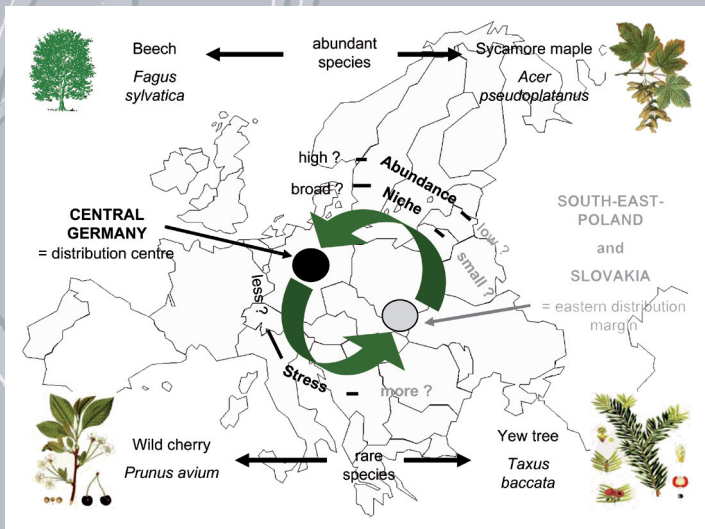Benjamin Köckemann

Abundance, niche breadth and stress in the centre and at the border of the distribution range

A macroecological study on
abundant and rare tree species

GEORG-AUGUST-UNIVERSITÄT
GÖTTINGEN

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Referentin/Referent: Prof. Dr. Christoph Leuschner

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Tag der mündlichen Prüfung:

I would like to dedicate this work to my grandparents and nature lovers

Dr. Alfons and Henriette Köckemann [†]

ABSTRACT

Macroecology investigates abundance and distribution patterns over large geographical scales. Some patterns, like the positive relationship between range size and abundance or niche breadth and the decrease of abundance and niche breadth from the distribution centre to the range margin, have been observed among different organism groups and in different habitat types.

Despite their obvious universality, these patterns have rarely been investigated for tree species and the methods used are mainly based on theoretical interpretation of large and already existing data sets, whereas physiological parameters are often neglected.

This study combines statistical pattern detection and ecophysiological studies to achieve a comprehensive assessment of macroecological patterns and the stress-exposure of Central European trees within their distribution range, with a focus on the eastern distribution margin in South-east Poland and Slovakia.

In contrast to most taxonomic groups, the relationship between abundance and range size was weak for Central European trees, which is probably caused by the ecological and phylogenetic heterogeneity within this rather species-poor assemblage. On the other hand, there was a positive relationship between a tree's niche breadth and its range size, which is a consequence of the fact that widespread species have a broader temperature niche but not necessarily a broader soil niche. Some tree species showed a decline of abundance from the distribution centre to the eastern range edge, whereas niche breadth did not differ between range positions. A niche shift to less fertile and partly also drier sites at the margin was detected, although there such sites were less abundant. Competition does not seem to be decisive, as we neither observed competitive displacement of weaker competitors at the range margin, nor a niche shift of superior competitors to ´better` sites. The investigation of leaf, fine root and growth-related traits in four adult trees did not provide convincing evidence that stress due to summer drought is a key factor reducing the vitality of adult trees in the marginal populations of South-east Poland. It is possible that the investigated common and rare species are controlled in their abundance at the eastern distribution margin not by water and nutrient availability, but other factors, such as winter and spring frost intensity. With respect to increasing drought frequencies in the future, marginal beech provenances revealed several traits characterizing this population as being better drought adapted than a central one from suboceanic Central Germany.

ZUSAMMENFASSUNG

Die Makroökologie untersucht Häufigkeits- und Verbreitungsmuster von Arten auf großen geographischen Skalen. Einigen Mustern wird universelle Gültigkeit nachgesagt, da sie bei einer Vielzahl verschiedener Artengruppen und Habitaten nachgewiesen wurden. Dementsprechend gibt es einen positiven Zusammenhang zwischen Häufigkeit bzw. Nischenbreite und der Arealgröße. Außerdem nehmen Häufigkeit und Nischenbreite vom Zentrum zum Rand kontinuierlich ab.

Ungeachtet ihrer vermeintlichen Allgemeingültigkeit wurden diese Muster selten bei Baumarten untersucht. Zudem verlässt sich die Makroökologie vorwiegend auf rein statistische Untersuchungen und lässt physiologische Parameter außer acht, welche jedoch wertvolle Hinweise auf die Ursachen der gezeigten Muster liefern könnten.

In dieser Studie kombinieren wir rein statistische mit ökophysiologischen Ansätzen zur Untersuchung von Häufigkeits-, Nischenbreite- und Verbreitungsmustern sowie der Stressbelastung mitteleuropäischer Baumarten innerhalb ihres Verbreitungsgebietes. Als Vergleich zum Zentrum wird der östliche Arealrand in Polen und der Slowakei betrachtet. Es zeigte sich nur ein schwacher Zusammenhang zwischen Häufigkeit und Arealgröße, was auf die ökologische und phylogenetische Heterogenität mitteleuropäischer Baumarten zurückzuführen ist. Es gab jedoch einen positiven Zusammenhang zwischen Nischenbreite und Arealgröße, welcher dadurch bedingt ist, dass weit verbreitete Arten eine große Nischenbreite hinsichtlich der Temperatur aber nicht notwendigerweise hinsichtlich der Bodenbeschaffenheit haben. Die Häufigkeit einiger Arten nahm vom Zentrum zum Arealrand ab, wohingegen die Nischenbreite keine Veränderung aufwies. Es gab eine Nischenverschiebung hin zu schlechter nährstoffversorgten und trockeneren Standorten am Arealrand, obwohl diese dort seltener vorkommen. Konkurrenzprozesse scheinen jedoch eine untergeordnete Rolle zu spielen, da weder eine Verdrängung schwächerer Arten am Arealrand, noch eine Verschiebung der Nische konkurrenzstarker Arten auf günstigere Standorte beobachtet wurde. Die Untersuchung physiologischer Parameter lieferte keine Hinweise darauf, dass durch Sommertrockenheit induzierter Stress die Vitalität adulter Bäume in marginalen Populationen nennenswert schwächt. Möglicherweise wird die Häufigkeit der untersuchten Arten am östlichen Arealrand nicht durch die Wasser- oder Nährstoffversorgung, sondern durch andere Faktoren, wie starke Winter- oder Frühjahrs-fröste gesteuert. Marginale Buchenprovenienzen zeigten eine erhöhte Resistenz gegenüber Trockenheit als zentrale Herkünfte, was im Hinblick auf die prognostizierte Zunahme von Trockenperioden forstwirtschaftlich bedeutsam sein könnte.

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Chapter I

General introduction

Macroecology - an alternative way of studying relationships between organisms and their environment

The term ´macroecology` was invented by Brown & Maurer (1989) who entered a new way of studying the relationships between organisms and their environment. The general aim of this young ecological discipline is to reveal statistical patterns of abundances, distribution and diversity of species on large spatial and temporal scales by analysing large, in most cases already existing data sets (Brown, 1995; Gaston & Blackburn, 2000). Prominent macroecological patterns, that have already been detected for many different organism groups, across different habitat types and across a range of spatial scales, include positive relationships between a species` abundance and range size (Bock & Ricklefs, 1983; Brown, 1984; Bock, 1984, 1987; Brown & Maurer, 1987, 1989; Morse *et al*., 1988; Gaston & Lawton, 1990; Lawton, 1993; Gaston, 1996; Kotze *et al*., 2003), between abundance and niche breadth (Brown, 1984), and the decrease of abundance (Brown 1984; Cox & Moore, 1985; Wiens, 1989; Sagarin & Gaines, 2002; Murphy *et al*., 2006) or niche breadth (Brown, 1984; Brussard, 1984; Bock, 1987; Gaston & Lawton, 1990) from a species` distribution centre towards the range edges.

Although such patterns are among the oldest and best known phenomena in ecology, they are still poorly understood and new statistical approaches (Brown, 1995; Brown, 1999; Gaston & Blackburn, 2000; Gaston & Blackburn, 2002) or models (Bell, 2001; Hubbell, 2001) are used to understand them. There is a plethora of hypotheses, which factors are most important for these patterns. Among the most likely factors are environmental ones like geology and soil, climate or land use, on the one side, and species-specific factors on the other side, like a species' life history, ecophysiological traits, and population dynamics (often triggered by environmental factors such as climate or interspecific interactions, as well). The underlying processes remained often still unclear though many patterns seem to be quite simple. Recent studies use novel approaches and consider functional parameters, plant energetics or flux of matter (e.g. West. *et al*., 1997; Enquist, *et al*. 1999; Gillooly, *et al*. 2001). Furthermore, macroecological patterns are described by evolutionary theory (Price, 2003).

It is known that macroecological processes act on several scales. For example, distribution patterns may be influenced by edaphic parameters on local or regional scales, whereas climatic factors have been found to dominate on a global scale (e.g. Pearson & Dawson, 2003). Species richness patterns on the other hand are mainly influenced on a global scale

by energy related climatic factors (Currie & Pacquin, 1987; Adams & Woodward, 1989; O´Brien, 1993), whereas patterns of community composition are shaped by local-scale topographic and geological factors (Woodward, 1987; Ellenberg, 1996). Both scales and the respective processes are linked to each other and ideally all have to be regarded when analysing macroecological patterns.

The importance of the discipline of macroecology is emphasised by Price (2003): "Setting distribution, abundance, and population dynamics in a macroevolutionary and macroecological framework places these central themes in ecology on a far larger scale than in the past, affording a comparative approach to the understanding of broad patterns in nature". He further argues that empirical pattern detection is the background of the development of theory, because development of factually and empirically based broad patterns and their mechanistic understanding will advance science in ecology more rapidly than any other approach. Furthermore, macroecology provides helpful tools to predict the effects of rapidly advancing Global Change on species abundances, distribution and biodiversity.

Global Change and its effects on macroecological patterns

Recent analyses by Sala *et al.* (2000) state changes in climate and land use as well as biotic exchange (i.e. biological invasions) to be among the most important threats to biodiversity subsumed under "global change". In this context, threat is not only the extinction of species but also the change in the macroecological patterns of abundance, diversity and distribution, which may lead to new patterns of the biosphere on several scales. These patterns may change dramatically due to global change, but the processes behind the general patterns are still poorly understood and prognoses about species abundance, niche or range shifts are associated with a high degree of uncertainty.

Over the past 100 years, the earth's climate has warmed by approximately 0.6°C due to increasing greenhouse gas concentrations in the atmosphere. There have been two major periods of warming. One lasted from 1910 to 1945 and the other from 1976 until today. What is special about the latter period is that its warming rate has been approximately double that of the first and greater than that of any other warming rate within the last 1000 years (Houghton *et al.*, 2001). Many long-term monitoring studies give proof of that

drastic climatic trend (Mann *et al.*, 1999). In addition, local and temporal weather anomalies have increased in size and duration in the past century (Reaser, *et al*. 2000). The effects of climate change act through local climate elements such as the temperature regime, wind, rain, snow, and ocean currents, as well as interactions among them (Stenseth *et al*., 2002). There is ample evidence amongst scientists of different research fields that climate change has a serious impact on the flora and fauna from community to ecosystem level and across different scales (Easterling *et al.,* 2000; Parmesan *et al.,* 2000). Besides effects on the physiology (Hughes, 2000) and phenology of organisms (Sparks & Menzel, 2002; Bairlein & Winkel, 2001) as well as the structure and composition of whole ecosystems (Pounds *et al*., 1999; Sagarin *et al*., 1999; Walther *et al*., 2002), climate change can have a strong influence on a species´ abundance and distribution, often through species-specific physiological thresholds of temperature and precipitation tolerance (Hoffmann & Parsons, 1997; Woodward, 1987). In order to compensate temperature and precipitation anomalies, species are expected to generally shift their distributions poleward in latitude or upward in elevation by progressive establishment of new local populations (Walther *et al*., 2002). A 3°C change in mean annual temperature corresponds to a shift in isotherms of approximately 300 - 400 km in latitude (in the temperate zone) or 500 m in elevation (Hughes, 2000). Global meta-analyses already documented significant range shifts averaging 6.1 km per decade towards the poles (Parmesan & Yohe, 2003). Accordingly, poleward and also upward shifts of species ranges could be observed across a wide range of taxonomic groups and geographical locations during the twentieth century (Hughes, 2000; McCarty, 2001; Walther *et al*. 2001; Easterling *et al*., 2000). There will probably also be an extinction of local populations along range boundaries at lower latitudes or lower elevations. In most cases, species whose distribution is affected by climate change, fall in two main categories: (i) species whose distributions are most obviously limited by climate, such as plants, and (ii) organisms that are highly mobile at some stage of their life cycle, such as flying insects, birds and marine invertebrates (Hughes, 2000). It seems evident that the first mentioned category of species, including trees, might be hit hardest by Global Climate Change due to their low mobility, i.e. their inability to rapidly follow climatic changes with range shifts.

The macroecology of Central European forest ecosystems in the scope of Global Change

Plants are among the best studied organisms in relation to environment. Thus the knowledge on many plant species' requirements and preferences for soil, water, nutrients and other resources are fairly well understood. Also, the study of specific communities has a long history. While many studies focus on global scales, there are only a few on a regional scale (e.g. Heikkinen & Neuvonen, 1997; Araújo *et al.*, 2001; Deutschewitz *et al.*, 2003; Kühn *et al.*, 2003). Furthermore, most of the studies that have investigated macroecological patterns, neglected tree species. Due to their immobility, trees will be hit by climate shifts directly over their lifespan. For Central European trees, the response period will be much longer than in more mobile taxonomical groups like fishes or birds which can adjust their distribution to the environmental conditions in a shorter time span. Thus, a high tolerance towards environmental stressors and a large niche breadth may be advantageous for tree species and the knowledge about both constitutes a precious tool for forest management and nature conservation.

There is general agreement that the 'realised niche' of a plant species (i.e. the ecological niche sensu Ellenberg) is variable and may change due to altered physical and biotic conditions. Thus, a plant species may occupy different niches in its geographical distribution range if climate and competing species differ regionally. At least two mechanisms may explain such niche shift: (a) a shift in niche position compensates for increasing stress in marginal regions of the range. This response is expressed by Walter's rule of the relative constancy of site conditions. (b) A species may face different competitors (or enemies) in different regions of its distribution range leading to competitive displacement along environmental gradients. For example, *Quercus petraea* competes widely with *Fagus sylvatica* in Central and Western Germany, but faces competition mainly by *Tilia cordata* and *Carpinus betulus* in Poland and Ukrainia. As a competitively inferior species, the realised niche of *Q. petraea* will be different in Central Germany and in Eastern Europe.

Regional comparisons of niche shifts have been conducted so far mainly by use of plant indicator values (e.g. Thompson *et al.,* 1993; Prinzing *et al.*, 2002). Such an approach may be imprecise in the case of tree species because many trees show a rather plastic response to the environment and, thus, indicator values often can only be poor proxies for the

ecological behaviour of these tree species. For example, beech, oak, spruce and pine are more or less indifferent with respect to soil acidity or soil fertility.

With this set of research articles, I present the results of an extensive study on macroecological patterns and environmental limits of Central European tree species. I tried to overcome common drawbacks of macroecological studies, such as scale limitation and the neglection of the species` physiology, by choosing a combination of different approaches.

On the one hand I sticked to theoretical pattern detection by analysing a wealth of literature in order to investigate the relationships between abundance, range size and niche breadth for all tree species, which have their distribution centre in Central Europe (Chapter II). To obtain precise data on abundance, niche breadth and niche position of three selected common (*Fagus sylvatica, Quercus petraea, Acer pseudoplatanus*) and three selected rare (*Prunus avium, Sorbus torminalis, Taxus baccata*) tree species in their distribution centre and at their eastern margin, we analysed forest inventory data bases (Chapter III).

On the other hand I investigated ecophysiological traits of four selected tree species (*Fagus sylvatica, Acer pseudoplatanus*, *Prunus avium, Taxus baccata*) in stands in the distribution centre and at the eastern range margin (Chapter IV). Furthermore, a growth experiment with seedlings of central (Germany) and marginal (South-East Poland) provenances of *F. sylvatica* was conducted to identify the drought tolerance of different ecotypes (Chapter V).

This combination of traditional „theoretical pattern detection" (Chapters II and III) with ecophysiological studies (Chapters IV and V) to date is unique in macroecological research. I am aware of no study that has investigated abundance and distribution patterns of Central European tree species on both global and regional scales. Besides testing macroecological hypotheses, a second objective of the study was to identify the causes determining the eastern distribution margin of Central European tree species.

Fagus sylvatica

Prunus avium

Quercus petraea

Sorbus torminalis

Acer pseudoplatanus

Taxus baccata

Distribution ranges of three common (*Fagus sylvatica*, *Quercus petraea*, *Acer pseudoplatanus*) and three rare (*Prunus avium*, *Sorbus torminalis*, *Taxus baccata*) Central European tree species investigated in this study (according to Meusel *et al*., 1965, 1978).

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Chapter II

The relationship between abundance, range size and niche breadth in Central European tree species

B. Köckemann, H. Buschmann, Ch. Leuschner

ABSTRACT

Aim Range size and niche breadth have been found to be positively related to abundance in many plant and animal groups. We tested these two relationships for the tree species flora of Central Europe, i.e. all 25 species that have their distribution centre in this region.

Location Eurasia with a focus on Central Europe.

Methods We devised an abundance and niche variable classification system to transform the existing literature data into a semi-quantitative assessment of abundance and niche breadth (soil chemical and physical variables, temperature) of the 25 tree species. Regression analyses between abundance, range size and niche breadth were conducted for the entire species sample and for subsets of species defined by their ecology or phylogeny.

Results The relationship between abundance in the distribution centre and range size was weak for the Central European tree species. However, significant abundance-range size relationships were found for phylogenetically or ecologically more homogenous species groups (e.g. trees of the order *Rosales*; mid-successional tree species). Realised niche breadth was positively related to range size in the case of temperature, but not for soil-related variables. No relationship existed between niche breadth and abundance in the distribution centre.

Main conclusions We hypothesise that the weak relationship between abundance and range size is primarily a consequence of substantial ecological and phylogenetic heterogeneity within this rather species-poor assemblage. The positive relationship between realised temperature niche breadth and range size emphasises the strong influence of climatic variables on plant distribution patterns over continental or global scales.

Keywords Distribution range, Eurasia, macroecology, realised niche breadth, soil chemistry, soil moisture, temperature, tree species abundance.

INTRODUCTION

The observation that widespread species tend to be more abundant than species with restricted distribution has been argued to be a macroecological keystone rule (Gaston, 1996). A positive relationship between abundance and range size has been observed in many different groups of organisms (Bock & Ricklefs, 1983; Brown, 1984; Bock, 1984, 1987; Brown & Maurer, 1987, 1989; Morse *et al.*, 1988; Gaston & Lawton, 1990; Lawton, 1993; Gaston, 1996; Kotze *et al.*, 2003), in very different habitat types (Blackburn *et al.,* 1998; Gaston *et al.,* 1998) and across a range of spatial scales (Gaston, 1996), regardless of the method used for measuring abundance and range size (Gaston *et al.*, 1998). In contrast, only a minority of studies on abundance-range size relationships have revealed no correlation (Gaston & Lawton, 1990).

The ecological niche of a species has received particular attention in the context of the abundance-range size relationship. Brown (1984) suggested that a species able to exploit a wide range of resources should occupy a larger number of sites, become locally more abundant and thus have a wider geographic range than a rare species, which is restricted to a narrower niche.

Attempts to investigate species distribution patterns should be based on the realised niche (Austin & Smith, 1989), which is usually assessed by environmental variables (Thuiller *et al.*, 2003b). In this context, it is important to specify the relevant niche dimensions and the relevant scale, because many definitions of the `ecological niche´ exist in the literature (Schaefer, 2003). For example, climatic factors have been found to dominate large-scale species distribution patterns much more than edaphic parameters (e.g. Pearson & Dawson, 2003), which seems to be particularly true for European tree species (Huntley,1990; Huntley *et al.*, 1995; Ellenberg, 1996; Sykes *et al.*, 1996; Rouget *et al.*, 2001; Thuiller *et al.*, 2003a,b; Svenning & Skov, 2005). Energy-related climatic factors seem to be responsible for global scale species richness patterns (Currie & Paquin, 1987; Adams & Woodward, 1989; O´Brien, 1993), whereas local-scale topographic and geological factors are more relevant for patterns of community composition (Woodward, 1987; Ellenberg, 1996). Further, climatic variables have a more direct physiological impact on general plant productivity, and also on plant survival under extreme environmental conditions (Bartlein *et al.*, 1986; Prentice *et al.*, 1991; Huntley *et al.*, 1995), whereas geology can be used as a proxy of soil type, nutrient supply and water availability, which control plant growth at the site level (Austin & Smith, 1989).

In fact, there is continuing debate on the role of niche breadth in generating macroecological patterns, although the relevant niche dimensions have rarely been measured. If data on niche dimensions are included in studies, they are most often easily accessible environmental variables such as temperature or rainfall. However, important site factors such as soil water and nutrient availability, or pollinator abundance are often neglected. Thus, the role of a species' niche in determining its abundance and distribution still awaits a quantitative treatment (Kouki & Häyrinen, 1991; Hanski *et al.*, 1993).

Most macroecological investigations have focused on birds, certain insect groups or herbaceous plants, while other life forms such as trees have mostly been neglected. Given the economic importance of trees and the prominent role forests play in the global carbon cycle, our limited understanding of the abundance-range size relationship and its link to niche breadth in trees is a serious shortcoming. This is particularly true for models dealing with the response of biomes and the biosphere to climate change.

To our knowledge, there exists only one study investigating abundance and distribution patterns of a tree flora. Murphy *et al.* (2006) analysed spatial datasets of the geographical range of eastern North American tree species to test macroecological hypotheses. They found that species with greater abundance somewhere in their distribution range tend to have larger range sizes, as predicted by basic macroecological theory. In this study abundance was not necessarily greatest in the distribution centre but often peaked in range edges (Murphy *et al.*, 2006). Comparable data for Central European tree species are lacking.

In the present study, we analysed the relationship between geographic range size, tree abundance and niche breadth in the distribution centre of Central European tree species. We hypothesised that (1) tree species which are abundant in their distribution centre occupy a large range, (2) abundant tree species have broader ecological niches than rare species, and (3) widespread species have broader niches than narrowly distributed species. We included all tree species with distributions centre in Central Europe (i.e. Germany, Czechia and parts of Poland) for which distribution is reliably documented on a global scale (i.e. 25 species from 15 genera and 11 families). Although it seems to be a rather small data set compared to other macroecological studies, it includes the entire set of species that have their distribution centre in Central Europe. By using the large body of information on abundance and niche breadth, we were able to characterise abundances in Central Europe and niche breadths for important niche axes semi-quantitatively. A similar

approach was taken previously for the entire Central European flora by Hoffmann & Welk (1999) but without attention to the woody plants.

METHODS

Estimating species´ distribution ranges

We determined the entire distribution range of all tree species that have their distribution centre in Central Europe using the range maps of Meusel *et al.* (1965, 1978). Tree species were defined as self-supporting woody species reaching at least 20 m in height (Tutin *et al.*, 1993) or species falling just short of this limit (More & White, 2003). The species included (acronyms in parentheses) were *Abies alba* Mill. *(Abiesalb), Acer pseudoplatanus* L. *(Acerpseud), Acer platanoides* L. *(Acerplat), Acer campestre* L. *(Acercamp), Alnus glutinosa* (L.) Gaertn. *(Alnusglut), Betula pubescens* Ehrh. *(Betpub), Carpinus betulus* L. *(Carpbet), Fagus sylvatica* L. *(Fagsyl), Fraxinus excelsior* L. *(Fraxexc), Populus tremula* L. *(Poptrem), Populus nigra* L. *(Popnig), Prunus avium* (L.) Moench *(Prunav), Prunus padus* Mill. *(Prunpad), Quercus petraea* (Mattuschka) Liebl. *(Quercpet), Quercus robur* L. *(Quercrob), Salix purpurea* L. *(Salpur), Salix alba* L.s.l. *(Salalba), Sorbus torminalis* (L.) Crantz *(Sorbtorm), Sorbus aria* (L.) Crantz *(Sorbaria), Sorbus aucuparia* L. *(Sorbaucup), Taxus baccata* L. *(Taxbac), Tilia cordata* Mill. *(Tilcor), Tilia platyphyllos* Scop. *(Tilplat), Ulmus glabra* Huds. *(Ulmglab)* and *Ulmus minor* Mill. *(Ulmminor)*.

The contour line of the distribution area of each species was reproduced on a digital map of Eurasia in which the borders of all European and Northern Asian countries are marked (National Geographic Society, 1995). Using Adobe Photoshop, we then calculated the size of each distribution area with the Image Analysis Method after Dietz & Steinlein (1996) by converting the total number of pixels in the entire distribution range into square kilometres. The area of each country was used as a reference. This approach yields the ´extent of occurrence` of a species (Gaston, 1991), covering not only all regions where the species is present, but also locations within the distribution range where it is locally absent. Quantifying the ´area of occupancy` of a species, which gives a more accurate reflection of the true distribution range, was not possible in our data set, because the distribution data

were not sufficiently precise in many Eastern European and Asian countries. Therefore, the range size data given for the 25 tree species are maximum values.

The degree of range filling of the species (R/P ratio), i.e. the ratio of realised range (R) to the potential range defined by climatic constraints (P), was calculated by Svenning & Skov (2004) for 13 of the tree species (*Abies alba, Alnus glutinosa, Betula pubescens, Carpinus betulus, Fagus sylvatica, Populus nigra, Populus tremula, Quercus petraea, Quercus robur, Salix alba, Taxus baccata, Ulmus glabra, Ulmus minor*). These data were used here to verify relationships between abundance and range size as well as between niche breadth and range size among the 25 tree species.

Quantifying species abundances

We conducted a thorough literature survey on abundance and realised niche breadth in the distribution centre for the tree species (for references see Supplementary material, Appendix S1). We defined Central Europe as the region between the Rhine River in the west, the Wisula River in the east, the North Sea and Baltic Sea in the north, and the Alps and western Carpathians in the south. This area mainly includes Germany and western Poland and Czechia, although the Alps are excluded. It is characterised by a gradient from an oceanic to a sub-continental climate. We searched the forest ecology and vegetation ecology literature from all regions of Central Europe for information on the regional abundance of the trees in order to generate a semi-quantitative classification of the mean abundance of these species. When selecting literature, we attempted to avoid regional ´clumping` of information on abundance and niche breadth in order to obtain data that were more or less evenly distributed in space. We did not consider vegetation relevés and floristic grid maps, as such information is not available for all species, and the different scales of the maps can result in misleading conclusions (Hoffmann & Welk, 1999).

