The north-eastern distribution range of European beech — a review

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Summary

Today, European beech (*Fagus sylvatica* L.) seems to be a markedly successful tree species in the north-east of its distribution range. The distribution area may be larger than originally assumed; past forest management is probably the main cause of the contraction in the postglacial European beech range. Numerous attempts consistently have failed to locate a distinct distribution edge for European beech. Therefore, we define northern and eastern Poland and the southern regions of the Baltic States as margins of European beech distribution. Ecophysiological approaches have identified the drought constraints for European beech in terms of (1) the critical limit for xylem cavitation and loss of hydraulic conductivity, reached at a shoot water potential of –1.9 MPa, and (2) a reduction in gross primary production and total ecosystem respiration when relative extractable soil water reaches 40 and 20 per cent, respectively. However, it is difficult to correlate European beech distribution margins with single macro-climatic factors. Moreover, the adaptation of European beech populations and provenances to drought and frost varies. The phenotypic plasticity and evolutionary adaptability of European beech appear to be underestimated. These characteristics may counteract a further contraction of the European beech range arising from climate change in the future.

Introduction

European beech (*Fagus sylvatica* L.), the main species in deciduous forests in Central Europe, is the most competitive tree species on sites with moderate soil moisture and acidity, widespread across this region (Bohn *et al.*, 2004). Leuschner *et al.* (2006) claims that European beech is the 'most successful Central European plant species'. However, since the medieval epoch, many forests with European beech were converted into agricultural land, and later into coniferous forests, particularly in its north-easterly range, north-eastern Germany and northern Poland, where mainly Scots pine plantations replaced many European beech and mixed deciduous forests (Ellenberg, 1988). In north-eastern Germany, for example, European beech covered 4.3 per cent of the forest area in the 1980s, which is only 10 per cent of its area of natural distribution in this region (Hofmann, 1996). A similar reduction in European beech forest area took place in northern Poland (Szafer, 1966). In contrast, Prussian foresters promoted European beech in some areas of Latvia, Lithuania and north-east Poland in the nineteenth century by planting European beech

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stands near or even outside the reputed range edge (Dreimanis, 2004). A 'renaissance' of European beech can be observed in the region in recent years when Scots pine forests were converted back to pure and mixed deciduous forests (Fritz, 2006), and as European beech spread more extensively throughout its eastern range spontaneously (Peters, 1997). Both the regional differences in human influence on European beech distribution over time and the loss of much of the natural or old deciduous forests in Europe (Bradshaw, 2005) create uncertainty about the current north-eastern edge of the European beech range. Moreover, the primary environmental factors determining the occurrence and competitiveness of European beech may be masked by anthropogenic activity (Bradshaw, 2004). The literature review presented in this paper addresses the following questions: (1) what are the historical and recent patterns of European beech distribution in its north-eastern range and (2) what ecological factors limit European beech occurrence in the region? The answers to these questions are important in view of the considerable interest in continuing the near-natural European beech forest restoration program in the region (see Tarp *et al.*, 2000); European beech contributes to both the high economic and ecological value gained from silvicultural measures for 'close-to-nature' and nature conservation aims (e.g. Fritz, 2006). Furthermore, the results will facilitate discussions about the possible response and adaptation potential of European beech to more frequent droughts anticipated as a result of climate change (EEA, 2004; IPCC, 2007).

European beech range and its north-eastern edge

In the last 150 years, over 40 publications have looked at the distribution of European beech forests and the edge of its range. One needs to differentiate between the natural range of European beech forests and the phytogeographic range of European beech itself, since the former defines the area in which it is dominant and the latter the area in which it is present. Although more than 20 maps of the European beech range have been published, these are not always based on separate studies (Markgraf, 1932, with a map from Abromeit, 1912; Szafer, 1932; Groß, 1934; Dengler, 1944; Firbas, 1952; Rubner and Reinhold, 1960; Meusel, 1965; Szafer and Zarzycki, 1972; Jalas and Suominen, 1972–1999; Mayer, 1984; Huntley *et al.*, 1989; Röhrig and Bartsch, 1992; Tarasiuk, 1992; Lang, 1994; Peters, 1997; Schröder, 1998; ; Tarasiuk, 1999; Otto, 2002; Institute of Geobotany, Halle University, 2006; Figure 1). Publications by Hofmann (1996, north-east Germany), Hofmann and Pommer (2004, Brandenburg, Germany), Szafer (1966) and Matuszkiewicz (1984, both entire Poland) and Bohn *et al.* (2004, Europe) include maps of the European beech forest area in north-eastern Central Europe.

