

Floristic Change at the Drought Limit of European Beech (*Fagus sylvatica* L.) to Downy Oak (*Quercus pubescens*) Forest in the Temperate Climate of Central Europe

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Abstract

An increase in drought could cause shifts in species composition and vegetation structure. In forests it limits the occurrence of drought sensitive tree species which become replaced by drought tolerant tree species and forest communities. Under temperate macroclimatic conditions, European beech (*Fagus sylvatica* L.) naturally dominates the forested landscape, except on extremely shallow soil in combination with high irradiation. On these sites beech reaches its drought limit, and is replaced by forests dominated by species like downy oak (*Quercus pubescens* s.l.) and English oak (*Quercus petraea* L.). Phytosociological and ecological data were collected in the transition (ecotone) between European beech stands and stands of more drought tolerant species in order to quantify the drought intensity threshold, above which beech is replaced by drought tolerant species. It was shown that favourable topographic and soil conditions partially compensated the unsuitable climatic conditions for beech. The ecotone between these forest types was found to be characterized by shallow soils with an available soil water storage capacity of 73 l/m² or less, and an irradiation intensity of 6000 MJ/m² or more during the growing season. This indicates that under conditions of climate change beech would naturally still remain the dominant tree species on the majority of central European forest sites.

Keywords: downy oak, *Quercus pubescens*, *Quercus petraea*, water supply

Introduction

European beech (*Fagus sylvatica* L.) would naturally dominate central European temperate forests because of its high physiological shade tolerance and competitiveness (Ellenberg and Leuschner, 2010). Natural limits of beech forest appear to be relatively abrupt, a result of the ongoing high competitiveness and shade tolerance of beech even when growing close to its distribution limits (Bolte *et al.*, 2007; Ellenberg and Leuschner, 2010). The species is able to grow under the temperate climate of central Europe in relatively dry to moist soils, yet under the sub-Mediterranean climate of southern Europe, the competitiveness of beech is increasingly limited by climatic drought. In southern Europe growth rates and

competitiveness of beech are reduced and controlled by environmental variables that indicate drought intensity (Czúcz *et al.*, 2011; Tegel *et al.*, 2014) and beech forests become replaced by submeridional forests composed of more drought tolerant species, mainly pines and oaks (Horvat *et al.*, 1974; Ellenberg and Leuschner, 2010). Therefore, beech is restricted to shady slopes and/or deep soils and/or higher elevations (Ozenda *et al.*, 1988; Peters, 1997; Reif and Löblich-Ille, 1999). In these locations, topography and soil compensate for the increasing macroclimatic drought, allowing for a “relatively constant” (Rubio and Sanchez-Palomares, 2006) water supply that favours beech. This example also demonstrates that there are various environmental factors influencing the distribution of plant species and plant communities with a scale dependent relative importance (Thuiller *et al.*, 2003) or, in other words, according to the “rule of relative site

constancy" (Walter, 1954), macro-climatic conditions that could potentially limit the distribution of a plant species can be partially counterbalanced by favourable, local topographic or soil factors. This explains, for example, the extrazonal distribution plant species and communities. At continental or global scale, macroclimatic variables have been proven sufficient to describe the distribution pattern of vegetation. But at local to landscape scales, disturbances, species interactions and direct physiologically effective parameters control the occurrence of plant species and plant communities. Variables influencing vegetation distribution can be broadly related to moisture, energy, nutrient availability and geomorphodynamics (Mellert *et al.*, 2011). To study drought or aridity-induced vegetation limits, moisture supply is the main factor to be considered. It has been shown, for example, that summer drought intensity in conjunction with late spring air temperature and precipitation are the determinant factors for beech distribution at low elevations in central Europe (Czúcz *et al.*, 2011). Moreover, soil water availability seems to actively control beech growth at its southern distribution limit (Tegel *et al.*, 2014).

Moisture supply is defined by the complex interactions of various factors, including soil water storage capacity, precipitation, air temperature, solar radiation intensity and wind speed. All of these factors influence a site's soil water balance (Thornthwaite, 1947; Thornthwaite, 1948; Thornthwaite and Mather, 1951). The interaction of these factors can have a counterbalancing effect (i.e. high values of available soil water capacity can partially counterbalance low precipitation). In effect it could either mitigate drought intensity or, contrary, synergize to intensify drought. Different combinations of drought factors lead to particular responses in species and thus specific vegetation types.

