Georg-August University
Göttingen

Albrecht-von-Haller Institute for
Plant Sciences

Response of European beech to decreasing summer precipitation under global climate change

Dissertation

zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades

„Doctor rerum naturalium“

der Georg-August University School of Science (GAUSS)

Promotionsstudiengang Biodiversität und Ökologie

vorgelegt von

Florian Knutzen aus Hamburg

Göttingen, Juli 2016

Betreuungsausschuss und Mitglieder der Prüfungskommission

Prof. Dr. Christoph Leuschner (Referent),

Abteilung Pflanzenökologie und Ökosystemforschung, Georg-August-Universität Göttingen

Prof. Dr. Markus Hauck (Korreferent),

Abteilung Pflanzenökologie und Ökosystemforschung, Georg-August-Universität Göttingen

Dr. Ina Christin Meier,

Abteilung Pflanzenökologie und Ökosystemforschung, Georg-August-Universität Göttingen

Weitere Mitglieder der Prüfungskommission

Prof. Dr. Christian Ammer,

Waldbau und Waldökologie der gemäßigten Zonen, Georg-August-Universität Göttingen

Prof. Dr. Erwin Bergmeier,

Abteilung Vegetationsanalyse und Phytodiversität, Georg-August-Universität Göttingen

Prof. Dr. Dirk Hölscher,

Abteilung Waldbau und Waldökologie der Tropen, Georg-August-Universität Göttingen

Prof. Dr. Hermann Behling,

Palynologie und Klimadynamik, Georg-August-Universität Göttingen

Tag der mündlichen Prüfung: 16. September 2015

Table of contents

Summary

Global warming-related summer precipitation reduction represents a major threat on tree vitality and persistence and hence on forest productivity over large parts of the temperate zone. European beech (*Fagus sylvatica* L.) is the most important broadleaf tree species of Central Europe's natural forest vegetation and one of the economically most important trees in Germany. Although this forest tree shows a wide tolerance toward a wide range of climatic and edaphic growing conditions, beech is known to be drought sensitive. Accordingly, the future role of *F. sylvatica* in Europe is under controversial debate. In order to broaden the knowledge of the response and the adaption potential of European beech to a drier climate likely to occur in the future, a gradient study was conducted. Measurements were taken along a natural rainfall gradient (855-576 mm y^{-1}) in 12 mature beech forest stands on comparable sandy geological substrate in the Central Northern German Lowlands was conducted. To consider the potential effect of soil water storage on the precipitation-response, this study was partly carried out in paired comparable beech stands growing on sites with contrasting soil texture (sandy vs. sandy-loamy). Influences on precipitation reduction during the growing season and the response of *F. sylvatica* trees were investigated by

(i) a common garden experiment with provenances from moist to dry climates under defined moisture conditions to investigate the short-term adaptive drought responses of young beech trees.

(ii) comparing tree ring chronologies along the gradient on two different soil types to define a critical precipitation limit under which growth decreases occur and to enlighten the role of the edaphic effect on growth dynamics

(iii) characterizing the vulnerability but also the adaptation potential to drought of *F. sylvatica* of sun-exposed branches with cavitron spinning technique and anatomical investigations

One option for forest managers to minimize the risk of failure is to use provenances of tree species which combine high productivity with drought tolerance. Beech sapling genotypes exposed to different precipitation regimes seem to have achieved only a limited number of specific drought adaptations. Surprisingly, provenance had only a minor influence on the morphology and growth. The main reason for this result may be the fact that genetic differences between populations were small, while genetic variation within populations was high in the study region. However, some physiological traits showed to be influenced by provenance: The modulus of leaf tissue elasticity ε was significantly higher in plants from moist origins. Hence, these plants may face a higher risk of hydraulic failure due to more rigid cell walls in leaf tissue. The high phenotypic plasticity observed in this study in terms of biomass partitioning, leaf and root morphology can be seen as the pivotal strategy of beech saplings to get along with the challenges of drought periods. The evolved adaptation of leaf water status adjustment has only minor effects on plant morphology and growth rate. Accordingly, selecting and translocating provenances across the investigated gradient is not recommended.

Comparing tree-ring series across this gradient, revealed that global warming already acts as a major stressor in *F. sylvatica* stands in the center of the species' distribution. Under a threshold of 350 mm precipitation during growing season or 600 mm during the year, basal area increment (BAI) has been constantly decreasing since the 1960s or 1970s. Even since the 1950s, sensitivity of mean ring width has increased, by decreasing autocorrelation of the forest stands. An increase in the occurrence of negative pointer years was observed since the 1960s. Surprisingly, the role of soil water storage for the growth dynamics of beech was not reflected in our results. These results call for careful tree species selection by foresters in forest regions where precipitation is already below the precipitation thresholds elaborated here. It is likely that *F. sylvatica* may lose part of its range in the managed and natural forest area of Central Europe upon climate warming.

Mature beech trees adapt their hydraulic architecture to long-term decreases in water supply with diminution of their vessels. We observed an increased appearance of smaller vessels along the gradient, while the frequency of larger vessels declined or remained unaffected. Surprisingly, leaf-specific conductivity decreased with increasing drought, while pit membrane thickness increased. Branches showed a larger embolism resistance with increasing drought at tree origin. Contrary to expectations, leaf-specific conductivity declined with decreasing precipitation. Due to branch wood modification, trees at the dry end of the investigated gradient were capable of tolerating more negative leaf water potentials. It may therefore reasonably be concluded, that the beech's branch hydraulic system has a distinct adaptive potential to respond to a precipitation reduction.

The observed high variability of traits and the physiological adaption potential within mature and young *F. sylvatica* populations, could be seen as a valuable tool for withstanding a future drier climate. However, the observed radial growth declines at the drier stands in our study region in the last decades, casts doubt on the ability of *F. sylvatica* to withstand the predicted intensification of aridity during the growing season even in the centre of its distribution.

CHAPTER 1

General Introduction

Global warming and regional consequences

Many natural climatic changes and variations with cycles of glacial advance and retreat have occurred throughout history (e.g. Akasofu 2010, Lamb 2013). However, the recent global warming trend, with a mean global land and ocean surface temperature increase of 0.85°C between 1880 and 2012, is of particular significance and it is very likely human-induced (IPCC 2013). Since the beginning of the industrialization from the mid-18th to the early 19th century, carbon dioxide (CO_2) has been released in large scale due to the burning of fossil fuels (coil, oil, and natural gas). A central indicator of the anthropogenic perturbation of our climate is the enrichment of the CO_2 concentration in the atmosphere which has increased from approximately 280 ppm in 1750 (Joos and Spahni 2008) to almost 400 ppm in 2013 (Nisbet et al. 2014). These fossil fuel emissions and the release of methane (CH_4), nitrous oxide (N_2O) and chlorofluorocarbon (CFC) absorb and emit radiation within the thermal infrared range, which traps the heat in the atmosphere (IPCC 2013). This leads amongst other factors to the so called "greenhouse effect", which is seen as the fundamental cause of global warming. Natural processes, for example changes of the intensity of solar radiation, are seen responsible to a far lesser extent (Thejll and Lassen 2000).