Quantifying species niche breadths

To characterise realised soil niche breadths, we collected data on the geological substrate, topsoil pH and base saturation, and typical soil moisture status of selected sites occupied by the tree species. These four soil-related niche axes were selected because they represent

good proxies for nutrient and water supply to the plant. To quantify temperature niche breadth we assessed the temperature width of the distribution range of each species by identifying extreme points of the range in north-western, north-eastern, south eastern and south-western directions. For each of these localities, we recorded the mean temperature (°C) in January and July by consulting climate diagrams of nearby cities (Supplementary material, Appendix S2, Table S1; Mühr, 2006). Temperature niche breadth was then defined as the difference between the lowest mean January temperature and highest mean July temperature. This was done at two different extents. First, we assessed a species' temperature niche breadth for Central Europe only, i.e. the region which represents the distribution centre of the species and can be directly related to the data on soil niche breadth. Most of the species occur throughout Central Europe. In these cases, Bremen in Germany, Elbing in Poland, Cracow in Poland and Freiburg im Breisgau in Germany were selected as localities in the extreme northwest, northeast, southeast and southwest, respectively, of this region. Second, we considered the temperature niche breadth for the entire range of a species, because several studies have found a substantial influence of temperature on a continental or global extent. All calculations of local tree abundance and soil niche breadth were translated into a rank-based classification system (six levels) by which soil niche breadth and the relative niche position on the niche axis could be measured semi-quantitatively. This was necessary because, in most cases, authors did not make quantitative statements on the four soil niche variables.

For tree abundance and species occurrence along the pH axis in the different regions of Central Europe, two classification systems with six levels each (absent to very abundant; extremely acid to neutral-basic) were established (Supplementary material, Appendix S2, Table S2 and S3). Based on the forest site classification system of Saxony-Anhalt in Germany (Hetsch *et al.*, 1998), the pH classes in Table S3 (Supplementary material, Appendix S2) are associated with classes of base saturation in the topsoil, i.e. the per cent contribution of exchangeable Ca, K, Mg and Na-ions to the total cation exchange capacity of the mineral soil. The soil moisture classification system (Supplementary material, Appendix S2, Table S4) contains six levels (very dry to very wet) and is based on the forest site classification system of the state of Hesse in Germany (Hetsch *et al.*, 1998). Variables used for characterising the mean soil moisture regime in the regions are soil depth, water storage capacity of the soil, position of groundwater surface and relief factors influencing local hydrology. Table S5 (Supplementary material, Appendix S2) contains the six-level classification system of geological substrates which were ranked according to

assumed nutrient supply rate (from very nutrient-poor, quartz-rich bedrock to nutrient-rich limestone and marl substrates) based on the quantitative data compiled by Leuschner *et al.* (2006). The geological substrate was included as a relevant niche axis, because it influences base saturation and pH of the soil, nitrogen and phosphorus supply, and soil hydrology, thus providing additional information on soil chemical and physical site factors.

Data analysis

The analysis was based on (i) the range size data set and (ii) the literature compilation on tree species abundance and habitat preferences in the various regions of Central Europe covered by the survey. Data analysis proceeded in five steps:

(I) The literature data on abundance and soil habitat occupation were transformed into rank values (see Supplementary material, Tables S2 to S5 in Appendix S2).

(II) The abundance scores from different regions of Central Europe were then averaged by calculating the median of each literature source, and all median values of a species were averaged.

(III) To quantify soil niche breadth with respect to the four variables of geological substrate, pH, base saturation and soil moisture status, we first counted the number of observations in each level of the classification systems. Niche breadth was then calculated with the following equation given by Dalbeck *et al.* (2001):

$$(1) \ p(k) = \frac{b(k)-e}{e} \ x \ 100$$

where

p(k) = relative measure of the breadth of niche k (large negative values indicate a large niche breadth),

b(k) = B(k) divided by N(k),

B(k) = sum over the six variable levels of s_{obs}^2/s_{exp} for a given species,

s_{obs} = number of observations of a species in a given variable level,

s_{exp} = theoretical number of expected observations of a species in a variable level in the case of equal occurrence along the niche axis,

N(k) = sum over the six variable levels of s_{obs}^2/s_{exp} for all species, and

e = number of variable levels with observations for a species divided by the total number of levels (6).

Soil niche breadth of a species with respect to a given variable was quantified as `realised niche breadth´ where both the number of occupied levels and the frequency of observations per variable level were considered.

To clarify extreme niche positions (very dry or wet sites, highly acid soils), observations made in levels 1, 2, 5, 6 were weighted when calculating niche breadth by multiplying the s_{obs}^2/s_{exp} of increasingly extreme niche positions with increasing weights (levels 3 and 4 = weight 1, levels 2 and 5 = weight 1.1, levels 1 and 6 = weight 1.3). This seemed reasonable because extreme niche positions are occupied less frequently than 'common' sites, and species able to grow on extreme sites are more likely to have a broader niche than species which do not. However, the results obtained with this alternative approach did not differ qualitatively from those obtained with unweighted data, and only the latter are presented here.

(IV) To quantify temperature niche breadth, ranks were allotted according to the temperature span across a species' range. The broader the temperature range, the higher the rank.

(V) After calculating the scores for abundance, range size and niche breadth variables (for soil and temperature), species were assigned an overall rank between 1 and 25. The soil niche breadth of a species was calculated by averaging over the four soil niche variables. By definition, species with a higher rank had a broader soil niche. The overall niche breadth was obtained by averaging the ranks for soil and temperature niche breadths. Using the ranked variables we correlated abundance in the distribution centre, range size and overall niche breadth (soil and temperature) with each other. We repeated these correlations with the original data (scores for niche variables and abundance, square kilometres for range size), but obtained similar results compared to the ranks. To distinguish between temperature and soil effects, we separately correlated temperature niche breadth in the Central European range, temperature niche breadth in the entire range of a species, and soil niche breadth with abundance in the distribution centre and range size.

To account for the functional diversity among Central European tree species, we pooled species of the same order, and we also grouped species according to abundance, range size, successional status and phylogeny (Supplementary material, Appendix S2, Table S6). For each group we examined the relationship between abundance in the distribution centre and range size. Moreover, we compared these species groups for significant differences in range size, abundance and overall niche breadth.

We also controlled phylogenetic relationships among the trees because abundance-range size relationships are often stronger among closely related species (Gaston *et al*., 1997). Separate analyses focused on the *Rosales*, *Fagales* and *Malpighiales*, which had sufficient species to conduct the calculations. In contrast, *Pinales, Sapindales, Lamiales* and *Malvales* did not contain enough species for order-level analysis.

To account for human influences on the abundance and range size of economically important tree species such as *Fagus sylvatica* and *Quercus petraea*, we omitted these species from the data set and repeated the analysis. However, the results of both analyses were the same, probably because the ranking method reduced any bias due to human influence on tree abundance in the original data, or because any non-climatic influence on abundance and distribution would be averaged out on a larger continent-wide scale (Prentice, 1986; Huntley, 1990).

We tested the significance of all relationships with Spearman's rank correlation coefficients using JMPIN Version 4.0.4 (SAS Institute, 2001). To test for significant differences in abundance, range size and niche breadth between the species groups, we used a Kruskal-Wallis-test for non-normally distributed data followed by a Mann-Whitney-U-test for pairwise comparisons. Due to the high number of analyses based on relatively few data points, we adjusted significance values using Bonferroni ($\alpha_{Bonferroni} = 0.0027$) and Sidak ($\alpha_{Sidak} = 0.003$) corrections (Abdi, 2007). After this procedure, all values indicating significance or marginal significance had to be rejected, except those for the relationships where range size and temperature niche breadth were involved. Nevertheless, P-values indicating (marginal) significance before adjustment are presented in the results section, although we are aware of their unreliability. By this we take an exploratory approach to document potentially interesting patterns within subsets of the data, as indicated by significance values ≤ 0.05 prior to adjustment. We consciously did not omit those results, which are questionable from a Bonferroni- and Sidak-perspective, as several macroecological explanations exist, which support the indicated patterns.

RESULTS

Abundance-range size relationship

The relationship between abundance in the distribution centre and range size was marginally significant when the whole data set was analysed (Fig. 1), thus only partly supporting our hypothesis (1). Nevertheless, the tendency for more abundant tree species to have larger ranges was also indicated by the significantly larger range size of the 12 most abundant species as compared to the 12 least abundant species ($z = 1.99$, $P < 0.05$, Fig. 2a). When considering more restricted samples, e.g. the 12 most abundant or the 12 least abundant species, or the 12 species with smallest or largest ranges, there was no correlation between abundance and range size ($0.16 > r_s > 0.01$, $P > 0.62$; results not shown). A relationship was also absent when the group of early- or late-successional species ($0.21 > r_s > 0.14$, $P > 0.64$, n = 7 and 6 for early- and late-successional species, respectively) or all members of the orders of *Fagales* or *Malpighiales* ($0.6 > r_s > 0.4$, $P > 0.47$, n = 6 and 4) were analysed.
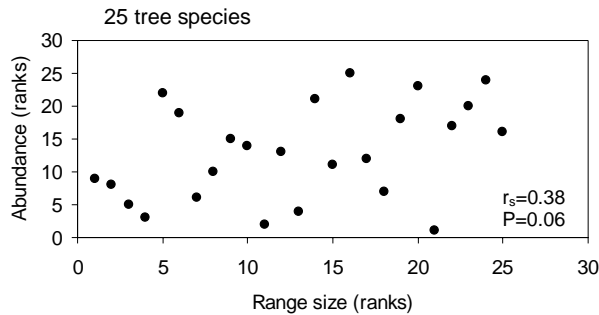

Figure 1 Relationship between abundance in the distribution centre and range size in the sample of 25 Central European tree species (ranks 1 to 25 with 1 = highest abundance or largest range).

However, we found significant positive relationships between abundance and range size for the group of mid-successional species (N = 12, $r_s = 0.66$, $P = 0.02$, results not shown) and for the species in the Rosales (N = 7, $r_s = 0.75$, $P = 0.05$, results not shown).
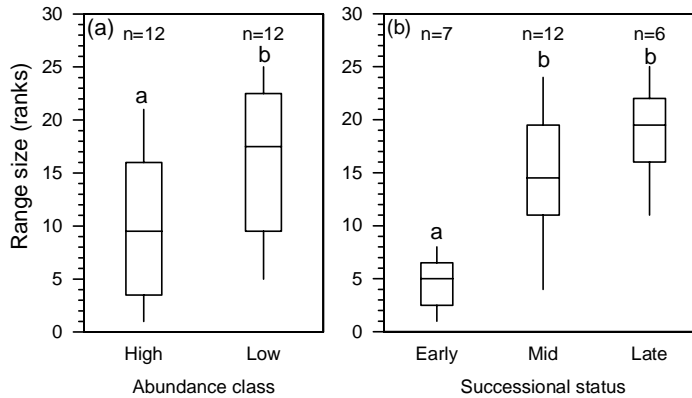
Figure 2 (a) Ranked range size of the 12 most abundant (High) and the 12 least abundant (Low) tree species (box-whisker- plots with median, range of 25-75% data points and non-outlying minima and maxima). (b) Ranked range size of early-, mid- and late-successional tree species (n = 7, 12, 6). Significant differences between the two abundance classes or successional groups are indicated by different letters.

A comparison of the median range size of the 10 groups of tree species in Table S5 (Supplementary material, Appendix S2) revealed significant differences between successional groups (Chi² = 13.8, P < 0.01), more precisely between early- and mid-successional species (z = -3.17, P < 0.01) and between early- and late-successional species (z = 2.93, P < 0.01) with early-successional trees having particularly large ranges (Fig. 2b). We also found a positive relationship between abundance in a species distribution centre and the extent of range filling, i.e. their realised range was closer to the range defined by climatic constraints (potential range, R/P ratio) (Fig. 3).
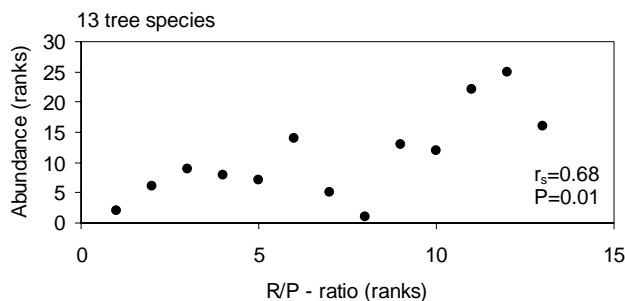

Figure 3 Relationship between abundance in the distribution centre and the degree of range filling (i.e. ratio of realised range to range as defined by climatic constraints; R/P ratio for 13 tree species as specified by Svenning & Skov, 2004) (ranked values).

Abundance and range size in relation to niche breadth

There was no relationship between overall realised niche breadth (soil and temperature variables) and abundance or range size when the temperature niche was defined for the Central European range only ($0.22 > r_s > 0.12$, $P > 0.28$, results not shown). However, a relationship between overall niche breadth and range size appeared when temperature niche breadth was analysed for a species' total range (Fig. 4a). In contrast, on the continent-wide scale, there was no relationship between overall niche breadth and abundance in the distribution centre (Fig. 4b). Also, soil niche breadth was not related to range size (Fig. 4c), but there was a highly significant relationship between temperature niche breadth and range size (Fig. 4d).
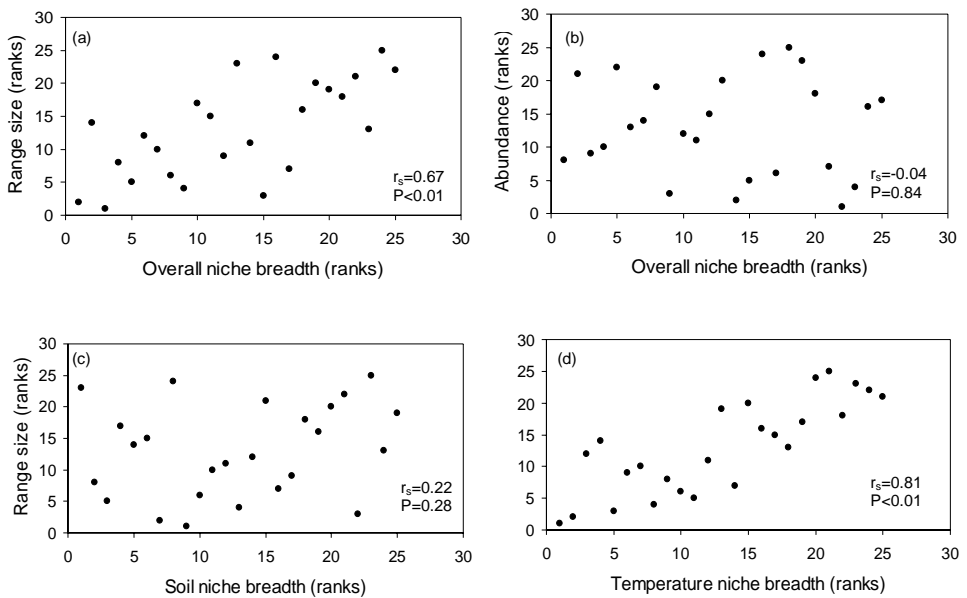
Figure 4 Relationship between overall niche breadth (mean of four soil variables and temperature span in the species' total range) and (a) ranked range size, and (b) ranked abundance in the distribution centre, and relationship between (c) ranked soil niche breadth (soil moisture, pH-value, base saturation, geological substrate) or (d) ranked temperature niche breadth (temperature span in the species' total range) and ranked range size among the 25 Central European tree species.

DISCUSSION

Ecological and phylogenetic factors influencing the abundance-range size relationship

In contrast to birds and mammals (Bock, 1987; Gaston, 1996; Blackburn *et al.*, 1997), Central European tree species showed only weak positive relationships between abundance in the distribution centre and range size. This is consistent with the results of an analysis of 134 tree species of eastern North America (Murphy *et al.*, 2006). Although there was a significant relationship between mean species importance value and range size in the larger North American data set (r = 0.23, P < 0.01), the relationship was even weaker than in the smaller Central European data set with correlation coefficients < 0.4 (Fig. 1). Grouping the species in abundance classes showed significant differences between the categories ´highly abundant` and ´rare` or ´sparse` in both regions, which suggests the existence of at least a weak abundance – range size relationship in temperate tree floras. However, it appears that this relationship is much stronger in other taxonomic assemblages than in trees (cf. Gaston, 1996).

In our study, the abundance-range size relationship was stronger in sub-samples of ecologically or taxonomically related tree species than in the whole data set of all 25 tree species that have their distribution centre in Central Europe. In the following, we address the questions (i) why is the abundance-range size relationship particularly weak in temperate trees, and (ii) why is this relationship stronger in some groups of trees than in others?

Niche breadth plays a central role in explaining positive relationships between abundance and range size (Gaston *et al.*, 1997). Species which are able to exist under a broader range of resource availabilities, i.e. that have a broader niche with respect to a given resource, are predicted to be locally more abundant and to have larger ranges, because they are able to grow in more habitats and to colonise additional regions with a different habitat spectrum than species with a smaller niche breadth (Brown, 1984). Since this explanation focuses on niche breadth, which has a strong effect on abundance and range size of a species, it is only applicable to species assemblages with similar niches that differ substantially in only a few niche dimensions. When ecologically dissimilar and distantly related species are considered, the correlation between abundance and range size will most likely be weak or absent (Brown, 1984).

We hypothesise, therefore, that the 25 Central European tree species of our data set are too dissimilar in their ecology and too different in their phylogenetic relationships to show significant positive relationships between abundance and range size. Nevertheless, a subgroup of 12 tree species revealed a significant abundance-range size relationship. This group comprises the mid-successional trees with similar adaptations in terms of light demand, height growth strategy, and maximum tree lifespan (Burschel & Huss, 2003), indicating that this group differs in fewer niche dimensions than the remaining tree species in the entire sample. This could indicate that Central European tree species are more dissimilar in their ecology than other taxonomic groups with stronger abundance-range size relationship.

Vegetation history could also weaken the relationship between abundance and range size in Central European trees. Due to the specific geography of Europe and the glaciation history of the Eurasian continent, the region has a more impoverished woody flora than, for example, temperate eastern North America and East Asia (Svenning & Skov, 2005, 2007). Re-immigration from the glacial refugia has been slow in some tree species and is still continuing in a few, such as *Fagus sylvatica*. It may well be that the climatically-defined potential range of some European tree species has not been completely filled, resulting in relatively small R/P ratios in these species (Svenning & Skov, 2004). Although we are aware of discussions about methodological approaches based on the Atlas Floraea Europeae of Jalas & Suominen (1972-1994, see Svenning *et al*., 2006; Welk & Bruelheide, 2006), incomplete range filling could contribute to the weak abundance-range size relationship we found. However, our data revealed a positive relation between abundance in the distribution centre and the degree of range filling as determined by Svenning & Skov (2004). Hence, species more abundant in their distribution centre fill more of their climatically-defined potential range in Eurasia than do rare species. Therefore, it is unlikely that the weakness of the abundance-range size relationship is caused by the rare tree species that have not yet completely filled their range. These species occupy ranges smaller than their potential ones, thereby enhancing the abundance-range size relationship instead of weakening it.

Phylogeny can also influence the relationship between abundance, range size and niche breadth, and failure to account for phylogenetic effects can seriously bias statistical tests in interspecific comparisons (Harvey *et al.*, 1991). Similar to species assemblages with diverse ecologies, positive abundance-range size relationships may become weaker with increasing taxonomic diversity of a sample (Brown, 1984). This is found in our data set, as

there is a positive relationship between abundance and range size among species of the same order (Rosales), but not for the whole data set which includes multiple orders. In our data set of 25 species, *Quercus petraea*, *Quercus robur,* and *Tilia cordata* and *Tilia platyphyllos* are the only species pairs that are closely related. However, the congeners are in both cases clearly different in their ecology (Ellenberg, 1996) and thus occupy different niches, which should minimise the risk of phylogenetic bias in our data set. For example, in contrast to *Q. petraea*, *Q. robur* tolerates soils with periodic anoxia and prefers substrates with a good nutrient supply (Röhrig & Bartsch, 1992; Ellenberg, 1996). Thus, the two species exhibit quite different p(k)-values despite being closely related. Moreover, in the woody flora of Europe, most rare species are neither overrepresented in certain families nor underrepresented in others, as is the case in many floras that are dominated by herbaceous plants (Haeupler & Muer, 2000). For example, the 12 least abundant tree species are members of seven families with mostly one species per family, in two cases two species per family (*Sapindiceae*, *Malvaceae*). This makes phylogenetic effects on distribution and abundance less likely in the case of the Central European tree flora. Here, we argue that the main effect of phylogeny is a weakening of the abundance-range size relationship because the tree flora of this region is poor in species but comprises a considerable number of orders and families that leads to a considerable taxonomic diversity at higher systematic levels.

Environmental factors influencing the range size-niche breadth relationship

The most important environmental variables explaining broad-scale patterns of plant distribution and diversity are widely believed to be water and energy (Prentice, 1986; Stephenson, 1990; O´Brien, 1993; Svenning & Skov, 2005). O´Brien *et al.* (2000) postulated that the smallest extent over which the influence of climate on tree diversity can be expected to be predominant at about 100 km. Our study was conducted over a large spatial extent that covers the entire distribution ranges of the species studied. We used temperature on two different spatial scales as an energy variable and soil conditions to characterise water availability. Regardless of scale, the abundance of Central European tree species seems to be insensitive to both of these environmental factors (Fig. 4b). This is in contrast to the findings of Hall *et al*. (1992), who reported a link between a positive energy balance of plant and animal species and their abundance. They postulated that rarity might

be due to insufficient energy use, and they considered temperature to be the main factor influencing abundance. Our data do not support this conclusion since there was no relationship between temperature niche breadth and abundance ($r_s = 0.09$, $P = 0.66$). The range size of Central European tree species is influenced by a species' niche breadth only when temperature niche breadth is considered on a continent-wide scale. Temperature-related variables such as winter minimum temperature, growing season length or summer mean temperature are known to have a strong influence on the diversity patterns of many plant and animal species (for a review see Hawkins *et al.*, 2003; and references therein), which obviously also is the case for distribution patterns of European tree species (Huntley,1990; Huntley *et al.*, 1995; Ellenberg, 1996; Sykes *et al.*, 1996; Rouget *et al.*, 2001; Thuiller *et al.*, 2003a,b; Svenning & Skov, 2005).

On a global scale, energy and water are the main factors postulated to be limiting to plant species richness (Currie & Paquin, 1987; Adams & Woodward, 1989; OʹBrien, 1993). In higher latitudes, energy has a stronger influence on species diversity patterns, whereas in energy-rich lower latitudes, water has been proposed to be the primary driving factor (Hawkins *et al.*, 2003). In the Northern hemisphere, the transition from energy to water control gradually takes place near 45° N, with energy being the most important explanatory variable between 45 and 60° N. Species from energy-poor, northern regions have developed a greater cold tolerance, enabling them to follow glacial-interglacial temperature oscillations better than species from energy-rich regions (Adams & Woodward, 1989; Svenning & Skov, 2004). In our study region, which is mostly situated north of 45° N, energy is most likely the main variable controlling distribution patterns, and species with large ranges that extend far into continental regions always have a broader temperature niche than narrowly distributed species ($z = 3.55$; $P < 0.01$; results not shown). This is crucial for species' survival in the energy-poor environments of higher latitudes.

Methodological considerations

We chose species' extent of occurrence to characterise range sizes. As this includes areas that are not actually occupied by a species, this measure is not as precise as the ´area of occupancy` to determine true range size. Gaston (1991) and Gaston (1994a) observed that positive abundance-range size relationships are weaker when range size is measured as extent of occurrence instead of area of occupancy. In our case it was not possible to

measure the area of occupancy because the data from Eastern Europe and Northern Asia are insufficiently precise (cf. Jalas & Suominen, 1972-94).

Measuring distribution ranges at the continental or global extent can further weaken macroecological relationships, as positive interspecific abundance-range size relationships may be weaker with increasing size of the investigated area (Gaston *et al.*, 1997). Possible reasons are that larger areas include a broader spectrum of habitat types and more diverse floras which may influence the behaviour of the species assemblage, and some mechanisms are based on assumptions which are unlikely to apply at larger spatial scales (Gaston, 1994b; Brown, 1995). Hence, the weak relationship between abundance in the distribution centre and range size among Central European trees may partly be a consequence of the very large ranges of some of its species and the size of Eurasia itself. A third possibility is that human activities can influence abundance-range size relationships. Central Europe has a long- history of forest management practices that can affect tree distributions. Conifers, particularly *Picea abies* and *Pinus sylvestris*, have widely been planted, whereas *Fagus sylvatica* and other broad-leaved species are less common now in parts of their range than in the past. We attempted to control for the influence of these human-induced abundance changes by excluding *F. sylvatica* and *Q. petraea* from our analyses, but this made no difference. Moreover, we used ranks instead of absolute abundance measures in all calculations, which emphasizes the relative abundance of the tree species instead of absolute frequencies and thus should reduce any confounding effects of forestry practice on tree abundance.

To further explore potential management-related biases in our data set, we based tree abundances on palynological evidence that exists for 11 of our 25 species (Firbas, 1949, 1952; Lang 1994; Ludemann, 2003; Nelle, 2003; Zerbe & Brande, 2003). Thus, we repeated the analyses using abundance values estimated by Tüxen (1956) and Zerbe (1998) for the potential natural forest vegetation. We again found a somewhat weak relationship between abundance and range size ($r_s = -0.54$, $P = 0.09$, results not shown), similar to the results of the full data set.

Finally, the ranges of several species of our sample have been extended by humans, including *Abies alba, Acer pseudoplatanus, Acer platanoides, Carpinus betulus, Fagus sylvatica, Populus alba, Populus nigra* and *Salix alba* (Jalas & Suominen, 1972-94; Haeupler & Schönfelder, 1988; Peterken, 1996, 2001). On the other hand, humans have caused range reductions at the distribution limit in a few species (Svenning & Skov, 2005). Nevertheless, changes in the distribution patterns of most European trees species seem to

be mainly caused by climate changes rather than by forest management in the past millennia (Prentice, 1986; Huntley, 1990). Human disturbance has likely facilitated changes in relative abundance and distribution at a local scale in some cases but, on a macro-scale they reflect climatic change rather than human impact (Prentice, 1986; Huntley, 1990).

