

The drought tolerance limit of *Fagus sylvatica* forest on limestone in southwestern Germany

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Abstract

Question: What components of drought influence the drought limit of *Fagus sylvatica* forests? This study contributes to the ongoing discussion regarding the future of *Fagus* as a major component of central European forests.

Location: The drought limit of *F. sylvatica* at its ecotone with forest dominated by *Quercus pubescens*, *Q. petraea* and their hybrids in two limestone regions (Klettgau, Schwäbische Alb) in southwestern Germany was compared.

Methods: Vegetation relevés were classified and a gradient analysis was performed. The vegetation pattern was analysed with several drought relevant variables. Classification trees were used to determine the drought limits of the *Fagus* forest.

Results: The *Fagus*, *Quercus* and the ecotone forests were floristically characterized. The lower humidity in the submontane Klettgau, compared to the montane Schwäbische Alb, was compensated for by greater soil moisture (ASWSC). Therefore, *Fagus* forest in the Schwäbische Alb grew on sites with ASWSC values similar to those of ecotone forest in Klettgau.

Conclusions: The interaction between climatic and edaphic drought related factors demonstrates that drought is a complex edaphic-climatic factor. Both components contribute to limiting the distribution of *Fagus*. For the two regions in southwestern Germany, and under the existing climatic conditions, it could be shown that *Fagus* is able to dominate forests on soils with very low ASWSC ($\geq 68 \text{ l.m}^{-2}$).

Keywords: Available water storage capacity; European beech; Local species distribution pattern; *Quercus pubescens*.

Nomenclature: Oberdorfer (1994).

Abbreviations: ASWSC = Available soil water storage capacity; DWD = Hechingen meteorological station; HI = Humidity index; MJ = Megajoule; P = Precipitation; PE = Potential evaporation; PET = Potential evapotranspiration; THI = Transeau's humidity index.

Introduction

Fagus sylvatica L. (European beech, hereafter *Fagus*) would naturally dominate central European temperate forests because of its high physiological tolerance and competitiveness (Ellenberg 1996; Ellenberg et al. 1992). In the southern part of its range, and at lower elevations, the competitiveness of *Fagus* is limited by increasing water stress, until finally it is replaced by submeridional forests composed of more drought-tolerant species (Ozenda 1966, 1981; Ozenda et al. 1988; Peters 1997), mainly *Pinus* and *Quercus* (Horvat et al. 1974; Ellenberg 1996). The focus of this paper is on the ecotone between *Quercus pubescens* Willd. forest and *Fagus* forest.

Over the last two decades many conifer plantations in central Europe have been converted to 'close to nature' forests with large proportions of *Fagus*. The drought limit and competitiveness of *Fagus* under a warmer and drier climate, expected as a result of climatic change (Anon. 2007), is currently being controversially debated (Ammer et al. 2005). *Fagus* is able to tolerate annual mean temperatures up to 14 °C, if sufficient water is available (Peters 1997; Kölling et al. 2007). Dittmar et al. (2003) studied the growth of mature *Fagus* using dendroecological methods. They concluded that *Fagus* is more water-stress tolerant than is often assumed. Simulations by Pretzsch & Ďurský (2002) have also indicated that increased growth of *Fagus* can be expected in a warmer climate. In Bavaria, *Fagus* achieves greatest height growth in dry-warm areas (Felbermeier 1993).

A number of ecophysiological studies involving young *Fagus* trees in laboratory and experimental settings simulated a changing climate (Rennenberg et al. 2004; Geßler et al. 2007). In these studies, an increasing frequency of drought reduced the growth and the competitiveness of *Fagus* (Geßler et al. 2007).

Despite these contradicting conclusions it is widely

agreed that, on sites where water is the growth-limiting factor, severe water deficits reduce increment growth. However, no long-term decrease in the competitiveness of *Fagus* has yet been observed (Ammer et al. 2005). Nevertheless, the competitiveness of *Fagus* will decrease if the length and frequency of dry periods increases (Bonn 2000; Leuschner et al. 2001; Ammer et al. 2005). As substantial information regarding the extent to which drought affects other plant species associated with *Fagus* is also lacking (Ammer et al. 2005; Geßler et al. 2007), the drought limit of *Fagus* forest in southwestern Germany was studied from a community ecology perspective.

Models have been designed to describe and predict the distribution of (syn)taxa along environmental gradients (Parmesan et al. 2005). The model outputs greatly depend on how unavailable data were estimated (Segurado & Araújo 2004; Araújo & Guisan 2006; Maggini et al. 2006). Therefore, knowing the abiotic thresholds of the range of a species with respect to site is an important input variable for distribution models. Knowledge of thresholds may reduce the overestimation of 'suitable habitats' for indicator species (Zaniewski et al. 2002; Araújo & Guisan 2006), and false positive errors whereby an absent species is predicted to be present in the model (Segurado & Araújo 2004; Allouche et al. 2006). Threshold values can be derived by studying the underlying factors that control the distribution of species and plant communities (Anderson et al. 2003; Parmesan et al. 2005).