It should be noted that global climate modelling cannot reduce uncertainties around future climate (Knutti and Sedláček 2013). The future development of greenhouse gases emissions for example is still unclear. Thus, for projecting future climate conditions, different scenarios are used, based on different amounts of CO_2 emissions. The scenario A1 assumes "a future world of very rapid economic growth, global population that peaks mid-century and declines thereafter, and rapid introduction of new and more efficient technologies" (IPCC 2013). This scenario is divided into three groups that describe diverging directions of future energy supply: fossil-intensive (A1FI), nonfossil energy sources (A1T), and a balanced use across all sources (A1B). In our research cooperation (KLIFF), scenario A1B is used. This scenario is based on a release of 16 Pg C per year, whilst the current level is 10 Pg C per year. In order to reach the politically agreed level of +2°C compared to pre-industrial temperature levels, less then 4 Pg C should be emitted by 2050 (Peters et al. 2013). Together with other uncertainties in the models themselves (Kjellström et al. 2013), forecasting climate trends is difficult.

It is a proven fact that the world´s surface temperature has increased substantially during the 20^{th} century, especially after the1960s (Jones and Moberg 2003). Paleo-climatic information, derived from natural long term archives like tree rings or ice cores, reconstruct that for the northern hemisphere "the period from 1983 to 2012 was likely the warmest 30-year period of the last 1,400 years" (IPCC 2013). Global climate warming at each of the last three decades was more severe than at any previous decade since 1850 (see Figure 1.1). A further increase of the global surface temperature by 3.2 to 5.4°C until the end of the current century above the mean temperature from 1850 to 1900 is expected by current climate models (IPCC 2013).

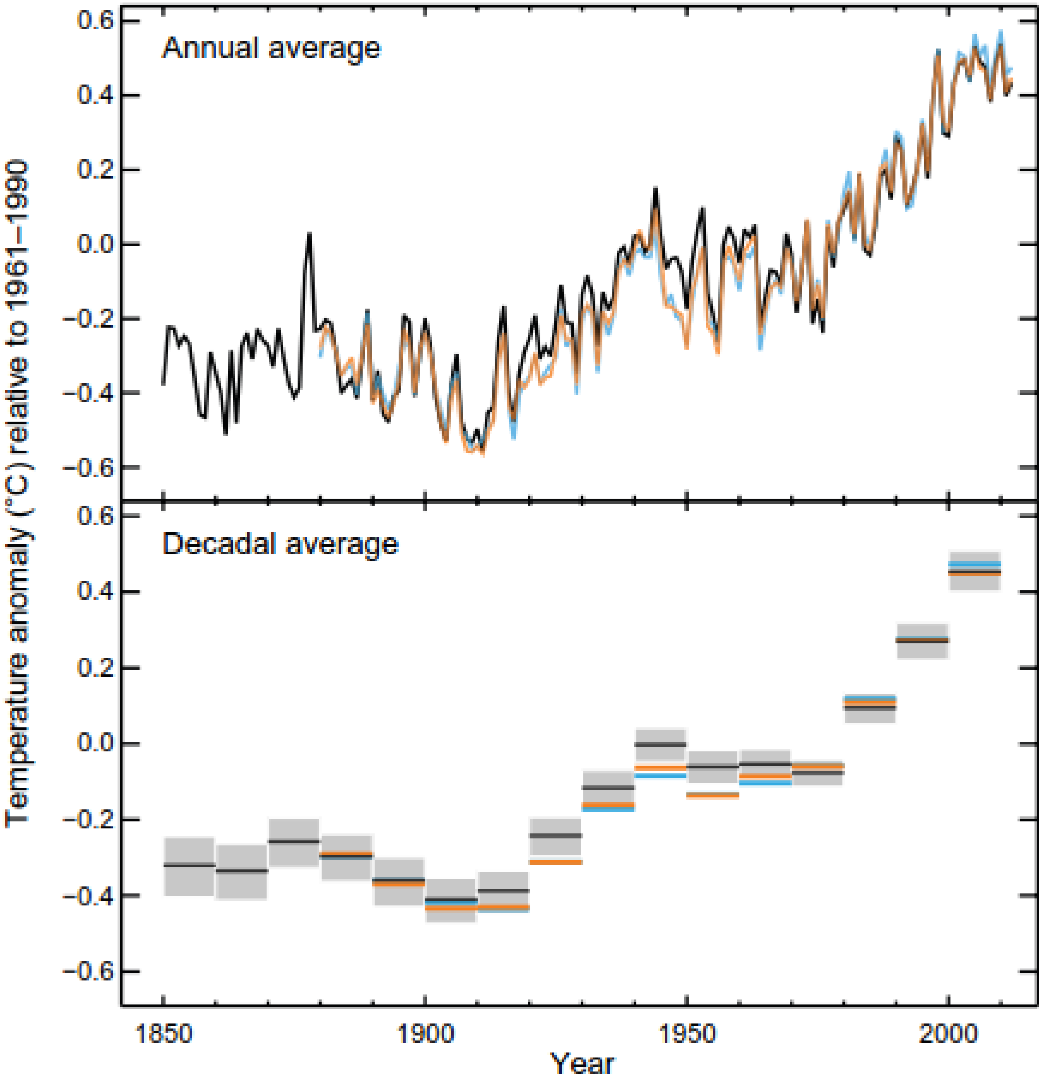

Figure 1.1. Observed mean combined land and ocean surface temperature anomalies from 1850 to 2012 (IPCC 2013, modified). Derived from three data sets (black, orange and blue line). Top panel: annual mean values. Bottom panel: decadal mean values with estimate of uncertainty for one dataset (black). Anomalies are relative to the mean of 1961−1990. For a listing of data sets and further details *cf.* IPCC 2013.

Further warming of the atmosphere will result in increases of evaporation and thus precipitation (Yang et al. 2003, Huntington 2006). One of the major consequences is an intensified and accelerated global water cycle, which has led to an increase of precipitation over land by about two percent globally averaged during the last century (Dai et al. 1997, Folland et al. 2001).

Although mean annual precipitation amounts are predicted to increase, changes in precipitation patterns will lead to decreasing summer precipitation (Rowell and Jones 2006) and to an increase in the appearance of summer heatwaves (Schär et al. 2004). In current regional climate change scenarios, drier summers over continental Europe are a common assumption.

The regional climate model ECHAM5-MPIOM (Max-Planck Institute for Meteorology, Hamburg), projects a decline in summer precipitation by up to 40 percent for parts of Germany accompanied by increasing temperatures by up to 3 °C (scenario A1B) until the end of the 21st century (Moseley et al. 2012, Belli et al. 2013, Jacob et al. 2013). For Lower Saxony, the scenario A1B of the regional systems REMO and CLM predicts an increase of the mean annual temperature of about 2.5°C and an increase of for mean precipitation in winter, spring and autumn. Summer precipitation in contrast, shall decline by about ten percent (Table 5.1).

Table 1.1. Climate change in Lower Saxony, simulated by regional climate models REMO and CLM. Both models are driven by global IPCC/AR4- climate simulations (coupled system ECHAM5-MPIOM, reference period 1971-2000). Data source: KLIFF.