CONCLUSIONS

Our analysis found weak relationships between abundance and range size for Central European trees, which is probably caused by ecological and phylogenetic dissimilarities within this rather species-poor assemblage. On the other hand, we found a significant positive relationship between a tree's niche breadth and its range size, which is a consequence of the fact that widespread species have a broader temperature niche but not necessarily a broader soil niche.

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Chapter III

Abundance, niche breadth, and niche preferences of Central European tree species in the centre and at the margin of their distribution range

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ABSTRACT

Aim How abundance, niche breadth and niche preferences of species change within the distribution range has been investigated in many taxonomic groups, but remains unresolved for tree floras. We compared populations of six European tree species in the distribution centre and at the eastern margin with respect to abundance, niche breadth, and preferential occurrence along several soil-related niche axes. We hypothesised that (i) abundance is higher, and niche breadth greater, in the distribution centre than at the margin, and (ii) niche preferences are different between central and marginal populations with species being restricted to more favourable soils at the margin.

Location Central Germany and Slovakia.

Methods We characterized niche preferences and niche breadth in a semi quantitative way. Forest inventory data and information from maps of the potential natural forest vegetation served for quantifying abundance in the central and marginal areas. The role of human impact is discussed in the light of evidence from paleoecology and forest dynamics research.

Results Five of the six species are more abundant in the centre than at the margin, at least in the natural vegetation prior to human intervention. In contrast to soil niche breadth, the preference for soil chemical and hydrological properties differed between centre and margin. A shift to less fertile and partly also drier sites at the margin was observed, although there such sites were less abundant.

Main conclusions While the abundant centre distribution hypothesis is supported by our data, we found no conclusive evidence of competitive displacement of weaker competitors and of a niche shift of superior competitors to more favourable sites at the range margin. Factors, other than competition must be responsible for the observed niche shifts. We conclude that increased drought stress apparently is not a limiting factor at the eastern margin, where dry sites were occupied more frequently than in the centre.

Key words Distribution range, macroecology, niche preference, realised niche breadth, tree species abundance.

INTRODUCTION

Macroecology investigates patterns, processes and relationships, which are visible only on a large geographic or time scale (Gaston & Blackburn, 2000). One such pattern, the ´abundant centre distribution`, predicts that the abundance of species declines from the centre to the margin of the distribution range (Brown, 1984; Cox & Moore, 1985; Wiens, 1989; Sagarin & Gaines, 2002; Murphy *et al.*, 2006). This pattern has been observed so constantly among many organism groups (see Sagarin & Gaines, 2002 for a review and references therein) that it has even been called a ´general rule` (Hengeveld & Haeck, 1982; Hochberg & Ives, 1999). However, other abundance patterns have been documented as well (Brown, 1984; Root, 1988; Wiens, 1989), which seem to represent exceptions to this rule. One of these exceptions is that locally rare species can be abundant elsewhere in their distribution range (Murray & Lepschi, 2004).

A crucial point in the test of macroecological hypotheses in woody floras is niche breadth. The importance of this variable for understanding abundance and distribution patterns of species and the inherent difficulties of measuring and interpreting this variable in macroecological studies have been comprehensively discussed (Collwell & Futuyma, 1971; Brown, 1984). Niche breadth, in addition to abundance, is also thought to be greatest in the distribution centre and to decline towards range edges (Brown, 1984; Gaston & Lawton, 1990). This pattern has at least been observed for abundant species, which seem to be able to best utilise prevailing site conditions in the distribution centre, where they consequently reach high abundances (Brown, 1984; Hall *et al.*, 1992).

Trees are among the least studied organism groups in macroecology, despite their outstanding importance for economy and global biogeochemical cycles. In fact, only very few studies have analysed the relationships among abundance, niche breadth and range size in tree floras (Lennon *et al.*, 2002; Murphy *et al.*, 2006).

A major problem when incorporating niche breadth into a study is the right choice of niche variables and the availability of data to describe the chosen variables. Another important aspect is the regarded scale, as many niche variables affect organisms differently on different scales. For a regional-scale perspective, physical and chemical soil parameters have been identified as the main predictors of plant distribution patterns (Austin & Smith, 1989; Ellenberg, 1996; Leuschner, 1999; Prinzing *et al.*, 2002). A further advantage of using soil parameters in tree studies is that detailed and reliable information is obtainable from forest inventory agencies. In contrast, energy related niche variables like temperature

have a greater power for describing distribution patterns on a global scale and are more closely related to the physiology of plant survival and growth (Prentice *et al.*, 1991; O´Brien, 1993; Huntley *et al.*, 1995).

In this study, we focus on Central European tree species, namely three common ones (*Acer pseudoplatanus* L., *Fagus sylvatica* L., *Quercus petraea* (MATT.) LIEBL.) and three rare species (*Prunus avium* (L.) MOENCH, *Sorbus torminalis* (L.) CRANTZ, *Taxus baccata* L.), which have their distribution centre in Germany and reach their eastern distribution margin in Slovakia or a few hundred kilometres further to the east. For these species we compared realised niche breadth and abundance between their distribution centres and their eastern distribution margins. According to general macroecological theory we hypothesise that (i) abundance and niche breadth of the six tree species decrease from the centre to the margin and that common species show a different pattern than rare species. We further hypothesize that (ii) the niche preferences of the investigated tree species differ between the distribution centre and the eastern distribution margin as is postulated by Walter's ´rule of relative site constancy` (Walter & Breckle, 1983) describing niche shifts along environmental gradients. This rule postulates that climatic gradients within a species' distribution range correspond to changes in niche preferences of the species to counteract the change in climate. We assume that marginal populations of a tree species should occupy "more favourable" sites compared to populations in the distribution centre counteracting increasingly unfavourable climatic conditions near the distribution limit.

A main objective of the study was to analyse the niche breadth and niche preference of the chosen species in an objective, at least semi-quantitative way. We selected four soil related variables (soil moisture, soil fertility, soil acidity/base saturation and bedrock type) as estimators of nutrient and water availability, because tree distribution is mostly under the control of these edaphic factors on a local and regional scale, and because detailed and reliable information is available for those important soil properties from forest inventories in Europe.

METHODS

Data bank query

To estimate abundance, niche preferences and occupied niche breadth of the three selected common and three rare tree species in their distribution centre and at their eastern distribution margin, we consulted forest inventory data on abundance and bedrock type, soil chemistry and soil moisture regime for both study regions, i.e. the state of Lower Saxony in Germany and the Republic of Slovakia.

Germany represents the distribution centre for all six species according to the distribution maps given by Meusel *et al*. (1965, 1978). In our analysis, we focused on the region of southern Lower Saxony in the centre of Germany. We considered data from forest stands between 100 and 500 m a.s.l. elevation only. The study region in Lower Saxony covers c. 304,600 ha of forested land, with 264,220 ha being located between 100 and 500 m a.s.l., covering the forest districts "Solling, Bramwald, Kaufunger Wald", "Mountainous region between Solling and Harz", "Harz", "Weserbergland" and parts of "Berglandschwelle", comprising 23 forest departments. The data bank query was conducted at the Niedersächsisches Forstplanungsamt in Wolfenbüttel, Germany.

For Slovakia at the eastern margin of the species` distribution ranges, a data bank query was conducted at Lesoprojekt Zvolen, a governmental forest management institute in Zvolen, Slovakia. In Slovakia, eight different altitudinal vegetation zones with a characteristic tree species composition are distinguished (Hančinský, 1972). In our study, we concentrated on the vegetation zones I (oak), II (oak-beech), III (beech-oak) and IV (beech), which are best comparable to the mountainous region of southern Lower Saxony with regard to the duration of the vegetation period (~160 days in both regions), mean annual temperature (~7°C in Slovakia and ~8°C in Southern Lower Saxony) and mean annual precipitation (~675 mm in Slovakia and ~650 mm in southern Lower Saxony). Similar to Lower Saxony, 500 m a.s.l. was chosen as the highest elevation in most cases. The vegetation zones I to IV cover an area of approximately 1,263,592 ha, for which the forest inventory data was analysed. Both study regions still have a forest cover > 40% and include a broad variety of forest sites in terms of topography and geology; such a fine-scale mosaic of substrates is characteristic for Central and East-Central Europe.

Estimating species abundance

The abundance of the six tree species in southern Lower Saxony is expressed in the forest inventory database as the area in hectares which is covered by a tree species in a forest compartment. The relative abundance of a tree species was calculated as the percental proportion of the total study region which is held by that species at elevations of 100 to 500 m.a.s.l. (Table 1).

For Slovakia, relative tree species abundance was obtained from the area a species is occupying on a certain soil type/subtype combination in each of the four vegetation zones. To calculate the abundance in the whole study region, we added the areas occupied in the vegetation zones I to IV and related their area to the study region`s total area (1,263,592 ha).

For the two most common species (*F. sylvatica* and *Q. petraea*), exact data on the size of the stands exist in Lower Saxony and Slovakia (Niedersächsisches Forstplanungsamt, 2004; Niedersächsisches Ministerium für den ländlichen Raum, Ernährung, Landwirtschaft und Verbraucherschutz, 2004; Ministry of Agriculture of the Slovak Republic, 2006). They were compared to the abundance data obtained from our analysis based on forest compartment or vegetation zone data. A good agreement was found for these two sources of abundance information.

For *Acer pseudoplatanus* and the rare species *Prunus avium*, *Sorbus torminalis* and *Taxus baccata*, stand size data for the whole study regions do not exist. Instead we had to build on the forest compartment or vegetation zone data.

Estimating soil nutrient availability and soil hydrology

A prominent goal of this study was to provide a semi-quantitative assessment of nutrient and water availability in the different stands of the six tree species that grow on the broad variety of geological substrates in Lower Saxony and Slovakia. We used the information on soil physical and chemical properties and nutrient availability provided by forest site type maps.

For southern Lower Saxony, the Soil Type Map for the Regions Göttingen, Hannover and Braunschweig (Niedersächsisches Landesamt für Bodenforschung, 1980) at a scale of 1:200.000 was used. Seventy-seven forest site types are identified in this map, giving

detailed information on soil moisture status, soil type and geological substrate for each forest site type. For Slovakia, we used the regional soil map (Office for Official Publications of the European Communities, 2005), which gives 17 soil types or sub type combinations. This pedological data was related to the information on forest type and tree species composition.

Information about the bedrock types was extracted from the Geological Map of Northwest Germany (Amt für Bodenforschung, 1954) and the Geological Map of Czechoslovakia (east) (Kodym *et al.*, 1967) in order to obtain additional information on soil fertility. Thus, information on soil chemical and physical status and fertility was obtained from two independent sources (pedological and geological maps) in order to improve data reliability. However, bedrock type was not included as a variable in the analysis of niche preference and occupied niche breadth of the six species, because the forest inventory data relates tree species abundance to soil type only, but not to bedrock type.

Observations on soil profile type, grain size distribution and soil moisture regime have been used by local experts to identify the different forest site type classes in the field. Soil fertility and soil acidity/base saturation are secondary variables derived from these field data which were estimated in the forest site type maps according to a wealth of soil chemical analyses conducted on forest soils by German forest research institutions. "Soil fertility" stands primarily as a proxy for soil nitrogen availability.

The information on soil parameters was transformed into a 6-level classification system (Supplementary material, Appendix S2, Tables S3, S4 and S7). In this system, each of the regarded niche parameters (soil moisture, soil acidity/base saturation, soil fertility) is classed into six levels ranging from low (1) to high (6). This allowed to compare soil-related data from two study regions with different soil and forest inventory systems.

The information on bedrock type is also encoded in six levels (Supplementary material, Appendix S2, Table S8), expressing a gradient from sites unfavourable for plant growth due to nutrient and/or water shortage (level 1) to favourable sites (level 6) with ample nutrient and water supply.

All maps were digitised and the frequency of a certain site type determined with the Image Analysis Method (Dietz & Steinlein, 1996), using the image analysis program Adobe Photoshop. This method yields the pixel number of a certain soil or bedrock type which subsequently is converted into hectares by referring to the map scale.

By using the semi-quantitative pedological and geological parameters and encoding systems in both regions, we were able to reach at a comparable niche classification system

in southern Lower Saxony and in Slovakia, expressing the abundance of the different level categories in both study regions.

Quantifying niche preferences and the occupied niche breadth of a species

The investigation of niche preferences and of the occupied niche breadth for the investigated six tree species in the two test regions based on the forest inventory data. In Lower Saxony, the forest inventory data bank gives information about the area of each forest site type which is covered by the different tree species. The forest site types themselves are characterised by certain soil types and specific soil moisture and fertility levels. Nutrient supply is given in six categories in the forest inventory data base of Lower Saxony. Hence, these categories were directly transferred into the six-level classification system used in our study (Supplementary material, Appendix S2, Table S7). The data base also provides 44 categories for the soil moisture regime and 70 categories for the soil type, which were classed into the six-level system of our study using information on soil acidity/base saturation and soil moisture regime (Supplementary material, Appendix S2, Tables S3 and S4). In Slovakia, the forest site type classification is mainly based on the identity of soil types and sub types found in the field. This information was translated into our six-level niche parameter classification system as well (Supplementary material, Appendix S2, Tables S3, S4 and S7) by referring to the description of the soil types/sub types in various pedological databases, mainly the World Reference Base for Soil Resources (FAO, 1998). From the transformation of these forest inventory data into the niche parameter classification system, we obtained the area a tree species is holding in the study regions in each of the six parameter levels, i.e. its niche occupancy with respect to soil resources.

Based on this information, we attempted to quantify niche preferences of the six species with respect to soil nutrient availability and soil hydrology. Both study regions offered a very broad spectrum of site types with soil chemical and physical conditions ranging from level 1 (low) to level 6 (high). We compared the relative abundance of a tree species in these six resource level classes with the relative abundance of these resource classes in the entire study region. We assumed that tree species with a low preference for a certain resource level (for example high soil moisture or low fertility) should occur in the six classes at a similar relative frequency as these classes occur in nature. Hence, such a

species would deviate in its preference of resource classes (´resource level occupation`) only marginally from the relative frequency distribution of the resource itself (´resource level availability`). In contrast, a species with large differences in its relative abundance in the resource classes compared to the resource class abundance in nature was assumed to have a smaller niche breadth because it occurred preferably in certain resource classes but was under-represented in others or totally absent. We used relative values of resource class frequency (i.e. fractions of 1) instead of absolute values to account for the contrasting abundances of the six tree species in the classes 1 to 6.

To quantify the deviation between resource level availability and resource level occupation for the six species in the two regions, we used the following equation:

$$D(f) = \frac{1}{n}\left[\left(\sum_{i=1}^{6} |S_{avail}(f) - S_{occ}(f)|\right) - n\right] \quad \text{(equation 1)}$$

with

$D =$ a quantitative measure of the deviation of resource level occupation and resource level availability for a given resource f and tree species.

$n =$ number of resource levels with stands of the species being present (1 to 6) divided by 6.

$S_{avail} =$ relative abundance of soils characterised by a given resource level of resource f given as a fraction of total forest area in the study region ($0 < S_{avail} < 1$).

$S_{occ} =$ relative abundance of a tree species in a given resource level of resource f given as a fraction of its total stand area in the study region ($0 < S_{occ} < 1$).

This equation sums up the absolute differences between S_{avail} and S_{occ} over all resource levels for a given resource and relates the total to the number of resource levels with occurrence of the species. Thus, the larger $D(f)$, the more is the resource level occupation deviating from the resource level availability in nature. A species that occurs in all six resource levels at equal abundance as these resource levels are present in nature, has a D value of -1. This species also has a maximal niche breadth. After calculating D values for soil moisture, soil fertility and soil acidity/base saturation, the three D values were averaged to obtain a mean value of the resource level availability – resource level occupation difference, which is treated as an estimator of the soil niche breadth of this species.

In order to have a second measure of niche breadth, we also counted the absolute number of resource levels of the three resource categories which were occupied by a tree species in the study area with a minimum relative frequency of species occurrence of 0.1.

Data analysis

All statistical analyses were conducted with the SAS routine JMPIN Version 4.0.4 (SAS Institute, 2001). Significance was determined at $P < 0.05$ in all cases. After data on tree abundance, niche availability, niche preferences and niche breadth had been tested for normal distribution and equality of variances, ANOVA was used to test for significant differences in abundance of the groups of common and rare species between the distribution centre and the eastern range margin. Data structure did not allow for analysing differences in abundance among the six species. Further, a Chi Square test was conducted to detect differences in the availability of soil resources and bedrock types in the distribution centre and at the eastern range margin.

We used a log-linear analysis to detect differences in niche preferences between distribution centre and range margin (for the six species and the groups of common and rare species). A separate analysis was performed for the variables "species" and "abundance".

To detect differences in niche breadth attributes between the central and marginal populations of the six species and of the groups of common and rare species, we conducted a nested ANOVA with the factors "abundance" (common, rare), "range position" (centre, margin), "abundance" nested in the factor "species identity", the interaction of "abundance" and "range position" and finally the interaction of "range position" and "abundance" nested in "species identity". In case of significant overall results we performed a post hoc Tukey test to reveal individual differences between factors.

To meet distributional assumptions for the analyses, the data on abundance was logarithmically transformed.

RESULTS

Tree species abundance in the central and marginal regions

As expected, the three common tree species (*Fagus sylvatica, Quercus petraea* and *Acer pseudoplatanus*) were much more abundant in terms of the percental proportion of forest area occupied in the two study regions (mean of the three species: 17.9±6.0%) than the

three rare species (*Prunus avium, Sorbus torminalis, Taxus baccata*: 0.4±0.3 %) ($F_{1,3} =$ 38.6, P < 0.01, Table 1). For the distribution centre (Central Germany), we obtained a mean percental abundance of the three common species of 18.5±9.3% and for the rare species of 0.8±0.7% (Table 1). At the eastern distribution margin in Slovakia, the mean percental proportion in forest cover of the common species was 17.1±9.5% and of the rare species 0.02±0.01% (Table 1). While the difference in abundance was highly significant between the common and rare species ($F_{1,3} =$ 38.6, P < 0.01), the abundance difference between central and marginal populations of common or rare species was not significant at P < 0.05 ($F_{1,3} =$ 5.0, P < 0.1). If the three rare species are analysed separately, a trend for a higher relative abundance of the rare species in Central Germany compared to Slovakia is appearing (mean abundance: 0.8±0.7% vs. 0.02±0.01%, $F_{1,3} =$ 6.2, P = 0.07). In contrast, the three common species were equally abundant in the two study areas ($F_{1,3} =$ 0.2, P = 0.7). We found no interaction between tree species relative abundance and central and marginal populations ($F_{1,6} =$ 2.9, P = 0.13).

Table 1 Absolute and relative abundance of the three common and three rare tree species in their distribution centre (Southern Lower Saxony, 100-500 m a.s.l., total area: 264,220 ha) and at their eastern range margin (Slovakia, vegetation zones I-IV, 100-500 m a.s.l., 1,263,592 ha). The relative abundance gives the percental proportion of the total forest area covered by the respective tree species.

Species	Distribution centre		Eastern distribution margin	
	ha	%	ha	%
F. sylvatica	98,043	37	434,546	34
Q. petraea	26,306	10	199,873	16
A. pseudoplatanus	22,657	8.6	17,537	1.4
P. avium	5709	2.2	555	0.04
S. torminalis	662	0.25	76	0.006
T. baccata	108	0.04	38	0.003

Comparison of chemical and physical properties of forest soils between the central and marginal regions

Both study regions comprise a broad variety of geological substrates from paleozoic, mesozoic and kenozoic formations representing the full spectrum of fertile to infertile, acid to basic and dry to wet soils. The percental proportion of the various soil and bedrock types

in the area of the study region differed significantly between Central Germany and Slovakia (Chi² > 40.4; P < 0.01, Fig. 1). In the distribution centre in Central Germany, glacial and fluvio-glacial sandy and loamy deposits (18% of total area) are much more abundant than at the eastern distribution margin in Slovakia (1%); this is also true for calcareous rocks (12 vs. 6%). In contrast, aeolian loamy deposits, mostly loess, and loamy and clayey alluvial and kolluvial sediments are more abundant in Slovakia than in Central Germany (25 and 24% vs. 16 and 4%). Thus, bedrock types which produce infertile soils (bedrock levels 1 and 2) are more abundant in Central Germany (about 23% of the area) than in Slovakia (about 2%, Fig. 1). In contrast, bedrocks which give rise to the development of more fertile soils (levels 5 and 6), such as loess and alluvial and kolluvial sediments, are more frequent in Slovakia with about 49% of the total area than in Central Germany (20%).
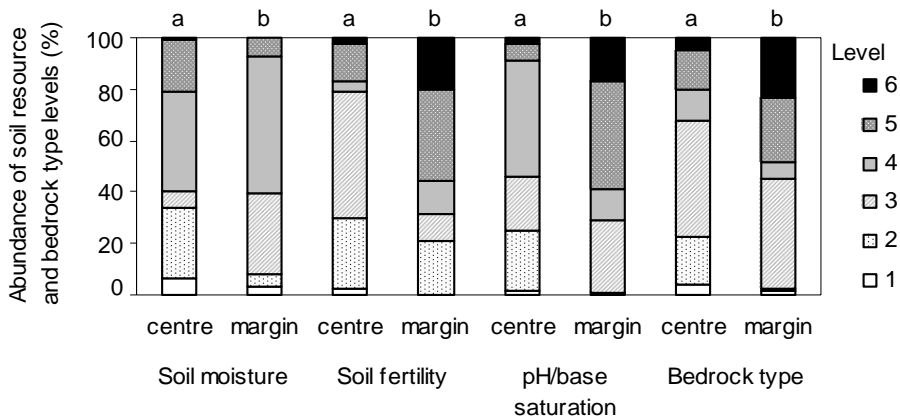

Figure 1 Relative frequency (in percent of the whole forested area) of the six resource availability classes (levels 1= very low to 6=very high) for three soil resource types (soil moisture, soil fertility and soil acidity/base saturation) and bedrock type in the two test regions in the distribution centre (Lower Saxony) and at the eastern distribution margin (Slovakia). Level 1 stands for the driest, poorest, most acidified sites with lowest base saturation and least favourable bedrock types, level 6 for the moistest, richest, most fertile and base-rich sites and bedrocks with most favourable properties. Different letters above the bars indicate significant differences between the distribution centre and eastern margin for each resource type. Chi^2 > 40 and P < 0.01.

The difference in geological substrate types between the distribution centre and distribution margin is mirrored in the relative abundance of soil types and the frequency of forest sites with moist or dry, acid or basic, fertile or infertile properties. With respect to soil hydrology, moderately dry (27%) and moist soils (39%) are the most abundant

categories in Central Germany, while ´moderately moist` soils (or soils with alternating moisture status) are quite rare (about 6%). In Slovakia, soils with a higher moisture status are more abundant, despite its more continental climate at the distribution margin. In this region, the bulk of forest soils refers to the soil moisture levels 3 and 4 (moderately moist and moist), while wet and dry soils, i.e. soils with a more extreme moisture regime, are much less abundant than in Central Germany (Fig. 1).

Similarly, there are differences between the two study regions with respect to soil chemical properties as estimated by the two variables ´soil fertility` and ´soil acidity/base saturation`. Forest soils in the distribution centre were, on average, more acid and less fertile than at the distribution margin. This difference is expressed by the dominance of soils with the properties ´medium fertility` (about 49%) and ´moderately acid` (about 46%) in Central Germany, while rich or very rich and weakly acid to neutral-basic soils represented 17 and 9%, respectively (Fig. 1). In contrast, Slovakian forest soils were dominated by profiles with the attributes ´rich` and ´weakly acid` while highly acid soils were very rare. Thus, the average forest soil in Central Germany was somewhat drier, more acid and less fertile than in Slovakia. Nevertheless, the spectrum of different soil types occurring in Central Germany and Slovakia was similarly broad.

Niche preferences in the central and marginal regions

Figures 2 to 4 contrast the ´availability patterns` of a soil resource for the six tree species, i.e. the abundance of soils in a given resource level class as a fraction of the soils of the whole study region, with the occupancy patterns, i.e. the relative abundance of the ´occupied` resource levels in the total area covered by the species in the study regions. Resource levels with a higher occupation than availability indicate preferred resource states, those with a lower occupation than availability stand for soil chemical and physical states where the species is less frequently found than would be expected from the abundance of that soil type. Figure 2 shows that the three common tree species (*F. sylvatica, Q. petraea, A. pseudoplatanus*) have a clear preference for moist sites (level 4) which are neither too dry nor not too wet, minimizing the threat of both drought and anoxia. This is also true for the rare species *Prunus avium*, while *Sorbus torminalis* seems to ´prefer` moderately dry or very dry sites. *Taxus baccata* occurred in Central Germany with nearly the same relative abundance in all moisture level classes as they existed in

nature, while this species was relatively abundant at very dry sites in Slovakia. Comparing the two study regions, indicates that the most distinct niche shift with respect to soil hydrology seems to occur in *Sorbus torminalis* and *Taxus baccata,* which reveal an apparently higher preference of dry sites at the eastern range margin than in the distribution centre. The other four species were relatively more abundant at very dry and also at moist to wet sites in Slovakia compared to Central Germany, indicating that the moisture niche was somewhat broader in Slovakia. While the first four abovementioned species showed a similar preference along the moisture axis in both study regions, it appears that drier and also wetter sites are more distinctly avoided in Central Germany than in Slovakia.

With respect to soil fertility, which may primarily stand for nitrogen availability, all six species showed a preference for sites with the levels 4 or 5 (good to rich) in Central Germany, and seemed to avoid sites with medium, poor and very poor nutrient availability (Fig. 3). However, this picture was markedly different in Slovakia where all species except for *T. baccata* showed a fertility preference which was by one level lower than in the distribution centre. In Slovakia, rich and very rich sites apparently were avoided in the sense that the species occurred at these sites less frequently than would be expected from the abundance of these soil types. Thus, all five broadleaved species exhibited a marked niche shift toward less fertile sites when moving from the distribution centre to the margin.

