies which showed that trees growing in admixtures could reduce the risk of drought by benefitting each other through resource complementarity, particularly in a good rainfall year, to compensate loss during years of drought

(McDowell et al., 2006; Metz et al., 2016). Significant decreasing trend of die-back in the upper crown with intraspecific interactions might be supported by a recent study of Gebauer et al. (2012) who showed that in conspecific neighbourhoods, beech trees did not exhaust soil water during the early summer because of lower canopy transpiration. With respect to interspecific interactions, Pretzsch et al. (2013) had postulated that the neighbourhood interactions in oak–beech mixed forests might facilitate growth of beech trees during drought periods because oak trees could hydraulically lift the water from low soil horizons and help beech trees to use it during the dry periods. The beech trees mostly growing under oak canopy might have access to water from upper soil horizons. A negative, but non-significant trend of die-back across the larger proportion of oak basal area in all study sites may support the hypothesis of Pretzsch et al. (2013). However, these positive interactions would change with stand dynamics that could not be assessed in this study. Our results are also in accord with the stress-gradient hypothesis, which asserts that under increasing stress from drought, competition between trees for resources can turn to facilitation in forest ecosystems (Bertness and Callaway, 1994) and that this effect is more pronounced in growth of the trees when the diversity of tree species increases (Isbell et al., 2015). Our result contradicts a recent finding that says larger trees are facing higher stress of drought driven mortality (Bennett et al., 2015). One probable explanation of this contradiction is the social position of the



**Fig. 8.** Frequency distribution of 224 living trees with different magnitudes of crown die-back (in green) and 59 dead trees (in blue) from five forest stands is shown. We observed that the maximum crown die-back for a still-living tree would be 58% of dead biomass in relation to their total possible biomass. When a beech tree crossed this threshold, it would die (i.e., 100% die-back), as was evidenced by the absence of living trees with more than 58% die-back in 5 forest stands from 3 locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

beech trees. The beech trees were intermediate to codominant in our study sites and growing at their drought limit (Gärtner et al., 2008; Sayer, 2000). In this context, other site factors like light and plant neighbourhood interactions also played a major role to control mortality. With increasing height, probability of getting light becomes higher which may decrease the die-back.

Trees try to adapt through physiological acclimatization at the intra-population level in the same location within a forest stand. Our study indicates that beech trees naturally growing in drought-stressed dry forests in temperate regions may be going through the processes of xeric physiological modulative adaptation by taking advantage of their natural habitat (e.g., soil available water, species diversity, positive neighbouring interactions etc.) (Jump et al., 2006; Larcher, 2003). The die-back threshold (i.e., 58% crown die-back in terms of above-ground biomass) shown here should be treated cautiously. This value may vary between regions within the same species and between species. In this context, a previous case study on beech trees growing on a southern aspect of gneiss outcrop in the Black Forest by Chakraborty et al. (2013) had found a die-back threshold of 40% for young and juvenile beeches. That study in 2013 included only seedlings and saplings compared to this study where saplings, intermediate and co-dominant beech trees were studied. Moreover, the impact of an extreme drought year of 2003 might have had a carry-over effect with the young beech trees studied by Chakraborty et al. (2013) which could be overcome by the beech trees studied in this study. Nevertheless, this study highlights that a crown die-back threshold in trees does exist in forests and that determination of this threshold may enhance understanding of the sensitivity of trees to drought while developing plausible management options. The lack of replication over time warrants a long-term monitoring of crown die-back of beech trees at their drought limit. The one-time measurement of some factors like light and plant–plant interactions has some limitations as these factors change with time, and also affect the partial crown die-back versus recovery as an environment-depending process. Yet, significant relationships between these factors and crown die-back highlight the importance of these factors in understanding the stress ecology of beech trees. The importance of severe climatic drought events (e.g. 2003 summer drought) as a trigger or predis-

posing factor on the mortality of beech trees cannot be directly studied due to lack of tree-ring data and permanent trial plots. However, future studies should also consider this aspect.