European beech distribution is concentrated in Central and west Europe (Figure 1). It is characteristic of maritime climates (Grisebach, 1872), with a special affinity to the Central European climate (Meusel, 1965). In the northern and eastern regions of Central Europe (south Scandinavia, north Germany, north Poland) as well as in some areas of western Europe (north France, south England), European beech occurs on the plains and in the hills and lower mountain ranges. In the cold climate prevailing in Masuria (north-eastern Poland), the northern and eastern margins of its distribution, European beech partially overlaps with the boreal coniferous species Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). There, European beech grows and dominates on loamy moraine soils in pure or mixed stands, usually with Scots pine. Admixed Scots pine may dominate and replace European beech on dry sandy soils with poor nutrition (sander sediments) (Rubner and Reinhold, 1953). Studies of the vegetation history in this region (Kaliningrad District, Warmia and Mazury) regarded the European beech range margin as the 'boundary between Central and eastern Europe' (Groß, 1934).

At the eastern edge of the European beech range in central and eastern Poland, where a continental climate prevails, deciduous tree species such as pendunculate oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.) and hornbeam (*Carpinus betulus* L.), in addition to Scots pine, may become more competitive than European beech and replace it in regions to the east and south of this range edge (Rubner and Reinhold, 1953).

However, the distinct location of the European beech range edge in this region remains unclear: some authors have described 'eroding' range

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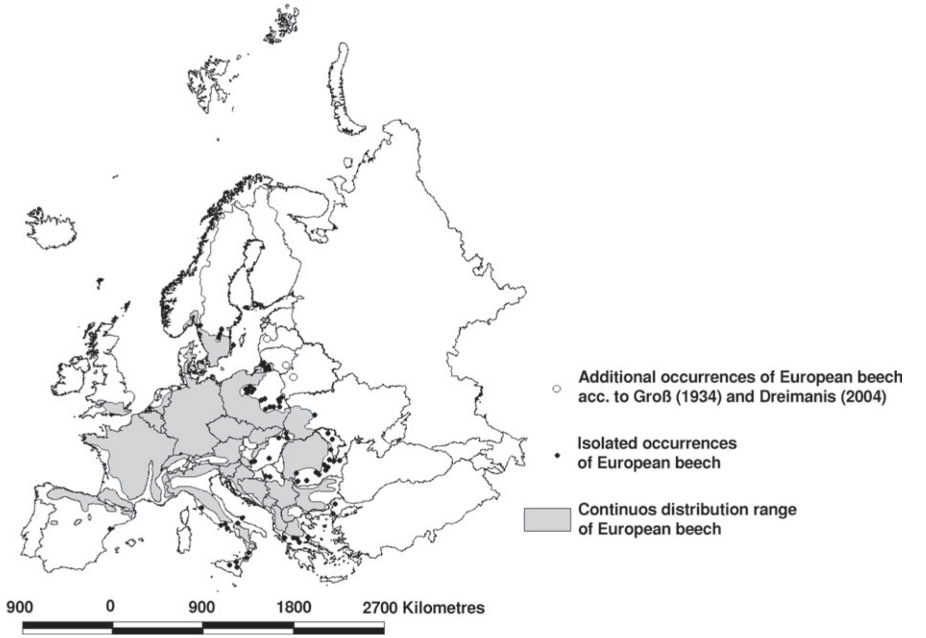

Figure 1. Map of the European beech distribution area with isolated occurrences, partly synanthropic (filled dots; Institute of Geobotany, Halle University, 2006), modified to include three additional occurrences from Groß (1934) and Dreimanis (2004) (unfilled dots).

margins (see Hampe and Petit, 2005) for European beech (Matuszkiewicz, 1984, 1989), whereas others separated its continuous range from the numerous isolated populations near the north-eastern range edge (Groß, 1934; Gostyńska-Jakuszewska, 1976; Röhrig and Bartsch, 1992; Tarasiuk, 1992; Lang, 1994; Otto, 2002). In the following discussion, the continuous European beech range in north-east Poland presented is extracted from four different publications (Figure 2; Markgraf, 1932; Groß, 1934; Szafer and Zarzycki, 1972; Tarasiuk, 1999). A new European beech distribution map (Institute of Geobotany, Halle University, 2006; Figure 1), which includes updated results from floristic surveys in Poland and Germany, shows its recent status.

Markgraf (1932) presented the most conservative estimate of the north-eastern European beech range edge in Central Europe, adopting a map from Abromeit (1912) and descriptions from Höck (1896), Drude (1896) and Lämmermayr (1926). The line representing the eastern edge commences south-west of Kaliningrad and continues southwards to Brodnica and Sierpc (Figure 2). Another line representing the northern edge heads west, and continues inland parallel to the Baltic Sea coast, yet excludes the Wisla River delta and floodplains and the Wisla Spit.