Soil acidity/base saturation was the factor that differentiated most between the distribution centre and margin and also between the species with respect to the preferred range. The three common tree species were much more abundant in Central Germany at highly acid sites and also at neutral-basic sites than expected from the abundance of those site types (Fig. 4). This pattern was markedly different from the situation in Slovakia where *F. sylvatica*, *A. pseudoplatanus, Q. petraea* and *P. avium* were most abundant in relative terms on moderately acid soils, i.e. they seemed to prefer less acidic soils than in Central Germany. There was also a marked difference in the behaviour of *P. avium* in the two regions: this species clearly preferred neutral-basic soils in Central Germany but did not so in Slovakia with a peak of occurrence on moderately acid soils. The two rare species *S. torminalis* and *T. baccata* showed a similar abundance pattern with respect to soil acidity in the two regions with a clear preference for neutral-basic soils. The niche preference of common and rare species differed in most cases significantly between distribution centre and distribution margin for the three resource types ($Chi^2 > 33.91$, $P < 0.01$).
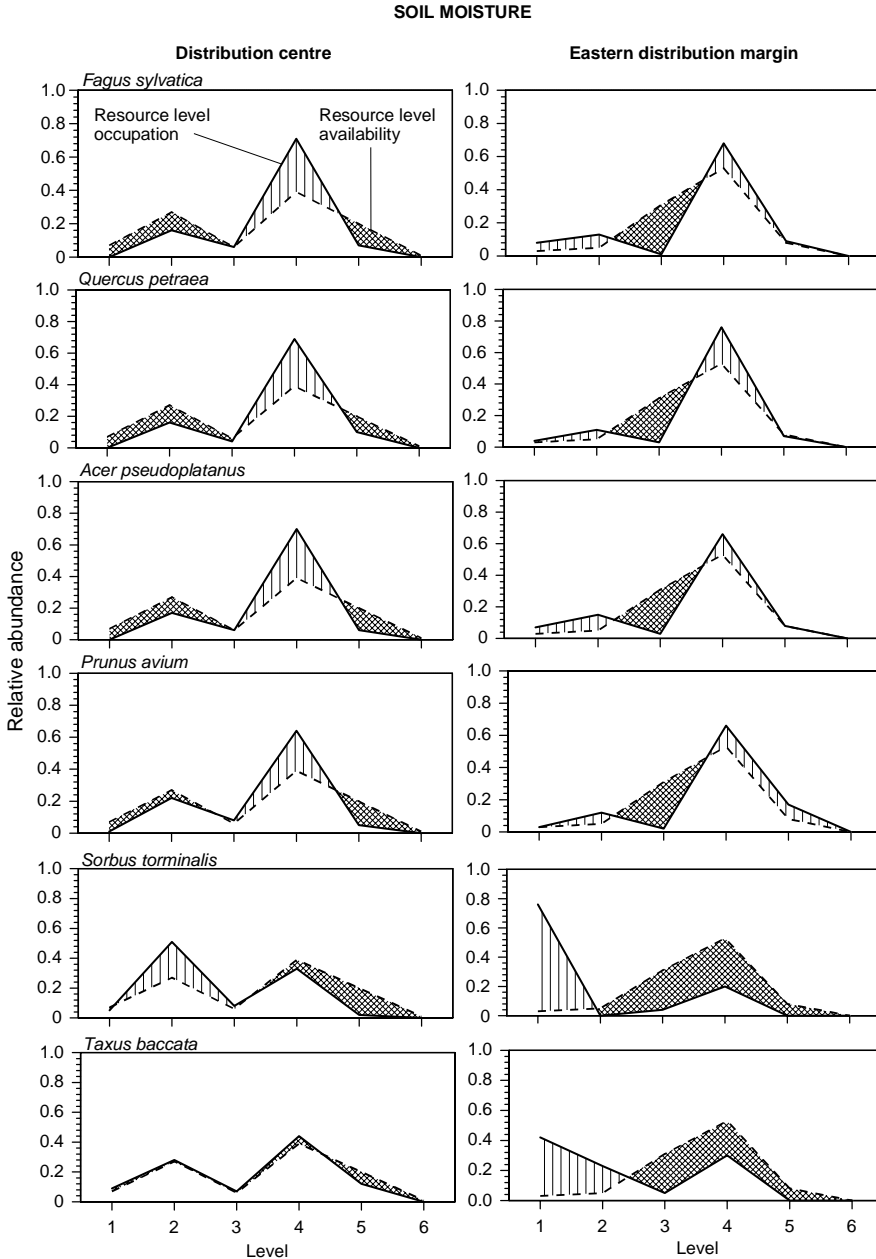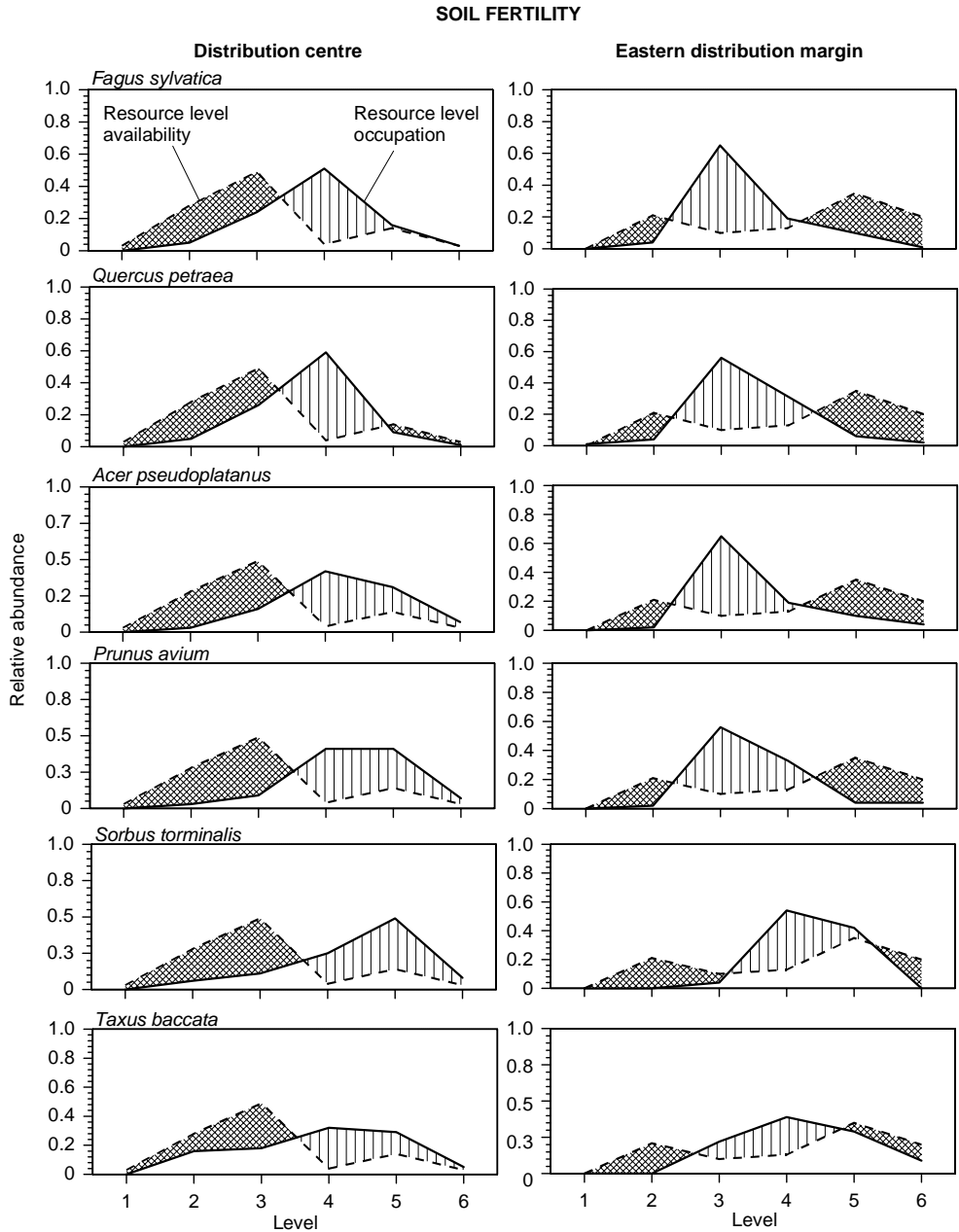
SOIL MOISTURE

Figure 2 Availability of soil moisture levels and occupation of these levels by stands of *Fagus sylvatica*, *Acer pseudoplatanus*, *Quercus petraea*, *Prunus avium*, *Sorbus torminalis* and *Taxus baccata* in the species` distribution centre and at the eastern distribution margin. Level 1 represents the driest and level 6 the wettest sites. The species is overrepresented on levels, where occupation is higher than supply (vertical hatching) and underrepresented on levels, where occupation is smaller than supply (cross-hatched).
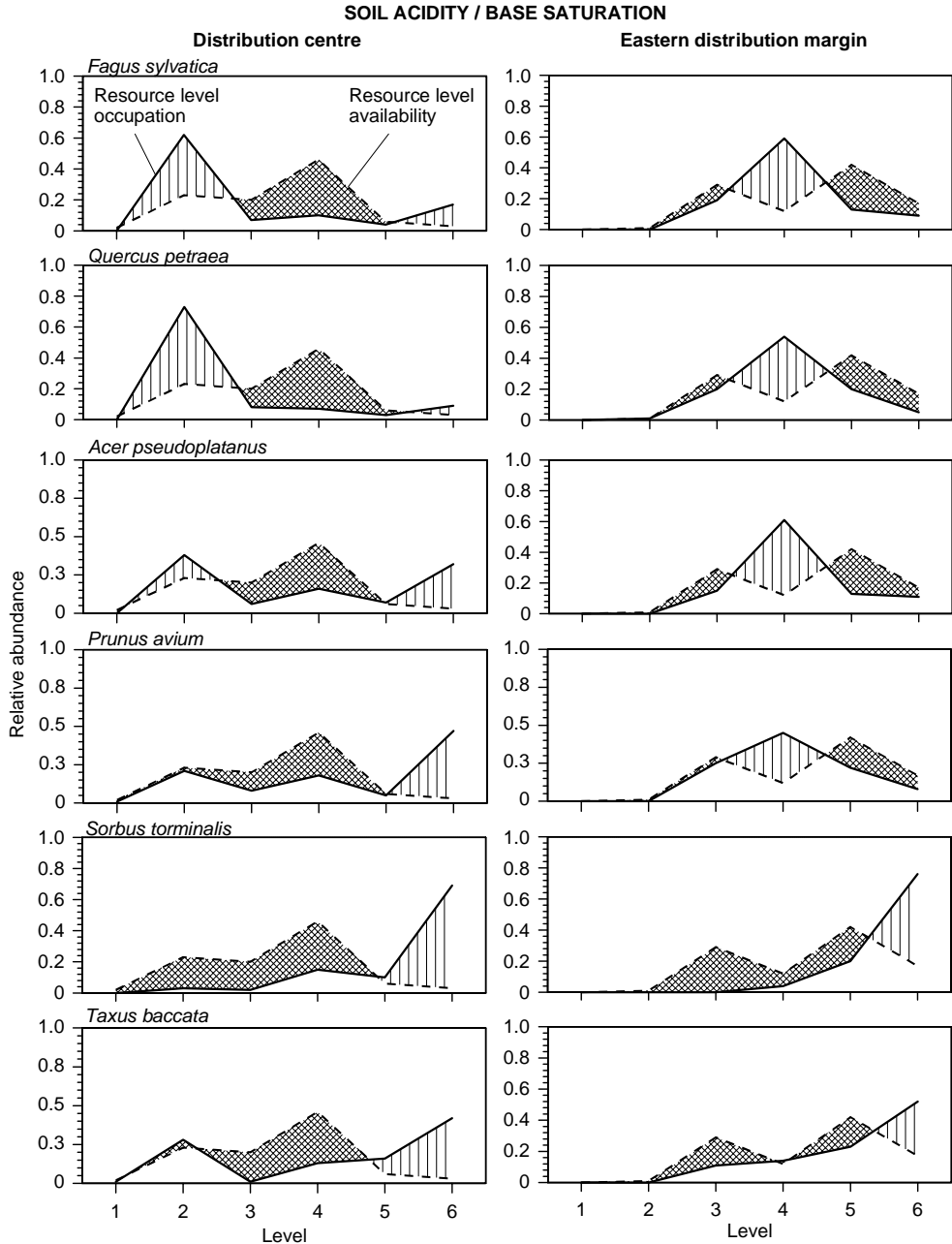
SOIL FERTILITY

Figure 3 Availability of soil fertility levels and occupation of these levels by stands of *Fagus sylvatica*, *Acer pseudoplatanus*, *Quercus petraea*, *Prunus avium*, *Sorbus torminalis* and *Taxus baccata* in the species` distribution centre and at the eastern distribution margin. Level 1 represents the least fertile and level 6 the most fertile sites. The species is overrepresented on levels, where occupation is higher than supply (vertical hatching) and underrepresented on levels, where occupation is smaller than supply (cross-hatched).

SOIL ACIDITY / BASE SATURATION

Figure 4 Availability of soil acidity/base saturation levels and occupation of these levels by stands of *Fagus sylvatica*, *Acer pseudoplatanus*, *Quercus petraea*, *Prunus avium*, *Sorbus torminalis* and *Taxus baccata* in the species` distribution centre and at the eastern distribution margin. Level 1 represents the sites with lowest pH-value/base saturation and level 6 the sites with highest pH-value/base saturation. The species is overrepresented on levels, where occupation is higher than supply (vertical hatching) and underrepresented on levels, where occupation is smaller than supply (cross-hatched).

Quantifying soil niche breadth

The overall test of differences in the size of the *D* value (i.e. deviation of resource level occupation and availability), as calculated with equation (1) between individual species, between common and rare species, and between central and marginal populations indicates a weak significance (F = 2.18, P = 0.05), which may be due to the different *D* values of the individual tree species (F = 3.1, P = 0.03). *P. avium* reached significantly lower *D* values, i.e. had a higher realised niche breadth, than *S. torminalis*. There is no difference in the deviation of *D* between common and rare species, between central and marginal populations, between the interactions of abundance (common, rare) and range position (centre, margin), and between the interactions of range position and species nested in abundance (F < 0.62, P > 0.14, Fig. 5).
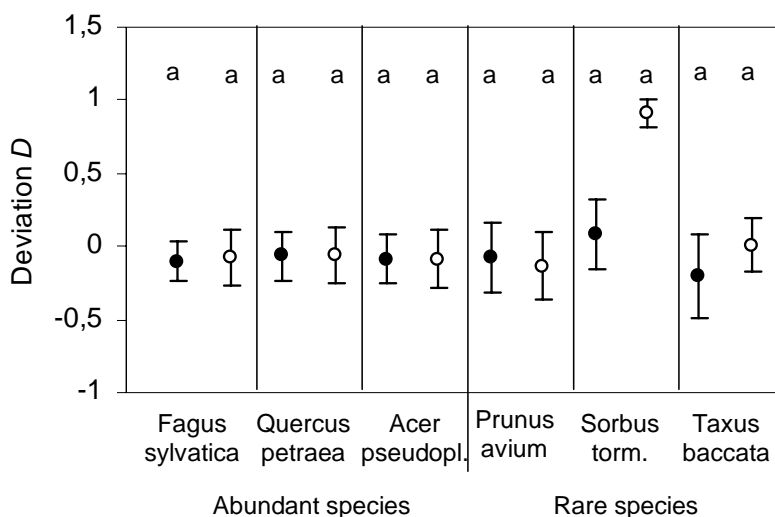

Figure 5 Deviation of resource level occupation and resource level availability for three common (FagSyl = *Fagus sylvatica*, AcerPseud = *Acer pseudoplatanus*, QuercPet = *Quercus petraea*) and three rare (PrunAv = *Prunus avium*, SorbTorm = *Sorbus torminalis*, TaxBac = *Taxus baccata*) Central European tree species in the distribution centre and at the distribution margin as calculated with equation (1) (see text); mean of the resource types soil moisture, soil fertility and soil acidity/base saturation (± standard error). A species that occurs in all 6 resource levels at equal abundance as these resource levels are present in nature, has a niche breadth value of -1. The larger the value, the more deviates the resource level occupation from the resource level availability. Filled circles = distribution centre, open circles = distribution margin. Different letters indicate significant differences between central and marginal populations.

An estimation of niche breadth from the simple count of the occupied resource levels shows that abundant and rare species, and central and marginal populations, do not differ systematically in occupied niche breadth. Only *T. baccata* tended to occur on more resource levels than the other species (Fig. 6).
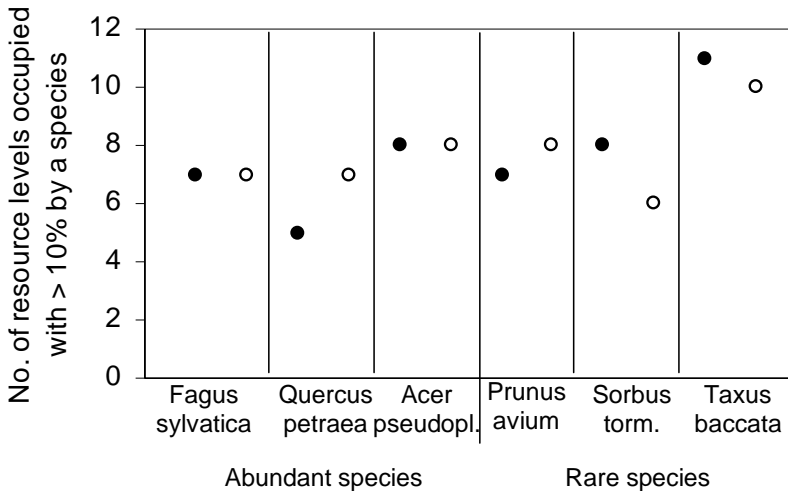

Figure 6 Number of resource levels occupied by a tree species with a relative frequency > 0.1 in the resource types soil moisture, soil fertility and soil acidity/base saturation in the two test regions. Maximum number of resource levels = 3 x 6 = 18. The larger the number of occupied resource levels, the broader the soil niche breadth of the species in the region.

DISCUSSION

Abundant-centre distribution of Central European tree species

Abundance patterns of species are strongly dependant on the quality of the environment (Kendeigh, 1974; Cox & Moore, 1985). A species achieves highest population densities where a maximum of its requirements are met in an optimal way. With increasing distance from an optimal site, the probability of meeting the multidimensional needs of a species decreases and, thus, population size declines (Brown, 1984). As niche factors are partly autocorrelated, nearby sites often provide rather similar living conditions and a change of site qualities with respect to a species` needs and should occur gradually rather than abruptly (Brown, 1984). This would be a geographical explanation why optimal sites will

most likely be found towards the centre of the distribution range and not close to the margin (Hengeveld & Haeck, 1982; Brown, 1984; Carey *et al*., 1995). Long-lived organisms such as trees may deviate from this pattern, because juvenile and mature plants often differ largely in their requirements. Mature trees can grow well in an environment where the seedlings of this species are only rarely successful because of summer drought, flooding or other stressful conditions (see Saxe *et al*., 1998 and references therein).

In fact, empirical evidence in support of the abundant-centre distribution theory is not strong. Sagarin & Gaines (2002) reviewed 22 studies on the abundant-centre distribution and found only 39% of the studies supporting the hypothesis. In the case of trees, a clear picture does not emerge. Murphy *et al*. (2006) analysed abundances and distribution ranges in the eastern North American tree flora and reported for about 60% of the species highest abundance at locations surrounding the centre, but not necessarily in the distribution centre itself. However, 40% of the investigated species did not change significantly in their abundance between the centre and the margin.

In the six Central European tree species of this study, a trend for higher abundances in the distribution centre (Central Germany) than at the eastern margin (Slovakia) was found for the three rare species and for the abundant species *A. pseudoplatanus*, while the abundant species *F. sylvatica* and *Q. petraea* were equally abundant in the recent forest vegetation in both regions. Before assessing this result in the light of the abundant-centre distribution hypothesis, two limitations have to be considered. First, the number of tree species in our sample is rather small for testing the hypothesis. Second, a careful consideration of human influence on tree species abundance in Central Europe is required, as human impact has influenced the natural forest vegetation since more than 7000 years (Lang, 1994), thereby reducing forest cover to about a third of the pristine conditions and altering tree species composition in the managed forest stands (Willis, 1993; Zerbe & Brande, 2003). This influence may be small or even negligible in the case of *P. avium*, *S. torminalis* and also *A. pseudoplatanus*, which were not in the focus of forestry and are species with only a small natural abundance in Central European forest communities (Ellenberg, 1996). Common Yew (*Taxus baccata*) is a rare conifer in Central European broadleaved forests which has lost ground due to intensive cutting for its valuable very hard timber, but also because its foliage is poisonous for horses, and the tree was eradicated in many places in the Middle ages for this reason. However, *T. baccata* is a light demanding, though shade tolerating tree, which must have been rare in the dark virgin beech or oak-hornbeam-linden forests of prehistoric Central Europe, but was promoted only on the forest clearings during the early

period of human settlement (Schütt *et al.*, 1994). Thus, it is likely that the recent abundance patterns of Yew are not that different from its natural abundance in Central Europe.

The situation is different with beech and sessile oak. *F. sylvatica* is the dominant tree species in Central Europe in the natural forest vegetation which presumably covered about 67% of the area of Germany prior to human intervention, forming mono-dominant, species-poor stands on a broad range of acid to basic bedrock types (Ellenberg, 1996; Leuschner, 1998). This species undoubtedly lost a large number of its original sites due to conversion to agricultural land or replacement by planted spruce and pine. The recent number of 37% of forested land occupied by beech in the test region of Southern Lower Saxony must be contrasted with an estimate of about 90% of that area which once may have been beech forest. This number is indicated by maps of the potential natural forest vegetation of that region (e.g. Bohn & Neuhäusl, 2000/2003), which base on a solid reconstruction of the former vegetation prior to human intervention using palynological evidence and virgin forest studies. The situation is different in Slovakia where the landnam and the conversion of broadleaved to coniferous forest were less intense than in Germany (Gerlach, 1970; Roering, 1999). According to the map of Bohn & Neuhäusl (2000/2003), beech may have occupied not more than about one third of the countries' area in the period before human intervention, thus being less abundant in a country wide perspective than in e.g. Central Germany. Beech is rare or absent from the planar and collin belts of lower elevation where *Quercus* species dominate in the more continental climate of Slovakia (Roering, 1999). In contrast, beech is the dominant species of the natural forest vegetation in the planar and collin belts of Western Germany (Ellenberg, 1996). Thus, while the figures of actual abundance of beech may be misleading due to forestry impact, information from well supported constructions of the potential natural vegetations give evidence that this species was once much more abundant in terms of total area covered in Central Germany than in Slovakia where its distribution is geographically restricted to the mountain ranges, leaving the lowlands to other broadleaved tree species (Roering, 1999).

Quercus petraea, on the other hand, was shown to be a species which already had lost most of its sites in Central Europe to the late invading species beech, when humans started to open the forests from about 7000 B.P. onwards (Schütt *et al.*, 1994; Ellenberg, 1996). Palynological data and observations on forest dynamics make it likely that *Q. petraea* was a relatively rare species in Central Germany in that time but was promoted by man through the opening of the forests and cattle ranging, and by direct planting in forestry (Hegi, 1981;

and see Schütt *et al.* 1994 and references therein; Küster 1997). Sessile oak only lost ground in recent time when forestry shifted to conifer monocultures and re-established beech which outcompetes sessile oak. In the more continental climate of lowland Slovakia, *Q. petraea* has a greater importance in the natural forest vegetation than in Central Germany (Roering, 1999). We assume that the percental figures of sessile oak in the two regions (10 and 16%) may be not too far from the potential natural abundance of the species in Germany and Slovakia.

We conclude that the available data from the six Central European tree species mostly can be judged as being supportive of the abundant-centre distribution hypothesis, despite the bias in the data caused by human influence on forest composition. In the case of five of the six species, abundance in the natural forest vegetations most likely was higher in the distribution centre than at the margin. In one case (*Q. petraea*), no decrease, or even an increase toward the eastern margin, may exist.

Niche breadth and niche preferences of central and marginal populations

Using a large base of semi quantitative data on soil properties and precise maps which allowed relating forest stands to edaphic characteristics, we were able to quantify the niche breadth and niche preferences of the six species in the central and marginal test regions. Both parameters must be assessed in the light of the availability of resources, i.e. the abundance of soils with certain qualities as sites for tree growth in the Central German and the Slovakian test regions. Differences in niche breadth and niche shifts can only be detected if the spectrum of site types is similarly broad in the two regions to be compared. This is the case for the Central German and Slovakian regions, which both comprise the full spectrum of fertile to infertile, acid to basic, and dry to wet soils. However, due to geologic and climatic particularities, the average forest soil in Central Germany was somewhat drier, more acid and less fertile than in Slovakia reflecting the higher abundance of loess and alluvial and kolluvial sediments in the latter region.

We found no convincing evidence for the hypothesis that species occupy a smaller niche at their distribution margin than in the centre. Such a tendency might appear in the data of *Sorbus torminalis* and *Taxus baccata*, but the difference was small and not visible in the other species (see Fig. 6). However, our data indicate a pronounced shift in the occupied soil niches between centre and margin in certain species.

All species, but most pronounced *S. torminalis* and *T. baccata*, were relatively more abundant at dry sites at the range margin than in the centre, which seems astonishing because we expected that the trees would avoid more drought affected sites in the eastern part of their distribution range with a more continental climate. However, annual temperature and precipitation were more or less similar in the two regions which leads us to the assumption that more extreme winter temperatures and a higher threat of late frost in spring in the continental climate may be more influential than is water shortage in summer for the growth and vitality of these species.

A niche shift was also evident with respect to the species` demand for soil nutrient supply, because all species (except for *T. baccata*) showed a fertility preference in Slovakia that was by one level lower than in the distribution centre. Thus, a marked niche shift toward less fertile sites was observed from centre to margin. This change was accompanied by a higher preference of soils with less acid to neutral reaction in the three common species in Slovakia as compared to Central Germany. Nevertheless, the common species are overrepresented on highly acid as well as neutral to basic sites only in their distribution centre.

Niche shifts as observed in our data can have three possible causes: first, species could meet a less favourable environment at the distribution margin, forcing them to colonize specific ´azonal` or ´extrazonal` sites with conditions that still fulfil the species` demands despite a generally unfavourable environment (Ellenberg, 1996). This behaviour is expressed by Walter`s ´rule of relative site constancy` (Walter & Breckle, 1983). With respect to soil moisture, we found no evidence in support of Walter`s rule.