This study focuses on the tree species composition change at the drought limit of beech in southwestern Germany and the Canton of Schaffhausen in Switzerland by studying stands at the ecotone between forests with downy oak (*Quercus pubescens* Willd.) including its hybrids with English oak (*Quercus petraea* (Matt.) Liebl.) and beech (Fig. 1) (Kätzler *et al.*, 2014). The objective was to compare these ecotones in two regions in southwestern Germany having different macroclimatic conditions. Because site conditions are expected to induce drought at the distribution limit of beech stands, we want to relate these conditions with changes in the species composition and the performance of beech at the ecotone. Only a few studies have analysed or quantified shifts in the components of water supply on comparable sites but with different macroclimates and related them to forest vegetation responses (Rigling *et al.*, 2013) or beech vitality (Chakraborty *et al.*, 2013; Chakraborty *et al.*, 2017).

Materials and Methods

Study regions and locations

The ecotones between beech and downy oak were studied at locations where forests were as near-natural as possible and the ecotone was large enough to sample along local gradients. For at least fifty years there was no harvesting in the five selected stands due to their low

productivity. Even though this is not a long time when considering the lifespan of a tree, (a) it was sufficient enough that a specific ground vegetation layer, which mirrors the natural site conditions, could establish; and (b) beech was not observed regenerating in the adjacent downy oak stands indicating the near-natural limits of beech.

Ecotones between near-natural stands of downy oak and beech were sampled at five locations on Jurassic limestones with shallow rendzina soils in (1) the submontane zone of the Klettgau, including one adjacent location in Osterfingen, Switzerland, and (2) the montane zone of the central Swabian Alb (Schwäbische Alb) (Fig. 1, Table 1).

Each of the locations had downy oak stands on the driest areas, i.e., southwest exposed upper slopes, surrounded by beech-dominated forests.

Vegetation assessment in the field

To determine site gradients and where the species turnover from beech to oak forest occurred, sample plots (relevés) 10×10 m in size were arranged in a systematic grid. The grid-lines ran in-line with the slope and had a distance of 25-30 m while these running along the slope had a altitudinal difference of 10-15 m, thus the horizontal distance varied. The relevé centres were positioned at the grid-line intersections.

For each 100 m² sample plot the vegetation was recorded. The percent cover of the vascular plants was estimated in three layers (herb, shrub and tree). A modified cover abundance scale *sensu* Braun-Blanquet was used (coverage <1%, 1-2 individuals: r; 2-5 individuals: +; 5-50 individuals: h; >50 individuals: m; coverage >1% to <10%: in 1% steps; coverage >10%: in 5% steps). The total cover of the three layers was estimated. Additional structure variables measured were (tree heights (m); canopy cover (%); crown diameters (m). Plant species were identified and named following Oberdorfer (2001). All introgressive hybrids between *Quercus petraea* and *Quercus pubescens* were morphologically identified following Aas (1998) and Müller