The maps from Groß (1934) and Szafer and Zarzycki (1972) appear similar; both maps include the Baltic Sea coastal region, i.e. Wisla River floodplains and delta, in the European beech distribution range (Figure 2). However, the map from Szafer and Zarzycki (1972) also draws the central Polish European beech range edge with its characteristic return westward along the 500-mm precipitation line from north of Warsaw to the Poznan region. Tarasiuk (1999) described a much larger European beech range; he extended the range more than 50 km eastward on average. The most recent European beech distribution map (Figure 1; Institute of Geobotany, Halle University, 2006) incorporates additional areas in the north-east, for example Samland, and in the south-western region of the Kaliningrad District in Russia and the Curonian Spit. It also records the isolated

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Figure 2. Beech forest distribution in north-eastern Central Europe (Bohn *et al*., 2004) and selected beech range edges.

and mostly synanthropic (i.e. planted and/or cultivated) occurrences of European beech throughout the Kaliningrad District, in western Latvia, in southern Lithuania and in western White Russia (Groß, 1934; Dreimanis, 2004). Of the different estimates of the European beech distribution range, we adopt Tarasiuk (1999), who suggested differentiating three European beech ranges in Poland: (1) the natural distribution (west of line A-A, Figure 3), (2) the synanthropic yet continuous distribution (west of line B-B-A, Figure 3) and (3) the synanthropic and isolated populations (east of line B-B-A, Figure 3). The latter distribution range places European beech in forests throughout Poland, although not necessarily always as the dominant species (Czajkowski *et al*., 2006). This reflects the high growth and regeneration capacity of European beech, even at its north-eastern range edge (Groß, 1934; Rubner and Reinhold, 1960; Matuszkiewicz, 1989; Tarasiuk, 1992), contradicting notions of a definite European beech edge in north-east and central Poland (Szafer and Zarzycki, 1972). In this context, reports about the recent spread of European beech to the east (Tarasiuk, 1992; Peters, 1997; Matuszkiewicz, 2002) can be regarded as the delayed filling in of its natural habitats (e.g. Giesecke *et al*., 2007). The delayed expansion of European beech in northern Central Europe over other tree species during the Holocene is attributed mainly to the warm, dry summers at the beginning of the Holocene, climatic conditions unfavourable for European beech and human impact (Tinner and Lotter, 2006).

Vegetation and forest management history in north-eastern Central Europe

With the retreat of glaciers at the end of the Vistula glacial period, pioneer open birch forests,

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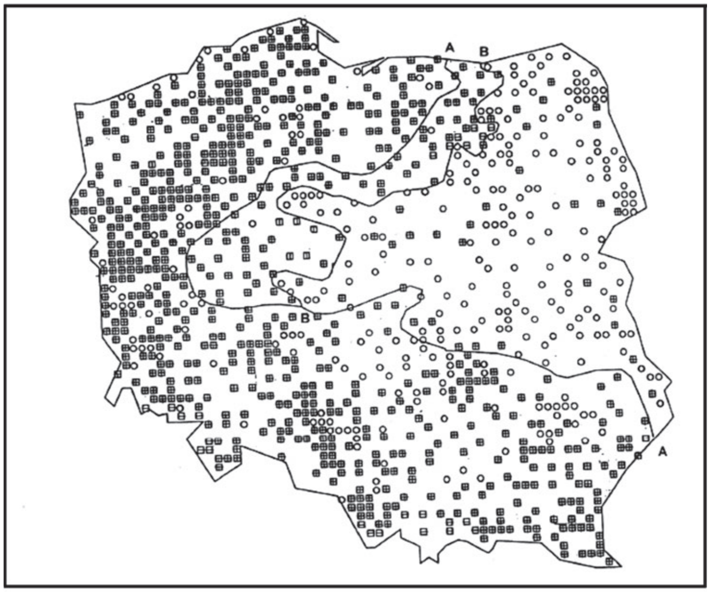

Figure 3. Management districts (i.e. subsection of a Forest Administration District) with European beech stands classified by the amount of precipitation in the vegetation period and number of frost days: line A-A reflects the eastern range edge from Szafer and Zarzycki (1972) and line B-B restricts the European beech range from Tarasiuk (1999) including introduced beech stands.