	Period 2021 - 2050	Period 2071 - 2100
Mean annual temperature	+ ~1.0°C	+ ~2.5°C
Length of growing season	+ ~23 days	+ ~60 days
Number of frost days	– ~31.5%	– ~66%
Number of spring frost days (after April 1st)	– ~40%	– ~90%
Length of warm periods	Uncertain	+ ~50%
Mean precipitation	+ ~7% in all seasons	Winter + ~18.5% Spring + ~11.0% Summer – ~10% Autumn + ~16.5%
Frequency of heavy rainfall	+ ~20% especially in autumn	Winter and Spring + ~40-50% Summer + ~8.5% Autumn + ~75%

Plant responses to changing climate

Climatic effects as a consequence of global warming such as increasing temperatures, extended growing season, and declining water availability are an ecological menace (e.g. Root et al. 2003, Thomas et al. 2004, Meier et al. 2012). Adaptation strategies that enable plants to respond according to changing environmental conditions occur mainly in three different ways, through:

(i) **phenotypic plasticity**, the range of phenotypes one genotype can express as a function of its environment (e.g. Garland and Kelly 2006; Nicotra et al. 2010; Bresson et al. 2011)

(ii) **genotypic variation**, what can be seen as adaption to recent stresses (e.g. Aitken et al. 2008, Hoffmann and Sgrò 2011) and

(iii) **migration**, shifting distributions to areas with better living conditions (e.g. Angert et al. 2011, Chen et al. 2011).

Distributional shifts and phenotypic plasticity are seen as ecological responses, while adaptation and gene flow are seen as evolutionary effects caused by changing abiotic conditions (Anderson 2012). Usually, a combination of ecological and evolutionary strategies can be observed. Little is known of the interaction of ecological and evolutionary processes against the background of global climate warming. Genotypic adaption and modification of the phenotype in response to environmental variations evolve to maximize fitness of an organism or a population (Dudley and Schmit 1996). In stable environments, specialization is preferred over plasticity due to its better cost-benefit ratio (DeWitt et al. 1998, Agrawal 2001). Phenotypic plasticity seems to play a major role in a successful adaption to quickly changing environments (Nicotra et al. 2010). This has been confirmed by the results of experiments where genetic and plastic contributions have been separated successfully: plasticity often seems to be more important (Hoffman and Sgrò 2011). Furthermore, different studies suggest that species can respond more quickly via phenotypic plasticity than via genotypic adaptation (e.g. Teplitsky et al. 2008, Ozgul et al. 2009). Generally, variation in physiological, morphological and anatomical traits is achieved by a combination of genotypic variability and phenotypic plasticity (Cordell et al. 1998). For plants it could be estimated that phenotypic plasticity will be high in variable environments, and genetic variability will be high in more constant habitats (Callaway et al. 2003).

Macroclimate plays a major role in shaping large-scale species distributions (Bale et al. 2002, Hickling et al. 2006). Climate conditions are the most important factors for the distribution of plants along elevational and latitudinal gradients (Halbritter 2013). Species exhibit measurable changes in their distribution during the last 140 years: range boundary moved on average about 6 km northward or 6 m upward per decade in the Northern hemisphere (Parmesan and Yohe 2003, Root et al. 2003). However, entire ecosystems do not shift their distributions in response to climate changes, but species and populations do (Parmesan 2006, Thomas et al. 2011). Consequently, biotic communities change, invasive species become more abundant and species interactions vary which puts existing species at risk and may even lead to their extinction (Thomas et al. 2004).

Forest trees under global warming

Because of their long generation time and limited migration abilities, it will be challenging for trees to cope with rapid anticipated global climate warming over the 21st century (Davis and Shaw, 2001). Predicted and observed climate trends with accompanying uncertainties call for flexible strategies in future forest management and ecosystem conservation. According to the International Union of Forest Research Organizations (IUFRO), the conservation of a constant global forest cover under global warming requires acclimatization as well as adaption (Seppälä et al. 2010). Acclimatization is seen as the potential of singular, already established trees to cope with environmental changes. Adaption in relation to climate change is here defined as “adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities”.

During the 20th century forest productivity trends for most regions in Europe were assessed mainly positively (Spiecker et al. 1996, Kahle et al. 2008), in the recent past however negative effects on growth performance and vigor were detected (Bigler et al. 2006, Vicente-Serrano et al. 2010). Mesic European tree species with a wide distribution seem to loose parts of their southern and lower altitude ranges (Cheaib et al. 2012, Herrero et al. 2013). In the Mediterranean several studies detected growth declines in a couple of conifer species due to reduced water availability (e.g. Linares et al. 2011, Sánchez-Salguero et al. 2010). Nevertheless, contrary observations in European forests to changing climate were also reported (e.g. Sánchez-Salguero et al. 2012, Rigling et al. 2013, Ruffault et al. 2013). The extended growing season length due to rising temperatures (Menzel and Fabian 1999) increased forest productivity in some cases (Spiecker 1999, Pretzsch et al. 2014), and promoted the expansion of thermophilic forest plants with more southerly distribution (van Herk et al. 2002, Pócs 2011, Jantsch et al. 2013).

Forest productivity and higher tree-growth rates are instinctively related with benefits for the vitality of trees and are often used for estimating drought adaptation potentials of species or genotypes (Dobbertin 2005). In fact, *Acer* seedlings originating from moister fieldsites grew faster under well-watered conditions, and had higher net photosynthesis rate, leaf conductance, and maximum carboxylation rate, than seedlings of provenances from drier field sites (Bauerle et al. 2003). In habitats with ample water supply, competition for light might be under higher selection pressure and therefore, faster growth is advantageous for competitiveness (Hartmann 2011). In habitats with frequent drought periods, natural selection might favor traits contributing to drought resistance (Montwé et al. 2015). Lower aboveground growth rates could impede an increased root: shoot ratio, leading to improved water uptake (Pretzsch et al., 2012). Different provenance studies have identified lower relative growth rates to be associated with higher drought tolerance in trees (e.g. Rose et al., 2009, Taeger et al. 2013). But consequences of selection processes for improving general plant fitness are complex (e.g. Jump and Peñuelas, 2005, Reusch et al., 2005), although it is likely, that "investments into safety mechanisms could contribute to growth limitations of the drought-resilient provenances" (Montwé et al. 2015).

How forest trees will respond or adapt to the expected strong evolutionary pressure through climate change is controversially discussed: Davis and Kabinski (1992) state that the genetic diversity of trees is not sufficient for adaptions to changing climate. The dispersion of trees might be too slow for migration to appropriate habitats, especially because of extensive fragmentation of the environment nowadays (Jump and Penuelas, 2005). On the other hand, several traits enable trees to withstand changes in their habitat (Hamrick and Godt, 1996). High phenotypic plasticity (Rehfeldt et al. 2002), gene flow through air-seeding (Petit and Hampe 2006), genetic diversity within, and moderately between populations (Buiteveld et al. 2007), are seen as advantageous for trees to stand challenges through a future warmer and drier climate. Actually, genotypic variability of drought tolerance and the drought adaption potential of trees and forest systems are not sufficiently known.

Transpired water passages from the soil to the plant and to the atmosphere along a continuum of gradually decreasing water potential (ψ); this relocation follows the equation

$$E = K_L(\psi_{soil} - \psi_{leaf}),$$

where E is the transpiration per unit leaf area, K_L is the leaf-specific hydraulic conductance at tree scale (Bréda et al. 2007), and $\psi_{soil} - \psi leaf$ (MPa) is the difference between the water potential of soil and leaf (Sperry and Tyree 1988). With decreasing soil moisture and / or increasing transpiration, leaf water potential declines and tensions in the xylem capillaries is intensified which can induce cavitation and embolism (Herbette et al. 2010). For the maintenance of tree vigour under drought, an effective water-conducting system is mandatory to avoid down-regulation of the photosynthesis rate (e.g. Rennenberg et al. 2006), and to preserve the water potential of the xylem above cavitation-threshold levels, otherwise tree mortality could be directly induce via hydraulic failure (Bréda et al. 2006). Consequently, cavitation resistance is seen as a key component of the potential of trees to withstand drought events (Anderegg et al. 2015, McDowell and Allen 2015). Water-conducting systems depend on the dimensions and structure of the conduits: Different studies revealed that reduced precipitation amounts cause narrower conduits by higher vessel densitiy (Carlquist 1977, Lens et al. 2004, Sterck et al. 2008, Gleason et al. 2012).