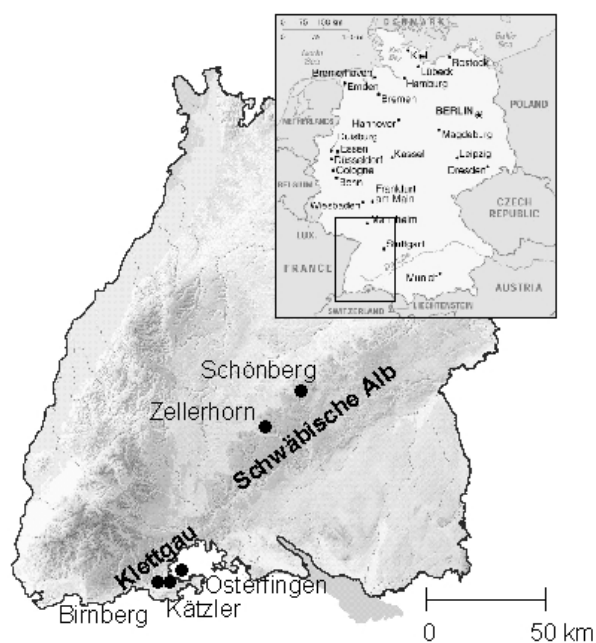


Fig. 1. The study areas

Table 1. The two study regions, incorporating five locations

Parameter	Klettgau region (incl. Osterfingen/CH)	Schwaebische Alb region
Location and number of relevés (F = <i>Fagus</i> forest; ec = ecotone stand; Q = <i>Quercus</i> forest)	Birnberg 47 (16F, 13ec, 18Q) Kaetzler 38 (29F, 9ec) Osterfingen 56 (22F, 15ec, 19Q)	Zellerhorn 42 (15F, 12ec, 15Q) Schoenberg 67 (10F, 45ec, 12Q)
Elevation of site locations	Birnberg 490-550 m Kaetzler 495-555 m Osterfingen 535-620 m	Zellerhorn 790-825 m Schoenberg 735-800 m
Altitudinal zone	Submontane	Montane
Length of phenological growth period	7.5.-13.10. (160 days)	17.5.-2.10. (139 days)
Length of climatic growth period (mean daily air temperature >5 °C)	23.3.-5.11. (226 days)	5.4.-25.10. (204 days)
Mean annual air temperature 1961-2003	9 °C	7 °C
Mean annual air temperature data corrected after interpolation	8.6 °C	5.5 °C
Mean annual precipitation 1961-2003	1012 mm	834 mm
Mean annual precipitation (data corrected after interpolation)	1012 mm	940 mm
Mean precipitation during climatic vegetation period (Deutscher Wetterdienst, 1953)	615 mm	468 mm
Mean precipitation during phenological vegetation period (Deutscher Wetterdienst, 1953)	452 mm	313 mm
Geology	Jurassic limestone	Jurassic limestone
Soil	Rendzina	Rendzina

(1999). To determine the proportion of oak and their hybrids, a crown map of each plot was drawn. After the species samples were identified, their proportions were calculated. Finally, for each plot Ellenberg's indicator values were calculated (Ellenberg *et al.*, 1992).

Assessment and calculation of soil and climate variables

Edaphic variables

The available soil water storage capacity (ASWSC) represents the edaphic water availability at each site (plot). It was derived from soil pit profiles which were distributed systematically at each location. For each profile, rooting depth, soil skeleton content, soil texture and bulk density were estimated. Humus content was analysed using the WOSTOFF-Method. Available soil water storage capacity was calculated in l/m², following Arbeitskreis Standortskartierung (1996).

Climatic variables

Air temperature and precipitation

Precipitation and air temperature for each location were obtained from the meteorological stations of Hallau (MeteoSchweiz) (27° 27' 34" E; 47° 41' 54" N) and Hechingen (Deutscher Wetterdienst) (8° 57' 54" E; 48° 21' 10" N). The observation period (1961-2003) was considered sufficient to represent the climatic standard.

Air temperature and precipitation data for the Swabian Alb relevés were estimated by interpolating the meteorological observations from several surrounding climatic stations using altitude as auxiliary variable (Schlenker and Müller, 1973) (Table 1). For the region of Klettgau no corrections were necessary due to the proximity

and elevational similarity of the Hallau climatic station to the study area.

PET and irradiation intensity

A widely used variable for describing vegetation distribution is potential evapotranspiration (PET) (Stephenson, 1998). It reflects the climatic and physiological moisture demand of a site. For the study area evaporation data was not available nor were comparisons for the best-fitting PET formulas elaborated. Instead, PET rates were estimated based on empirical formulas making use of the available weather observations. The unavailability of many climatic data variables ruled out the use of the physically based FAO Penman-Monteith formula which is considered to be the best for calculation of reference PET when it is not measured directly (Allen *et al.*, 1998). PET therefore was obtained by means of three different irradiation-temperature formulas after Caprio (1974); Jensen and Haise (1963); and Turc (1961), all found in (Xystrakis and Matzarakis, 2010). The final PET values for each plot were calculated as the average of the three above-mentioned PET values.

Irradiation intensity is an indirect variable affecting the distribution of vegetation (Sternberg and Shoshany, 2001) by affecting a site's energy balance. It highly depends on latitude, though its values can be locally modified by slope aspect and inclination. Irradiation intensity was calculated for each plot by means of DACHRAD (Fischer and Gilgen, 2002). This software calculates monthly values of irradiation intensity in MJ/m² based on latitude, but also incorporating slope aspect and inclination, elevation and sky view factor (horizon limitation).

Although irradiation is integrated in the PET calculations, for comparison reasons irradiation has been also included separately into the set of our explanatory variables. All the calculations of PET and irradiation intensity refer to the growing season (Fischer, 1994).

Humidity index

The relationship between water supply (precipitation, P) and evaporative demand (potential evaporation, PE) are an adequate substitute for the estimation of climatic water availability. Both factors are combined in Transeau's humidity index ($HI = P/PE$) (Tuhkanen, 1980). In this study potential evaporation was replaced by PET in the HI, and humidity index was calculated as $HI = P/PET$, being suitable for comparison of climatic water availability between different sites and regions. The higher the index value the more water is available on a site. HI was calculated for the growing season for every plot.