Most studies correlating drought-related variables with (syn)taxa distribution along drought gradients, and the analysis of threshold values, have focused on a continental to regional spatial scale. Variables describing the humidity are generally preferred (Mather & Yoshioka 1968; Woodward & Williams 1987; Arundel 2005). Distribution thresholds at such large scales are important as most of the stress-inducing changes that result in vegetation pattern shifts or even species extinction have a regional to global extent (Cornwell & Grubb 2003). On a local scale, small-scale heterogeneity of environmental factors is crucial for the analysis of (syn) taxa occurrence (Palmer & Dixon 1990; Sankaran et al. 2005). An example of a practical application might be the selection of alternative tree species in forestry, chosen to regenerate stands in accordance with altered climate conditions.

The objective of this study was to characterise the drought limits of *Fagus*, by combining vegetation, soils and topographies for five locations in two regions in southwestern Germany. The aims were to:

1. Ascertain which climate and soil variables determine the floristic gradient at the ecotone between *Fagus* and *Q. pubescens* forest;
2. Define the drought threshold responsible for the transition from *Fagus* to *Q. pubescens* forest.

Material and Methods

Study area and sampling design

Five locations with *Fagus* and *Q. pubescens* forest were sampled on Jurassic limestone substrate with shallow rendzinic soils: (1) two in the submontane zone of 'Klettgau' (Birnberg and Kätzler, DE) and one in the nearby Osterfingen (CH) and (2) another two in the montane zone of the 'Schwäbische Alb,' located at: Schönberg and Zellerhorn (DE) (Fig. 1, Table 1).

These five locations were selected because they provided (1) the most natural tree species compositions possible and (2) represented the drought limit of *Fagus*. Each location contains stands of *Fagus* and *Q. pubescens*, and the ecotones between them, and has been unmanaged for at least 50 years. Although this is not a long time in the life of a tree, (1) it was sufficient in that the ground vegetation layer mirrored the natural site conditions and (2) *Fagus* regeneration was not invading the adjacent *Q. pubescens* stands, indicating the near-natural limits of *Fagus*.

At each of the locations, *Q. pubescens* stands occurred on the driest sites, i.e. southwest facing upper slopes, surrounded by *Fagus* dominated stands. To sample the ecotone between *Fagus* and *Quercus*, the relevés (10 m × 10 m) were arranged in a systematic grid. The grid lines ran 25–30 m apart, parallel to the slope. The lines running perpendicular to the slope occurred with ca. every 10–15 m change in elevation. A relevé was recorded at each intersection.

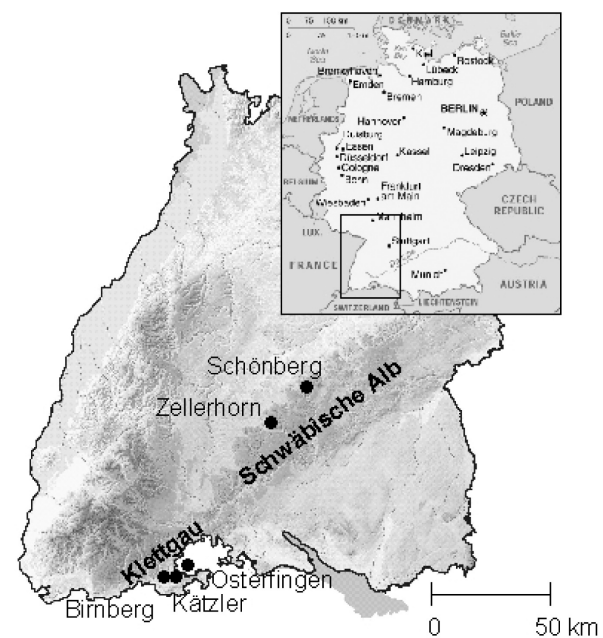


Fig. 1. Map of the two regions (Klettgau and Schwäbische Alb) and the five study locations in southwestern Germany.

Table 1. Natural settings of the two study regions, including the five study sites.

	Klettgau region (incl. Osterfingen/CH)	Schwäbische Alb region
Name of the location and number of relevés	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 study sites (m a.s.l.)	Birnberg 490 - 550 Kaetzler 495 - 555 Osterfingen 535 - 620	Zellerhorn 790 - 825 Schoenberg 735 - 800
Elevation zone	submontane	montane
Mean annual air temperature (DWD and MeteoSwiss)	8.6 °C	5.5 °C data corrected after Schlenker & Müller (1973)
Mean annual precipitation (DWD and MeteoSwiss)	1012 mm	900 mm data corrected after Schlenker & Mueller (1973)
Length of climatic vegetation period, (DWD and MeteoSwiss)	23rd March - 5th November (226 days)	5th April - 25th October (204 days)
Mean precipitation during climatic vegetation period (DWD and MeteoSwiss)	620 mm / 656 mm	

(F = *Fagus* forest; ec = ecotone stand; Q = *Quercus* forest; climatic vegetation period = mean daily air temperature > 5 °C.)