with juniper (*Juniperis communis*), aspen (*Populus tremula*) and Scots pine (*Pinus sylvestris*), gradually replaced the early tundra vegetation in the northern regions of Central Europe, south Scandinavia and England from about 8700 BC. Thereafter, mixed forests comprising the species hazel (*Corylus avellana*), elm (*Ulmus* ssp.), black alder (*Alnus glutinosa*), lime (*Tilia cordata*, *T. platyphyllos*) oak (*Quercus petraea*, *Q. robur*) and ash (*Fraxinus excelsior*) in different compositions dominated until the arrival of European beech (Birks, 1989; Hahn and Fanta, 2001). According to a recent study by Magri *et al.* (2006) based on paleobotanical and genetic data, European beech began colonizing Central Europe from its northerly glacial refugia in southern France, in Slovenia and Istria and possibly even in southern Moravia and Bohemia; Mediterranean refugia did not contribute. European beech spreads into Central Europe after a climate change around 6200 BC, when the climate became increasingly colder and more humid (Tinner and Lotter, 2001). The expansion of European beech into the lowlands of northern Central Europe in waves during the second half of the Holocene succeeded a comparatively long phase of minor European beech occurrence in small and isolated populations (Giesecke *et al.*, 2007). It reached the southern Baltic shores of Poland and northern Germany between 1500 and 1000 BC; European beech then became abundant and dominant on almost all suitable sites between 500 and 1000 AC, when it reached its recent range (e.g. Giesecke *et al.*, 2007). European beech pollen has been found in

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southern Lithuania, in the eastern Baltic States, as well as in eastern and southern White Russia (Bobruisk and Prypjat depression, Gerassimow, 1930; Kulczynski, 1930; Groß, 1934). However, the low percentages of European beech pollen indicate that it resulted mainly from isolated occurrences and not from large stands. After investigating the etymology of place names, Groß (1934) claimed that, in the Kaliningrad District and northern Masuria, i.e. former East Prussia, the European beech range edge (continuous beech distribution) has remained constant since the Bronze Age. Beyond this edge of the distribution range, he found no Lithuanian or Masurian place names referring to European beech. In contrast to Groß's (1934) estimates, Szafer (1966) found place names associated with European beech further east than the reputed range edge in eastern Poland and western Ukraine.

Recent studies of the paleoecology and forest management history in south Scandinavia revealed that European beech has not yet recolonized its natural range since the last ice age. Although European beech cannot invade old growth forests easily, it is spreading northwards in unmanaged forests in south Sweden (Björkman and Bradshaw, 1996; Björse and Bradshaw, 1998; Björkman, 1999; Diekmann *et al.*, 1999; Hannon *et al.*, 2000; Bradshaw, 2005; Bradshaw and Lindbladh, 2005). This spontaneous spread of European beech may be the 'completion' of its incomplete postglacial invasion (Lang, 1994).

Postglacial climate change, forest site development and natural forest succession are seen as important factors for the natural expansion of European beech forests in Central Europe (Ellenberg, 1988; Pott, 2000). However, recent paleobotanical studies from several regions in northern Central Europe and northern Europe (Björkman and Bradshaw, 1996; Karlsson, 1996; Björkman, 1999; Bradshaw, 2005; Giesecke *et al.*, 2007) support the theory that anthropogenic activities, having increased forest disturbances, for example through burning and clearing forest areas, were a major stimulus for the successful spread of European beech and localized changes in forest vegetation over the last 2000 years (Lindbladh *et al.*, 2000). Thus, human management activities may influence the occurrence of European beech at the margins of its northern distribution range. Some older studies addressed the question, whether European beech stands had been planted or had established spontaneously. Reports by Hryniewiecki (1911) and Szafer (letter quoted by Groß, 1934) claimed that there were no naturally established European beech stands in east Poland (today White Russia, Ukraine and Lithuania), whereas Caspary (1864) argued the reverse. Groß (1934) maintained that the natural European beech occurrences in Nowogrodek and Wilna/Vilnius arose from the seed dropped by birds. This theory is supported by the fact that no large European beech stands were planted in the Kaliningrad District, Warmia or Mazury until the twentieth century. In this region, the inhabitants commonly did not use timber from European beech. Moreover, European beech forests were less favourable than oak forests for cattle grazing and feeding of mast pigs because European beech mast years were infrequent (Groß, 1934) and the ground vegetation usually sparse (Ellenberg, 1988).

However, by removing Scots pine and hornbeam, thought to be the preferred firewood species in medieval times, probably the establishment of European beech in forests was favoured indirectly, and ultimately resulted in it dominating forests in north-eastern Central Europe. This management regime may have favoured European beech expansion in subsequent forest successions due to its excellent ability to regenerate and grow in the region (Groß, 1934; Rubner and Reinhold, 1960; Matuszkiewicz, 1989). The small-scale benefits to European beech expansion may have been assisted on larger scale by sudden reductions in human influence brought about by war, epidemics and the consequent abandonment of settlements (Rubner and Reinhold, 1960; Jahn, 1979, 1983, 1990; Pott, 1997; Speier, 1998; Küster, 1999). This theory is in keeping with the results of the vegetation history in south Sweden discussed earlier.