## 5. Conclusions

We conclude that under temperate macroclimatic conditions soil water storage capacity plays a crucial role in maintaining beech tree vitality at the level of growing environment for individual trees. Future studies on growth and survivability of beech trees should not omit this abiotic factor. The facilitative interactions between plants can be an additional factor in maintaining the vitality of trees in the drought stressed forests. This study is the first to report that multiple abiotic and biotic stressors can differently influence die-back in upper, middle and lower crown compartments within the same tree. We have also provided the first evidence that tree species diversity can significantly reduce crown die-back in beech trees under an increasing gradient of soil drought. To summarize, our results support the hypothesis of Bertness and Callaway (1994) because we found that positive interactions between trees complement each other in reducing stress in a drought-stressed forest ecosystem.

Our results also support the theoretical concept of stress and strain proposed by Levitt and adapted by Schulze (Levitt, 1980; Schulze et al., 2005) based on field ecological research. When beech trees are exposed to moderate drought stress, e.g. a dry year after a sequence of less dry years, they first respond elastically to this stress by surviving through partial crown die-back. However, response to strain gradually becomes plastic under severe drought stress after an extremely dry year, resulting in complete die-back when it crosses a threshold. This finding is also in accord with Dobbertin's plant vitality model (Dobbertin, 2005). We suggest future studies on beech trees growing in forests should also combine dendroecology and dendrochemistry (e.g., stable isotope analysis) at a microsite level to further elucidate the intrinsic physiological acclimatization strategies of trees to drought.

## Author contribution statement

TC and AR jointly developed the research concept and study designs. TC collected field data, performed all laboratory and statistical analyses and wrote the manuscript. SS involved in field data collection and provided useful suggestions on this research. AM provided meteorological data and helped in calculation of potential evapotranspiration.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.flora.2017.02.012>.

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**Supplemental Material**

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

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**Running title:** Crown die-back of the European beech trees

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## **Appendix A1: Assessment of soil physical properties**

### **Calculation of soil bulk density**

Data were collected to calculate bulk density for each soil profile by volume replacement method specifically used for the Rendzina soils, containing large roots and stones, where bulk density cylinder could not be used (Rowell, 2014). Therefore, a 30 cm × 30 cm × 20 cm pit was dug in the center of each 10 m × 10 m plot, and the excavated earthen material was weighed in the field. A sub-sample was collected from the excavated material in a polythene bag and weight of the polythene was recorded in the field. Then the pit was filled up with dry fine sand and the volume of the sand was also recorded. Finally bulk density was calculated in the laboratory after oven drying of the collected sub-samples at 105 °C as per Rowell (2014).

### **Calculation of available soil water storage capacity**

After finishing the measurements for bulk density, we continued digging 1 m wide soil profile until we reached the compact bedrock. Another set of soil parameters were measured from different soil horizons like of the respective profile which were as follows: soil depth, type of soil horizon boundary, volume percentage of stone content, and colour of soil from different horizons using Munsell Soil Color Charts (Munsell, 1994) to calculate available soil water storage capacity (AWC) after the German Soil Classification Working Group (Arbeitskreis Standortkartierung, 2016) and Food and Agriculture Organization of the United Nations (FAO, 2006). Horizon specific soil samples were collected in polythene bags to analyse soil texture and soil organic matter content as well as for soil chemical analysis in the laboratory. See Chakraborty (2010) and Chakraborty et al. (2013) for more detailed description of the calculation of AWC.



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## **Appendix A2: Assessment of light availability**

Percentage of light availability of inventoried beech trees was measured using Canon EOS DIGITAL REBEL XSi digital camera with fish-eye lens for the acquisition of hemispherical photography. Most of the sampled trees were overtopped and intermediate, and located under the dominant and co-dominant canopy trees. Therefore they were generally not receiving vertical direct light, but the lateral light in their stretched lateral branches (Dawkins and Field, 1978; Clark and Clark, 1992). We wanted to capture the neighbourhood light availability for our sampled beech trees. Photos were taken at 1.3 m height on a fixed tripod stand under the over cast cloud condition, either in dawn or in dusk. Photos were taken on the top of the plant when height was 1.3 m or lesser. For the rest, allometry of tree size (DBH) and crown expansion area was used to calculate the circumference and radius of each tree's crown. Crown hemispherical photographs were then taken within that circle at the radial position of three different compass angles of East, South and West as plants were located on south facing slopes. Photos were taken at each 1 m interval of that circle of crown expansion area. Number of photographs per plant ranged from 3 to 9 that were related to the size of the respective plant. Hemispherical photographs were analysed in the WinSCANOPY 2008 software (Regent Instruments Inc., 2008). The light availability values obtained from multiple photographs were then averaged for the respective tree.