Smaller cells, with comparable cell-wall thickness, resist more negative sap pressure without cavitation than larger cells (Hacke et al. 2001). On the other hand, an increased lumen diameter is far more efficient for water conduction (Tyree and Zimmermann 2002). Accordingly, hydraulic efficiency and safety is mainly driven by vessel size and vessel size distribution (Tyree et al. 1994). Cavitation and subsequently the formation of embolism are caused by rupture of the water column in water-conducting systems (Tyree and Zimmermann 2002). The consequences, such as stomatal closure followed by lowered carbon assimilation, can be harmful for trees.

Stomatal adjustment is of high importance for plant water relations, because stomatal closure is one of the primary responses to drought in order to reduce transpirational water losses (Farquhar et al. 1989). Furthermore, closed stomata decrease the CO_2 concentration in the gas compartments of the leaves, which can reduce photosynthetic activity. Additionally, controlling the transpiration has also the function to keep up the maintenance of the water potential with the positive effect of avoiding embolism within the vessels and thus xylem cavitation (Cochard et al. 1996). Embolism resistance is connected to several traits, e.g. vessel size (Carlquist 1977, Tyree et al. 1994, Maherali et al. 2006), pit structure (Jansen et al. 2009, Plavcová et al. 2013; Bouche et al. 2014), hydraulic conductivity (Maherali et al. 2006, Markesteijn et al. 2011) and wood density (Hacke et al. 2001, Jacobsen et al. 2007). Thus, studies on traits effecting xylem safety, growth and leaf water relations are needed for a better understanding of the adaption potential of European beech tree.

European beech

In Central Europe, European beech (*Fagus sylvatica* L.) is of high economical importance, the most abundant deciduous forest tree in Germany and plays a significant role for landscape ecology (Schraml and Volz 2004). *F. sylvatica* would dominate Central Europe´s potential natural vegetation in large parts (Peters 1997). This species can occupy a broad range of habitats from poor and highly acidic to neutral soils (Ellenberg and Leuschner 2010). Currently *F. sylvatica* covers about 17 percent of the German forest area, 21 percent of the area where it would naturally dominate (BMEL 2014). The success of European beech has two pivotal reasons: seedlings and saplings show a high shadow tolerance while mature trees are able to cast deep shade.

F. sylvatica is characterized by an extensive distribution in Europe from southern Sweden to Central Italy and from Northern Portugal to Greece (Figure 1.2). In the north, *F. sylvatica* is limited by the growing season length, which has to be at least 140 days (Peters 1997). In the south, conditions get too dry during summer. Eastwards, *F. sylvatica* is restricted by temperature, especially by late frost (Peters 1997, Ellenberg and Leuschner 2010).

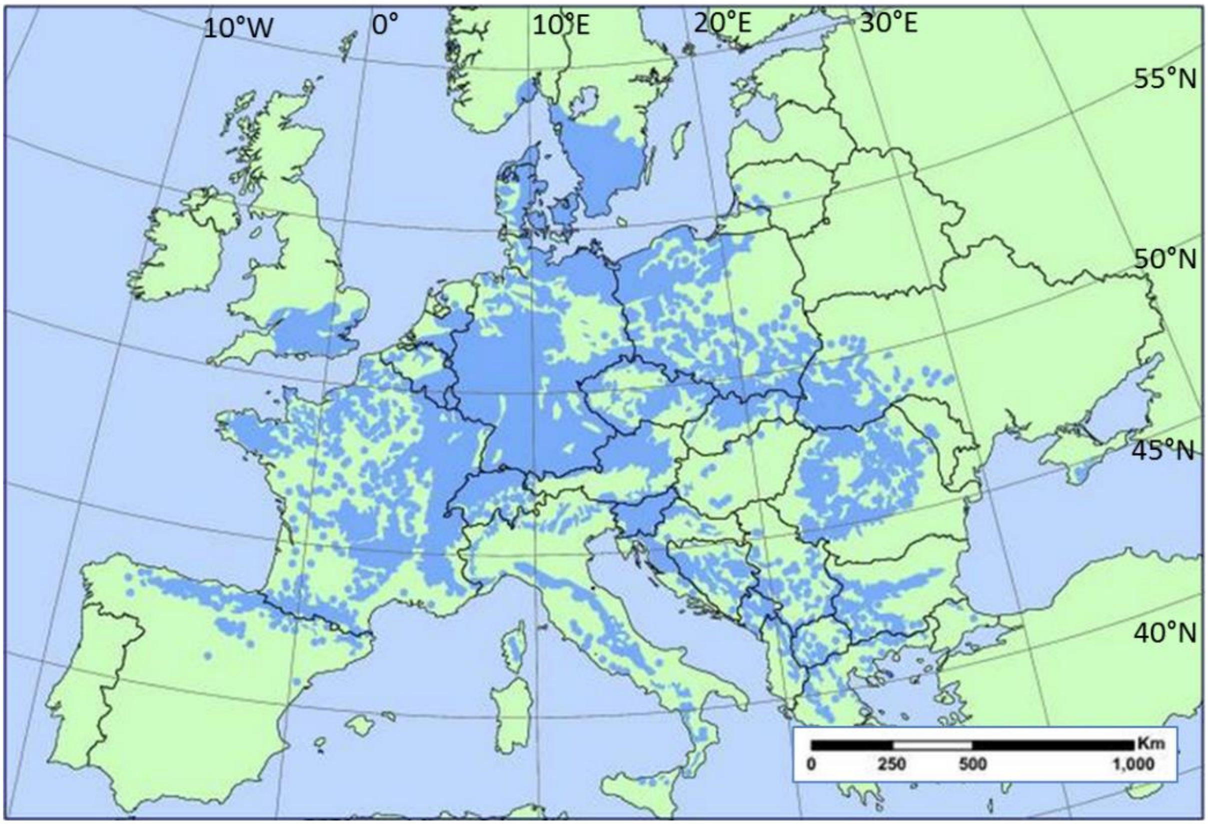

Figure 1.2. Distribution map of beech (*Fagus sylvatica*; EUFORGEN 2009, modified).

The climate history shows that European beech has experienced a lot of partially harsh climate changes. During the last ice age (Weichsel ice age) about 10,000 years ago, European beech began to spread from its few refugee areas in the Cantabrian mountains, the Pyrenees, Croatia, Slovenia and Italy (Magri et al. 2006, Magri 2008). The full recolonization of Central Europe may have taken 7,000 years (Saltre et al. 2013). Beech arrived in Germany during the late Atlanticum around 3,000 years before present. During Bronze Age (2,200 to 1,200 years before present) climate conditions were generally colder, a time optimal climate for beech followed only about thirty years B.C.E., until again, a phase of coldness set in approximately in the year 250 and lasted about 200 years (Glaser 2001). After the Medieval warm period, with the beginning of the 15th century, a colder phase began, which is often called "the little Ice Age" (Glaser 2001). Finally, the human-induced global warming began by the year 1850 (Akasofu 2010). These examples show that, *F. sylvatica* had to respond to many climate changes during its history, but is nevertheless assumed to be vulnerable to rapid environmental changes (Davis and Shaw 2001, Beck and Heußner 2012). Because of long generation times or cultivation periods, temperate forest trees will not be able to adapt fast enough to keep pace with the predicted changes (Hamrick et al. 2004, Spellmann et al. 2007).