Data collection

Vegetation assessment in the field

For each 100-m² relevé, all vascular plant species were recorded. The percent cover was estimated for each species in three layers (herb, shrub and tree). A modified cover abundance scale *sensu* Braun-Blanquet was used: r = cover < 1%, 1-2 ind.; + = 2-5 ind.; h = 5-50 ind.; m = > 50 ind.; cover > 1% - < 10%, in 1% steps; cover > 10%: in 5% steps).

The introgressive hybrids occurring between *Quercus petraea* Liebl. and *Q. pubescens* were identified morphologically (Aas 1998; Müller 1999). To determine the cover of the *Quercus* species and their hybrids, a crown map of each of the relevés was drawn. After the species samples were identified their proportions were calculated.

Assessment of soil and climate variables

Available soil water storage capacity

The available soil water storage capacity (ASWSC) represents the edaphic water availability at each site (relevé). It was derived from soil profiles distributed systematically at each location. For each profile, the rooting depth, soil skeleton content, soil texture and bulk density were estimated. Humus content was analysed using the WÖSTOFF method (Schlichting et al. 1995). ASWSC was calculated in liters per m², after Arbeitsgemeinschaft Standortkartierung (Anon. 1996).

Air temperature and precipitation

Precipitation and air temperature data for each location were obtained from the meteorological stations at Hallau (MeteoSwiss) (27° 27'34" E; 47° 41'54" N) and Hechingen (DWD) (8° 57'54" E; 48° 21'10" N). Hallau is located 8.6 - 9.6 km from the three Klettgau sites. Given the proximity and similar elevation of the climate station, no corrections were necessary. There is an altitudinal difference of ca. 200 m between the Hechingen climate station (DWD) and the two Schwäbische Alb sites, Schönberg (13.7 km) and Zellerhorn (4.5 km). Therefore, annual precipitation data from ten climate stations located at the same elevation, and also on the windward side of Schwäbische Alb, were used to extrapolate the precipitation for the year and the vegetation period. The observation period (1961-2003) is considered sufficient to represent the climatic standard.

Potential evapotranspiration and irradiation intensity

A commonly used variable for describing vegetation distribution across spatial scales is potential evapotranspiration (PET), reflecting the demand for water consumption (Stephenson 1998). Neither evaporation data from nearby climate stations nor comparisons for the best-fitting PET formulas were available for the study locations.

PET was, therefore, calculated by averaging the results of three different irradiation-temperature formulae after Caprio (1974); Jensen and Haise and Turc cited by Zimmermann & Roberts (2001). The choice of the PET formulas was based on the fact that irradiation-temperature formulae (a) perform better in the prediction

of PET than temperature-based formulas (Lu et al. 2005; Xu & Singh 1998); and because their use, when the application of physically based formulas is not possible, was supported by Kirnak et al. (2002) and (b) the effect of slope and aspect are included as they are embodied in the estimation of irradiation intensity.

Irradiation intensity is an indirect variable affecting the distribution of vegetation (Sternberg & Shoshany 2001). Increased irradiation intensity increases the evapotranspiration rates (Bendix 2004; Lauer & Bendix 2004) and is highly correlated with slope, aspect and elevation. Irradiation intensity was calculated for each relevé using RADICAL (Fischer 1994). This software calculates monthly irradiation intensity values in $\text{MJ}\cdot\text{m}^{-2}$ based on latitude, including the aspect and slope; elevation and sky view factor (horizon limitation). These topographic variables were assessed additionally.

Although irradiation is integrated into the PET calculation, it has also been included separately for comparison purposes. All the calculations of PET and irradiation intensity used in this study refer to the climatic vegetation period.

Humidity index

Water supply (precipitation, P) and evaporative demand (potential evaporation, PE) are elements of the climatic water balance (Stephenson 1998). Both variables are combined in Transeau's humidity index ($\text{THI} = P/\text{PE}$) (Tuhkanen (1980)). Potential evaporation is highly correlated to PET and responds in a similar fashion to the climatic variables affecting PET (Allen et al. 1998). In this study, potential evaporation was replaced by PET in the humidity index (HI), which was calculated as $\text{HI} = P/\text{PET}$, being suitable for comparing climatic water balance between different sites and regions. The higher the index value, the more water is available at a site. The HI used was that for the climatic vegetation period for every relevé; therefore, the values were lower than annual values often found in the literature.

Data analysis

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 programme (Wildi & Orlóci 1996) with the following analysis sequence (Wildi 1989):

1. Classification of relevés (transformations: extracting the sixth root and normalisation; resemblance measure: covariance; cluster algorithm: minimum variance);
2. Extracting the main gradient (transformations: extracting the sixth root and double normalisation of the

contingency values; correspondence analysis);

3. Classification of species (transformations: extracting the sixth root and normalisation; resemblance measure: chord distance; cluster algorithm: minimum variance);

4. Ordination of the relevé and species groups with a concentration analysis;

5. Reduction of the species using Jancey's ranking.

The methods and resulting forest types are described in Sayer (2000).