Classification of forest vegetation

Vegetation data were classified based on the floristic composition and cover values of the species transformed to percent, and using the MULVA 5 program package (Wildi and Orlóci, 1996) with the following analysis sequence (Wildi, 1989):

- Clustering to get relevé groups (Transformations: extracting the 6. root; normalization; resemblance measure: covariance; Cluster algorithm: minimum variance).
- Ordination the species and relevés along the main gradient by applying a correspondence analysis (transformations: extracting the 6. root, double normalization of the contingency values; correspondence analysis).
- Clustering to get species groups (transformations: extracting the 6. root, normalization; resemblance measure: Chord distance; Cluster algorithm: minimum variance)
- Ordination of the relevé and species groups along the gradient by applying a concentration analysis
- Reduction of the species list to the discriminating ones by using Jancey's ranking based on F-values.
- The resulting forest types and their floristic differentiation were described in detail in Sayer (2000).

Gradient Analysis

The entire data set (257 relevés from all five locations) was analysed using a Principal Component Analysis (PCA) (ter Braak and Prentice, 1988, ter Braak, 1990). Ordination through a Detrended Correspondence Analysis of all relevés showed a standard deviation of 2.6 units with respect to the first axis, and allowed the application of a PCA (Lepš and Šmilauer, 2003). Afterwards the principal components were correlated with the measured environmental variables. We used indirect methods since we wanted to optimally project the samples in the floristic space and later to try and explain the floristic axis of the PCA.

The PCA was carried out based on the correlation matrix of the 6th root transformations of the species cover values. The reason was to linearise the relationship between the species as a basic assumption of applying the ordination

method and to highlight the ecological meaning between the species. Ordination diagrams were projected in Euclidian distance and performed using CANOCO for Windows 4.52 (Fischer and Gilgen, 2002).

Results

General vegetation patterns and environmental causes

The results of the multivariate analysis of the floristic data were compared with the existing phytosociological classification (Oberdorfer, 1992) and summarized as "beech forest", "oak forest" and "ecotone forest" (Table 2; see also Sayer, 2000; Gaertner *et al.*, 2008). The term "oak forest" was used to summarize relevés which were classified as *Quercetum pubescenti-petraeae* Imchenetzky 26 n. inv. Heinis 33, comprising sub-Mediterranean deciduous forest near its northern limit (Oberdorfer, 1992). In southern Germany, this association is rare and can be found only as isolated stands surrounded by the more frequent *Carici-Fagetum* Moor 52 (dry limestone beech forest) (Oberdorfer, 1992) to which the majority of the relevés of the "beech forest" belong. In Klettgau, few relevés of the beech forest on less dry sites were classified as *Galio odorati-Fagetum* Rübel 30 ex Sougnez et Thill 59. The transition between oak and beech forest is gradual; however, the "ecotone forest" was clearly distinct in species composition from the beech forest. Floristically, it also was classified as *Quercetum pubescenti-petraeae*, because the difference between ecotone and oak forest was mainly due to tree species cover rather than ground flora. The species listed in Table 2 are reduced to those which differentiate the forest types in the two regions. A complete vegetation table containing all 257 relevés can be obtained from the authors on request.

In both regions (Klettgau and Swabian Alb) the tree species and ground vegetation change completely at the ecotone (Fig. 2, Table 2). On soils having higher SWSC, beech is dominant with some ash (*Fraxinus excelsior* L.) individuals mixed in. SWSC appears to be the main limiting factor for the occurrence of beech. Therefore, the more drought tolerant oak forest community is restricted to soils with a SWSC of up to 73 l/m², and an irradiation of 6000 MJ/m² or more during the climatic growth period (Fig. 3). High irradiation combined with shallow soil are the site factors restricting the competitiveness of beech thus allowing oak to dominate.

The oak forests are composed of oak species and their hybrids, mixed with some other tree species, whereas most adjacent beech forests belong to the *Carici-Fagetum* (Sayer, 2000) (Table 2, Fig. 2). The ecotone between these two forest types floristically resembles the oak forest, but beech trees with low vitality, low heights and partial crown dieback can still be found. Climatic parameters and ground vegetation composition between the two regions are different (Tables 1, 2).