European beech under global warming

European beech is known to respond more sensitively to drought than numerous other broad-leaved tree species in Central Europe (e.g. Leuschner et al. 2001, Bréda et al. 2006). However, genotypic variability and phenotypic plasticity of mature beech trees coping with lack of water have so far not been sufficiently disentangled (Bolte et al. 2007, Meier and Leuschner 2008a). As a consequence, the climate response and future distribution of *F. sylvatica* to global warming is controversially discussed (e.g. Kölling et al. 2007, Kramer et al. 2010).

Rennenberg et al. (2004) assumed that by the end of the present century beech will no longer be in its optimum range in numerous locations where it is dominating nowadays. Peuke et al. (2002) presumed that beech will be impaired in its physiological capacity, its growth, and competitiveness. Hacke and Sauter (1995) assumed that plant nutrition will be degraded. Kint et al. (2012) showed evidence of drought-induced growth reduction throughout the distribution of *F. sylvatica*. Reduced water availability results in lower nitrogen uptake from the soil and can therefore result in reduced tree growth (Fotelli et al. 2001, 2002). *F. sylvatica* trees located in France reached only 15% of their predrought values in stomatal conductance during the pan-European drought year 2003 (Ciais et al. 2005). Also in France, decreasing radial and height growth of European beech with a reduction of BAI by 5 %, beginning in the 1990s, was observed (Bontemps et al. 2009, Charru et al. 2010). In Spain (e.g. Peñuelas and Boada 2003, Jump et al. 2006) as well as in Central and Southern Italy (Rita et al. 2014) a climate change related growth decline of this species was reported.

Pre-senescent leaf shedding during summer droughts (Bréda et al. 2006, Granier et al. 2007), radial growth declines due to decreasing precipitation (Weber et al. 2013), lower pre-dawn leaf water potential during times of aridity (Aranda et al. 2001, Köcher et al. 2009), and increased fine root turnover as well as mortality upon lower soil moisture (Leuschner et al. 2001, Meier and Leuschner 2008a, Hertel et al. 2013) have also been reported. Even in the center of the species distribution i.e. in Switzerland and Germany growth decline was observed (Scharnweber et al. 2011, Weber et al. 2013, Zimmermann et al. 2015).

However, in Albania and Macedonia, an increase of radial growth was revealed, which might be explained by the prolonged growing seasons and the increased availability of atmospheric CO_2. Thus, it is likely that *F. sylvatica* might expand northwards while losing habitats in the south (Kramer et al. 2010). Beech trees have a notable potential to recover after drought periods (van der Werf et al. 2007) and show a high drought tolerance through a strong allocational plasticity (Schall et al. 2012, Müller-Haubold et al. 2013). Dittmar et al. (2003) find on one hand an apparent regional decline of *F. sylvatica*, but on the other an increased growth potential due to global warming-induced landscape changes. Other authors also see a warmer climate as no harm or even as a benefit for *F. sylvatica* (Döbbeler and Spellmann 2002, Sabaté et al. 2002). According to Peters (1997) an annual average temperature up to 14°C is no harm for beech, as long as the soil is not too shallow. In fact, dendroecological analyses showed a conspicuous high and stable growth level of *F. sylvatica* at lower altitude sites in Central Europe (e.g. Dittmar and Elling 1999, Dittmar et al. 2003).

The potential of European beech to rejuvenate may also be critically affected by the predicted climate change (Peuke et al. 2002). Besides the competition for light, competition for water plays another key role between *F. sylvatica* seedlings and other competitors in the forest understorey (Fotelli et al. 2002, 2004, Robson et al. 2009). Therefore, increased frequency and duration of summer droughts will possibly harm the natural regeneration of this forest tree (Gessler et al. 2007). It should be noted though, that comparing ^{13}C-signatures of different functional groups in the scrub of beech forests in southern Germany showed better tolerance to dry conditions of beech saplings then other co-occurring woody and herbaceous species (Fotelli et al. 2003). The response of beech seedlings and saplings to climate effects as a consequence of global warming deserves to be studied intensely, since rejuvenation is generally considered to be particularly sensitive to drought stress, and the main level at which adaptation through natural selection takes place (St. Clair and Howe 2007).

Pivotal for the future of forestry is the right choice of seed material for a changing climate, a topic which is therefore controversially discussed (e.g. Rennenberg et al. 2004, Ammer et al. 2005, Mette et al. 2013). *F. sylvatica* is known for a grand genetic variability within and between ecotypes (e.g. Nielsen and Jörgensen 2003, Buiteveld et al. 2007, Carsjens et al. 2014). European beech provenances from different origins exhibit different variations in numerous traits (e.g. Gregorius and Kleinschmitt 1999, Peuke and Rennenberg 2011, Robson et al. 2012).

Some studies on the drought tolerance of *F. sylvatica* detected better adaptation of trees originating from drier than moister origins in significant traits; higher ABA levels in leaves (Bauerle et al. 2004), reduced stomatal conductance (Tognetti et al. 1997) or more negative foliar $\delta^{13}C$ signatures (Lauteri et al. 1997) were reported. Meanwhile, other studies detected only weak significant differences in the drought adatption of beech genotypes (e.g. Rose et al. 2009, Robson et al. 2012, Thiel et al. 2014). It may be possible that provenances from the southern margin of the distribution can cope better with predicted climate warming in Central Europe (Rennenberg et al. 2004, Eilmann et al. 2014). In contrast, Ammer et al. (2005) warn against translocating ecotypes for sylvicultural purposes, as requirements on habitat or climate might not be clear. There will still be an ongoing discussion about increasing yield by selecting special ecotypes with higher growth rate, stress tolerance or other advantages for silviculture. Nowadays, the physiological basis of differences in drought stress tolerance between provenances or genotypes is not well understood.

Main study objectives

Global warming and the resulting climate changes, such as increasing occurrence and dimension of summer drought periods in most parts of Europe (Schär et al. 2004, IPCC 2013) may threaten tree vigor and forest productivity. A deeper understanding of the ability of important tree species to cope with rapid climate variation is required. In this investigation of beech forest stands across a precipitation gradient (855 – 576 mm yr^{-1}) in northwestern Germany, species-specific vulnerability and adaption to a changing climate should be elucidated. The results of this work are expected to shed light on specific questions concerning future climate responses of *F. sylvatica* in the center of its natural distribution.

This investigation is divided into three sub-studies focusing on different aspects of drought response in young and mature European beech trees.

Major study goals were to:

(i) investigate short-term responses of beech saplings to water shortage

(ii) investigate long-term response of stem increment of mature beech trees to increasingly drier summers in consideration of the soil texture

(iii) identify long-term adaptations in the hydraulic system of mature beech trees to reduced precipitation

This study was supported by grants provided by the Ministry for Science and Culture of Lower Saxony (Germany) in the research co-operation KLIFF (Klimafolgenforschung in Niedersachsen - Climate impact and adaptation research in Lower Saxony).

This research program aims to increase the knowledge base of consequences of global climate warming at regional and local scales, with the aim to develop sustainable adaptation strategies for the management of natural resources in Lower-Saxony, Germany.

Methodological approach

In this precipitation transect study the drought response of *F. sylvatica* was investigated simultaneously at different levels. Studies were conducted with both beech saplings and mature forest stands, with an experimental and an observational *in situ* approach.