Analysis of gradients

Ordination through a detrended correspondence analysis (DCA) of all relevés showed a standard deviation of 2.6 units with respect to the first axis and allowed the application of principal components analysis (PCA; Lepš & Šmilauer 2003) for the 257 relevés. Afterwards, the principal components were correlated (Pearson correlation) with the measured environmental variables. Indirect methods were applied so as to optimally project the samples in the floristic space, and then to explain the floristic axis of the PCA.

The PCA was carried out based on the correlation matrix of the sixth root transformations of the species cover values. The reason for this was to linearise the relationship between the species as a basic assumption of applying the ordination method, and to emphasise the ecological significance of the proportion between the species. Ordination diagrams were projected in Euclidian distance and performed using CANOCO for Windows 4.52 (ter Braak & Šmilauer 1997).

Analysis of the threshold between the forest types using classification trees

The following variables reflecting the drought intensity for each of the relevés were used to determine the thresholds between the forest types in the two regions: annual irradiation (ir_ann) in $\text{MJ}\cdot\text{m}^{-2}$; irradiation during the climatic vegetation period (ir_cl_p) in $\text{MJ}\cdot\text{m}^{-2}$; mean annual temperature (T_an) in $^{\circ}\text{C}$; mean temperature during the climatic vegetation period (T_vp) in $^{\circ}\text{C}$; precipitation during the climatic vegetation period (P_cl_p) in mm; average PET during the climatic vegetation period (PET_a_cl) in mm; humidity index sensu Transeau (HI) and the available soil water storage capacity (ASWSC) in $\text{l}\cdot\text{m}^{-2}$.

The dataset was subdivided recursively into subsets using classification tree methods. These were increasingly homogeneous with respect to the defined groups, providing a tree-like classification and an associated dichotomous key to classify unknown samples into groups (Urban 2002). This nonparametric method is more robust than discriminant analysis (Mairdonald & Braun 2007) when dealing with ecological data. The calculations were performed using r-part, R version 2007-02-23 (Anon. 2006).

Table 2 displays the predictive accuracy of the analysis. The cross-validated error rate was used to determine the number of splits of the classification tree. The cross validated error rate was 19.3% for seven splits and 20% for eight splits (calculated by: root node error × minimum of cross validated error). This small difference shows that eight splits are only marginally better than seven (Table 2). The root node error was 0.72047, calculated by dividing the 183 misclassified samples of the first split by the total 257 samples. The tree was therefore pruned after seven splits.

The HI and ASWSC for the different forest types and the two regions were compared using Kruskal-Wallis tests and Mann-Whitney U tests as *post-hoc* tests, the results of which were integrated in box-plots.

Results

Floristic differentiation between beech and oak forests in the two elevation zones

The results of the multivariate analysis of the floristic data were used to define the forest types, compared with an existing phytosociological classification (Oberdorfer 1992) and summarised as ‘*Fagus* forest’, ‘*Quercus* forest’ and ‘ecotone forest’ (for detailed results see Sayer 2000). ‘*Quercus* forest’ was used to summarise relevés classified as *Quercetum pubescenti-petraeae*, which comprises submediterranean deciduous *Quercus* forest near its northern limit (Oberdorfer 1992). This association is rare in southern Germany and can only be found as isolated stands surrounded by the more frequent *Carici-Fagetum* (dry limestone *Fagus* forest) (Oberdorfer 1992), to which the majority of the ‘*Fagus* forest’ relevés belonged. At one location in Klettgau, a few relevés within the *Fagus* forest were on slightly moister sites and included species of the *Galio odorati-Fagetum*. The ecotone between *Quercus* and *Fagus* forest types is gradual, but narrow; the species composition of the ‘ecotone forest’ was clearly distinct from that of the *Fagus* forest. Ecotone plots could also be classified as *Quercetum pubescenti-petraeae*, the divergence from the *Quercus* forest mainly due to the tree species composition and cover (occurrence of some stunted *Fagus* trees with partial crown dieback). The species listed in Table 3 are those that differentiate the forest types in the two regions. A complete vegetation table containing all species and 257 relevés was published by Sayer (2000) and can be obtained from the authors on request.

Table 2. Predictive accuracy of the classification tree (cp = complexity parameter; rel error = relative error; x-error = cross validated error; xstd = cross validated error standard deviation).