At the north-eastern range margin of European beech, European beech forests were first documented in the Pasłęk region (Masuria, northern Poland) in 1297 and 1308. Since the fourteenth century, European beech forests (old German: 'Buchwälder') were recorded in the German Knightly Order (Groß, 1934). The indirect support for the establishment of European beech forests ended at the beginning of the eighteenth century, after which the exploitation and devastation of

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the forests intensified during the next 200 years. From the beginning of the nineteenth century, conifers were planted and grown on sites formerly dominated by European beech. After the World War I, European beech was planted on a few sites as underplantings in older Scots pine stands to prevent insect infestation and to improve soil nutrition on nutrient-poor, dry sandy sites such as those in the Puszcza Piska (southern Masuria). Recently, Czajkowski *et al.* (2005) found 100-year-old European beech stands in this region, which Groß (1934) had predicted would fail.

Site requirements for European beech

European beech is a distinct shade tree species that is able to grow on a wide variety of sites (Figure 4). Its ability to reduce the below-canopy irradiance, often below 5 per cent of the open-field irradiance (Emborg, 1998; Collet *et al.*, 2001), enables European beech to compete successfully against other species, as European beech is virtually the only species able to regenerate under such limited light conditions (Ellenberg, 1988). European beech occurrence is not constrained by soil acidity, soil nutrition (Le Tacon, 1981; Ellenberg, 1988; Leuschner, 1993, 1998; Leuschner *et al.*, 1993) or humus type (raw humus to mull). The highest European beech growth rates are recorded on base-rich, moderately moist but well-drained (calcareous) cambisols (Mayer, 1984). Sites with extremely dry soils and stagnic soil types or sites with flooding and high groundwater levels are less favourable (Ellenberg, 1988). Thus, European beech reputedly does not grow on very dry sandy soils, in floodplains, in peat lands or on many gleyic soils (Szafer, 1932; Dengler, 1944; Rubner and Reinhold, 1960; Schubert, 1979; Röhrig and Bartsch, 1992; Lang, 1994; Otto, 2002). Leuschner's (1997) ecogram provides a comprehensive overview of European beech presence and dominance in relation to soil moisture and soil acidity in Central Europe (Figure 4). It shows that European beech dominates all other tree species under the moderate site conditions widespread throughout Central Europe (Bohn *et al.*, 2004). European beech prefers a maritime, temperate climate with mild winters and moist summer conditions. It avoids the pronounced continental climate. Long, severe winters and summer drought seem to limit its distribution in the east (Dengler, 1944; Röhrig and Bartsch, 1992; Tarasiuk, 1999).

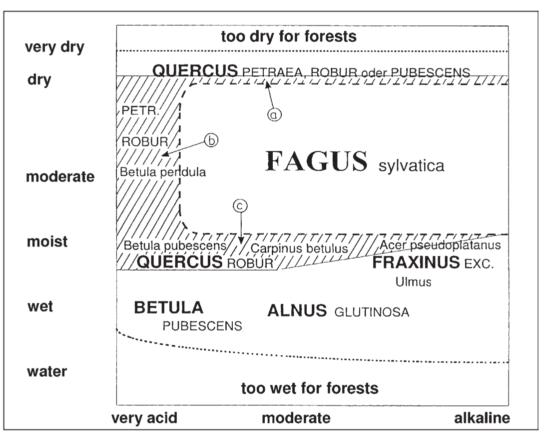

Figure 4. Ecogram of forest tree species in the submontane altitudinal zone in temperate–submaritime climates in Central Europe (Leuschner, 1997, modified). Deviations from an earlier ecogram from Ellenberg (1988) are highlighted by hatched areas; without human influence, European beech most likely would be the dominant tree species in (a) oak–hornbeam forests, (b) very acid and nutrient-poor sites with an intact humus layer and (c) moist sites as well.