(i) Morphological, physiological and growth related short-term responses to increasing drought were studied on provenances of beech saplings originating from moist to dry climates under defined moisture conditions in a common garden experiment in the Experimental Botanical Garden of the University of Göttingen.

(ii) Levels of annual increment of *F. sylvatica* trees were investigated through a dendroecological approach. Because of the dependence of drought intensity on soil water storage, a two-factorial plot design was used in order to characterize climatic and edaphic drought effects of the *in situ* long-term growth performance.

(iii) The vulnerability but also the adaptation potential to drought of *F. sylvatica* was investigated with cavitron spinning technique and anatomical investigations on branches of the sun canopy in cooperation with INRA, University of Bordeaux, UMR BIOGECO, Talence, France.

Study sites

The investigated forest stands are located along a 130-km long precipitation gradient in the northwestern German lowlands in the federal states Lower Saxony and Saxony-Anhalt in the regions Lüneburg Heath, Wendland and Altmark in the centre of the distribution range of European beech (Figure 1.3). The locations of the forest stands are: Sellhorn (*Se*), Unterlüss (*Un*), Oerrel (*Oe*), Göhrde (*Go*), Klötze (*Kl*) and Calvörde (*Ca*, abbreviation in brackets). In these six forest stands, twelve study sites were established. The gradient represents a transition from a sub-oceanic to a sub-continental climate, with a continuous decline of mean annual precipitation amounts from 855 to 576 mm yr^{-1} by a moderate increase in mean annual temperature from 8.4 to 9.1 °C from Sellhorn in the northwest to Calvörde in the southeast (Figure 1.4).

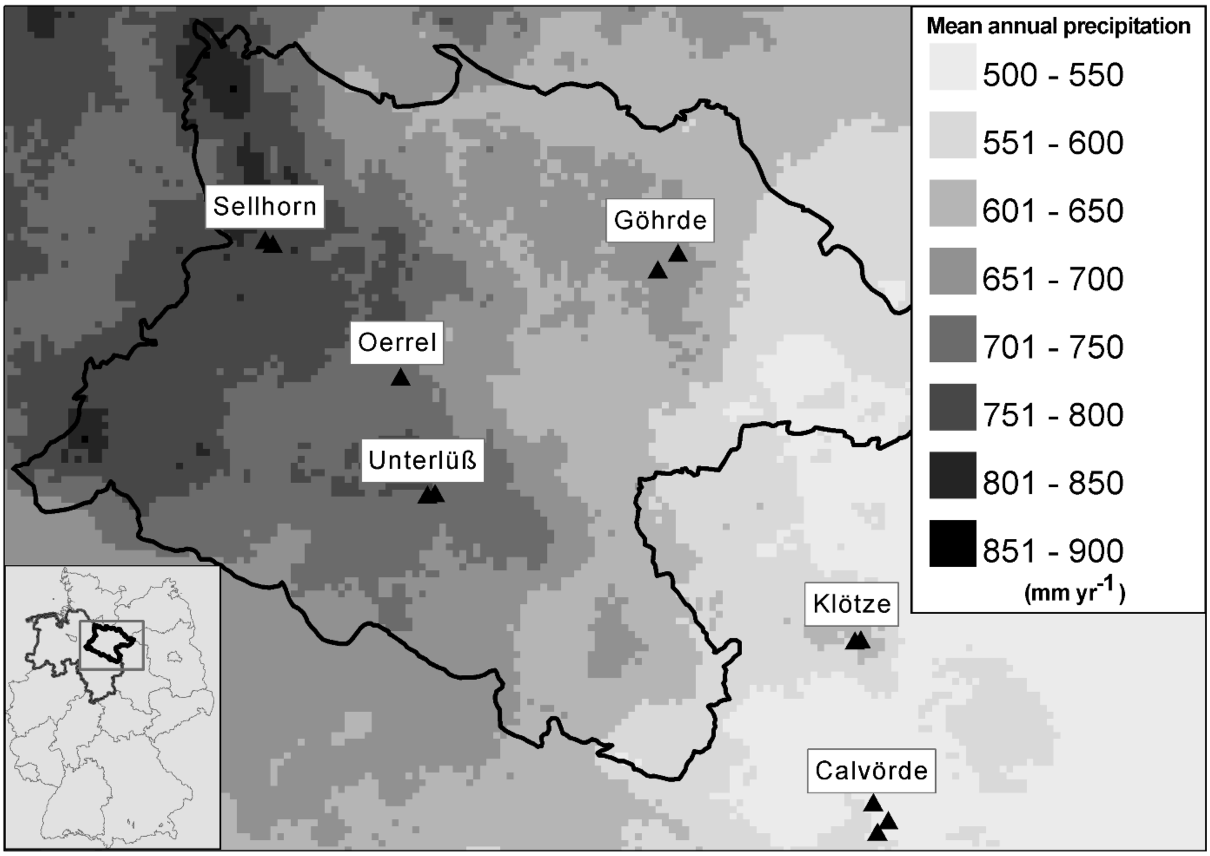

Figure 1.3. Map of the study region in northwestern Germany with the forest stands along a precipitation gradient from northwest to southeast (triangles: location of plots). The black line encircles the area of the Lüneburg Heath. Mean annual precipitation is calculated for the period 1971-2000. Climatic data from Deutscher Wetterdienst, Offenbach. Layout by C. Döring.