Second, niche shifts could result from competitive displacement when species meet other competitors at the range margin or competitive balances change when moving from the centre to the margin (Austin & Austin, 1980; Walter & Breckle, 1991). Especially species, which are susceptible to competitive displacement or abiotic or biotic stressors, should show stronger niche variation between geographic regions than generally more competitive species in order to compensate their disadvantage (Prinzing *et al*., 2002). Accordingly, species with a higher competitiveness should be able to displace less competitive species from the best sites. This pattern does not seem to be applicable to our study, as highly competitive species such as *F. sylvatica* and *A. pseudoplatanus* do not prefer better sites at the eastern distribution margin than in the centre. Furthermore, the rare species, which should be displaced towards "worse" sites at the margin as a result of their weaker competitiveness, occupy at least as good sites at the margin as in the range centre. Hence,

competitive displacement as a consequence of unfavourable site conditions in marginal areas is not evident in our six species. A similar observation was made by Prinzing *et al*. (2002), who investigated the influence of competition and stress on the niches of plant species on a between-region scale, which is comparable to ours, and only found a negligible influence. They observed that niche variation is not higher in species, which are subject to competitive displacement, nor is it higher in species that reach their distribution limit and suffer from increased stress. Comparable conclusions were drawn by other authors for observations on the community level (Diekmann, 1995; Diekmann & Falkengren-Grerup, 1998).

A third factor possibly responsible for niche shifts is the influence of forestry. The impact of forestry generally seems to be lower in Slovakia than in Central Germany (Roering, 1999; Niedersächsisches Ministerium für den ländlichen Raum, Ernährung, Landwirtschaft und Verbraucherschutz, 2004; Ministry of Agriculture of the Slovak Republic, 2006), leaving a greater proportion of the forest areas in a near-natural state in Slovakia (49%) than in Central Germany (less than 5%). Forest management and land use decisions are undoubtedly responsible for a number of ´niche preferences` that appear from our analysis and are hardly explained by the species` physiological preferences or competitive interactions. The apparent ´avoidance` of *F. sylvatica, Q. petraea* and *A. pseudoplatanus* of sites with medium soil acidity levels (3 and 4) is most likely a consequence of replacement of beech by faster growing spruce on these sites. However, other niche preferences evident from our analysis cannot be explained by the activity of forestry, notably the more abundant occurrence of all species on drier sites in Slovakia and the apparently higher tolerance for acid soils in Slovakia of most species. In particular, in the case of the three rare tree species, forestry has adopted management and planting rules that are largely based on the natural site preference of these species in order to maximize yield. Thus, at least for these species, actual niche occupancy should be not too different from natural niche occupancy.

CONCLUSIONS

Our analysis of three common and three rare Central European tree species indicates that the majority of species is more abundant in the distribution centre than at the margin, thus supporting the abundant-centre distribution hypothesis. However, it appears that the niche

breadth with respect to soil chemical and hydrological properties is not markedly different between central and marginal populations of a species, while some niche shifts were recognized. Even though forest management has exerted a profound influence on the species composition of Central European forests, the data allows the conclusion that neither competitive displacement of weaker competitors at the range margin, nor a niche shift of superior competitors to ´better` sites is important in this species sample. It is possible that these species are controlled in their abundance at the eastern distribution margin not by water and nutrient availability, but other factors not investigated here such as winter and spring frost intensity, or herbivore damage. Physiological studies have to reveal whether any of these stressors is more intense at the eastern range margin. In our study, we only addressed the eastern distribution margin of the species since this border is rather distinct for several Central European tree species. A deeper understanding of macroecological patterns in the Central European tree flora would require an investigation towards southern, western and northern distribution limits as well, because there patterns could be different again (cf. Ferguson & McLoughlin, 2000; Sagarin & Gaines, 2002; Murphy *et al.*, 2006). Furthermore, other critical factors operating on large geographical scales, like species turnover, post glacial migration processes or species genetic variability, to mention just a few, will also have to be considered in this context.

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Chapter IV

Are Central European trees at their eastern distribution margin more stress-exposed than in the distribution centre?

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ABSTRACT

Aim Four Central European tree species (*Fagus sylvatica* and *Acer pseudoplatanus* as common species, *Prunus avium* and *Taxus baccata* as rare species) were investigated for symptoms of drought stress and the degree of leaf herbivory in populations at the distribution cenre (Central Germany) and at the eastern distribution margin (South-East Poland). We hypothesized that trees from marginal populations exist under less favourable environmental conditions and thus are more affected by drought stress and leaf herbivory than trees from central populations where growth conditions should be closer to the species' optimum. We further hypothesized that rare tree species are more stressed at the distribution margin than common species.

Location Central Germany and South-East Poland

Methods In two summers (2005: average climatic conditions, 2006: relatively dry), we investigated more than 15 leaf, fine root and growth-related traits in adult trees of the four species comparing 23 stands in Central Germany to 17 stands in South-East Poland.

Results Neither foliar $\delta^{13}C$ signature, specific leaf area (SLA), nor fine root biomass density or mean tree ring width during the past 50 to 80 years gave evidence of a higher drought exposure of trees of the marginal populations. Moreover, dendrochronological analyses revealed no higher climate sensitivity of stem increment in the continental climate of South-East Poland as compared to the sub-oceanic climate of Central Germany. Leaf herbivory hit a larger number of leaves in the marginal populations of *F. sylvatica*, *A. pseudoplatanus* and *P. avium* in the drier summer 2006 as compared to the central populations, but this difference was absent in the summer 2005.

Main conclusions Adult trees of the four species do not seem to generally be more stressed by drought events or leaf herbivory at the eastern margin of their distribution range than in their distribution centre. Further, we found no evidence of a higher stress exposure of the rare species. We speculate that seedlings and saplings may be more sensitive than adult trees and that other stressors such as winter and/or late frosts may be more decisive in determining tree vitality at the eastern distribution margin.

Key words Central European tree species, distribution centre, eastern range edge, ecophysiological stress, macroecology, leaf parameters, fine root density

INTRODUCTION

A higher abundance and greater niche breadth in the distribution centre than at the margin is a macroecological pattern found in many systematic groups (Brussard, 1984; Bock, 1987; Gaston & Lawton, 1990; Sagarin & Gaines, 2002). A reason for the reduced abundance and niche breadth at range edges may be increased environmental stress, forcing species to explore only the most favourable sites, thereby reducing realized niche breadth (Brown, 1984; Hall *et al.*, 1992). However, this pattern may not be universally valid. For example, Leuschner *et al.* (Chapter III) tested this niche reduction hypothesis for Central European tree species, but found no reduction of soil niche breadth from the distribution centre to the eastern range margin. They concluded that environmental stress on mature forest trees at the range edge may not be as severe as expected, or that other factors than the tested soil variables are limiting the tree species at their distribution range. Beside temperature extremes, drought is a stressor which often is associated with range edges not only in the South, but also in the East, of the plant´s distribution areas where increasing continentality may coincide with reduced precipitation. In order to asses the degree of drought stress experienced by mature trees, it is feasible to investigate different tree organs in consecutive seasons (Leuschner *et al*., 2001), because leaves, roots and stems may differ in their sensitivity to drought (Westgate & Boyer, 1985). Meaningful variables, that integrate over longer time spans, are the $\delta^{13}C$ signature of leaves (e.g. Dawson *et al*., 2002), the live/dead-ratio of fine roots (Jentschke *et al*., 2001; Godbold *et al*., 2003; Vanguelova *et al*., 2005), specific leaf area (e.g. Cornelissen *et al*., 2003), stem increment growth chronologies (Schweingruber, 1996), and possibly leaf asymmetry (see Palmer & Strobeck, 1986 for a review).

Numerous studies have compared the drought response of trees from habitats differing in soil water availability. However, most of them dealt with seedlings in common garden experiments or glasshouses, (Tognetti *et al*., 1995; Peuke *et al.*, 2002; Nielsen & Jørgensen, 2003; Peuke & Rennenberg, 2004; Aspelmeier & Leuschner, 2004, 2006), whereas mature trees growing at sites with contrasting water supplies have been studied in less detail (e.g. Meier & Leuschner, 2008a, b; Meier & Leuschner, in press). Comparisons between tree populations in the distribution centre and at the margins may not only serve for testing macroecological hypotheses, but can also give valuable indications on the possible response of tree species to expected climate change. Many Central European tree species reach their eastern distribution margin in Eastern Poland or

Ukrainia where a distinct transition from a sub-continental to a continental climate with colder winters and a higher frequency of summer drought occurs. For parts of Central Europe, recent IPCC scenarios (IPCC, 2007) predict an increase in summer temperatures and a decrease in summer precipitation, i.e. a 'continentalisation' of the climate in the coming decades. Thus, a comparison of tree vitality in sub-oceanic Central European and sub-continental Eastern European populations might serve as sort of a space-for-time substitution of climate change effects on Central European trees.

In this study, we compared the vitality and drought stress symptoms of two common (*Fagus sylvatica* L., European beech; *Acer pseudoplatanus* L., Sycamore maple) and two rare (*Prunus avium* (L.) MOENCH, Wild cherry; *Taxus baccata* L., Yew tree) tree species from populations in the distribution centre (Central Germany) and the eastern range margin (South-eastern Poland). We tested the hypotheses (i) that trees from marginal range positions with a sub-continental to continental climate are more drought-affected than those from central locations with a sub-oceanic climate, and (ii) that the rare species in general suffer more from drought stress than common species. We focused on adult trees that have been studied less frequently than seedlings and saplings, and investigated more than 15 different morphological and physiological parameters at leaf, stem and root levels for characterizing tree vitality in two subsequent years.

METHODS

Tree species and study sites

Two common (*Fagus sylvatica, Acer pseudoplatanus*) and two rare Central European tree species (*Prunus avium, Taxus baccata*) were chosen for study. All four species have their distribution centre in Germany and reach their eastern distribution margin in South-eastern Poland or western Ukrainia. A total of 40 stands containing these species was selected in two areas in Central Germany close to the distribution centre, and in South-eastern Poland close to the eastern distribution margin. The central area encompassed forest stands in Southern Lower Saxony, Northern Hesse and Western Thuringia. The marginal area includes stands in an area between Cracow, Kielce and the Polish-Ukrainian and Polish-Slovakian borders. In both areas, each 8 to 10 adult stands per species were selected (*Taxus baccata* in the centre: 7, at the margin: 6) which grew on geological bedrock types that are

typical for these species in the distribution centre and margin (see Chapter III). In the case of *Acer pseudoplatanus*, *Prunus avium* and *Taxus baccata*, this were base-rich rocks (mostly limestone with partial loess cover); the beech stands grew on both base-rich and acidic base-poor substrates (limestones and sandstones). Typically, two or three of the forest species occurred together in the stands. The two study regions are well comparable with regard to elevation (100-500 m a.s.l.) and the mosaic of geological substrates (see Chapter III).

Leaf and root sampling

Fourteen leaf and fine root morphological and chemical traits were investigated in order to assess tree vitality and to detect possible stress symptoms among the four species. Sampling was conducted in the two consecutive summers of 2005 (no pronounced summer droughts) and 2006 (several rainless periods in summer). In each stand, three trees per species, which reached the upper canopy, were chosen by random. One branch of the upper sun canopy per tree was extracted using a fishing line which was shot into the crown with a crossbow. Branches of *T. baccata* were collected with secateurs as the trees reached a maximum height of 4 m only.

The 30 youngest leaves (in the case of *T. baccata* needles) of each branch were collected for analysis. Immediately after sampling, all 30 leaves were photographed with a digital camera from a top view and leaf area, leaf area loss due to herbivory and leaf asymmetry analysed with the software Adobe Photoshop using the Image Analysis Method after Dietz & Steinlein (1996). The degree of leaf asymmetry was calculated from the size difference of the left and right leaf halves. The proportion of damaged leaves was assessed by counting all leaves that showed damage due to herbivory, regardless of whether large or small parts had been lost. Leaf area loss was defined as the leaf area eaten up by herbivores (unit: cm²).

After drying (70°C, 48 h), specific leaf area was calculated for every leaf. The concentrations of C and N and the $\delta^{13}C$ signature were detected in the ground leaf mass with a C/N elemental analyser (NA1110, CE-Instruments, Rodano, Milano, Italy) in the Stable Isotope Laboratory (KOSI) of the University of Göttingen, those of Ca, K and Mg by atomic absorption spectroscopy (AAS vario 6, analytic jena, Jena, Germany). Foliar

concentration of phosphorous was detected by yellow-dying after digestion with 65% HNO_3 at 195°C and subsequent photometric measurement.

Fine roots (< 2 mm in diameter) were analysed for root density (mass per soil volume) and the live/dead-ratio of root mass in the topsoil, two variables that may characterize the vitality of the fine root system of trees. Because sampling in the 40 stands was rather time-consuming, we conducted a rotating sampling scheme to guarantee temporal comparability of the German and Polish samples. In both study years, root sampling and subsequent analysis were conducted in two rounds. In 2005, the first batch was taken in Poland in the period July 23 to 28 during maximum summer drought; the second batch was taken from October 15 to 19. In Central Germany, two sampling campaigns were conducted from August 2 to 5, and from October 24 to 28, 2005. In 2006, alternating sampling was conducted in Poland in the periods July 22 to 24 and October 2 to 3, and in Germany from August 3 to 8 and October 11 to 13.

In each of the 40 stands, 6 tree individuals per species were randomly chosen and the fine root biomass and necromass was sampled twice in 2005 and 2006. Each one soil core (10 cm depth, 3.3 cm in diameter) per tree was extracted at a stem distance of 1.5 m in northern direction. The samples were stored in a cooling box and transported immediately to the laboratory where processing of the stored roots (4°C) took place within 6 weeks. The root material was soaked in water and carefully washed out over a sieve with 0.2 mm mesh width to recover even finest root fragments. We only considered roots < 2 mm in diameter (fine roots). Fine root fragments > 10 mm in length were picked out by hand. Based on earlier work of this group (Hertel & Leuschner, 2002) and other authors (Persson, 1978; Murach, 1983), we used a morphological key to distinguish the roots of the respective target species from smaller amounts of other root species that were discarded. Criteria of species identification were the morphology and colour of the root periderm, fine root branching patterns, and the morphology and abundance of fine roots tips (cf. Scherfose, 1990; Hertel, 1999; Hölscher *et al.,* 2002); this was done under a binocular with 10x magnification. Live and dead fine roots were distinguished by colour, elasticity and degree of cohesion of cortex, periderm and stele under the microscope (see Persson, 1978; Leuschner *et al.*, 2001). In order to sort out the finest root fragments for distinguishing between live and dead roots following the criteria established by Hertel (1999) and Leuschner *et al.* (2001), we transferred the residue of each sample onto a piece of filter paper (diameter 100 mm) that was cut into 4 sectors, and analysed each sector carefully for even finest root segments under a stereo-microscope at a magnification of 40x.

The root material was dried at 70°C for 4h, weighed and related to the volume of the soil core to give biomass or necromass root density per soil volume (g L^{-1}). In total, more than 750 root samples were analysed in the two years. All analyses were conducted by two persons with a standardised protocol to minimise bias in the recognition of the root fractions.

Stem increment analysis

In July and August 2005 and 2006, we extracted wood cores from stems of *Fagus sylvatica*, *Acer pseudoplatanus* and *Prunus avium* in each four stands of the two study regions and analysed stem increment and climate sensitivity of growth in the different stands. *Taxus baccata* was excluded from the dendrochronological analysis because its wood has a very high density. Five dominant and vital trees per stand and species were selected by random with vitality assessed visually according to Kraft´s tree classification system (class 2 and higher, Kraft, 1884). Each one 5 mm core was extracted at 1.3 m height with a Suunto increment corer (Suunto, Finland). For minimising twisting upon drying, the cores were glued into wooden slates. Chalk was applied to increase the visibility of the annual rings. Ring width and the number of rings per core length were analysed at a precision of 1/100 mm with the tree Samples Analysis Program TSAP (Version 0.59, Rinn 2007) using the computer-aided positioning system LINTAB and a stereo-microscope. In total, each 20 cores per species were analysed in the central and the marginal test region.

All chronologies were cross-dated visually and with statistical methods to create a species-specific mean chronology per stand (Norton & Ogden, 1990). As quality criteria, we considered the co-linearity of increment (Eckstein & Bauch, 1969), the t-value after Baillie & Pilcher (1973) and Hollstein (1980), and the cross-dating index (Grissino-Mayer & Dobbertin, 2003). We accepted cross-dating of a chronology as being reliable, when it reached a minimum co-linearity of 70 % for a 50-year overlap (Eckstein & Bauch, 1969; Frech, 2006), a minimum t-value of 3.5 (Baillie & Pilcher, 1973; Hollstein, 1980), and a minimum cross-dating-index (CDI) > 20 (Müller, 2007). Our chronologies reached a mean co-linearity of 70.4 % (min. 60 %, max. 83 %; results not shown) for a mean overlap period of 40.6 years (min. 15 years, max. 68 years). The mean t-value of Baillie & Pilcher

(1973) was 4.3 (min. 0.2, max. 7.1), the mean t-value of Hollstein (1980) was 3.68 (min. 0, max. 6.9) and the mean CDI value was 30 (min. 1, max. 61).

As parameters for quantifying the climate sensitivity of increment we used the mean sensitivity (MS) (Fritts, 1976; Schweingruber, 1996) and the autocorrelation of the chronologies as calculated with TSAPWin.

We conducted pre-trend elimination procedures for the mean chronology of every stand in a first step (Baillie & Pilcher, 1973), based on a 5-yr running average, as is commonly done in dendrochronological analyses, and on a 11-yr running average, which seemed better suited to account for the relatively short length of our chronologies compared to other studies. The use of pre-trend elimination procedures may lead to a loss of information about important growth trends and their use is controversially discussed in dendrochronology (Müller, 2007). Therefore, we considered both the original data and the data sets with indexation based on 5- or 11-yr averages. There was no qualitative difference in mean sensitivity of the three data sets (F = 0.3, P = 0.74, results not shown). However, autocorrelation differed for *F. sylvatica* and *A. pseudoplatanus* between the original data and the data based on the 5-yr running average, as well as between original data and data based on the 11-yr running average. For *P. avium*, the mean sensitivity differed between all data sets (F = 81.4, P < 0.01, results not shown). Therefore, we considered all data sets when evaluating mean sensitivity and autocorrelation.

Soil chemical and physical analyses

In all 40 stands, we analysed the chemical and physical properties of the topsoil in October 2005. Each five samples per stand were taken at random locations with a soil corer (diameter 5.3 mm) to a depth of 100 mm. The fresh soil was analysed for pH in water and KCl. Soil moisture, i.e. the water content (in % of dry weight) was analysed gravimetrically. The concentrations of salt-extractable cations were determined by percolating 2.5 g of soil with 100 ml of 1 M NH_4Cl solution for 4 h. The solution concentrations of K, Mg, Ca, Mn, Al and Fe were analysed by atomic absorption spectroscopy (AAS vario 6, analytic jena, Jena, Germany). Fe was assumed to be Fe^{2+}. The concentration of hydrogen ions at the cation exchangers was calculated from the observed pH change during the percolation process. The effective cation exchange capacity (CEC_e) was calculated as the sum of all extractable cations in the NH_4Cl extraction (Meiwes *et al*.,

1984). The base saturation gives the percentage of Ca, K and Mg in CEC_e. From base saturation and CEC_e, we calculated the concentration of exchangeable bases per soil dry mass. Total carbon and nitrogen were determined with a C/N elemental analyser (vario EL III, elementar, Hanau, Germany).

Climate data

The two study regions were characterized with respect to annual temperature, temperature of the vegetation period (May – September), annual precipitation (mm), and precipitation in the vegetation period of the years 2004, 2005 and 2006, and with respect to the long-term means of temperature and precipitation (Table 1). For the Central German study region, we averaged the data of the meteorological stations of Göttingen and Kassel; in South-eastern Poland, we calculated means of the meteorological stations of Rzeszow and Roztocze National Park.

Table 1 Climatic characteristics (means ± standard error, vegetation period = May - September) of the study regions (meteorological stations in Germany: Göttingen and Kassel; in Poland: Rzeszow and Roztocze National Park). Different letters indicate significant differences between the two regions (P < 0.05).

Parameter	Period	Year	Central Germany	South-East Poland
Mean temperature (°C)	Annual	1901-2002	8.0 ± 0.16 [a]	7.8 ± 0.09 [a]
		2004	9.0 ± 1.8 [a]	8.3 ± 2.2 [a]
		2005	9.3 ± 1.8 [a]	8.0 ± 2.4 [a]
		2006	9.7 ± 2.2 [a]	8.4 ± 2.7 [a]
	Vegetation period	1901-2002	14.6 ± 0.2 [a]	15.7 ± 0.1 [b]
		2004	15.0 ± 1.2 [a]	15.6 ± 1.3 [a]
		2005	15.4 ± 0.9 [a]	16.3 ± 1.1 [a]
		2006	16.8 ± 1.4 [a]	17.0 ± 1.3 [a]
Precipitation (mm)	Annual	1901-2002	640 ± 50.6 [a]	664 ± 34 [a]
		2004	714 ± 6.9 [a]	710 ± 12.2 [a]
		2005	660 ± 5.5 [a]	709 ± 7.4 [a]
		2006	589 ± 6.3 [a]	612 ± 9.8 [a]
	Vegetation period	1901-2002	318 ± 18.9 [a]	394 ± 17 [b]
		2004	355 ± 11.1 [a]	364 ± 27.1 [a]
		2005	324 ± 8.2 [a]	388 ± 8.6 [a]
		2006	294 ± 13.2 [a]	349 ± 19.5 [a]

For those 8 stands, in which we took increment cores (Supplementary material, Appendix S2, Table S9), we analyzed a 100-yr record of climatic data (1901 to 2002). With respect to the long-term (1901 to 2002) annual mean of temperature and precipitation, no differences between the study regions in Central Germany and South-East Poland existed ($F < 0.45$, $P \geq 0.53$, Table 1). In the vegetation period, however, mean temperature and precipitation are normally higher at the marginal than in the central study region ($F > 8.64$, $P \leq 0.03$, Table 1). This was not true for the years 2004, 2005 and 2006 immediately before and during the study, when centre and margin did not differ in weather conditions, both in the vegetation period and the whole year ($F < 1.17$, $P \geq 0.31$, Table 1).

Statistical analysis

For statistical data analysis, we used the SAS program JMPIN Version 4.0.4 (SAS Institute 2001). Significance was determined at $P \leq 0.05$ throughout the study. First, all data were tested for normal distribution and equal variances. Subsequently, we tested for significant differences between the populations in the range centre and at the eastern range margin and between the 4 species. For each parameter and each year (2005 and 2006), we conducted a separate 2-way ANOVA with the influencing variables "species", "range position" and the interaction species*range position, followed by a post-hoc Tukey-test.

To meet the distributional assumptions for the analyses and to remove the heterogeneity of variances, most data were log- or square root-transformed. In some cases, where distributional assumptions were not met, we performed a non-parametric Kruskal-Wallis test to detect differences between species and range positions followed by a post-hoc Mann-Whitney U-test.

RESULTS

Differences in soil physical and chemical properties between central and marginal stands

The soils of the central populations were on average richer in exchangeable base cations (F = 11.52, P < 0.01), and had a higher base saturation (Z = -4.24, P < 0.01) and pH (H$_2$O)-value (F > 7.72, P < 0.01) than the soils of the marginal populations (Table 2). The soil water content as determined once during the sampling campaign in October 2005 tended to be higher in the central populations, but this difference was not significant (Z = -1.91, P = 0.06, Table 2). No difference existed for soil nitrogen content and C/N-ratio (F = 1.48, P = 0.19, Table 2).

Table 2 Soil chemical and physical properties (means ± standard error) in the central and marginal stands. Each five samples per stand, 17-23 stands per region. Significant differences (P < 0.05) between the populations of a species are indicated by an asterisk (*).

Parameter	*Fagus sylvatica*		*Acer pseudoplatanus*		*Prunus avium*		*Taxus baccata*	
	Centre	Margin	Centre	Margin	Centre	Margin	Centre	Margin
Soil moisture (% DW)	28±2.2	22±3.1	27±2.7	22±4.1	24±1.5	19±2.6	27±1.6	31±8.5
Base saturation (%)	43±10.1	40±9.9	67±8.2	46±13.2*	65±7.0	29±5.6*	75±9.5	25±15.1*
Exchangeable bases ($\mu mol_c\, g^1$)	172±62	177±81	240±64	208±99	226±51	58±14	356±115	442±416
pH (H$_2$O)	4.9±0.3	5.0±0.4	5.7±0.3	5.3±0.5	5.7±0.2	4.7±0.2	6.0±0.4	4.8±0.5
pH (KCl)	3.8±0.3	4.3±0.4	4.5±0.3	4.5±0.5	4.4±0.3	3.8±0.1	5.0±0.5	4.1±0.5
C/N ratio	16.3±1.1	15.8±0.6	14.4±0.5	16±0.5	13.9±0.5	16.0±0.5	17.6±0.9	15.7±0.6
N content (mmol g^{-1})	0.23±0.03	0.24±0.04	0.23±0.04	0.25±0.06	0.22±0.03	0.21±0.03	0.3±0.05	0.45±0.26

Leaf trait differences between central and marginal populations

Analyses of variance covering all four species revealed only minor differences between central and marginal populations in the 11 leaf traits tested (Table 3). Most variables differed not significantly between the two regions in both years (e.g. leaf K and Mg concentration, leaf δ^{13}C and asymmetry; F ≤ 1.92, P ≥ 0.17, Table 3), or did so only in one

of the two years (e.g. leaf Ca content and SLA in 2005, leaf area loss in 2006; F > 10.6, P < 0.01, Table 3). An exception was leaf C/N ratio which was significantly higher in central than in marginal populations in the species sample (F > 6.22, P ≤ 0.01, Table 3). In addition, all three broad-leaved trees were subjected to a significantly higher leaf damage due to herbivory in their marginal populations in the summer of 2006 with extended drought periods (F = 5.37, P < 0.01, Table 3). In contrast, in the less drought-affected summer 2005, the proportion of damaged leaves tended to be higher in the distribution centre than at the margin (F = -2.52, P = 0.01, Table 3).

As expected, large differences existed between the four species with respect to certain leaf traits. For example, leaf nutrient concentrations were in most cases higher in *Prunus avium* and *Acer pseudoplatanus* than in *Fagus sylvatica* and *Taxus baccata* (F > 13.2, P < 0.01, Table 3), as was the loss of leaf area due to herbivory (F > 7.74, P < 0.01, Table 3). The conifer *T. baccata* was the only species not visibly affected by herbivory. Although differences in foliar $\delta^{13}C$ signature existed between the species (F > 5.07, P < 0.01), they were generally small with all means ranging between -27.2 and -28.8 ‰ (Table 3). Significant interactions between species and range positions were found for certain traits in one of the two years, but never occurred in both years (2005: C/N ratio, P and N content, SLA; 2006: K content, $\delta^{13}C$, damaged leaves; F > 2.81, P ≤ 0.04, Table 3).