	CP	n-split	rel error	x-error	x-std
1	0.311475	0	1	1	0.039083
2	0.174863	1	0.68852	0.68852	0.043543
3	0.092896	2	0.51366	0.53552	0.042394
4	0.071038	3	0.42077	0.51366	0.042049
5	0.060109	4	0.34973	0.45902	0.040973
6	0.038251	5	0.28962	0.34426	0.037611
7	0.032787	6	0.25137	0.32787	0.036992
8	0.010929	7	0.21858	0.27869	0.034887
9	0.01	8	0.20765	0.26776	0.034364

Forest types along the elevation and drought gradient

The vegetation of all 257 relevés was ordinated (Fig. 2). With the first four principal components 33.5% of the species variance was extracted (Eigenvalues 1st axis: 0.12; 2nd axis 0.10; 3rd axis 0.07 and 4th axis 0.04). The species-environment correlations were 0.53 for the first and 0.79 for the second axis, 48% of the species-environment relationship was explained by the environmental variables included.

The main floristic gradient, depicted by the first axis, goes from *Fagus* to *Quercus* forest from left to right (Fig. 2). The differentiation between the forest types is an overlay of the classification results. Along axis 1, the vegetation changed from *Fagus* forest with tall

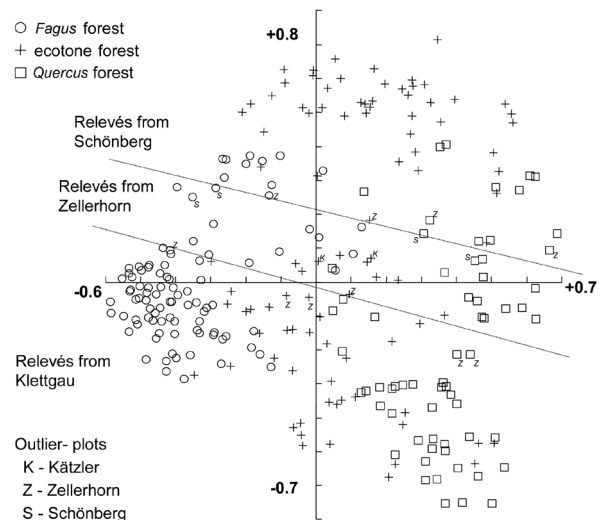


Fig. 2. Distribution of the forest types and regions along the principal components. The first (horizontal) axis separates the *Fagus* dominated relevés from the ecotone and *Quercus* dominated relevés. The second (vertical) axis separates the regions Klettgau (Kaetzler, Birnberg, Osterfingen) and the Schwäbische Alb (Zellerhorn, Schönberg).

trees, large crowns and a higher number of shade tolerant taxa amongst the ground flora to *Quercus* forest comprised of smaller trees with many light-demanding taxa amongst the ground flora. The ASWSC showed the highest correlation with the first axis, indicating soil with decreasing ASWSC from *Fagus* to the *Quercus* forest (Fig. 2 and Table 4).

The second axis shows a differentiation between the two regions, from Klettgau below the first axis to the Schwäbische Alb in the upper part of the diagram (Fig. 2). This floristic gradient is directly reflected in the high correlation of the second axis with the elevation ('elev', Fig. 3 and Table 4) and precipitation. Precipitation during the climatic vegetation period increases with increasing elevation ('P_cl_p', Fig. 3 and Table 4), from the submontane Klettgau to

the montane Schwäbische Alb. However, the annual precipitation ('P_an', Fig. 3 and Table 4) decreases. The annual irradiation ('ir_ann', Fig. 3 and Table 4) is higher in the Schwäbische Alb than in the Klettgau region. Another indicator of the regional differentiation by climate is the humidity index ('HI'; Fig. 3 and Table 4), which shows higher humidity in the Schwäbische Alb region during climatic vegetation period.

In both regions (Klettgau and Schwäbische Alb), the ASWSC is higher in the *Fagus* forest, followed by the ecotone and then the *Quercus* forest (Fig. 4a). When analysing the climatic factors of the different regions, HI during the climatic vegetation period is higher in the Schwäbische Alb than Klettgau (Fig. 4b). In the less humid Klettgau, all forest types occur on

Table 3. Frequency (F) and mean coverage (mC) in % of the differentiating species of the forest types dominated by *Quercus pubescens*, *Fagus sylvatica* and in the transition (ecotone). Data obtained from plots at five locations in Klettgau (including Osterfingen/CH) and the Schwäbische Alb.

Elevational zone Forest type [all numbers are %]	Klettgau submontane ecotone				Schwäbische Alb montane ecotone				<i>Fagus</i>			
	<i>Quercus</i>		<i>Fagus</i>		<i>Quercus</i>		<i>Fagus</i>		F	mC		
	F	mC	F	mC	F	mC	F	mC	F	mC		
Species typical of <i>Quercus</i> forest in both regions												
<i>Quercus petraea</i> x <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 <i>Quercus</i> 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 clinopodium</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 purpurocaeruleum</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 <i>Quercus</i> forest (Schwäbische 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

Table 4. Correlation coefficients (Corr. Coef) for the relationship of the environmental variables with the first (PCA AX1) and the second PCA axes (PCA AX2).