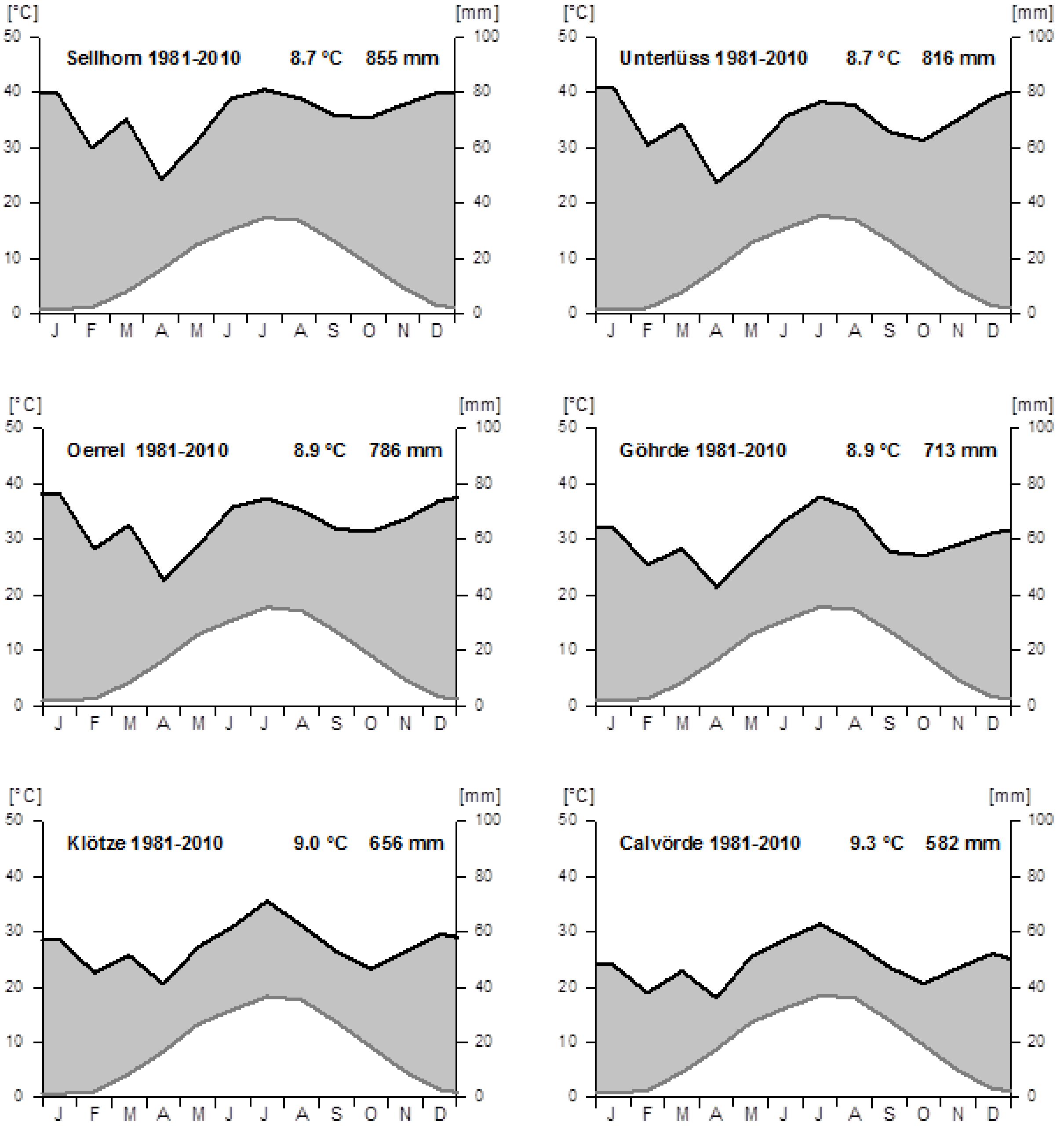

Figure 1.4. Climate diagrams for the six investigated forest stands in northwestern Germany. Values are given for the long-term averages from 1981 to 2010. Data obtained from the 1 x 1 km grid data set from Deutscher Wetterdienst, Offenbach. Precipitation: black line, Temperature: grey line.

The forest sites are situated at elevations of 72 to 125 m a.s.l. in plane or slightly sloping terrain. All study plots are located on highly acidic and nutrient-poor sandy or sandy-loamy soils deriving from fluvio-glacial sands or moraine deposits of the penultimate ice age, the Saale glaciation (Drenthe and Warthe stadial moraines) covered by periglacial drift sand. The mineral soils (dystric or umbric Arenosols or podsolic soils) are overlain by an organic layer with a thickness of 4 to 9 cm. Additional criteria of stand selection were: a closed canopy (mono-layer with additional tree or shrub layers mostly absent), mature and even-aged stand structure (85-125 years old; extreme: 180 years), absent or low admixture of other tree species (*Se*S, *Un*S *Kl*S *Ca*L: 3 - 19% *Quercus petraea*, *Oe*S 39%; *Go*S: 6% *Pseudotsuga menziesii*), last forest management activities at least ten years ago, and tree origin from natural regeneration (with the exception of *Oe*). Overall characteristics of the 12 forest sites used for this transect study are given in Table 1.1 at the end of this chapter.

Edaphic gradient

in the dendroecological investigation an additional focus was placed on the effects of soil texture. Next to the climatic influence on soil moisture conditions, we aimed at adding an edaphic component: we selected each two study sites with a sandy and a sandy-loamy soil texture, respectively, at six locations along the gradient. In Oerrel only one site with sandy texture was available, while in Calvörde, at the dry end of the gradient, one site with sandy-loamy, and two sites with sandy textures were set up (Figure 1.5). All study sites were fenced and had a size of 30 x 30 m.

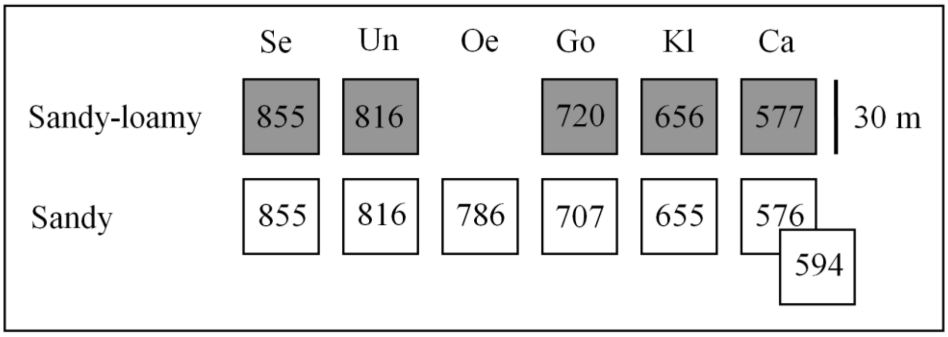

Figure 1.5. Schematic study plot design. In Oerrel only a sandy site, in Calvörde one sandy-loamy and two sandy sites were set up. Mean annual precipitation, calculated for the period 1981-2010, is given for each plot in the squares. Climatic data from Deutscher Wetterdienst, Offenbach. Layout by H. Müller-Haubold, modified.

The sandy-loamy sites are located on loam-richer sandy deposits with a higher content of silt and clay and mainly a higher water storage capacity (WSC). The sandy plots are located on more coarse-grained meltwater sands with low silt and clay content and a smaller WSC. The soils had a pH (KCl) 4.2-4.4 (mean: 4.3) at the sandy-loamy and 4.0-4.3 (mean: 4.2) at the sandy sites (Table 1.2). C:N ratio ranged by 12-26 mol mol^{-1} (mean: 18) at the sandy-loamy and 13-26 mol mol^{-1} (mean: 20) at the sandy sites. A base saturation of 7-24 % (mean: 14) at the sandy-loamy and 3-13 % (mean: 8) at the sandy sites was determined. Nitrogen concentration of the top mineral soil was 0.28-0.46 g kg^{-1} (mean: 0.38) at the sandy-loamy sites and 0.33-0.78 g kg^{-1} (mean: 0.49) at the sandy sites. Phosphorous concentration was for sandy-loamy sites 59-126 mg kg^{-1} (mean: 88), and 79-238 mg kg^{-1} (mean: 123) at the sandy sites (data according to Müller-Haubold et al. 2013).

Table 1.2. Summary of climatic, edaphic, and stand structural properties of the 12 beech stands in north-western Germany. Mean annual precipitation (MAP) and temperature (MAT) refer to the period 1981-2010 (regionalised by C. Döring from the national weather stations network data base provided by DWD, Deutscher Wetterdienst). Mean tree height refers to all beech trees constituting the upper canopy layer. Mean diameter in breast height considers all beech trees > 7 cm stem diameter; stem density and cumulative basal area refer to all trees > 7 cm stem diameter in a plot and may include a few individuals of other species in certain plots (see Methods section). Soil chemical properties refer to the upper 30 cm of the mineral soil (N: total nitrogen; Al: NH4Cl-exchangeable aluminium; P: total phosphorus; data provided by M. Jansen and C. Döring, unpublished). Fine-grained soil particles include fine sand, silt and clay (particles size < 200 µm) expressed in % of total soil mass (0 – 120 cm soil profile). The water storage capacity is calculated for the upper 120 cm of the mineral soil. Edaphic and stand structural properties refer to Müller-Haubold et al. 2013).