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### **Appendix A3: Preparation of allometric biomass equations for quantification of crown die-back**

#### **Sampling**

In total, 96 beech saplings and trees were harvested to estimate total above-ground biomass, including stem with bark and branches with leaves. Only healthy trees (i.e. trees without die-back symptoms) were felled down for this purpose to maintain the accuracy of equations to estimate biomass. We choose trees systematically from both dry and less-dry plots based on their diameter at root collar (DRC) class from the inventory dataset. The range of DRC was 1.1–21.5 cm for the harvested trees. Since the stands are located in dry sites, we observed morphological stunted growth in many of the beech trees and saplings. To capture this phenomenon, plants' DRC was used as independent variable for the biomass model (Chakraborty et al., 2013, 2016).

We calculated: total above-ground biomass, stem with bark biomass and branch with leaf biomass separately to prepare three different biomass equations to quantify both living and dead biomass of each single tree. After felling, plant height and crown length (length of crown measured from crown tip to the origin of lowest living branch on stem) were recorded. Fresh weight of the whole tree was measured directly in the field using portable spring scale (precision 0.5 kg). From our inventory data which was collected before tree felling, we knew diameter and length of all branches originating from the stem for each inventoried tree. From this record, we had prepared a size class of branches. From each harvested tree, we collected sample branches for each size class. Depending on crown length, tree crown was vertically divided in three equal compartments. Our pre-selection for branch collection was generally systematically distributed throughout the three crown compartments; for this reason, we had to collect at least three

branches from each crown compartment of each harvested trees. In total, we collected 326 living branches. Likewise, 84 terminal branches were also collected from the top of the tree according to the diameter class from the inventory dataset. Then the tree was separated in two different portions: main stem with bark without branches and all branches with leaves. Fresh weight of main stem with bark and the length was measured. Sub-samples from stem in terms of stem disks of 10 cm length were collected first at 10 cm above forest floor, and then consecutively in 1-meter interval until the tip or the terminal base of the plant was reached. Fresh weight of individual disks, branches, terminal branches and total leftover branches from the whole tree were measured in the field by using portable spring scale and portable electronic scales (precision 0.5 kg and 0.001 kg, respectively) depending on their size and mass. Finally, sub-samples collected in the field (branches with leaves, terminal branches with leaves and stem disks with bark) were brought to the laboratory for accurate dry biomass calculation through determining the moisture content and regression equations (Chakraborty et al., 2013, 2016).

### **Drying**

Collected disks were weighed before putting in oven at 105 °C for complete drying until constant weight was achieved. Similarly, sampled branches were chipped and dried in oven at 105 °C. All fractions weights were determined with  $\pm 0.1$  g precision. Dry weight of each part was calculated as:

$$\text{Total dry weight of parts} = \frac{X_{dry}}{X_{fresh}} \times \text{Total fresh weight of parts}$$

where  $X_{dry}$  and  $X_{fresh}$  were the dry and fresh weight of the plant part.

### **Allometric equations**

Three regression equations based on dry biomass and diameter were prepared: branch equation, terminal branch equation, and stem equation for each stand. At first, we performed *post-hoc*

model testing with 12 linear and non-linear regression functions to develop equations for biomass. In those regression model tests, we used the dry weight as dependent variable and the diameter of the respective branch and stem as independent variables. Finally, we found that non-linear regression with power function could explain the maximum amount of variation (resulted in the highest adjusted  $R^2$  value) in the data. This also supported some recent study that had shown that the biomass of almost all European broadleaved tree species followed a non-linear power function relationship with the diameter in young stages (Zianis et al., 2005). Finally, three non-linear regression models (for branches, terminal branches and stem axis) were formulated for each stand with dry biomass and diameter (see Table A2 for the regression equations) according to the following formula:

$$Y = a \times d^b$$

where  $Y$  = dry biomass,  $a$  = coefficient constant,  $b$  = regression coefficient and  $d$  = diameter.