Environmental variables	Corr.Coeff. PCA AX1	Corr.Coeff. PCA AX2
Annual irradiation (ir_ann) (MJ·m ⁻²)	0.098	0.358
Annual precipitation (P_an) (mm)	-0.388	-0.756
Aspect (°)	-0.092	-0.266
Available soil water storage capacity (ASWSC) (L·m ⁻²)	-0.436	-0.214
Av. pot. evapotranspiration climatic vegetation p. (PET_a_cl) (mm)	-0.203	-0.280
Elevation (elev) (m a.s.l.)	0.374	0.703
Humidity index (HI)	0.235	0.353
Inclination (inclin) (%)	0.080	-0.022
Irradiation during climatic vegetation period (ir_cl_p) (MJ·m ⁻²)	-0.110	-0.096
Precipitation during climatic vegetation period (P_cl_p) (mm)	0.388	0.756

sites with significantly higher ASWSC, compared to the same forest types in the Schwäbische Alb (Fig. 4a). For each forest type in Klettgau, the lower humidity is counterbalanced by ASWSC (Fig. 4). *Fagus* in the Schwäbische Alb was able to grow on sites with ASWSC values as low as those of the ecotone forest in the less humid Klettgau region (Fig. 4). Proportionally, the ecotone forest in the Schwäbische Alb occurred on sites with ASWSC values similar to those of the *Quercus* forest relevés in Klettgau (Fig. 4). The consistency of this pattern demonstrates a gradual drought-dependent shift in the occurrence of forest types between those regions. This interaction between climatic and edaphic drought-related factors demonstrates that drought is a complex edaphic-climatic factor requiring the combination of both components.

Threshold values of the components of drought

In both regions, the distribution of *Fagus* was limited by increasing drought. Out of the eight drought indicating variables, two separated the forest types between and within the two study regions, namely mean annual air temperature (T_an) and ASWSC (Fig. 5). The first split of the samples in the data set separated the regions according to T_an. Taking the left branch of the classification tree, the mean annual temperature is $\geq 8.1^\circ\text{C}$ separating the Klettgau region. On the right, the annual temperature in the Schwäbische Alb is less. Within each region, the differentiating criterion is the ASWSC. On the left branch, the *Fagus* forest occurs when the ASWSC is $\geq 68.7 \text{ l}\cdot\text{m}^{-2}$. The *Quercus* forest occurs when the ASWSC is $< 60.8 \text{ l}\cdot\text{m}^{-2}$. The ecotone forest in Klettgau occurs on sites with ASWSC values between 60.8 and $68.7 \text{ l}\cdot\text{m}^{-2}$.

In the montane climate of the Schwäbische Alb, a similar ASWSC threshold of $67.5 \text{ l}\cdot\text{m}^{-2}$ limits the *Fagus* forest type. However, the occurrence of the ecotone forest appears to be wider than in Klettgau, and extends further onto drier soils. The threshold is $55.2 \text{ L}\cdot\text{m}^{-2}$; below which only *Quercus* forest occurs.

The result of the dendrograms can be used to predict the occurrence of the forest types. The validity of the prediction model is reflected in the percentage of misclassifications (Table 5). Of 257 relevés, 40 were misclassified based on a cross validation. Of the *Fagus* forest relevés, only 8.3 and 7.7% were misclassified as ecotones. The patterns were less clear in the case of *Quercus* forests, where 18.2 and 24.4% of the relevés were misclassified. This means that the floristic composition of these *Quercus* forest relevés occurred on slightly less shallow soils than predicted. This may have been due to a latent, historical human influence (elimination of *Fagus*), resulting in a floristic classification not clearly reflecting the natural separation between *Quercus* and ecotone relevés.

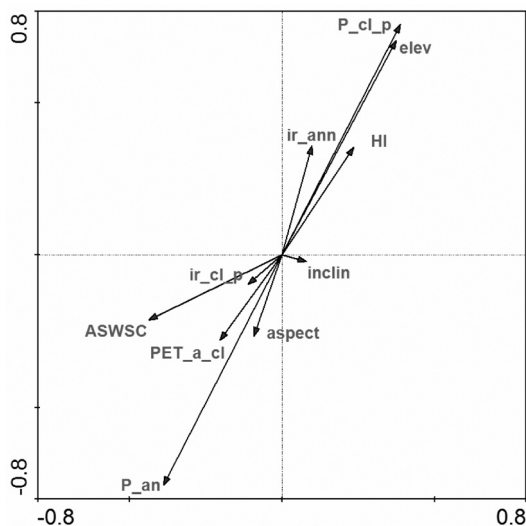


Fig. 3. Projection of the various environmental variables in the floristic space of the two first principal components (for the abbreviations of the environmental variables and the correlation coefficients see Table 4).