Vegetation and site conditions in the Klettgau ecotone

In the less humid Klettgau region the ecotone represents a more abrupt transition between beech and oak forest. On the ecotone and in the oak forest, downy oak (*Quercus pubescens*) and its hybrids (*Quercus petraea* × *pubescens*) prevail (Figs. 4, 5). Another frequent tree species is *Sorbus*

Table 2. Importance (= combination of frequency and coverage) of diagnostic species of the forest formations dominated by downy oak (*Quercus pubescens*), beech (*Fagus sylvatica*), and in the transition (ecotone). Compiled data from the regions Klettgau (including the adjacent locality Osterfingen/CH) and the Schwabische Alb

Climate (elevational zone) Forest formation	Klettgau (incl. Osterfingen/CH) Osterfingen/CH						Schwabische Alb					
	Submontane						Montane					
	<i>Quercus</i>		Ecotone		<i>Fagus</i>		<i>Quercus</i>		Ecotone		<i>Fagus</i>	
	Frequency	Average cover	Frequency	Average cover	Frequency	Average cover	Frequency	Average cover	Frequency	Average cover	Frequency	Average cover
[All numbers are %]												
Species typical of oak forest in both regions												
<i>Quercus petraea</i> × <i>pubescens</i>	100	53.9	92	33.0	46	5.2	85	17.9	67	12.6	40	6.2
<i>Fragaria viridis</i>	41	0.2	27	0.1			26	0.1	14	0.1		
Species mainly in submontane oak forest (Klettgau)												
<i>Quercus pubescens</i>	62	7.4	51	6.8	6	0.4	48	5.7	9	1.1	4	0.6
<i>Calamintha menthifolia</i>	78	0.3	57	0.2			37	0.2	2	<0.1	4	<0.1
<i>Sorbus torminalis</i>	14	0.8	32	1.2	11	0.2						
<i>Coronilla emerus</i>	73	0.3	65	0.2	41	0.1						
<i>Dictamnus albus</i>	51	0.2	43	0.2	15	<0.1						
<i>Asperula tinctoria</i>	27	0.1	14	<0.1	1	<0.1	4	<0.1				
<i>Lithospermum purpureocaeruleum</i>	16	<0.1	30	2.5	1	0.1	4	<0.1			8	0.1
<i>Teucrium chamaedrys</i>	73	0.5	32	0.2					2	<0.1		
<i>Melittis melissophyllum</i>	95	0.4	81	0.3	56	0.2						
<i>Euonymus europaeus</i>	62	0.2	70	0.2	45	0.1	7	<0.1	2	<0.1	8	<0.1
<i>Hedera helix</i>	97	0.5	92	0.5	96	0.4	7	<0.1	63	0.9	72	0.5
Species mainly in montane oak forest (Schwab. Alb)												
<i>Laserpitium latifolium</i>					1	<0.1	89	0.8	37	0.1	20	<0.1
<i>Thesium bavarum</i>							67	0.1	28	<0.1	4	<0.1
<i>Calamagrostis varia</i>							63	16.0	40	2.6	36	1.5
Mesophytic species of deciduous forest												
<i>Fagus sylvatica</i>	5	1.4	46	10.2	100	64.9	11	1.7	67	18.4	92	45.7
<i>Phyteuma spicatum</i>					7	<0.1	41	0.1	53	0.2	76	0.2
<i>Convallaria majalis</i>	24	0.1	19	0.2	52	0.3	11	0.1	54	0.4	68	0.5
<i>Asarum europaeum</i>							22	0.1	79	2.1	88	0.9
<i>Abies alba</i>											16	0.9
Light demanding tree species												
<i>Quercus petraea</i>	59	7.5	68	7.7	49	4.3	96	23.6	89	31.8	48	6.2
<i>Fraxinus excelsior</i>	32	1.6	57	10.0	44	6.8	67	9.3	77	14.7	68	13.7
<i>Acer campestre</i>	16	0.6	43	2.0	18	0.6	33	1.0	47	6.6	36	2.9
Light demanding species of the ground flora												
<i>Brachypodium pinnatum</i>	11	0.1	5	<0.1	1	<0.1	63	11.0	26	1.3	4	1.8
<i>Geranium sanguineum</i>	11	<0.1	5	<0.1			78	0.2	11	<0.1		
<i>Sesleria varia</i>	32	0.1	8	<0.1			30	1.5	42	1.5	40	3.0

torminalis (L.) Crantz. In the understory the thermophilous shrub *Hippocrepis emerus* (L.) Lassen subsp. *emerus* (= *Coronilla emerus* L.) and the herbs *Dictamnus albus*, *Asperula tinctoria* L., *Aegonychon purpureocaeruleum* (L.) Holub (= *Lithospermum purpureocaeruleum* L.), *Teucrium chamaedrys* L. (Table 2) along with other species were found.