Differences in root traits and stem increment between central and marginal populations

Root coring in the topsoil (0-10 cm) revealed a higher live/dead ratio of fine root mass in the central populations than at the margin in both study years (2005: F = 20.35, P < 0.01; 2006: Z = -2.9, P < 0.01, Table 4). This was a consequence of a higher necromass density in the marginal compared to the central populations (2005: Z = 3.46, P < 0.01; 2006: F = 4.96, P = 0.03, Table 4). In contrast, we found no significant difference in fine root biomass density (root mass per soil volume) between centre and margin in any of the two years (F < 0.33, P ≥ 0.56, Table 4).

Table 3 Leaf traits (means ± standard error) of Central European tree species from central and marginal provenances measured in the two consecutive years (yr) 2005 (05) and 2006 (06). Significant differences (P < 0.05) between a species' populations are indicated by an asterisk (*).

Leaf trait	Yr	Fagus sylvatica Centre	Fagus sylvatica Margin	Acer pseudoplatanus Centre	Acer pseudoplatanus Margin	Prunus avium Centre	Prunus avium Margin	Taxus baccata Centre	Taxus baccata Margin
SLA (m² kg⁻¹)	05	15.5±1.0	18.4±1.1	15.3±0.7	19.5±1.6*	16.1±1.0	23.2±1.0*	16.0±1.8	13.7±0.6
	06	23.3±4.4	22.0±7.2	14.2±1.7	10.2±1.6	20.2±1.1	22.7±1.6	14.0±1.3	13.9±1.7
Damaged leaves (%)	05	71.3±6.6	66.7±5.6	92.7±1.6	79.0±4.7*	88.3±1.5	75.5±3.0*	0	0
	06	32.2±4.3	57.3±8.2*	36.4±6.7	61.2±5.0*	36.2±3.7	70.1±6.0*	0	0
Leaf area loss (cm²)	05	0.5±0.1	0.7±0.1	1.9±0.2	1.6±0.5	1.9±0.2	1.5±0.3	0	0
	06	0.7±0.4	0.9±0.3	1.1±0.4	2.2±0.4	1.2±0.4	2.1±0.3	0	0
Leaf asym-metry(cm²)	05	0.1±0.04	0.3±0.08	0.3±0.06	0.4±0.16	0.3±0.07	0.2±0.06	0.01±0.003	0.01±0.002
	06	0.3±0.17	0.2±0.07	0.2±0.05	0.6±0.14	0.4±0.2	0.1±0.05	0.01±0.002	0.01±0.002
C/N ratio	05	23±0.4	22±0.6	21±1.0	19±0.9	23±0.3	19±0.6*	25±1.6	28±1.1*
	06	21±1.3	19±0.6	20±2.5	16±0.5	21±1.2	18±1.0	28±2.2	28±1.4
$\delta^{13}C$ (‰)	05	-28.8±0.19	-28.5±0.16	-28.0±0.27	-28.0±0.4	-27.2±0.16	-27.8±0.21	-27.4±0.31	-27.4±0.24
	06	-28.4±0.24	-28.2±0.19	-28.5±0.27	-27.9±0.25	-27.5±0.24	-27.7±0.32	-27.6±0.12	-28.4±0.22
K (µmol g⁻¹)	05	179±14	193±12	319±26	303±31	514±16	550±33	316±22	317±17
	06	170±9	208±11	369±33	338±27	537±18	527±35	338±29	268±21
Ca (µmol g⁻¹)	05	209±19	206±22	325±23	279±45	433±31	290±34*	180±27	143±35
	06	197±15	243±18	343±18	325±28	430±23	420±33	192±31	153±24
Mg (µmol g⁻¹)	05	60±3.8	49±4.2	78±5.8	73±12.4	131±6.3	133±11.7	54±9.4	73±10.8
	06	69±4.5	62±4.0	93±4.3	90±9.2	156±6.3	164±10.5	74±8.7	80±11.7
N (µmol g⁻¹)	05	1.8±0.04	1.9±0.05	1.9±0.06	2.1±0.07*	1.7±0.01	2.0±0.05*	1.7±0.07	1.5±0.03
	06	2.0±0.15	2.1±0.06	2.0±0.13	2.4±0.04	1.8±0.11	2.2±0.1	1.5±0.07	1.5±0.04
P (µmol g⁻¹)	05	0.009± 0.0008	0.013± 0.0008	0.014± 0.0012	0.018± 0.0015	0.015± 0.0015	0.018± 0.0012	0.017± 0.019	0.014± 0.0003
	06	0.012± 0.0006	0.009± 0.0006	0.015± 0.0013	0.014± 0.0014	0.016± 0.0012	0.017± 0.0016	1.6± 0.002	0.013± 0.0009

Table 4 Live/dead ratio of fine root mass (< 2 mm in diameter) and density of fine root bio- and necromass in the topsoil of 6 to 10 stands per species and region. Mean ± standard errors of each two sampling occasions (July/August and October) in the years (yr) 2005 (05) and 2006 (06). Significant differences (P < 0.05) between the populations of a species are indicated by an asterisk (*).

Fine root parameter	Yr	*Fagus sylvatica*		*Acer pseudoplatanus*		*Prunus avium*		*Taxus baccata*	
		Centre	Margin	Centre	Margin	Centre	Margin	Centre	Margin
Biomass density (g L^{-1})	05	2.7±0.39	2.0±0.38	1.3±0.23	1.8±0.18	1.7±0.2	1.5±0.3	1.6±0.4	2.2±0.6
	06	2.1±0.21	1.8±0.4	1.0±0.22	1.5±0.3	1.1±0.17	1.5±0.2	0.9±0.31	0.6±0.13
Necromass density (g L^{-1})	05	1.5±0.39	1.7±0.36	0.2±0.03	0.9±0.21*	0.9±0.11	1.2±0.18	0.7±0.28	2.1±0.54*
	06	1.4±0.48	1.1±0.34	0.1±0.04	0.4±0.08	0.4±0.14	0.7±0.09	0.4±0.15	0.7±0.21
Live/dead ratio	05	1.8±0.4	1.2±0.27	7.0±2.49	2.1±1.8	1.9±0.42	1.2±0.3	2.2±2.05	1.0±0.79
	06	1.4±0.74	1.5±0.49	8.2±50.5	3.9±1.4*	2.5±0.95	2.0±0.53	2.0±0.94	0.8±0.24*

The dendrochronological analysis of each 20 wood cores per species showed no significant differences between the central and marginal populations (Table 5), regardless of the calculation procedure considered (original data, 5-yr running average, 11-yr running average (F ≤ 1.94, P > 0.14). Although not significant, the polish beech, maple and cherry trees tended to have a greater mean stem growth (and a higher autocorrelation of ring width, F ≤ 2.57, P > 0.06) than the trees in Central Germany. Moreover, we found no indications of a higher climate sensitivity of stem growth of the marginal populations.

Table 5 Mean annual ring width, mean climate sensitivity of annual increment and autocorrelation of ring width in central and marginal populations of three species (n = 20 cores per species and region). Significant differences (P < 0.05) between the populations of a species are indicated by an asterisk (*).

Parameter	*Fagus sylvatica*		*Acer pseudoplatanus*		*Prunus avium*	
	Centre	Margin	Centre	Margin	Centre	Margin
Ring width (mm)	2.03±0.14	2.64±0.24	2.04±0.57	2.78±0.4	1.93±0.46	2.67±0.25
Mean sensitivity	0.17±0.006	0.18±0.027	0.22±0.027	0.20±0.009	0.25±0.027	0.19±0.012
Auto-correlation	0.48±0.125	0.63±0.112	0.37±0.049	0.64±0.109	0.56±0.118	0.78±0.043

DISCUSSION

Our comparative investigation which included four tree species with up to 20 stands each revealed no unequivocal evidence of a higher drought stress exposure of populations close to the eastern distribution margin in South-eastern Poland as compared to populations in the distribution centre in Germany. Neither the δ^{13}C signature of sun canopy leaves nor leaf SLA, stem increment growth and its mean climate sensitivity, or fine root biomass density showed a significant and consistent change in the two studied summers that would indicate a reduced tree vitality of the marginal populations. These variables have been found to indicate increasing drought stress in other studies investigating the drought response of trees along precipitation gradients (e.g. Stewart *et al.*, 1995; Bonn, 1998; Leuschner *et al.*, 2001; Wright *et al.*, 2001; Lebourgeois *et al.*, 2005; Meier & Leuschner, 2008b). Foliar δ^{13}C is expected to increase upon water shortage, whereas SLA and tree ring width typically decrease. In many cases, our study revealed contrasting results in the two study years, and this inter-annual difference was in general greater than the difference between the central and marginal populations. Moreover, certain results may even indicate a lower vitality of the central populations, as exemplified by the tendency to higher stem increments of the marginal populations or the higher SLA of sun leaves of Polish *Acer pseudoplatanus* and *Prunus avium* trees compared to Central German trees. This finding allows the conclusion that drought stress may not be greater at the eastern distribution margin with a continental climate than in the suboceanic climate of the distribution centre. This holds true at least for summers with average rainfall and temperature and when the forests of South-eastern Poland are compared to stands in Central Germany.

One explanation for the absence of a drought effect is the nature of the climatic gradient from Central to Eastern Europe as covered in this study. Despite a more continental climate with higher summer temperatures and a higher evaporative demand, South-east Poland receives on average slightly more rainfall in summer than Central Germany (394 vs. 318 mm), and did so in the study years 2005 and 2006 as well. Yet, rainfall typically occurs more irregular with a higher frequency of drought periods in continental climates where convective rainfall is more important. Thus, soil water deficits may not be greater in average summers in South-east Poland than in Central Germany.

Years drier than average may change the situation as is indicated in the summer 2006 which was warmer than the 100-yr mean and received about 50 mm less rainfall in South-east Poland. Our data revealed a significantly higher leaf damage in the marginal

populations of the three broad-leaved species, possibly indicating a weaker defence because foliar N concentrations were not significantly different. However, a difference in herbivory attack between the two regions was only visible in 2006 but not in 2005 (when *A. pseudoplatanus* and *P. avium* showed even greater attack in Central Germany). Other drought-sensitive traits, however, were not affected. In any case, our data from two summers are not sufficient to test the hypothesis that leaf herbivory represents a more severe stressor for broad-leaved central European trees at their eastern, continental range limit than in central populations. Further, more precise data on soil water status in the forest stands are needed to understand the putative role of summer drought for the vitality of adult forest stands at their eastern distribution margin. In the absence of continous soil moisture measurements in the studied stands, a comparison of the drought exposure in the summer months is difficult for the two regions.

The absence of significant differences in stem growth patterns between central and marginal populations is surprising, since annual ring width and its sensitivity to rainfall are known to be reliable archives of past effects of drought on tree vitality (Schweingruber, 1996; Worbes *et al.*, 1995; Bonn, 1998; Andreu *et al.*, 2007). The high annual increment is even more astonishing as the growing season is about 4 wk shorter in South-east Poland than in Central Germany. These results are probably the most convincing evidence for our conclusion that the eastern distribution limit of *F. sylvatica*, *A. pseudoplatanus*, *P. avium* and *T. baccata* is not caused by drought effects on adult trees that increase towards the margin.

The fine root system of trees was found to respond particularly sensitive to water shortage, either by an increased mortality and root turnover, or by a reduction in size in drought-affected stands (e.g. Pregitzer *et al.*, 1993; Joslin & Wolfe, 1998; Gill & Jackson, 2000; Meier & Leuschner, 2008b). In our study, the live/dead ratio of fine root mass in the topsoil is the single parameter that could point at a more stressful environment in South-east Poland, as it was significantly higher in the central than in the marginal populations of the four species. This could indicate a higher mortality of fine roots due to environmental stress, including soil drought, or might point at a reduced decomposition rate of dead fine roots that persist in the soil for longer time spans (Nisbeth & Mullins, 1986; Norby & Jackson, 2000; Leuschner *et al.*, 2004). Our data indicate that the shift to a reduced live/dead ratio towards the marginal populations was most likely a consequence of reduced root necromass decomposition, as is shown by elevated necromass densities in the Polish stands, in particular in *A. pseudoplatanus* and *T. baccata*. A higher fine root mortality,

compensated by higher fine root growth rates, however, would also explain the data, and cannot be ruled out in the absence of direct observations of fine root turnover. Lower pH-values and base saturations in the soil of the marginal populations could be indicators of a soil environment reducing fine root longevity and increasing mortality (e.g. Jentschke *et al.*, 2001; Godbold *et al.*, 2003). Higher soil acidity and lower base saturation of the soils in stands at the eastern distribution margin as compared to central stands were also reported by Leuschner *et al.* (Chapter III) who compared populations of 6 tree species in Central Germany and Slovakia. On the other hand, if summer drought is more pronounced in extreme years at the eastern margin, this could hamper root decomposition as well resulting in the accumulation of organic material in the soil as is evidenced by the Chernozems of Eastern continental Europe. In conclusion, the evidence for an increased fine root mortality at the eastern range limit is weak in our data.

In the absence of clear drought effects on the vitality of adult trees, other factors must limit the distribution of these species in Eastern continental Europe. In the case of *F. sylvatica*, the climatic factors being responsible for the species´ eastern distribution limits are still disputed (Czajkowski *et al.*, 2006). Extreme winter frosts and severe late frosts in spring are supposed to be important. Both factors increase towards continental Eastern Europe. Moreover, it might well be that seedlings and saplings, which lack deep-reaching roots, are more sensitive to drought, frost or other climatic hazards in Eastern Europe than are adult established trees. Seedlings of *F. sylvatica* were found to be sensitive to soil drought and environments with dry air (e.g. Schraml & Rennenberg, 2002; Lendzion & Leuschner, in revision) and to temperatures below –17°C (Czajkowski & Bolte, 2006). Rose *et al.* (Chapter V) could show that marginal populations of European beech generated offspring that was better adapted to soil drought than central populations, which makes a higher drought exposure of beech offspring at the eastern margin likely. Thus comparative studies exposing young and adult individuals of the same species to the drought or cold stress must show whether the bottleneck of tree survival at the eastern range margin is in the juvenile stage or not.

We also found only weak evidence in support of our second hypothesis: only the leaf δ^{13}C signature gave hints that rare tree species are more affected by drought stress than common ones. *P. avium* and *T. baccata* had by about 1 ‰ higher δ^{13}C values than *F. sylvatica* and *A. pseudoplatanus* indicating that stomatal limitation of CO_2 assimilation could have been more severe in the rare than the common species. However, no consistent shift in δ^{13}C values towards weaker ^{13}C discrimination at the eastern margin was visible which could

indicate increased water shortage. In addition, species-specific traits such as growth form and light demand might also be responsible for these differences. Neither stem increment nor fine root data supported a higher drought sensitivity of the two rare species.

CONCLUSIONS

This study provides no convincing evidence that adult individuals of four Central European tree species are more drought-affected at their eastern distribution margin than in the distribution centre. This conclusion is based on the analysis of a multitude of leaf, root and stem-growth traits including decade-long stem increment and foliar $\delta^{13}C$ signatures. In most cases, significant differences visible between central and marginal populations in leaf, stem and root sometimes reversed in the second year. We conclude that stress due to summer drought is not a key factor reducing the vitality of adults of the four species in the marginal populations of South-east Poland. Some indications were found for the assumption that this may be different in extremely dry summers. We also found no convincing evidence for a higher drought sensitivity of rare tree species compared to common ones.

Since our study only covered two summers, we cannot rule out the possibility that drought damage to the canopy or root systems, or high leaf herbivory rates in extreme years are important factors reducing the vitality of adult trees of the four species at their eastern range margin. In addition, there is evidence that other stressors such as winter and/or late frost events may severely damage adult trees of beech and other Central European tree species in continental Eastern Europe (Röhrig & Bartsch, 1992; Czajkowski *et al.*, 2006; Czajkowski & Bolte, 2006). Finally, this study explicitly focused on adult trees, but did not consider seedlings and saplings which may be more sensitive to drought, frost and herbivory than older stages of the same species. This warrants a comparison of juvenile and adult trees in their response to relevant stressors.

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Chapter V

Are marginal beech provenances a source for drought tolerant ecotypes for future forestry?

L. Rose, H. Buschmann, B. Köckemann, Ch. Leuschner

ABSTRACT

Aim According to recent climate change scenarios the number and intensity of summer droughts are expected to increase in Central Europe in the next decades. Therefore the identification of drought-tolerant ecotypes of silviculturally important tree species may be an adaptive strategy of forestry to cope with these challenges. This study aims at identifying drought tolerance of beech seedlings (*Fagus sylvatica* L.) from marginal and central provenances in Central Europe.

Methods A common garden experiment with a beech provenance from the center (Central Germany) and from the eastern margin (South-East Poland) of the species' distribution range was conducted. Fourteen-wk-old seedlings were exposed to three different drought treatments (40, 20 and 10% soil water content) for 8 weeks. The responses of different morphological, physiological, biochemical and growth parameters to drought were analyzed.

Location Central Germany and South-East Poland

Results The relative growth rate of the marginal provenance was generally lower than that of the central provenance. Because of the significantly higher mass of its seeds, the marginal seedlings showed a tendency to higher total biomass by the end of the experiment in all treatments. Drought generally resulted in lower biomass production but to a lesser extent in the marginal provenance. Root/shoot ratio decreased with increasing drought stress in both provenances and was lower in the central than in the marginal provenance. A lower SRA of the marginal provenance especially in the control treatment indicates higher root tissue densities and, thus, a better adaptation to low xylem water potentials than in the central provenance. Under moderate drought, lower leaf $\delta^{13}C$ signatures indicated lower stomatal limitation in the marginal compared to the central provenance.

Main conclusions We conclude that marginal beech provenances from the eastern range limit of the species may exhibit a better drought adaption than central ones.

Key words *Fagus sylvatica*, drought, root/shoot ratio, seedlings, RGR, $\delta^{13}C$

INTRODUCTION

Climate warming is predicted to increase winter precipitation, but to decrease summer rainfall in parts of Central Europe (IPCC, 2007; Schär *et al.*, 2004). This may affect forestry in particular because of the long lifespan of trees. European beech (*Fagus sylvatica* L.) is a highly competitive species in Central Europe with a wide tolerance of contrasting soil chemical conditions (Ellenberg, 1996; Leuschner, 1998). However, beech is known to be sensitive to drought which is also reflected in its distribution area in a mostly sub-oceanic climate (Bohn, 2004). Due to its great economic importance in European forestry, much research has recently focused on the drought response of juvenile and adult beech plants and the mechanisms of drought tolerance of this species (e.g. Grossoni *et al.*, 1998; Peuke & Rennenberg, 2004; Löf *et al.*, 2005; Meier & Leuschner, 2008a; Meier & Leuschner, in press). In comparison to other Central European broad-leaved tree species, a sensitivity of beech upon drought was found particularly with respect to embolism in its conducting system (Cochard *et al.*, 2005), stem increment reduction in dry summers, pre-senescent leaf shedding in drought periods (Granier *et al.*, 2007), and a reduced fine root biomass in dry soil (Meier & Leuschner, 2008b). In addition, beech seedlings were also found to be sensitive to dry air (Lendzion & Leuschner, in revision). This has stimulated a vital debate on the future of Central European beech forests and the proper choice of tree species for forestry under the prospect of a drier and warmer climate (e.g. Rennenberg *et al.*, 2004; Ammer *et al.*, 2005).

Species that occupy large geographic ranges respond to contrasting environmental conditions by genotypic variation and phenotypic plasticity (Abrams *et al.*, 1992; Peuke & Rennenberg, 2004; Kriebitzsch *et al.*, 2005). Several case studies have investigated the drought sensitivity of beech provenances along a gradient of decreasing precipitation from northern to southern Central Europe and to the Mediterranean region (García-Plazaola & Becerril, 2000; Nielsen & Jørgensen, 2003; Peuke *et al.* 2006), but fewer studies have been conducted on drought sensitivity of beech at the eastern margin of its distribution area. Czajkowski & Bolte (2006) conducted a drought experiment with beech seedlings from eastern provenances, but focused on aboveground drought responses only and gave no attention to root responses to drought which may be crucial in drought tolerance of beech (Meier & Leuschner, 2008b).

Since the frequency of extreme drought and frost events is increasing in Central Europe with the growing continentality of the climate from west to east (Ellenberg, 1996), eastern

provenances might therefore be important sources for drought and frost resistant ecotypes (Wilmanns, 1990; Czajkowski *et al.*, 2006).

We conducted a growth experiment with beech seedlings from a provenance in the distribution centre (Central Germany) and a provenance from South-eastern Poland close to the eastern range margin and observed the response of about 20 physiological, morphological and growth-related parameters in moderately or severely drought-stressed plants relative to the well watered control. Based on earlier beech provenance trials conducted by Nielsen & Jørgensen (2003), Peuke *et al.* (2006) and Meier & Leuschner (2008a), we tested the following hypotheses: (i) beech provenances from the eastern range margin with a more continental climate are less sensitive to soil drought, and (ii) the root system of beech seedlings is particularly sensitive to drought and thus represents a bottleneck in the strategy of young beech plants to cope with drought.

METHODS

Plant material

Fagus sylvatica seeds from Central Germany (Neuhaus, Solling) and South-east Poland (Lutowiska, Podkarpackie) were chosen for study in order to compare autochthonous provenances from the centre and the eastern margin of the species' distribution range (Fig. 1).
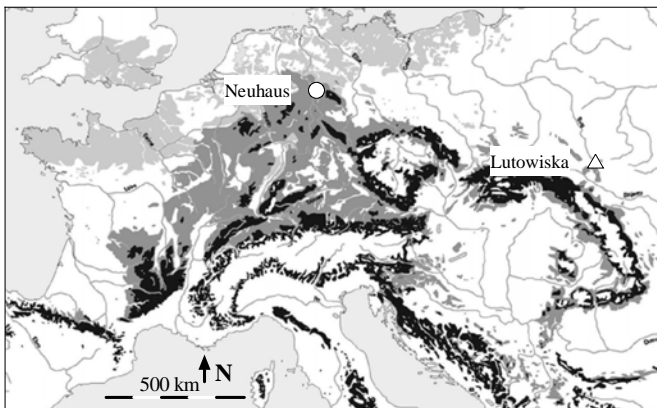

Figure 1 Location of the seed origin areas in the geographic range of beech after Bohn (2004), modified. ○ planar (-hilly), ◕ hilly – mountainous, ● mountainous – high mountainous beech populations.

The seeds originated from several tree individuals of each one stand per region (forestry district Neuhaus, No. 81009; forestry district Lutowiska). We focused on a single stand per region because the genetic diversity of *F. sylvatica* is typically higher within a given stand than the diversity between different stands. For example, in a sample covering six beech forests in Central Germany (Hesse), Sander *et al*. (2000) found 99% of the diversity within the stands and only 1% of the diversity between the stands. Climatic data of the two regions are given in Table 1.

Table 1 Climatic data of the marginal and central provenances
(after Lorenc, 2005 and Schipka, 2002)

Provenance	Marginal	Central
Country	Poland	Germany
Place of harvest	Lutowiska	Neuhaus
Geographical Position	49°15'N, 22°41'E	51°45'N, 9°31'E
Elevation a.s.l	approx. 800 m	440 m
Mean annual temperature	7.5°C	6.9°C
Mean annual precipitation	approx. 650 mm	1040 mm
Mean precipitation in the vegetation period	405 mm	535 mm

Cultivation

For germination, the seeds were placed in regularly watered pots filled with loamy sand (Einheitserde B) in a climate chamber at 15/20°C (night/day), after weighing 10 seeds per provenance for subsequent determination of the RGR (see below). On April 19, 2006, the seedlings were planted in the centre of circular plastic containers (2 L) filled with a mixture of one part loamy sand, one part Perlite (Perligran G, Deutsche Perlite GmbH, Dortmund, Germany) and one part humus material (v : v : v). A commercial NPK-fertilizer (Triabon, COMPO GmbH & Co. KG, Münster, Germany; 16-8-12/N-P-K) was added. The experiment took place in the Experimental Botanical Garden of the University of Göttingen between May 10, 2006, and September 21, 2006, under a mobile plexiglass roof equipped with a rain sensor, which automatically covered the plants when it rained. The roof was removed automatically a few minutes after the rain stopped. Thus, the beeches

grew under local temperature and light conditions, but with complete control of soil water supply. To minimize potential influences of environmental gradients at the experimental site, the provenances and treatments were randomly positioned in alternating order and the positions were changed randomly every 4 times during the experiment.

The pots were well watered until the drought treatment was initiated after 14 weeks (July 25, 2006). In total, 36 plants per provenance were cultivated with each 12 plants treated with a different moisture regime, i.e. a control (40%), a moderate stress (20%), and a high stress (10% soil water content) treatment. The limited volume of the pots made it necessary to add water every two days after water loss had been determined by weighing the pots.

Harvesting

At the end of the experiment (September 21, 2006), all leaves were removed from the stem, and the remaining shoot was cut off at the root collar after measuring shoot length and diameter of the stem and counting the number of leaves. All leaves were scanned with a flatbed graphics scanner, and the images were analyzed with the software WinFolia (WinFolia 2005b, Régent Instruments Inc., Québec, Canada) to determine leaf area and calculate specific leaf area (SLA, in $cm^2 \, g^{-1}$ DM). The roots of the trees were harvested by carefully sifting the root-containing soil material of each pot through a sieve and washing the roots to clean them of soil residues. They were sorted by diameter (fine roots < 2 mm, coarse roots > 2 mm). The roots were spread out in water, scanned and the digitized images processed using the software WinRhizo (WinRhizo 2005c, Régent Instruments Inc., Québec, Canada) which calculates the surface area of each root.

All plant organs were dried (70°C, approx. 80 h) and weighed. Specific root area (SRA, in $cm^2 \, g^{-1}$ DM), total fine root surface area, root dry weight, and fine root/leaf area ratio were calculated from these data for each tree. The relative growth rate (RGR, in g $g^{-1}day^{-1}$) was calculated for the whole seedling by subtracting seed biomass from total harvested biomass and relating the difference to the duration of the experiment.

One day before the harvest, predawn water potential (Ψ_{pre}) of the leaves was measured at 4:00 a.m. using a Scholander pressure chamber (Scholander *et al.*, 1965). The relative water content of the leaves (θ_l) harvested around noon was determined by drying (fresh weight - dry weight / fresh weight).