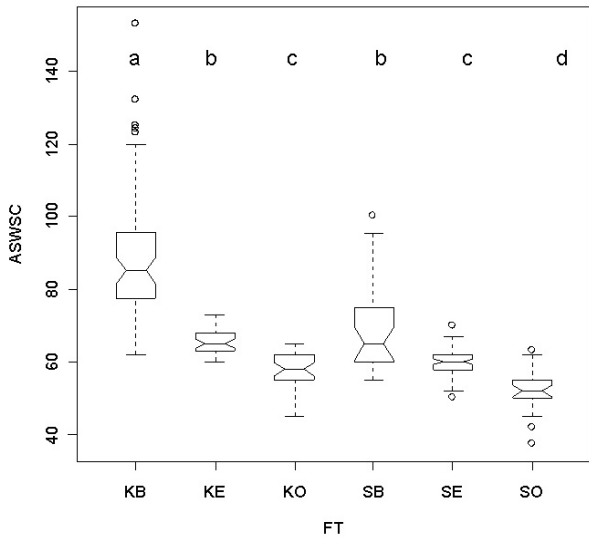


Fig. 4a. Median and range of the available water storage capacity (ASWSC) in the two regions (K = Klettgau; S = Schwäbische Alb) and for the different forest types (B = *Fagus* forest; E = ecotone forest; O = *Quercus* forest). Letters above the box-plots indicate the result of the Mann-Whitney *U*-test; identical letters indicate no significant difference.

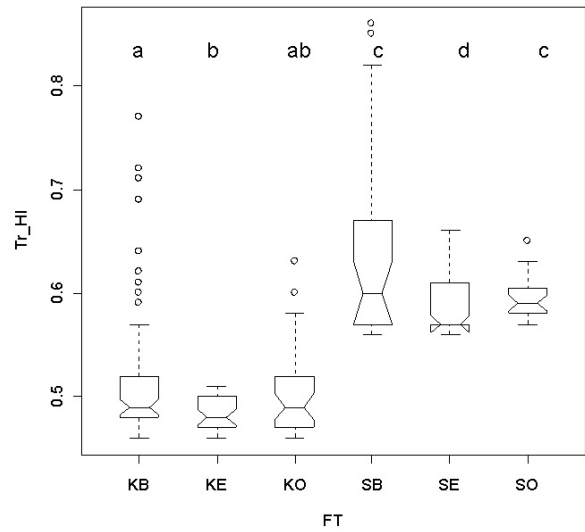


Fig. 4b. Median and range of the humidity index in the two regions (K = Klettgau; S = Schwäbische Alb) and for the different forest types (B = *Fagus* forest; E = ecotone forest; O = *Quercus* forest). Letters above the box-plots indicate the result of the Mann-Whitney *U*-test; identical letters indicate no significant difference.

Discussion

Drought effects near the ecotone between Fagus and Quercus

Drought stress is caused by different combinations and interactions associated with limited ASWSC, a lack of precipitation and increased evapotranspiration (Stephenson 1998; Thornthwaite 1948). Analyses of floristic and environmental gradients and thresholds are important for the occurrence of species, e.g. *Fagus* (Rubio & Sánchez-Palomares 2006; Kölling et al. 2007).

PCA and Classification and Regression Tree (CART) analyses showed that in both study regions, the ASWSC discriminates the forest types (Figs. 3, 4a, 5), while the climatic variables (precipitation during climatic vegetation period; potential evapotranspiration during

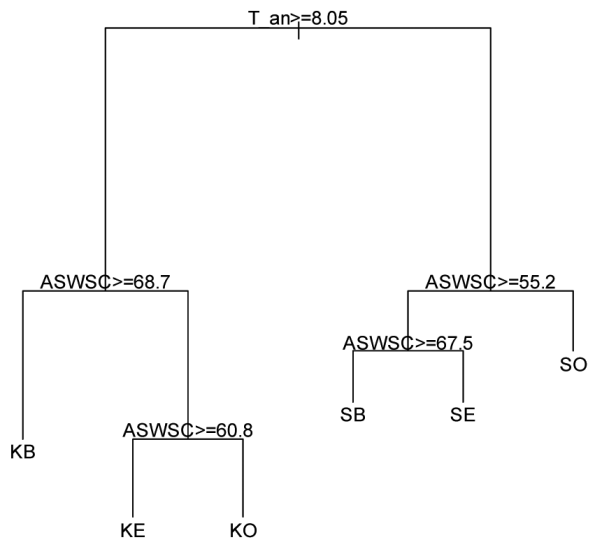


Fig. 5. Classification tree for the three forest types (B = *Fagus* forest; E = ecotone forest; O = *Quercus* forest) in the two regions (K = Klettgau and S = Schwäbische Alb) based on the environmental variables indicating the drought thresholds, namely ASWSC (available soil water storage capacity) and mean annual temperature (T_{an}).

Table 5. Misclassification table for the classification tree (K = Klettgau; S = Schwäbische Alb; B = *Fagus* forest; E = ecotone forest; O = *Quercus* forest; N = number of samples; Misc = number of misclassifications; % = percentage of misclassifications).