Vegetation and site conditions in the Swabian Alb ecotone

In the montane Swabian Alb the ecotone boundaries are slightly less abrupt. Downy oak is able to grow only on the driest sites and was absent on the ecotone relevés (Figs. 2, 4). The hybrids *Quercus petraea* × *pubescens* were also reduced in terms of frequency and cover (Figs. 2, 5). Instead of oaks, beech, *Quercus petraea* (Fig. 6), *Acer campestre* L, *Fraxinus excelsior* L. and *Sorbus aria* (L.) Crantz were more prominent, resulting an ecotone relatively rich in tree species (Fig. 2). Overall the tree species cover was lower and the ground vegetation cover higher. Differential species include *Laserpitium latifolium* L., *Thesium linophyllum* subsp. *montanum* (Schrad.) Čelak. (= *Thesium bavarum*

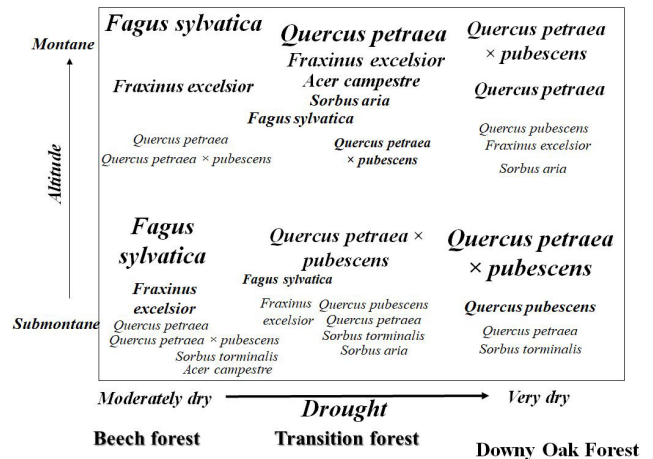


Fig. 2. Ecogram of the principal tree species occurring in limestone forests in the ecotones between beech and downy oak forests. The drought and altitude gradients lead to a distinct shift in the competitiveness of the tree species. The font size represents the relative significance of the species (mean coverage rates)

Schrank) and *Calamagrostis varia* (Schrad.) Host (Table 2).

Interactions of drought components

In the submontane Klettgau region temperatures and precipitation are higher and the growing season longer compared to the montane Swabian Alb region (Table 2).

In both regions, beech was able to grow on sites reflecting similar SWSC values (Fig. 3). However, the ecotone in the Swabian Alb occurred on sites with slightly lower SWSC values as those of the oak forest in Klettgau (Fig. 7). Beech forest in Klettgau was confined to soils having a SWSC of >65 l m⁻², whereas in the more humid Swabian Alb region beech was able to survive in soils having a SWSC of 60 l m⁻² (Fig. 7).

The Transeau's humidity index (Tuhkanen, 1980) during the growing season expressed as humidity index HI was higher in the Swabian Alb than in the Klettgau (Fig. 7). This is reflected in the SWSC of the ecotone representing

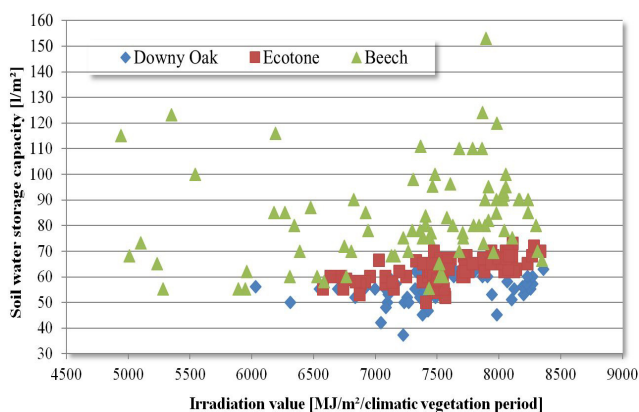


Fig. 3. The relationship between soil water storage capacity (SWSC), irradiation value during the climatic growth period, and forest formation. Oak forest is restricted to soils with a SWSC of up to 73 l/m², and an irradiation of 6000 MJ/m² or more