Descriptive analyses of climatic constraints in northern Central Europe

Over about the last 150 years, numerous attempts have been made to define the climatic factors limiting European beech distribution in north-eastern Central Europe. The results have been inconsistent and often contradictory (Table 1). Most authors have used values of the mean precipitation rate per year or vegetation period, the winter and/or summer (monthly) temperature and the vegetation period length. Some focussed on a single parameter, for example winter temperature (Willkomm, 1887; Hueck, cited by Lämmermayr, 1923; Hueck, 1936), length of vegetation period or length of a period above a certain threshold temperature (Grisebach, 1872; Enquist, 1929). However, most authors adopted a combination of at least two different climatic parameters to describe thermic and hygric

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constraints to European beech occurrence. From Table 1, the following minimum requirements for European beech presence may be defined: (1) precipitation rates of 500 mm per year, or ~250 mm between May and September; (2) a July mean temperature less than 19°C; (3) fewer than 141 frost days with a daily minimum temperature below 0°C; (4) a January mean temperature above −3°C and (5) more than 217 days with a daily mean temperature of 7°C or more. Furthermore, in addition to these long-term climatic factors, the presence of European beech depends on the absence of extreme drought and heat, winter frosts (<−35°C) and severe late frosts as the intensity and frequency of these events affect its performance. The local site topography, particularly the relief, degree of slope and orientation of the site modify the microclimatic conditions in favour of European beech, e.g. high humidity in valleys and near lakes lessens the above-mentioned adverse macro-climatic effects (Czajkowski and Bolte, 2006b). The complexity of and variation in these interacting macro- and microclimatic factors may be the reason for the inconsistent descriptive assessments of the influence of climate on the distribution of European beech. Alternatively, the different responses of European beech populations to climatic stress may reflect variation in the adaptation and competition status of European beech populations in different regions within its distribution range (see Tognetti *et al.*, 1995). Therefore, functional studies on stress physiology and competition ecology are crucial in the assessment of climatic and site limitations of European beech.

Functional approaches for defining critical limits of European beech occurrence

The European beech seedlings and mature trees present along the margin of its distribution range in central Poland may respond to the frequent and intensive droughts by reducing growth, by restricting nutrient uptake and through xylem embolism when water availability is limited (Geßler *et al.*, 2007). Recent dendroecological studies revealed that mature beech growth is highly sensitive to drought and extreme soil water depletion (Dittmar *et al.*, 2003; Lebourgeois *et al.*, 2005; Jump *et al.*, 2006; Beck and Müller, 2007). For various forest ecosystem types, including European beech forests, Granier *et al.* (2007) identified 40 and 20 per cent of relative extractable soil water as critical limits below which gross primary production and total ecosystem respiration decreased, respectively, during the summer drought of 2003. The delayed growth response of European beech growth to drought is known, and often results in a more pronounced reduction in growth in the year after drought (Löf and Welander, 2000; Czajkowski *et al.*, 2005; Granier *et al.*, 2007). The reduction in assimilation and transpiration due to a decreased canopy conductance, which draws the water and nutrients from soil–root interfaces up to the leaves (Bréda *et al.*, 2006), restricts European beech growth. When the water supply is sufficient, canopy conductance in European beech is closely related to atmospheric water balance (Granier *et al.*, 2000). Yet, extreme drought events disrupt this relationship by reducing stomatal conductance, for example, to only 15 per cent of the 2002 values in eastern France in summer 2003 (Ciais *et al.*, 2005). Stomatal control is important for preventing the internal water status from falling below a critical shoot water potential of −1.9 MPa (Hacke and Sauter, 1995), which would lead to a loss of hydraulic conductivity (Tognetti *et al.*, 1995; Schipka, 2002) due to xylem embolism (Cochard *et al.*, 1996). At a shoot water potential of −2.0 to −3.0 MPa, a 50 per cent loss of hydraulic conductivity has already occurred (Cochard *et al.*, 1999; Cruziat *et al.*, 2002). The ability of European beech to recover actively from drought-induced embolism within the vegetation period is unknown; full recovery seems to occur only after the new year ring has developed (Cochard *et al.*, 2001). Vulnerability to xylem cavitation is thought to be a key component of drought tolerance. The greater susceptibility of European beech to xylem cavitation than the Central European oak species and Norway spruce may make it more drought sensitive than these species (Maherali *et al.*, 2004; Bréda *et al.*, 2006). Furthermore, several studies of drought response showed that, in European beech, stomatal control alone often is unable to maintain the shoot water potential above the critical limit and thereby prevent loss of hydraulic conductivity (Tognetti *et al.*, 1994, 1995; Aranda *et al.*, 2000; Fotelli *et al.*, 2001; Schipka, 2002; Schraml and Rennenberg, 2002; Czajkowski and

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Table 1: Some definitions, listed chronologically, of minimum climatic factors for the occurrence of European beech in north-eastern Central Europe