Chemical analyses

The dried plant material of all organs of a plant was pooled and ground. The leaf $\delta^{13}C$ signature and N concentration were determined by mass spectroscopy (Delta Plus, Finnigan MAT, Bremen, Germany) in the Stable Isotope Laboratory (KOSI) of the University of Göttingen. For analysing plant cation concentration, 100 mg of plant powder were digested with 3 ml HNO_3 at 185°C for 5 hours and the concentrations of Ca, K and Mg measured by atomic absorption spectrometry (AAS vario 6, analytic jena, Jena Germany).

Statistical analyses

All statistical analyses were performed with SAS Version 8.02 (SAS Institute Inc., Cary, USA) and JMP (JMPIN Version 4.0.4, SAS Institute 2001). Significance was determined at $p < 0.05$ throughout. Before statistical analyses, all data were tested for normal distribution (Shapiro-Wilk test) and homogeneity of variances (Bartlett test). To achieve normal distribution and homogeneity of variances, the data of fine root biomass and leaf calcium content were logarithmically transformed. Two-way analyses of variance with the model parameters treatment, provenance and their interaction were performed by the ANOVA procedure for balanced data of the variables maximum shoot length, number of leaves per plant, seed weight, total biomass, leaf biomass, root/shoot ratio, RGR and leaf N concentration. In the case of unbalanced data (fine root biomass, SLA, leaf calcium content, leaf potassium content), general linear models (GLM) were calculated. Differences between two treatments were analysed with a Scheffé test, except for root/shoot ratio and RGR which were analysed with a posthoc Tukey test.

For non-normally distributed data, the influences of provenance and treatment were investigated with a Kruskal-Wallis test (leaf water content, pre-dawn leaf water potential, root collar diameter, shoot biomass, SRA, FR/LA ratio, $\delta^{13}C$, leaf magnesium content). Differences between two treatments were analysed with a U-test after Mann & Whitney. A summary of the results of the different tests comparing the plant morphological, physiological and chemical variables between different drought treatments and different provenances is given in the Table S10 (Supplementary material, Appendix S2).

RESULTS

Plant water status

Neither predawn leaf water potential Ψ_{pre} nor leaf water content θ_l measured at noon were influenced by the provenance in the three treatments (Table 2).

Table 2 Some morphological, physiological and chemical properties of beech seedlings from marginal or central provenances under three different drought treatments (means ± SE). Different letters represent different means.

Treatment	Control				Moderate stress				Severe stress			
Provenance	Marginal		Central		Marginal		Central		Marginal		Central	
Total bio-mass (g)	4.62± 0.47	a	4.36± 0.54	a	3.71± 0.21	ab	3.17± 0.29	ab	2.60± 0.16	b	2.45± 0.16	b
Number of leaves per plant	15.08± 1.47	a	17.58± 1.81	a	16.17± 1.63	a	15.08± 1.59	a	11.41± 1.8	a	14.00± 1.04	a
Root collar diameter (mm)	5.23± 0.27	a	5.00± 0.29	ab	5.04± 0.16	a	4.42± 0.16	bc	4.05± 0.25	c	4.05± 0.14	c
Shoot length (cm)	18.99± 1.23	a	20.68± 1.70	a	21.84± 1.02	a	18.18± 1.38	a	17.05± 1.01	a	19.90± 0.85	a
SLA (cm² g⁻¹)	202.71± 4.01	ab	182.83± 6.52	a	210.29± 4.55	b	194.50± 5.36	ab	208.25± 5.03	b	203.36± 4.80	ab
Total leaf area (cm² plant⁻¹)	182.95± 19.78	a	160.48± 18.41	a	184.89± 14.81	a	154.69± 15.18	a	148.28± 17.18	a	143.04± 12.90	a
Leaf water content	0.54± 0.01	ab	0.55± 0.01	a	0.50± 0.02	b	0.49± 0.03	b	0.31± 0.04	c	0.32± 0.05	c
Pre-dawn water po-tential(MPa)	-0.30± 0.02	a	-0.3± 0.03	a	-0.77± 0.21	b	-0.85± 0.24	b	-2.51± 0.54	c	-2.38± 0.45	c
Leaf Ca con-centration (g kg⁻¹)	18.29± 1.40	a	18.57± 0.42	a	18.91± 1.10	a	18.44± 0.76	a	17.43± 1.76	a	18.52± 0.80	a
Leaf N con-centration (mmol g⁻¹)	1.55± 0.05	a	1.68± 0.05	a	1.50± 0.03	a	1.54± 0.03	a	1.52± 0.04	a	1.55± 0.05	a

Leaf $\delta^{13}C$ was not significantly different between the central and marginal provenances under ample soil moisture supply (control treatment), but was significantly higher (less negative) in the central beech population under moderate drought stress (Fig. 2). As expected Ψ_{pre} and θ_l decreased with increasing drought but the response was not different

between the provenances. A large and significant increase in $\delta^{13}C$ occurred in both provenances between the control and the moderate stress treatment, but no further increase was visible toward the severely stressed plants.
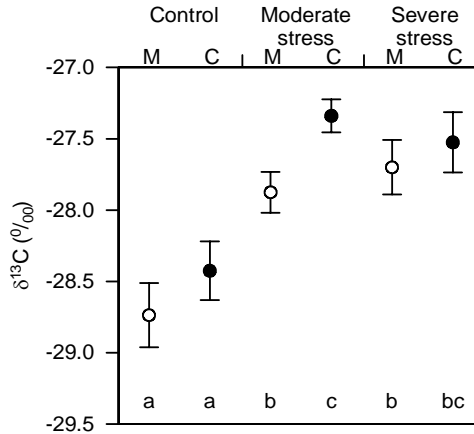

Figure 2 Leaf $\delta^{13}C$-values at the time of harvest of marginal (M – open circles) and central (C - filled circles) provenances under three different drought treatments. Different letters represent different means (U-test: n = 12, p < 0.05).

Parameters of morphology and growth

The marginal provenance exhibited significantly higher seed weights than the central provenance (0.25 vs. 0.16 g, T-test < 0.001, F = 19.05). The relative growth rate (RGR) was significantly influenced by both provenance and treatment. Seedlings of the central provenance had a higher RGR in all treatments (difference significant only for the control and high-stress treatment, Fig. 3). The decrease in RGR with increasing drought was roughly similar in the two provenances. Total biomass produced at the day of harvest, however, was not different between the two provenances despite a higher RGR of the central provenance. This holds true under ample water supply and in the drought treatments and was a consequence of the considerably higher seed weight of the marginal provenance. The number of leaves produced per plant and the shoot length at harvest were affected neither by the drought treatment nor by provenance. However, drought reduced the root collar diameter significantly (Table 2).
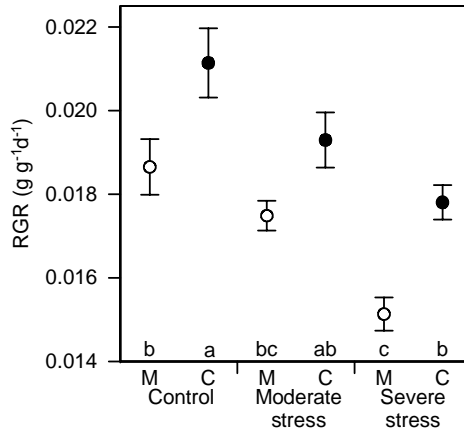
Figure 3 Relative growth rate of beech seedlings of two provenances (M - marginal, open circles; C - central, filled circles) in the period April 19 to September 21, 2006, under three different drought treatments. Different letters represent different means (Tukey: n = 12, p < 0.05).

Total fine root biomass per plant was significantly lowered by drought. However, the marginal provenance showed only a small and non-significant difference in fine root biomass between the control and the severe stress treatment, whereas the central provenance exhibited a significant decrease (Fig. 4A). The root/shoot ratio was lower in the stressed than in the control plants, and lower in the central as compared to the marginal provenance (Fig. 4B).
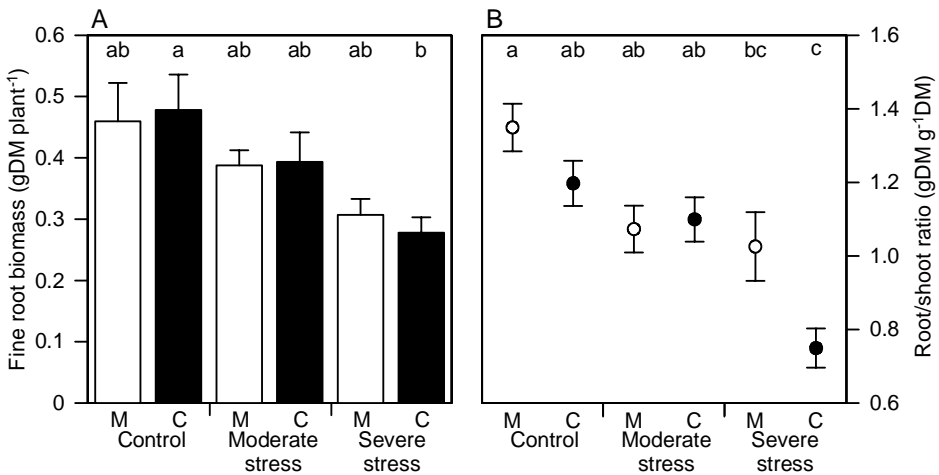
Figure 4 Fine root biomass (A) and root/shoot ratio (B) at the time of harvest of marginal (M - open bars/circles) and central (C - filled bars/circles) provenances under three different drought treatments. Different letters represent different means (A: Tukey: n = 12, p < 0.05; B: Scheffé: n = 9-12, p < 0.05).

Root/shoot ratio decreased with increasing drought stress in both provenances, but to a greater extent in that from the distribution center than in the marginal one. Specific root area (SRA) of the central provenance significantly declined with increasing drought in contrast to nearly constant values in the marginal provenance (Fig. 5A). In other words, the proportion of finest roots decreased upon drought in the central but not in the marginal provenance. SLA was neither affected by drought nor provenance (Table 2).

The ratio of fine root to leaf area (FR/LA) was found to be significantly lower in stressed than in control plants. While the central provenance showed a significant decrease of FR/LA with increasing drought, the response of the marginal provenance was less pronounced (Fig. 5B). Thus, FR/LA of both provenances showed similar values in the severely stressed treatment, although FR/LA of the well-watered central seedlings was significantly higher than that of the marginal ones.
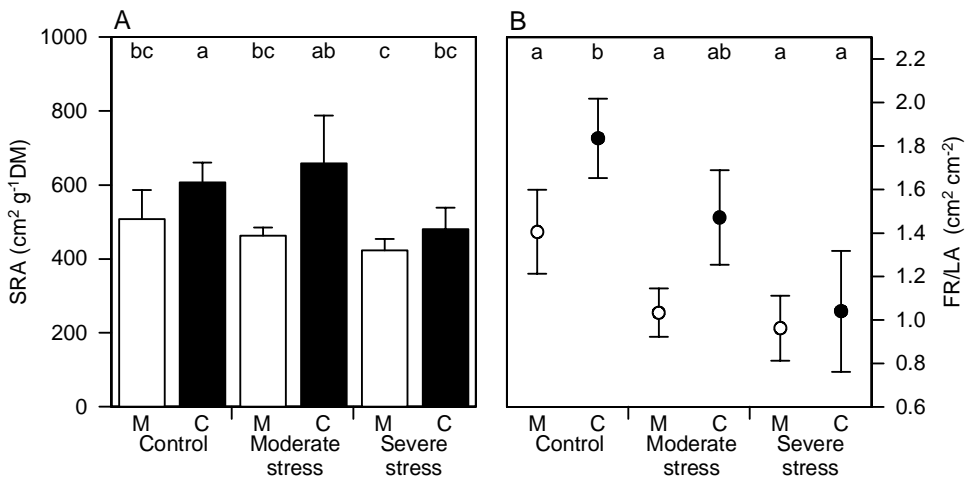

Figure 5 Specific root area (SRA) (A) and fine root/leaf area (FR/LA) ratio (B) at the time of harvest of marginal (M - open bars/circles) and central (C - filled bars/circles) provenances under three different drought treatments. Different letters represent different means (U-test: n = 9-12, p < 0.05).

Leaf nutrient concentrations

The N concentration of the leaves was neither affected by soil moisture treatment nor provenance as was the leaf concentration of calcium (Table 2). The potassium concentrations of the leaves, however, were found to be influenced by both drought and

provenance. The central provenance showed significantly lower means than the marginal one, which contained highest amounts of K in the moderate-stress treatment (Fig. 6).
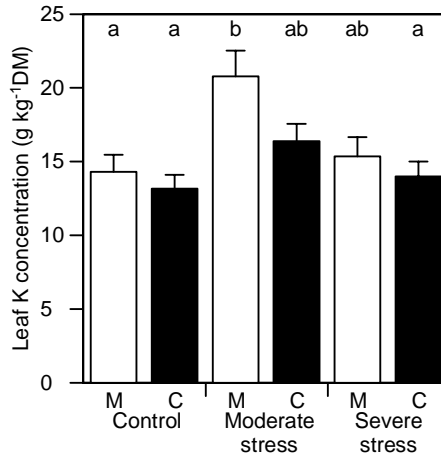

Figure 6 Leaf K concentration at the time of harvest of marginal (M - open bars) and central (C - filled bars) provenances under three different drought treatments. Different letters represent different means (Scheffé: n = 11-12, p < 0.05).

DISCUSSION

The main differences between the two provenances to be compared in this study were detected with regard to seed weight, relative growth rate of the seedlings and carbon allocation patterns. Although seeds of the central provenance showed considerably lower weights than those of the marginal one, which may reduce the fitness of the embryo, this initial disadvantage was compensated by higher subsequent growth rates of the seedlings from the range centre. These differences are thought to be genetically determined and may indicate different adaptations to the climate in Central Germany and South-East Poland. A reduction of biomass is a frequently observed response to drought in beech seedlings (Madsen & Larsen, 1997; Fotelli *et al.*, 2001). However plants can prevent productivity losses to some extent by completing growth before the onset of drought stress (Schraml & Rennenberg, 2002). Thus, how severely drought will affect the biomass production of juvenile beeches seems to depend on the timing of drought relative to the growth period. Nevertheless, Tognetti *et al.* (1995) found beech seedlings from drier regions always to produce less biomass than equally treated seedlings from regions with ample water supply,

irrespective of the drought treatment. García-Plazaola & Becerril (2000) showed similar results for the leaf biomass of beech seedlings. The overall lower relative growth rates of the marginal provenance in our study could therefore be interpreted as an adaptation to drier habitats.

In contrast to seedlings, mature trees can use water resources deeper in the soil because of their fully developed root system (Bolte & Roloff, 1993). The allocation of carbon and nutrients between root and shoot may be crucial for the success of tree seedlings at sites with temporal water shortage. A higher seed mass may support the early development of a deep-reaching primary root which may protect the seedling from damage by summer droughts. A more frequent occurrence of dry spells in summer in the more continental climate of South-East Poland could have fostered a selection process towards beech plants with higher seed masses to increase the survivorship of the seedlings (Blossey & Nötzold, 1995). That the strategy of providing larger acorns in a drier climate is successful is indicated by the fact of marginal seedlings having produced similar amounts of biomass after 22 weeks as compared to central ones despite lower relative growth rates.

A second important adaptive trait seems to be the root/shoot ratio which was higher in the marginal provenance than in the central one. Similarly, Tognetti *et al.* (1995) found higher root/shoot ratios in beech seedlings originating from drier regions. This may be an important adaptation securing access to soil water resources in a drier climate, since beech seedlings seem to be particularly sensitive to drought effects on the fine root system: various studies exposing beech seedlings to drought found a greater reduction of root than of shoot biomass, resulting in a decrease, and not an increase of root/shoot ratio upon drought (Davidson *et al.*, 1992; Fotelli *et al.*, 2001; Löf *et al.*, 2005; Meier & Leuschner, 2008a). In our experiment as well, shoot biomass was less affected by drought than root biomass. A similarly sensitive response of the fine root system was also reported for adult beech trees in a rainfall gradient studied by Meier & Leuschner (2008b). Thus, beech provenances with an inherently higher root/shoot ratio should have advantages in a drier environment, given the low belowground drought tolerance of beech. Moreover, there is evidence that beech provenances from drier environments have a less drought-sensitive root system than provenances from more humid climates. Hamp *et al.* (1999) found that the root/shoot ratio of beech seedlings was reduced to a greater extent in plants from moister habitats than in plants of a drier origin. Similarly, the relatively small reduction of the root/shoot and fine root/leaf area (FR/LA) ratio in the marginal provenance as compared to the central provenance in our study may be interpreted as a better adaptation

to drought of the Polish plants. This is supported by a reduction in fine root biomass in the drought treatments that was significant only in the central, but not in the marginal provenance indicating a higher drought tolerance of the latter. An explanation of the greater reduction in fine root biomass upon drought of the central provenance could be the higher specific root surface area in these plants, indicating a greater proportion of very fine roots (i.e. roots <0.5 mm in diameter) in total root mass and/or a lower average root tissue density. Both traits would support a faster root growth rate and a higher water and nutrient uptake per root mass, but should result in a greater sensitivity to drought (Ryser, 1996). The significant reduction of SRA of the central provenance under drought must be viewed as an acclimatisation which reduces the drought exposure of the most sensitive elements of the root system. Different phenologies of growth may be another explanation of the greater drought-induced reduction of root biomass in the central provenance. Nielsen & Jørgensen (2003) found drought tolerant beech seedlings to complete growth 18 days earlier than equally treated drought sensitive plants, thereby avoiding drought stress at least partly. We may speculate that root growth may have occurred mostly before the onset of drought in the marginal provenance as did leaf and shoot growth, whereas root growth of the central provenance occurred later under less favourable conditions. However, direct observation of root growth activity with minirhizotrons is required to test this hypothesis.

This study focused on above- and belowground growth, morphology and carbon partitioning patterns while only a few physiological variables were investigated. Remarkably, parameters of leaf water status (Ψ_{pre} and θ_l) did not differ significantly between the central and the marginal provenances, neither under ample nor reduced water supply. However, the about 0.6 ‰ lower $\delta^{13}C$ signature of the leaves of the marginal provenance under moderate drought stress may indicate that stomatal limitation must have been higher in the plants of the central provenance (e.g. Ehleringer & Cooper, 1988; Virgona & Farquhar, 1996). If valid, these plants from a humid environment should have responded more sensitively to soil drought by partial stomatal closure. However, a negative effect of stomatal closure on CO_2 assimilation is unlikely since RGR was higher, and not lower, in the seedlings of the central provenance as compared to the marginal one. According to Damesin & Lelarge (2003), the contrasting $\delta^{13}C$ values could also be a consequence of different phenologies of growth: $\delta^{13}C$ tends to increase with proceeding growth in beech with the consequence that slower growing plants (as in the marginal provenance) discriminate more against ^{13}C than faster growing ones. In a genotype

comparison of droughted *Betula pendula* seedlings, Aspelmeier & Leuscher (2004) also found generally lower $\delta^{13}C$ signatures in plants from drier origins.

Calcium, which is mostly transported by the xylem sap and accumulates in the leaves, was remarkably constant across the provenances and drought treatments. A comparison of leaf K concentrations revealed particularly high values in the moderately stressed plants of the marginal provenance. A possible explanation is that these plants conducted a more active osmoregulation in the leaf tissue than those from the central provenance. This hypothesis needs testing by pressure-volume-curve analysis of the different provenances.

CONCLUSIONS

We conclude that the marginal beech provenance from a subcontinental to continental climate with a higher probability of summer drought reveals several traits characterizing this population as being better drought adapted than a central one from suboceanic Central Germany. Due to a considerably higher acorn mass, the seedlings of the marginal population may be more successful in surviving drought in the first year. Further, marginal plants were less sensitive to a drought-induced reduction in fine root biomass allowing them to maintain higher root/shoot and root surface area/leaf area ratios under drought than central plants. This is probably a consequence of a root morphology and/or root growth phenology better adapted to more frequent summer droughts at the range margin. The $\delta^{13}C$ signature points at a lower stomatal limitation of photosynthesis of the marginal plants. We suggest that a combination of morphological, physiological and phenological adaptations enable beech seedlings of the marginal provenance to maintain an equal or even higher biomass production upon drought as compared to plants of the central provenance, even though their inherent relative growth rate seems to be lower.

Hence, marginal beech provenances may be a source for beech cultures to be founded under the prospect of increasing drought frequencies in the future. However, further results about the drought response and its underlying mechanisms among different beech provenances are needed to confirm the long term drought resistance of promising provenances.

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Chapter VI

Synthesis

Introduction

Macroecology is a recently emerged discipline that investigates patterns which are only visible on large geographic or temporal scales (Gaston & Blackburn, 2000). Common macroecological patterns include a positive relationship between abundance, range size and niche breadth (Bock & Ricklefs, 1983; Brown, 1984; Bock, 1984, 1987; Brown & Maurer, 1987, 1989; Morse *et al*., 1988; Gaston & Lawton, 1990; Lawton, 1993; Gaston, 1996; Kotze *et al*., 2003), and a decrease of abundance (Brown 1984; Cox & Moore, 1985; Wiens, 1989; Sagarin & Gaines, 2002; Murphy *et al*., 2006) and niche breadth (Brown, 1984; Brussard, 1984; Bock, 1987; Gaston & Lawton, 1990) from the distribution centre to the range margin. Those patterns have been observed among many different organism groups and across different habitat types and therefore seem to be of universal validity. The knowledge about macroecological patterns of species assemblages is important mainly for two reasons. First, empirical pattern detection is the background of the development of theory, because development of factually and empirically based broad patterns and their mechanistic understanding will promote ecological science more rapidly than any other approach (Price, 2003). Second, macroecological tools may be helpful in future Global Change research.

Plant species, especially temperate tree floras, may be affected by global climate change much more severely than other, more mobile taxonomic groups. An already established forest community will be able to track altered temperature and precipitation patterns with a range shift only from one generation to the next, which may take several decades.

Trees have been widely neglected in macroecological studies although they have an outstanding importance for economy and global biogeochemical cycles. I am aware of only one recent study, addressing abundance and distribution patterns of temperate trees (Murphy *et al.*, 2006). It was the study`s aim to fill this gap with the following approaches:

  (i)   We investigated for all tree species that have their distribution centre in Central Europe, if they show a relationship between abundance in the distribution centre and range size and between niche breadth in the distribution centre and range size (chapter II). According to the general macroecological believe we hypothesized, that species with a great abundance and a broad niche in their distribution centre have larger ranges than rare species with a smaller niche breadth.

(ii)   According to the ´abundant-centre` hypothesis we investigated how abundance and niche breadth differ within the distribution range, as both are ment to decrease from the distribution centre towards the range margin (chapter III).

(iii)   In chapter IV we studied the question if trees are more stressed at their eastern range margin than in their distribution centre. This physiological approach might clarify the reasons for the existence of the eastern range edge and might further explain the presence or absence of macroecological patterns among trees.

(iv)   We identified the drought tolerance of beech seedlings (*Fagus sylvatica* L.) from marginal and central provenances in Central Europe (chapter V), which may be of major concern in the course of global climate change to prevent loss of trees due to drought.

To achieve our aims, we combined different approaches. In chapter II we chose a semi-quantitative assessment of abundance and niche breadth in the species` distribution centre based on a thorough literature review. We then correlated abundance, niche breadth and range size to each other for detecting patterns within ecologically similar subgroups of the whole sample set. The assessment of the variation of abundance and niche breadth from centre to margin (chapter III) was based on a wealth of already existing forest inventory data for the central (Southern Lower Saxony, Central Germany) and marginal (Slovakia) study regions. Here we aimed at detecting (i) differences in the availability of soil resources and bedrock types, (ii) in species niche preferences and (iii) in niche breadth attributes between the central and marginal populations of the six investigated tree species. For analysing the stress exposure of central and marginal tree populations (chapter IV) we collected leaf, fine root and soil samples as well as increment cores in several forest stands in Central Germany and South East Poland. The identification of drought-tolerant beech ecotypes (chapter V) was achieved with an experimental approach with seedlings from two autochthonous provenances from Central Germany and South-East Poland. They were grown under three controlled soil moisture regimes (control, moderate drought stress, high drought stress) and morphological, physiological and growth-related responses to drought of 14-week old seedlings were analyzed.

Do Central European tree species show the widely recognized macroecological patterns and relationships?

In contrast to most other taxonomic groups, Central European trees generally showed only few macroecological patterns. Trees, which are abundant in Central Europe, do not necessarily have larger distribution ranges than rare species (chapter II). Trees which vividly mirror this phenomenon are the two *Populus* species and *Fagus sylvatica*. *Populus tremula* has by far the largest distribution range of all species in the study (27,381,800 km²) but only reaches rank nine in abundance in Central Europe. Its congener *Populus nigra* has the fifth largest distribution range (11,888,150 km²) but is a very rare species (rank 22). *F. sylvatica*, on the other hand, is the most dominant and abundant tree species in Central Europe (rank 1), but has a rather small distribution range (1,954,152 km², rank 21). However, there are also examples of relatively abundant species, like *Salix alba* and *Alnus glutinosa* (ranks 5 and 6), which indeed have large distribution ranges (*S. alba*: 14,124,900 km², rank 3, *A. glutinosa*: 9,422,800 km², rank 7). Furthermore, the spectrum of different soil conditions which are tolerated by a species in its distribution centre, does not seem to be related to its ability of colonising large areas (chapter II). *Salix alba*, for example, populates most of Europe and its distribution range extends into Asia and Afrika (14,124,900 km², rank 3) but the species is mainly limited to wet sites with a good nutrient supply along riverbeds in its distribution centre (niche breadth rank 22) (Schütt *et al.*, 1994). *Carpinus betulus*, on the other hand, is rather tolerant with regard to soil conditions in the distribution centre (Schütt *et al.*, 1994; Ellenberg, 1996) (rank 4) but has only a small distribution range (3,321,500 km², rank 17) compared to the other 24 investigated tree species. Beside from not being related to the range size of Central European tree species, the soil niche breadth of *Fagus sylvatica, Quercus petraea, Acer pseudoplatanus, Prunus avium, Sorbus torminalis* and *Taxus baccata* also did not narrow towards the eastern distribution margin (chapter III), as was hypothesized according to general macroecological believe.