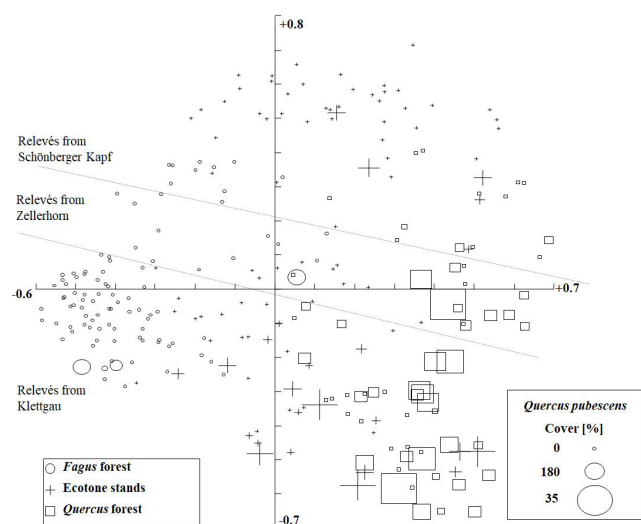


Fig. 4. *Quercus pubescens* was found with higher cover values in the *Quercus* forests and ecotone stands of the submontane Klettgau, compared to the montane Schwäbische Alb (Schönberger Kapf, Zellerhorn). PCA of the whole data set. The symbol form represents the forest type, its size indicates the coverage of the species

the drought limit of beech. In the less humid Klettgau, all thresholds between the forest types occur on sites with significantly higher SWSC compared with the Swabian Alb (Fig. 7).

The consistency of this pattern demonstrates a drought-dependent shift of the ecotone and the occurrence of intermediate forest types between those regions. The climatic and edaphic factors between these regions are different.

Discussion

It can be expected that climate change will also affect the growth and vitality of beech or eventually influence its distribution limit as shown by many studies (Gessler *et al.*,

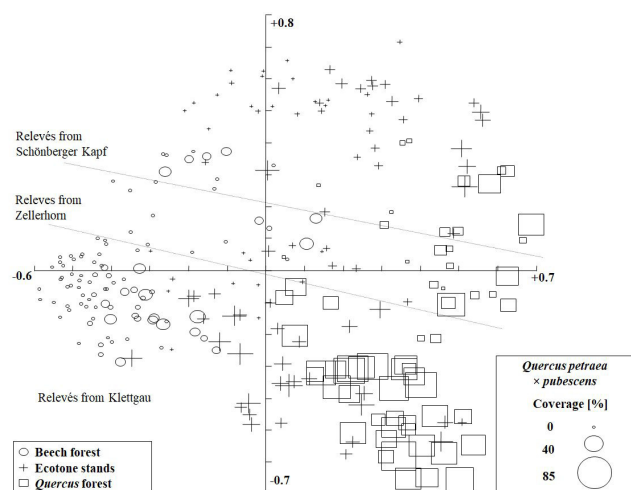


Fig. 5. The hybrid *Quercus petraea* × *pubescens* was the most important taxon in the *Quercus* forest and the ecotone stands of the submontane Klettgau region. In the montane Schwäbische Alb (Zellerhorn, Schönberger Kapf), the hybrid was less dominant. PCA of the whole data set. The symbol form represents the forest type, its size indicates the coverage of the species

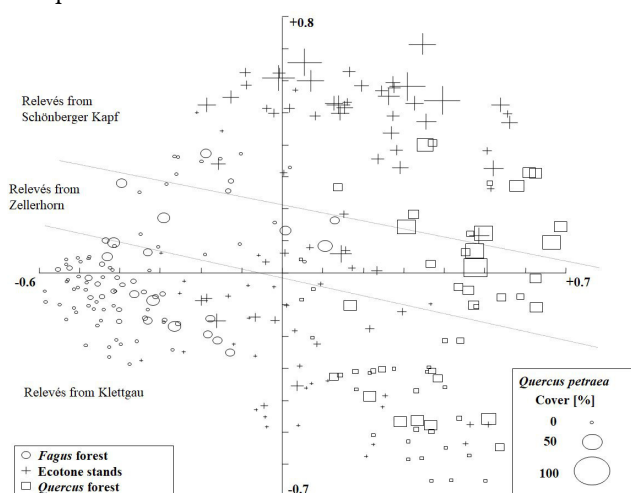


Fig. 6. In the montane Schwäbische Alb (Schönberger Kapf, Zellerhorn), *Quercus petraea* dominates the ecotone stands and was found with high cover values in the *Quercus* forest, whereas it was infrequent in the submontane Klettgau plots. PCA of the whole data set. The symbol form represents the forest type, its size indicates the coverage of the species