Author	Precipitation	Temperature	Other factors
De Candolle (1855)	≥7 rainy days per month	Mean winter temperature >−6.25°C	–
Grisebach (1872)	–	–	Length of vegetation period (≥150 days)
Willkomm (1887)	–	Mean winter temperature –6.25 to −5°C	–
Hempel and Wilhelm (1889)	–	–	Length of vegetation period (≥150 days) + maritime climate
Köppen (1889)	–	January temperature >−3°C; February temperature >−2°C	Length of vegetation period ≥8 months with temperature more than 10°C; winter ≤3 months
Mayr (1925)	≥250 mm during the vegetation period	Annual mean temperature 7–12°C, May to August 16–18°C	Air humidity May to August: ≥70%
Pax (1918)	≥660 mm per year	–	Elevation about sea level
Jedliński (1922)	–	≤3 months with temperature <0°C; May temperature >8°C, May temperature amplitude <10°C	Late frost (topography and site conditions may lesson frost impact)
Lämmermayr (1923)	Climate continentality (summer drought, duration of winter: ≤4 months)		
Hueck according to Lämmermayr (1923)	–	January isotherm –2.5°C	–
Enquist (1929)	–	≥217 days with temperature ≥ 7°C or 245 days with temperature ≥5°C	–
Steffen (1931)	Climate continentality (summer drought and winter frost), January temperature ≥4 months		Length of vegetation period
Goetz (1935)	≥500–750 mm per year	–	Late frost, topography, site conditions
Hueck (1936)	–	January temperature ≥−3°C	–
Ilinskij (1937)	Summer drought, precipitation: evapotranspiration ~100–120%	Yearly temperature amplitude: 15–25°C, winter temperature ~0°C	–
Hjelmqvist (1940)	≥550 mm per year	≥213 days with temperature ≥7°C or 216 days with temperature ≥6.5°C	Topography and no stagnic moisture
Tarasiuk (1999)	≥320 mm May to October	≤141 days with temperature <0°C	–
Hofmann (2001)	≥550–580 mm per year (European beech dominance)	July temperature <18–19°C (European beech dominance)	Mild winter, high air humidity

Bolte, 2006a). This is particularly true for European beech regeneration when young European beech seedlings with limited rooting space must compete with surrounding regeneration, overstorey trees and ground vegetation for limited water and nutrient resources (Madsen, 1994; Fotelli *et al.*, 2001, 2005; Ammer, 2002; Coll *et al.*, 2003, 2004). Not only does water shortage have

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an adverse effect on the European beech water budget but it also restricts its nitrogen supply (Geßler *et al.*, 2004). Thus, a drought-induced decrease in nitrogen may also be an additional, important factor in explaining drought effects on European beech (Geßler *et al.*, 2007).

Severe frost with minimum temperatures below –20°C as well as extreme late frosts may damage the cambium of oak species and European beech, possibly leading to bark lesions and fungal infections later on (Thomas and Hartmann, 1992; Jönsson, 2000). Winter frosts with temperatures between –17 and –21°C have been found to kill 50 per cent of the European beech saplings present (Višnjić and Dohrenbusch, 2004; Czajkowski and Bolte, 2006a). Furthermore, frequent late frosts in north-eastern Central Europe adversely affect xylem activation in spring (Cochard *et al.*, 2001). A late frost of below –4°C may kill young shoots and lead to misshapen branches (Holmsgaard, 1962). Plant tissue appears to be frost resistant between –1 and –4°C (see compilation by Dittmar *et al.*, 2006). At temperatures a few degrees below zero, flowers and young acorns may be damaged, resulting in less frequent mast years than in western Europe (Lindqvist, 1931; Groß, 1935). Yet, definite critical limits cannot be derived because the effects of frost are heavily dependent on the season, the extent of frost hardening and the site conditions (Jönsson, 2000).

Adaptation potential of European beech to changing environmental factors

The adaptation of forest trees to adverse climatic and site conditions depends upon two different processes: (1) phenotypic plasticity, ensuring short-term persistence of several years or a decade, and (2) long-term evolutionary adaptation over one or more generations (see Hamrick, 2004). The plasticity of European beech to drought is apparent in its capacity to reduce the transpiring leaf area in relation to the water-absorbing root surface area or conductive elements. It achieves this by shedding leaves or alternating biomass partitioning and carbon allocation between the aboveground and belowground tree components (Bréda *et al.*, 2006). European beech is known for its high plasticity in biomass partitioning (e.g. Bolte *et al.*, 2004, Löf *et al.*, 2005) and its ability to vary fine root morphology and soil space sequestration to increase soil resource uptake (e.g. Schmid, 2002; Bolte and Villanueva, 2006). These distinct elements of phenotypic plasticity may contribute to European beech's adaptability to drought and its competitiveness.