	KB	KE	KO	SB	SE	SO	N	Misclass	%
KB	66	6	0	0	0	0	72	6	8.3
KE	3	25	2	0	0	0	30	5	16.7
KO	2	6	35	0	0	0	43	8	18.6
SB	0	0	0	12	1	0	13	1	7.7
SE	0	0	0	10	51	2	63	12	19
SO	0	0	0	3	5	25	33	8	24.2

climatic vegetation period) follow in importance. This demonstrates the need to study soil properties when downscaling studies to the local stand level, at which forest management planning takes place. Similar results were obtained from studies dealing with the small-scale distribution of vegetation patterns, e.g. of more resource-demanding shrubs and trees compared to the more stress-tolerant grasses in semi-arid ecosystems (Meinzer et al. 1983; Sankaran et al. 2005; Svoray et al. 2007).

Elevation is the most important factor for the discrimination of the two study regions (Fig. 3). Elevation is frequently used as an indirect variable for the description of vegetation gradients (Austin 2002). Its explanatory power is due to the integration of several climatic variables that are often highly correlated with elevation (Rouget et al. 2001; Austin 2002), e.g. elevation has been used instead of precipitation and air temperature gradients (Rouget et al. 2001).

Elevation must be treated carefully when it is used as an explanatory variable for vegetation patterns as (1) it does not have any direct ecological or physiological effects on species. For this reason, the use of variables with a direct physiological effect is recommended (Stephenson 1998; Pausas & Austin 2001) and (2) Elevation may be oppositely correlated with other climatic variables (e.g. precipitation amount) when different periods are considered. The results demonstrated that the annual precipitation is higher in Klettgau than in the Schwäbische Alb, but that precipitation during the climatic vegetation period is higher in the Schwäbische Alb (Table 1). Therefore, elevation is negatively correlated with annual precipitation while positively correlated with precipitation during vegetation period. This exhibits (1) the inclusion of seasonality when climatic parameters are applied (Ohmann & Spies 1998; Rouget et al. 2001) and (2) the need for consideration of the different macroclimatic conditions of the regions under study (Rubio & Sánchez-Palomares 2006).

Isolated interpretations of the simplistic variable 'precipitation' may also generate misleading conclusions, e.g. in the characterisation of the gradient of the second PCA axis (Figs. 2, 3). To conclude on the basis of the higher annual precipitation that the Klettgau region has a more favourable water supply is shown to be incorrect when the higher annual evaporative demand (PET) is considered (Table 1). This supports the use of combined variables such as humidity/aridity indices to describe the climatic water balance, vegetation gradients and species thresholds (Tuhkanen 1980; Box 1981; Weber et al. 2007).

Therefore, the humidity index during the vegetation period appears to be the most suitable variable to express the climatic water balance between the two regions, indicating a more favourable water supply for the Schwäbische Alb.

Fagus sylvatica – a tree species with a future in central Europe

Climatic change will affect the tree species composition of central European forests (Anon. 2007). The future of *Fagus* in central Europe appears unclear, as reflected by the controversial debate taking place between ecologists (Ammer et al. 2005) and physiologists (Rennenberg et al. 2004). It must be assumed that a changing climate will affect the vitality of *Fagus* (Geßler et al. 2007). Near its drought limit, *Fagus* will probably give way to tree species more tolerant of drought stress. The first effects will presumably be greater mortality of regenerating and understorey *Fagus* near its drought limit (Kohler et al. 2006).

Certainly there is more than one abiotic factor controlling species distribution and if competition, historical contingency, source-sink dynamics and dispersal limitations are considered (Pulliam 2000; Thuiller et al. 2004), then species reactions remain far too complicated to be comprehensively understood, described and quantified with accuracy. Distribution modelling is still in its 'infancy,' and further research into the abiotic environmental limitations of species distribution based on fundamental ecological and site classification research will provide valuable information for modellers studying niche-related aspects. The link between ecological theory and modelling tools has to be strengthened, and greater use made of existing data (Guisan et al. 2006). The quantification of the leading limiting factor for the distribution of species, and the setting of a distinct threshold for its occurrence, may help in the development and evaluation of such models.

This study showed that distribution limitations are highly dependant on mesoscale factors. In drought assessments, in particular, it is necessary that each climatic region be treated independently due to the complexity of the drought factor. It could be shown for two regions in southwestern Germany that, under existing climatic conditions, *Fagus* is able to dominate forests on soils with very low ASWSC. Higher air temperature and lower humidity in the Klettgau forced the *Fagus* forest to retreat only slightly, and permitted *Quercus* to advance onto soils with an ASWSC ca. only 5 l·m⁻² higher than that of the Schwäbische Alb. As the majority of central European forest soils have a much higher ASWSC than the threshold for *Fagus*, of ca. 65-70 l·m⁻² (Landesamt für Geologie Rohstoffe und Bergbau - Regierungspräsidium Freiburg 2007), it must be assumed that *Fagus* will continue to dominate the potential natural vegetation of central Europe (Ammer et al. 2005). In most central European regions, the area of *Fagus* is likely to increase even, due to the ongoing decline of *Picea abies* (spruce) in managed forests as a result of storm and insect damage

(Kölling et al. 2007).

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