There may be two explanations why Central European tree species differ in their macroecology from other organisms. First, the Central European tree species may be too different in their ecology from each other to show a strong relationship between abundance and range size (e.g. Brown, 1984). This explanation is emphasized by the presence of a relationship between abundance and range size among mid-successional tree species, which constitute a subgroup with similar ecological niche dimensions (Burschel & Huss

2003). Second, phylogenetic diversity within a species assemblage can further weaken abundance relationships (Brown, 1984), which might also be the case in the Central European tree flora, as it is rather poor in species but contains a considerable number of orders and families which lead to a high taxonomic diversity at higher systematic levels. Furthermore, niche breadth is often stated as the key variable controlling abundance and distribution patterns (Brown, 1984; Gaston *et al.*, 1997). In this context, it is important to specify what niche dimensions and scales are considered, because contrasting definitions of the ´ecological niche` exist in literature (Schaefer, 2003). Soil niche breadth in the distribution centre does not seem to be influential in our tree species sample (chapter II). This variable stays more or less constant from the distribution centre towards the eastern range margin in three common and rare species, although a general niche shift was observed, which is directed to generally less productive sites at the margin (chapter III). This might indicate that temperature is a more influential variable in controlling abundance and distribution patterns among Central European trees, than are soil attributes (chapter II). As soon as tolerance of extreme low and high temperatures on a continent-wide scale is incorporated into the analysis of niche breadth, a positive relationship appears between niche breadth and range size of Central European tree species. The role of temperature might be important when attempting to explain the eastern distribution margin. In fact, low temperature extremes, or increasing summer drought, or other factors such as increasing herbivory could limit the tree species at their eastern distribution edge with a more continental climate.

Ecophysiological traits of Central European tree species and their influence on macroecological patterns

The investigation of a number of ecophysiological traits of central and marginal provenances of *F. sylvatica*, *A. pseudoplatanus*, *P. avium* and *T. baccata* did not reveal symptoms of pronounced drought stress in marginal nor in central populations (chapter IV). It seems more likely that the eastern limit of the aforementioned species is primarily caused by damage to seedlings as well as to flowers and fruits of mature trees which results from a higher frequency and intensity of late frost events. Especially seedlings may suffer from extreme low temperatures, making them more vulnerable to diseases. The limiting effect of frosts has especially been observed in *F. sylvatica* which shows a much lower

frequency of masting years in Eastern Poland compared to the distribution centre (Ellenberg, 1996).

At least for *F. sylvatica* seedlings, we could prove that increased drought at the eastern range margin does not seem to be a limiting factor if acting alone (chapter V). Seeds from marginal provenances of *F. sylvatica* seem to be better adapted in their physiology and phenology to drought periods than plants from central populations.

It seems most likely that a tree species` tolerance towards temperature extremes defines its abundance and distribution patterns on a global, i.e. macroecological, scale. This conclusion agrees with the findings of other authors (Currie & Pacquin, 1987; Adams & Woodward, 1989; O´Brien, 1993) who report that in the Northern hemisphere, between 45 and 60° N, temperature is the most important single variable, explaining diversity patterns and probably also the distribution range of species.

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Supplementary material

Appendix S1 Literature used in the survey on abundance and niche breadth of the Central European tree flora

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Appendix S2 Classification system used to transform literature data into a semi-quantitative assessment of abundance and niche breadth of Central European tree species in their distribution centre

Table S 1 Mean January and mean July temperature (°C) (1961-1990) of cities on north-western, north-eastern, south eastern and south-western range edges of the Central European and global distribution ranges of 25 Central European tree species. For abbreviations see methods section.

Central European distribution range

Range edge	City	Species	Mean temperature (°C)	
			Jan.	Jul.
North-West	Berlin	*Popnig, Prunav*	0.5	18.4
	Bremen	*Alnusglut, Betpub, Carpbet, Fagsyl, Fraxexc, Poptrem, Prunpad, Quercpet, Quercrob, Salalba, Salpur, Sorbaucup, Taxbac, Tilcor, Ulmminor, Ulmglab*	0.8	16.8
	Dortmund	*Abiesalb, Sorbtorm*	1.9	17.6
	Flensburg	*Acercamp*	0.6	16.0
	Hamburg	*Acerpseud*	0.5	16.8
	Cologne	*Acerplat, Sorbaria*	1.8	17.8
North-East	Cracow	*Prunav, Sorbaria*	-3.3	17.5
	Elbing	*Acercamp, Acerplat, Acerpseud, Alnusglut, Betpub, Carpbet, Fagsyl, Fraxexc, Popnig, Poptrem, Prunpad, Quercpet, Quercrob, Salalb, Salpur, Sorbaucup, Sorbtorm, Taxbac, Tilcor, Ulmminor, Ulmglab*	-2.4	16.8
	Posen	*Tilplat*	-2.0	18.0
	Warsaw	*Abiesalb*	-3.3	17.9
South-East	Wroclaw	*Sorbtorm*	-1.8	17.6
	Cracow	*Abiesalb, Acercamp, Acerplat, Acerpseud, Alnusglut, Betpub, Carpbet, Fagsyl, Fraxexc, Popnig, Poptrem, Prunav, Prunpad, Quercpet, Quercrob, Salalba, Salpur, Sorbaria, Sorbaucup, Taxbac, Tilcor, Tilplat, Ulmminor, Ulmglab*	-3.3	17.5
South-West	Augsburg	*Ulmminor*	-0.7	17.8
	Freiburg i. Br.	*Abiesalb, Acercamp, Acerplat, Acerpseud, Alnusglut, Betpub, Carpbet, Fagsyl, Fraxexc, Popnig, Poptrem, Prunav, Prunpad, Quercpet, Quercrob, Salalba, Salpur, Sorbaria, Sorbaucup, Sorbtorm, Taxbac, Tilcor, Tilplat, Ulmglab*	1.8	19.9

Global distribution range

Range edge	City	Species	Mean temperature (°C)	
			January	**July**
North-West	Birmingham	*Carpbet, Popnig, Prunav, Salalba, Sorbaria, Sorbtorm*	3.1	15.8
	Bodoe	*Betpub*	-2.2	12.5
	Brest	*Fagsyl*	6.3	15.9
	Gardermoen	*Acerplat*	-7.2	15.2
	Göttingen	*Abiesalb*	1.0	17.4
	Karlstadt	*Taxbac*	-4.3	16.4
	Kiel	*Ulmminor*	0.7	16.3
	La Hague	*Tilplat*	4.5	17
	Leeming	*Acercamp*	3.3	15.5
	Orland	*Tilcor*	-0.7	12.7
	Stornoway	*Alnusglut, Fraxexc, Poptrem, Prunpad, Quercpet, Quercrob, Salpur*	4.2	12.7
	Trornsoe	*Sorbaucup, Ulmglab*	-12.8	13.5
	Vlissingen	*Acerpseud*	3.2	16.9
North-East	Arkona	*Acerpseud*	0.2	16.2
	Bergen	*Quercpet, Quercrob*	1.5	15.0
	Elbing	*Sorbtorm*	-2.4	16.8
	Goeteborg	*Fagsyl*	-0.9	16.6
	Jakutsk	*Poptrem*	-41.1	18.7
	Kanin Nos	*Sorbaucup*	-9.6	9.0
	Karaganda	*Salalb, Tilcor*	-13.6	20.8
	Kasan	*Prunav, Ulmglab, Ulmminor*	-13.1	19.4
	Lugansk	*Acercamp*	-5.9	21.7
	Marnitz	*Tilplat*	-0.8	16.9
	Murmonak	*Prunpad*	-9.6	9.0
	Orenburg	*Salpur*	-13.6	21.9
	Oulu	*Alnusglut*	-11.1	16.0
	Stockholm	*Carpbet*	-2.8	17.0
	Tallin	*Fraxexc, Taxbac*	-5.2	16.3
	Tura	*Betpub*	-36.1	16.6

	Warsaw	*Abiesalb*	-3.3	17.9
	Wologda	*Popnig*	-12.7	16.9
	Zamosc	*Sorbaria*	-4.4	17.4
South-East	Aschchabad	*Ulmminor*	2.2	30.9
	Bukarest	*Abiesalb, Sorbaria, Tilplat*	-2.1	22.4
	Burgas	*Fagsyl*	2.1	21.9
	Hakkari	*Carpbet*	-4.7	24.7
	Karraganda	*Popnig, Prunpad*	-13.7	20.8
	Kars	*Betpub, Salpur, Sorbtorm, Tilcor*	-9.9	17.3
	Machackala	*Acercamp, Fraxexc, Ulmglab, Quercpet, Taxbac*	0.3	24.8
	Chengchu	*Poptrem*	5.5	25.3
	Omsk	*Acerplat*	-17.4	19.7
	Orenburg	*Quercrob, Sorbaucup*	-13.7	21.9
	Patigorsk	*Prunav*	-3.7	20.9
	Taschkent	*Salalba*	0.5	27.6
	Van	*Alnusglut*	-4.5	21.9
	Varna	*Acerpseud*	1.9	22.0
South-West	Barcelona	*Acerplat*	9.8	24.0
	Cabo Bonifati	*Fagsyl*	8.0	22.6
	Campobasso	*Fraxexc*	3.8	21.5
	Crotone	*Prunpad*	9.2	25.0
	Gela	*Prunav, Tilplat*	11.6	23.1
	Gibraltar	*Alnusglut*	13.4	23.7
	Kalamai	*Taxbac, Ulmminor, Ulmglab*	10.2	26.5
	Lugano	*Betpub*	2.5	20.3
	Malaga	*Salalb*	12.2	24.8
	Melilla	*Popnig, Sorbaria*	12.2	24.8
	Palermo	*Quercpet*	12.5	25.6
	Thessaloniki	*Tilcor*	5.0	26.5
	Toulouse	*Abiesalb*	5.1	21.2
	Trapani	*Acercamp, Acerpseud, Carpbet, Poptrem, Quercrob, Salpur, Sorbaucup, Sorbtorm*	11.6	24.7

Table S 2 Abundance classification table used to transform literature information on a species' abundance into abundance levels and finally ranks. Literature was surveyed for abundance terms or synonyms alternatively.

Level	Abundance classification term	Attributes used by the authors to quantify abundance
1	absent	absent, missing
2	very rare	at a few specific sites; single records; very low frequency
3	rare	small quantities; occurring in single-stem admixtures; very scattered
4	sparse/scattered	regionally common; occurring in groups; trees admixed in stands; occurring in parts of the respective region
5	abundant	large forests; pure stands; common; occurring without interruption or only with regional gaps
6	very abundant	dominant; main tree species; very common

Table S 3 pH and base saturation classification table used to transform literature information on the pH value and the base saturation at which a species appears into levels and finally ranks. Literature was surveyed for terms of acidity, numerical values or correlating attributes.

Level	Classi-fication term	Literature data for topsoil		Attributes used by the authors to characterize the soil status			
		pH (KCl)	Base satura-tion (%)	Substrate types	Soil types	Humus types	Herb layer species
1	extre-mely acid	< 3,2	< 12	very silicate-poor substrates, dune sands, quarzit etc.	Podsol	mor	*Calluna, Leuco-bryum, Erica* spec.
2	highly acid	3,0 – 4,0	10 – 18	silicate-poor rocks, glacial sands etc.	Brown Earth-Podsol	raw moder	*Des-champsia, Erica* spec.
3	mode-rately – highly acid	3,5 – 4,5	15 – 30	sandstone, granite, greywacke, agrillaceous shale, moderately acid loess	pod-solic Brown Earth	moder	*Luzula, Calama-grostis* species
4	moder-ately acid	4,0 – 5,0	25 – 45	silicate rocks rich in bases, sedimentary rocks: diorit, gneiss, mudstone	Brown Earth or Lessivé	mull-like moder	*Lamiastrum galeob-dolon*
5	weakly acid	4,5 – 6	> 40	base-rich rocks: diabas, gabbro, basalt;	base-rich Brown Earth	mull	herbs, *Mercurialis perennis*
6	neutral-basic	>6	> 40	limestone, dolomite	Rend-zina, Terra fusca	mull	*Mercurialis perennis,* orchids

Table S 4 Soil moisture classification table used to transform literature information on the soil moisture status at which a species occurs into moisture levels and finally ranks. Literature was surveyed for precise soil moisture terms or correlated soil attributes alternatively.

Level	Soil moisture status	Attributes of the soil used to characterize soil moisture status
1	very dry	very shallow soil; very low water holding capacity
2	moderately dry	intermediate to shallow soil depth; low water holding capacity
3	moderately moist or alternating moisture status	soils with stagnic properties; low to medium water holding capacity
4	moist	deep soils; medium to high water holding capacity
5	wet	medium to high ground and backwater levels; transition from terrestrial soils to gleyic soils
6	very wet	weakly fluctuating ground and backwater; wet gley; mor-gley; mor

Table S 5 Classification table of geological substrates ranked according to soil grain size or soil type.

Level	Geological substrates	Correlating soil categories
1	silicate-poor glacial deposits	highly acidified sandy soils on glacial sands or dune sands
2	silicate-poor rocks: sandstones, schists, granite	acidified sandy to silt-rich soils
3	decalcified loess substrates	acidified loamy light soils
4	silicate-rich rocks: basalts, diabas	moderately base-rich sandy to loamy soils
5	claystones, marls	moderately base-rich loamy to clayey compact soils
6	limestones	carbonate soils rich in clays

Table S 6 Groups of species with similar attributes in terms of abundance, range size, successional status or phylogeny that were analysed for relationships between abundance, range size and niche breadth variables. For abbreviations see methods section in chapter II.

Attribute	Species group	Species
Abundance in the distribution centre	Most abundant species (n=12)	*Acercamp, Alnusglut, Betpub, Carpbet, Fagsyl, Fraxexc, Prunpad, Poptrem, Quercpet, Quercrob, Salpur, Salala*
	Least abundant species (n=12)	*Abiesalb, Acerplat, Acerpseud, Prunav, Popnig, Sorbaria, Sorbaucup, Sorbtorm, Taxbac, Tilcord, Tilplat, Ulmminor*
Range size	Species with largest ranges (n=12)	*Alnusglut, Betpub, Popnig, Prunpad, Poptrem, Quercrob, Salalba, Sorbaucup, Salpur, Tilcord, Ulmminor, Ulmglab*
	Species with smallest ranges (n=12)	*Abiesalb, Acercamp, Acerplat, Acerpseud, Carpbet, Fagsyl, Prunav, Quercpet, Sorbaria, Sorbtorm, Taxbac, Tilplat*
Successional status	Early-successional species (n=7)	*Alnusglut, Betpub, Popnig, Poptrem, Salalba, Salpur, Sorbaucup*
	Mid-successional species (n=12)	*Acercamp, Acerplat, Carpbet, Fraxexc, Prunav, Prunpad, Sorbaria, Sorbtorm, Tilcor, Tilplat, Ulmminor, Ulmglab*
	Late-successional species (n=6)	*Abiesalb, Acerpseud, Fagsyl, Quercpet, Quercrob, Taxbac*
Phylogeny	Fagales (n=6)	*Alnusglut, Betpub, Carpbet, Fagsyl, Quercpet, Quercrob*
	Rosales (n=7)	*Prunav, Prunpad, Sorbaria, Sorbaucup, Sorbtorm, Ulmusminor, Ulmusglab*
	Malpighiales (n=4)	*Popnig, Poptrem, Salalba, Salpur*

Table S7 Nutrient status classification table used to transform forest inventory information on the nutrient status into a six-level system in order to standardise the data from Lower Saxony and Slovakia. This assessment refers mainly to N availability as indicated by soil C/N ratio.

Level	Soil fertility	Related soil types according to FAO classification
1	very poor	haplic Arenosol, (haplic) Podzol, podzolic Ranker, Regosol, Syrosem, (mor/podzol) Gley
2	poor	endoeutri-gleyic Albeluvisol, (typical/gleyic/podzol) Brownearth, dystric/gleyic Cambisol, dystric Gleysol, Gley, gleyic Pseudogley, (humous) Podzol, typical Ranker, (skeletal/typical) Stagnogley, carbonatic Syrosem
3	medium	kolluvial/mesotrophic/gleyic Cambisol, molli-gleyic Fluvisol, dystric-gleyic/kolluvial Luvisol, (endoskeletic) Umbrisol, alluvial/calcaric/brown Gley, pelosolic Pseudogley, brown Ranker
4	good	chernic Chernozem, Luvisol, ranker Cambisol, haplic Phaeozem, calcaric/alluvial Regosol, alluvial Syrosem, gleyic Fluvisol, andosolic Luvisol, andosolic Ranker, Terra Rossa
5	rich	Andosol, andosolic/eutric Cambisol, calcic/typical/brown Chernozem, calcarous/eutric/brown Fluvisol, (dystric-lithic) Leptosol, calcaric-fluvic Phaeozem, alluvial Regosol, (loess/protorendzina) Pararendzina, protorendzina/brown Rendzina, (loess/luvic/gleyic) Terra Fusca
6	very rich	calcaric Fluvisol, rendzic Leptosol, calcarous Rendzina

Principal decrease of soil C/N ratio

Table S8 Geological bedrock type classification table with correlating soil fertility and soil moisture characteristics used to transform information from geological maps into a six level system.

Level	Bedrock type	Substrate	Ecological characteristics
1	silicate-poor rocks	quartzite, pure sands (compacted)	nutrient-poor, unfavourable water balance
2	glacial and fluviatile sediments	mainly sand, gravel	moderately fertile, unfavourable water balance
3	silicate-rich rocks	plutonic rock, magmatic rock (crystallin basement, i.e. granite), metamorphic rocks (gneiss), volcanite (basalt, andesite), sedimentary rock (clay, mudstone, marl, bunter, sandstone)	medium to high nutrient availability, (un) favourable water balance
4	calcareous rocks	limestone, marl	high nutrient availability, unfavourable water balance
5	aeolian deposits	loess	high nutrient availability, favourable water balance
6	alluvial and kolluvial sediments (holocene)	heterogeneous grain size distribution	very nutrient-rich, favourable water balance

Table S9 Study sites with their location, the tree species present (F = *Fagus sylvatica*, A = *Acer pseudoplatanus*, P = *Prunus avium*, T = *Taxus baccata*) and their geology. Stands where increment cores have been taken are marked with an asterisk (*).

Central Germany			
Stand	**Coordinates**	**Species**	**Geology**
Hünstollen	51°34´45.01´´N 10°02´59.77´´E	F, A	limestone
Totenberg	51°31´38.68´´N 9°38´47.22´´E	F	sandstone
Dreyberg	51°43´35.94´´N 9°33´13.18´´E	F	sandstone
Sababurg	51°32´37.69´´N 9°30´23.66´´E	F	sandstone
Reinhausen Abt. 6/7	51°34´02.19´´N 10°02´51.22´´E	P	limestone
Reinhausen Abt. 15	51°34´54.41´´N 10°03´20.97´´E	P	limestone
Reinhausen Abt. 27	61°35´34.95´´N 9°59´06.60´´E	F, A, P	limestone
Reinhausen Abt. 156	51°34´03.74´´N 9°57´28.33´´E	F, A, P	limestone
Billingshäuser Schlucht	51°34´43.40´´N 9°58´56.48´´E	A	limestone
Barlissen	51°26´20.18´´N 9°47´24.81´´E	P	limestone
Deiderode*	51°25´27.51´´N 9°50´53.82´´E	F, A, P	limestone
Bovenden	51°35´21.34´´N 9°57´28.07´´E	T	limestone
Meensen	51°26´02.02´´N 9°45´36.70´´E	T	sandstone
Atzenhausen	51°25´33.58´´N 9°47´26.95´´E	T	sandstone
Brackenberg	51°26´06.80´´N 9°44´31.05´´E	T	limestone
Taufsteinweg (Lichtenhagen)	51°25´58.82´´N 9°59´54.27´´E	T	sandstone
Münden	51°24´11.93´´N 9°47´20.60´´E	T	limestone
Schradersrottweg	51°26´54.32´´N 9°59´53.51´´E	T	sandstone
Ruine Reichenbach*	51°10´25.40´´N 9°46´31.27´´E	F, A, P	limestone

Hohestein*	51°14´45.37´´N 10°02´59.90´´E	F, A	limestone
Niestehänge	51°17´30.76´´N 9°42´52.94´´E	F	sandstone
Lindig (Hainich)*	51°05´24.03´´N 10°31´28.11´´E	F, A, P	limestone
Fuchsfarm (Hainich)*	51°06´11.90´´N 10°28´04.96´´E	P	limestone

South-East-Poland

Stand	Coordinates	Species	Geology
Ojcow Grota Łokietka*	50°12´20.27´´N 19°48´11.36´´E	F, A	limestone
Ojcow Wawóz Jamki	50°12´17.01´´N 19°48´33.48´´E	F, A	limestone
Ojcow Wawóz Pradła	50°12´00.43´´N 19°48´46.24´´E	P	limestone
Ojcow Wawóz Dziekowiec	50°12´03.81´´N 19°48´17.81´´E	P	limestone
Radomice	50°44´26.00´´N 20°39´11.31´´E	T	sandstone
Cisów*	50°46´48.34´´N 20°54´29.10´´E	F, A	limestone
Zamczysko	50°46´55.43´´N 20°57´07.95´´E	F, A	limestone
Roztocze Jarugi	50°38´17.81´´N 23°01´43.95´´E	F, A, P	limestone
Roztocze Mokra Debra*	50°37´49.43´´N 23°01´40.12´´E	F, A, P	limestone
Roztocze Czerkies	50°35´30.45´´N 23°02´39.10´´E	F	limestone
Roztocze Kąty	50°38´11.21´´N 23°01´48.93´´E	P	limestone
Kretówki A	49°42´51.90´´N 21°54´29.50´´E	F, A, P, T	calcareous rocks
Kretówki B	49°42´38.33´´N 21°55´21.09´´E	F, P, T	calcareous rocks
Malinówki*	49°42´39.52´´N 21°55´12.13´´E	P, T	calcareous rocks
Igiełki A	49°30´34.18´´N 21°38´36.31´´E	P, T	sandstone
Igiełki B	49°30´37.30´´N 21°38´46.80´´E	T	sandstone
Przełom Jasiołki	49°27´30.71´´N 21°44´06.37´´E	F, A, P	limestone

Table S10 Summary of results of three different statistical tests comparing various plant morphological, physiological and chemical variables between different drought treatments (DT) and different provenances (Pro). Pro x DT = influence of the interaction between provenance and drought treatment; K-W, Kruskal-Wallis; df, degrees of freedom. ***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; m, $p \leq 0.1$; n.s., $p > 0.1$

		Pro		**DT**		**Pro x DT**		**Pro**		**DT**	
	df	1		2		2		1		2	
	Test	F	p	F	p	F	p	χ^2	p	χ^2	p
Number of leaves	ANOVA	1.07	n.s.	2.96	m	0.88	n.s.				
RGR	ANOVA	24.01	***	17.50	***	0.31	n.s.				
Shoot length	ANOVA	0.09	n.s.	0.97	n.s.	4.13	*				
Total biomass	ANOVA	1.29	n.s.	16.63	***	0.18	n.s.				
Fine root biomass (ln)	GLM	0.02	n.s.	7.22	**	0.25	n.s.				
Leaf Ca content (ln)	GLM	0.52	n.s.	0.36	n.s.	0.44	n.s.				
Leaf K content	GLM	6.08	*	8.80	***	0.74	n.s.				
Root/shoot ratio	GLM	5.94	*	16.46	***	2.55	m				
SLA	GLM	10.46	**	3.46	*	1.26	n.s.				
$\Delta^{13}C$	K-W							3.85	*	20.44	***
FR/LA ratio	K-W							3.46	m	13.36	***
Leaf Mg content	K-W							1.10	n.s.	8.50	*
Leaf water content	K-W							0.14	n.s.	28.25	***
Predawn water potential	K-W							0.47	n.s.	49.15	***
Root collar diameter	K-W							2.82	m	18.52	***
SRA	K-W							10.11	**	8.77	*
Stem biomass	K-W							1.10	n.s.	8.50	*

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CURRICULUM VITAE

Personal data

Name	**Benjamin Köckemann**
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Place of birth	Düsseldorf
Nationality	German

Work experience

May 08 – dato	**Reader** Quelle & Meyer Verlag, Wiebelsheim, Germany
Jan 05 – Mar 08	**Scientific Assistant** Department of Ecology and Ecosystem Research, Albrecht-von-Haller-Institute for Plant Sciences, Georg-August-University of Göttingen, Germany
May - Dec 04	**Graduate Assistant** Institute of Silviculture, Albert-Ludwigs-University of Freiburg, Germany

Education

Apr 05 - dato	**Phd study programme „Biological Diversity"**, Georg-August-University of Göttingen, Germany
Apr 02 - Mär 04	**Sustainable Forestry and Land Use Management** Albert-Ludwigs-University of Freiburg, Masterthesis: Comparison of biomass and carbon stocks in two silviculture systems in sub-tropical Australia
Mar 98 - Jan 02	**Forestry**, Technical University of Applied Sciences Hildesheim/Holzminden/ Göttingen, Diplomathesis: „Kommerzialisierung der forstlichen Öffentlichkeitsarbeit am Beispiel des Kommunalverbandes Ruhrgebiet"

Studies-related activities and internships

May 07 - Okt 07	**XLAB - Göttinger Experimentallabor für junge Leute e.V.** Trainer in the course „Interdependencies and Productivity in Forest Ecosystems"
Nov 03 - Jan 04	**University of Queensland, Australia**, collection and analysis of data for the masterthesis; scholarship of the Landesstiftung Baden-Württemberg
Jul 02 - Sep 03	**Institute of Forestbotany und Treephysiology**, Albert-Ludwigs-University of Freiburg, Germany, undergraduate assistant
Okt 02	**Tutor** in the study course „Sustainable Forestry and Land Use Management"
Dez 00 - Feb 01	**Queensland Parks and Wildlife Service** in Queensland, Australia, Internship at the "Centre for Tropical Restoration"
Okt 96 - Apr 97	**Gräflich von Spee´sche Forstverwaltung Heltorf**, Ratingen, Germany internship

Coloured cover images by Göttingen Centre for Biodiversity and Ecology (legend top to bottom)

1 Mixed deciduous forest in the Hainich region (Central Germany)
2 Different insect taxa on the flowers of a thistle (*Cirsium* sp.)
3 *Glomeris* sp., a member of the decomposing soil fauna in forest ecosystems
4 *Pleodorina californica* (Chlorophyceae), colony-forming freshwater phytoplankton species
5 Grasshopper *Tettigonia cantans*, distributed from the Pyrenees to Northeastern China
6 *Microcebus berthae* (Cheirogaleidae), the smallest extant Primate species (Madagascar)
7 Tropical rain forest (Greater Daintree, Australia)
8 *Lethocolea glossophylla* (Acrobolbaceae), a liverwort of alpine mountain ranges in South America
9 Part of a coral reef in the Red Sea

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