Mean of observed and modeled values from allometric equations were compared by  $t$ -test and showed no significant difference. Hence, the allometric equations were accepted. Finally, the total above-ground biomass of 224 inventoried living saplings and trees was calculated as the summation of dry weight of stems with bark and branches (all lateral and terminal) including leaves.

**Table A1:** Regression equations developed to predict dry biomass for different trunk compartments of five forest stands. DRC: diameter at root collar (in cm), BR: lateral branch biomass with leaves (in gram), TR: terminal branch biomass with leaves (in gram), ST: stem biomass with bark (in kg).

Stand	Biomass components	Equations	$N$	$R^2$	$p$ value
Innerberg	BR	$34.361 \times (\text{diameter})^{2.605}$	86	0.937	< <b>0.001</b>
	TR	$62.602 \times (\text{diameter})^{2.537}$	28	0.973	< <b>0.001</b>

	ST	$0.02 \times (\text{DRC})^{2.65}$	28	0.974	< <b>0.001</b>
Schönberg	BR	$30.077 \times (\text{diameter})^{2.914}$	77	0.960	< <b>0.001</b>
	TR	$48.821 \times (\text{diameter})^{2.637}$	19	0.981	< <b>0.001</b>
	ST	$0.021 \times (\text{DRC})^{2.744}$	20	0.978	< <b>0.001</b>
Kätzler	BR	$42.153 \times (\text{diameter})^{2.739}$	30	0.980	< <b>0.001</b>
	TR	$74.914 \times (\text{diameter})^{2.57}$	11	0.992	< <b>0.001</b>
	ST	$0.026 \times (\text{DRC})^{2.668}$	12	0.988	< <b>0.001</b>
Steimüri	BR	$34.612 \times (\text{diameter})^{2.75}$	62	0.945	< <b>0.001</b>
	TR	$55.855 \times (\text{diameter})^{2.589}$	17	0.953	< <b>0.001</b>
	ST	$0.009 \times (\text{DRC})^{3.114}$	18	0.966	< <b>0.001</b>
Steinbruch	BR	$34.407 \times (\text{diameter})^{2.709}$	71	0.976	< <b>0.001</b>
	TR	$42.774 \times (\text{diameter})^{2.988}$	16	0.945	< <b>0.001</b>
	ST	$0.009 \times (\text{DRC})^{2.976}$	18	0.982	< <b>0.001</b>

### Calculation of dead above-ground biomass

Many living beech plants in our plots had dead terminal and partial branches, twigs and stem with varying magnitude of crown die-back. In addition, we had 59 standing dead beech trees in our inventory dataset. Those dead branches were either broken from the base or broken at a certain length from the base because of the branch shedding process. Practically, it was impossible to calculate the actual weight of that dead branch once it was green. We therefore developed a novel approach to simulate the weight of a dead branch from the diameter recorded during field inventory using the above-mentioned site specific allometric biomass equations. The diameter of such a dead branch was measured at the base where the mortality started that was still visible during the field inventory. For a single tree, all dead branches were summed up to calculate the total simulated weight of the dead branches. Similarly like the dead branches, above-ground biomass of standing dead beech plants were calculated from the regression model prepared for the whole living above-ground biomass of single tree (see Table A2 for the regression equations) (Chakraborty et al., 2013).

**Table A2:** Regression equations developed to calculate dry biomass (in kg) of standing dead beech trees (snags) from the five forest stands. DRC: diameter at root collar (in cm).

Stand	Equations	<i>N</i>	<i>R</i> <sup>2</sup>	<i>p</i> value
Innerberg	$0.047 \times (\text{DRC})^{2.445}$	54	0.992	< <b>0.001</b>
Schönberg	$0.044 \times (\text{DRC})^{2.611}$	64	0.976	< <b>0.001</b>
Kätzler	$0.057 \times (\text{DRC})^{2.529}$	22	0.988	< <b>0.001</b>
Steimüri	$0.027 \times (\text{DRC})^{2.867}$	34	0.985	< <b>0.001</b>
Steinbruch	$0.026 \times (\text{DRC})^{2.819}$	44	0.982	< <b>0.001</b>

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**Appendix A4: Tabular results of the generalized linear model (supplementary to Fig. 7A to 7D of the Result section)**