The assessment of the evolutionary adaptation potential of European beech is still a considerable challenge. DNA marker analyses have not revealed any distinct differences in genetic structure between different European beech populations or provenances, but a high genetic diversity within populations (Hamrick, 2004; Lefèvre *et al.*, 2004; Vornam, 2004). However, European beech provenances exhibit different adaptive behaviour to climatic factors such as late frost (spring flushing) (Engler, 1908; Hjelmqvist, 1940; Rzeźnik, 1976; Kleinschmidt, 1985; Tarasiuk *et al.*, 1998; Chmura and Rożkowski, 2002; Višnjić and Dohrenbusch, 2004). This shows that knowledge about genetic control over the phenotypic variation in European beech is still lacking. As less sensitive individuals are selected from a large number of young beech trees at the regeneration stage, this stage is most important for the evolutionary adaptation of European beech to different climatic conditions. Shallow roots and competition from the overstorey expose European beech seedlings and saplings to drought, and therefore intensify the selective pressure (Czajkowski and Bolte, 2006b). The longevity and number of successful recruitment events are important in the adaptation process (Hamrick, 2004). To date, few ecological studies have dealt with the evolutionary adaptation of European beech to drought. Investigations suggesting that young European beech populations at the drought-induced distribution range margin in central Poland are better adapted to drought than those populations inside the distribution range (Czajkowski *et al.*, 2005, Czajkowski and Bolte, 2006b) support the results from Tognetti *et al.* (1995) and Schraml and Rennenberg (2002), who also found that European beech provenances from dryer regions were better adapted to drought than those from more humid regions. Studies of 'rear' edge European beech populations (see Hampe and Petit, 2005) like those in central Poland are of great importance for our understanding of the acceleration of adaptation processes under extreme environmental conditions. Both the influence of

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evolutionary adaptation and the above-mentioned high phenotypic plasticity appear to be underestimated in assessments of the drought sensitivity of European beech from short-term studies of seedlings originating from the centre of the European beech range. The different adaptation status of the various European beech provenances in north-eastern Central Europe may also explain the diversity in the European beech distribution range margins reported. Therefore, one can agree with Tarasiuk (1999), who regards large tracts of Poland as margin areas where European beech may or may not be present.

Conclusions about the future of European beech in the face of climate change

Any assessments of the impact of climate change on the future distribution of European beech will be crude as regional climatic predictions in the eastern and north-eastern extent of its range are unavailable as yet (see EEA, 2004). Moreover, the success of the mitigation strategies in reducing greenhouse gases remains unclear. Nevertheless, European climate-warming projections, e.g. like the SCEN projection (Schär *et al.*, 2004), predict a large increase in temperature anomalies in Central Europe up until 2100, which, in addition to other changes, will result in more frequent and intensive drought periods. Although European beech is a drought-sensitive species (Aranda *et al.*, 2000; Geßler *et al.*, 2004), its adaptation potential to such drought periods via evolutionary processes and its phenotypic plasticity appear to be underestimated. This may counteract theories claiming that the European beech range is becoming narrower due to climate change in north-eastern Central Europe. The way in which changes in interspecific competition should be incorporated into predicting shifts in the European beech distribution range arising from climate change is still unsolved (see Davis *et al.*, 1998). There are some indications that the competitive ability of early successional species such as ash (*Fraxinus excelsior*) will increase compared with European beech (e.g. Rust and Savill, 2000; Saxe and Kerstiens, 2005). However, reliable information about the climate change-induced variation in competition dynamics of European beech and its competitors in one generation is lacking.

Nevertheless, silviculture will play an important role in the future performance of European beech in the region when directed to improving water availability for natural European beech regeneration (e.g. Madsen, 1994) by reducing competition from the shelterwood, which exacerbates the climate-induced adverse effects of drought on European beech regeneration through root competition and reduces the limited water resources further and also the availability of light (Czajkowski *et al.*, 2005). The latter reflects the limited ability of overtopped European beech regeneration to cope with water shortage (Aranda *et al.*, 2001) given their lower osmotic potential and lower root/shoot ratios (Eschrich *et al.*, 1989, Löf *et al.*, 2005). This, in turn, suggests that the optimization of soil water resource management through future silvicultural practices will be crucial for successful European beech regeneration in forest stands. Thus, a marked reduction in the canopy after the successful establishment of young European beech plants will reduce the risk of water stress, provided competition from ground vegetation is controlled. Irregular shelterwood systems creating gap openings with an initial area of up to 20 m in diameter will provide those conditions, particularly in gap centres.

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Conflict of Interest Statement

None declared.

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