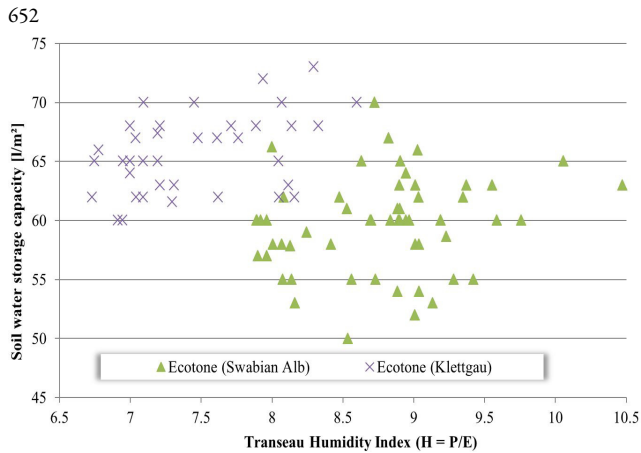


Fig. 7. The relationship between water supply in the soil, vegetation and the Transeau Humidity Index ($H = P/E$; P = precipitation, E = potential evaporation). The Humidity Index clearly shows the mesoclimatical differences between the two regions (submontane Klettgau and montane Schwabische Alb)

2007, Scharnweber *et al.*, 2011, Cavin *et al.*, 2013, Tegel *et al.*, 2014, Zimmermann *et al.*, 2015). An increase in temperature alone can be tolerated by beech as it is able to grow in regions with a mean annual temperature of 14 °C (Peters, 1997, Kölling *et al.*, 2007) and may even grow faster when sufficiently supplied with water (Felbermeier, 1993, Pretsch and Ďurský, 2002)). Cavin and Jump (2017) found that populations of European beech at the driest part of its distribution exhibit particularly high resistance to drought and showed little evidence of recent drought-linked growth decline. Instead the greatest sensitivity and lowest resistance was observed in populations near the core of the species range.

In this study it was shown that at a local scale and under temperate macroclimatic conditions beech was the dominant tree species in all forests except those found on extremely shallow soils combined with high irradiation on south-western facing slopes. At this ecotone beech trees showed higher mortality, lower resilience and higher climate dependency compared to the adjacent less dry sites (Chakraborty *et al.*, 2013, Chakraborty *et al.*, 2017). This supports the argumentation that drought affects the vitality and growth rates well before it induces distribution shifts (Weber *et al.*, 2013).

In both regions of this study, drought intensity that limits the occurrence of beech is defined by the interaction of edaphic and climatic drivers which supports the argumentation of a simultaneous climatic-edaphic expression of drought (Weber *et al.*, 2013). Our results demonstrated that the consideration of the relative site constancy rule, i.e. the interaction of edaphic and topographic features can be used to improve the quantification of drought and compare sites that do not share the same macroclimatic conditions. It is generally agreed that with a more local the scale, edaphic, landscape and biotic factors should gain in importance in explaining species distribution (Pearson and Dawson, 2003). The relatively high precipitation in the Klettgau region results in

an higher humidity (“lower demand”), which allows beech to advance to slightly shallower soils (“lower supply”), providing “relatively” the same water supply. From this point of view the drought stress intensity on the ecotone can be regarded as similar in both regions. This combination of soil, topographic and climatic data allows for the quantification and description of the ecological features of the ecotone between oaks and beech in great detail. However, we cannot exclude the possibility that additional parameters other than those considered here may also play a role.

Between the two regions examined there are also differences that are related to the length of the growing season. The lower temperatures, precipitation and humidity along with a shorter growing season in the Swabian Alb result in less plant growth (biomass production), compared to the Klettgau region. This affects the vitality, frequency and percent ground cover of all species including the ground vegetation and the tree species composition.

Conclusions

Our results demonstrate the need to include edaphic and topographic variables in modelling procedures in order to increase the accuracy of the quantification of the distributional limits of tree species (Fang and Lechowicz, 2006). Our results, combined with further research in additional sites, are a stepping stone for the analysis of the interactions between factors acting at different spatial scales. It is proposed that in species distribution modelling, the importance of local, topographic variations should always be tested even when the distribution modelling refers to large geographic areas before assuming that only climate is sufficient to explain distribution patterns at large scales (Austin and Van Niel, 2011).

Based on our findings it can be expected that beech will be replaced on sites near its drought limit in central Europe. The first effects will presumably be increased regeneration and understory beech mortality (Chakraborty *et al.*, 2013, Chakraborty *et al.*, 2017).

Acknowledgements

This work was supported by the Deutsche Forschungsgemeinschaft grant number RE 579/1-3.

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