<b>Dependent variable</b>	<b>Coefficients:</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>crown die-back for the whole tree</b>	Intercept	5.342104	0.813078	6.570	<b>3.86e-10</b>
	Available soil water storage capacity	-0.007437	0.003030	-2.454	<b>0.01493</b>
	Plant height	-0.080775	0.028081	-2.877	<b>0.00443</b>
	Light availability (total site factor)	-3.520412	1.140654	-3.086	<b>0.00230</b>
	Bulk density	-0.229724	0.242312	-0.948	0.34419
	Intra-specific interaction	-0.026733	0.009281	-2.880	<b>0.00438</b>
	Inter-specific interaction	-0.007404	0.003925	-1.886	0.06064
	Tree species diversity	-0.262665	0.224879	-1.168	0.24411
	Structural diversity	0.270084	0.367366	0.735	0.46304
	Proportion of oak basal area	-0.005160	0.002912	-1.772	0.07784
	Potential evapotranspiration	-0.343583	0.238880	-1.438	0.15183
	Interaction of soil pH (pH of Ah:pH of B)	-0.011510	0.016503	-0.697	0.48626
<b>Crown die-back for the upper crown</b>	Intercept	8.424631	1.099163	7.665	<b>6.45e-13</b>
	Available soil water storage capacity	-0.010944	0.004097	-2.672	<b>0.008140</b>
	Plant height	-0.156837	0.037961	-4.132	<b>5.19e-05</b>
	Light availability (total site factor)	-6.919451	1.541999	-4.487	<b>1.19e-05</b>
	Bulk density	-0.638592	0.327571	-1.949	0.052564
	Intra-specific interaction	-0.067428	0.012547	-5.374	<b>2.03e-07</b>
	Inter-specific interaction	-0.019169	0.005306	-3.613	<b>0.000379</b>
	Tree species diversity	-1.027160	0.304004	-3.379	<b>0.000867</b>
	Structural diversity	0.728146	0.496626	1.466	0.144086
	Proportion of oak basal area	-0.002406	0.003936	-0.611	0.541709



Crown die-back of the European beech trees

	Potential evapotranspiration	0.097116	0.322931	0.301	0.763914
	Interaction of soil pH (pH of Ah:pH of B)	-0.013088	0.022309	-0.587	0.558070
<b>Crown die-back for the middle crown</b>	Intercept	5.719007	0.979774	5.837	<b>1.98e-08</b>
	Available soil water storage capacity	-0.001585	0.003652	-0.434	0.66461
	Plant height	-0.038382	0.033838	-1.134	0.25796
	Light availability (total site factor)	-3.763317	1.374509	-2.738	<b>0.00671</b>
	Bulk density	0.079525	0.291991	0.272	0.78562
	Intra-specific interaction	-0.049377	0.011184	-4.415	<b>1.61e-05</b>
	Inter-specific interaction	-0.014551	0.004730	-3.076	<b>0.00237</b>
	Tree species diversity	-0.088633	0.270984	-0.327	0.74393
	Structural diversity	-0.112490	0.442683	-0.254	0.79966
	Proportion of oak basal area	-0.002694	0.003509	-0.768	0.44345
	Potential evapotranspiration	-0.385572	0.287855	-1.339	0.18186
	Interaction of soil pH (pH of Ah:pH of B)	-0.011851	0.019886	-0.596	0.55185
<b>Crown die-back for the lower crown</b>	Intercept	2.9924095	1.1244619	2.661	<b>0.00839</b>
	Available soil water storage capacity	0.0071243	0.0041909	1.700	0.09061
	Plant height	0.0633619	0.0388345	1.632	0.10426
	Light availability (total site factor)	0.3590763	1.5774899	0.228	0.82016
	Bulk density	0.0102582	0.3351108	0.031	0.97561
	Intra-specific interaction	0.0085937	0.0128357	0.670	0.50390
	Inter-specific interaction	0.0002782	0.0054284	0.051	0.95917
	Tree species diversity	-0.0713554	0.3110011	-0.229	0.81875
	Structural diversity	0.2515519	0.5080563	0.495	0.62103
	Proportion of oak basal area	0.0060082	0.0040269	1.492	0.13719
	Potential evapotranspiration	-0.6264637	0.3303637	-1.896	0.05929
	Interaction of soil pH (pH of Ah:pH of B)	-0.0325465	0.0228226	-1.426	0.15533