Site code	Se	Se	Un	Un	Oe	Go	Go	Kl	Kl	Ca	Ca	Ca
Texure	L	S	L	S	S	L	S	L	S	L	S	S
Coordinates	53°10' N 09°57' E	53°10' N 09°57' E	52°50' N 10°19' E	52°50' N 10°19' E	52°59' N 10°14' E	53°07' N 10°49' E	53°09' N 10°52' E	52°37' N 11°14' E	52°37' N 11°15' E	52°24' N 11°16' E	52°23' N 11°17' E	52°22' N 11°16' E
Elevation (m a.s.l.)	127	130	120	117	90	85	85	102	85	72	75	105
MAP (mm) / MAT (°C)	855 / 8.7	855 / 8.7	816 / 8.7	816 / 8.7	786 / 8.9	720 / 8.9	707 / 9.0	656 / 9.0	655 / 9.1	577 / 9.3	576 / 9.4	594 / 9.3
Stand age (yr)	127	127	115	115	95	142	133	c.125	c.125	131	97	87
Mean tree height (m)	31.4	28.0	28.4	25.3	27.2	30.2	24.6	33.8	30.2	28.3	23.8	25.5
Stem density (no. ha^{-1})	156	367	411	611	500	122	289	267	478	300	711	578
Mean diameter in breast height (cm)	46.7	29.6	26.1	18.6	21.7	51.0	30.7	43.3	29.0	36.6	23.4	24.9
Stand basal area (m^2 ha^{-1})	31.0	30.7	28.5	24.3	32.3	26.6	24.4	44.9	40.8	33.3	33.2	32.6
Proportion of beech (% of basal area)	100	95	100	81	61	100	94	100	81	97	100	100
Timber volume (m^3 ha^{-1})	490	395	378	227	287	407	289	758	516	454	374	402
Thickness of organic layer (cm)	7.5	9.1	6.5	7.3	6.9	9.0	8.8	4.1	6.4	7.5	6.6	8.0
pH value (H_2O) of mineral soil	4.2	4.2	4.4	4.3	4.0	4.3	4.3	4.4	4.3	4.2	4.3	4.1
C/N ratio of mineral soil (g g^{-1})	15.6	24.2	25.8	24.1	17.8	22.9	25.5	11.9	15.7	15.9	13.2	19.0
N concentration of mineral soil (g kg^{-1})	0.28	0.46	0.40	0.47	0.78	0.41	0.51	0.46	0.49	0.34	0.42	0.33
P concentration of mineral soil (mg kg^{-1})	63	79	71	106	238	59	97	121	97	126	111	133
Al concentration of mineral soil (g kg^{-1})	0.53	0.52	0.58	0.31	0.42	0.46	0.79	0.48	0.54	0.38	0.57	0.38
Cation exchange capacity (µmol$_c$ g^{-1})	16.1	27.5	18.4	24.2	22.7	20.2	26.5	21.3	17.3	18.6	14.7	14.2
Base saturation of mineral soil (%)	24.3	9.7	14.8	8.3	13.0	6.7	2.8	14.4	9.7	7.4	5.0	6.9
Fraction of fine-grained (< 200 µm) soil particles (%)	51	42	52	46	25	41	14	62	46	61	24	14
Water storage capacity mineral soil (mm 120 cm^{-1})	90	111	95	79	59	78	107	124	90	140	81	46

References

Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. *Science*, **294**, 321-326.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomeas for tree populations. *Evolutionary Applications*, **1**, 95-111.

Akasofu, SI (2010) On the recovery from the Little Ice Age. *Natural Science*, **11**, 1211.

Ammer C, Albrecht L, Borchert H, Brosinger F, Dittmar C, Elling W, Ewald J, Felbermayer B, Gilsa VH, Huss J, Kenk J, Kölling C, Kohnle U, Meyer P, Mosandl R, Moosmayer HU, Palmer S, Reif A, Refuss KE, Stimm B (2005) Zur Zukunft der Buche (*Fagus sylvatica* L.) in Mitteleuropa–kritische Anmerkungen zu einem Beitrag von Rennenberg et al. (2004) *Allgemeine Forst und Jagdzeitung*, **176**, 60-67.

Anderegg RL, Meinzer FC (2015) Wood anatomy and plant hydraulics in a changing climate. *Functional and Ecological Xylem Anatomy*. Springer International Publishing, Switzerland, 235-253.

Anderson JT, Panetta AM, Mitchell-Olds T (2012) Evolutionary and ecological responses to anthropogenic climate change. *Plant Physiology*, **160**, 1728–1740.

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677-689.

Aranda I, Gil L, Pardos J (2001) Effects of thinning in a *Pinus sylvestris* L. stand on foliar water relations of *Fagus sylvatica* L. seedlings planted within the pinewood. *Trees – Structure and Function*, **15**, 358-364.

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1-16.

Bauerle WL, Whitlow TH, Setter TL, Bauerle TL, Vermeylen FM (2003) Ecophysiology of *Acer rubrum* seedlings from contrasting hydrologic habitats: growth, gas exchange, tissue water relations, abscisic acid and carbon isotope discrimination. *Tree Physiololgy*, **23**, 841-850.

Bauerle WL, Whitlow TH, Setter TL, Vermeylen FM (2004) Abscisic acid synthesis in *Acer rubrum* L. leaves - A vapor-pressure-deficit-mediated response. *Journal of the American Society for Horticultural Science*, **129**, 182-187.

Belli R, Frisia S, Borsato A, Drysdale R, Hellstrom J, Zhao JX, Spotl C (2013) Regional climate variability and ecosystem responses to the last deglaciation in the northern hemisphere from stable isotope data and calcite fabrics in two northern Adriatic stalagmites. *Quaternary Science Reviews*, **72**, 146-158.

Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems*, **9**, 330-343.

BMEL (2014) Der Wald in Deutschland – Ausgewählte Ergebnisse der dritten Bundeswaldinventur. Berlin: Bundesministerium für Ernährung und Landwirtschaft.

Bolte A, Czajkowski T, Kompa T (2007) The north-eastern distribution range of European beech a review. *Forestry*, **80**, 413–429.

Bontemps JD, Hervé JC, Dhôte JF, (2009) Long-term changes in forest productivity: a consistent assessment in even-aged stands. *Forest Science*, **55**, 549-564.

Bouche PS, Larter M, Domec JC, Burlett R, Gasson P, Jansen S, Delzon S (2014) A broad survey of hydraulic and mechanical safety in the xylem of conifers. *Journal of Experimental Botany*, **65**, 4419–4431.

Breda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625–644.

Bresson CC, Vitasse Y, Kremer A, Delzon S (2011) To what extent is altitudinal variation of functional traits driven by genetic adaptation in European oak and beech? *Tree physiology*, **00**, 1-11.

Buiteveld J, Vendramin GG, Leonardi S, Kamer K, Geburek T (2007) Genetic diversity and differentiation in European beech (*Fagus sylvatica* L.) stands varying in management history. *Forest Ecology and Management*, **247**, 98-106.

Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions among plants. *Ecology*, **84**, 1115–1128.

Carlquist S (1977) Ecological Factors in Wood Evolution - Floristic Approach. *American Journal of Botany*, **64**, 887–896.

Carsjens C, Nguyen Ngoc Q, Guzy J, Knutzen F, Meier IC, Müller M, Finkeldey R, Leuschner C, Polle A (2014) Intra-specific variations in expression of stress-related genes in beech progenies are stronger than drought-induced responses. *Tree Physiology*, **34**, 1348–1361.

Charru M, Seynave I, Morneau F, Bontemps JD (2010) Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. *Forest Ecology and Management*, **260**, 864-874.

Cheaib A, Badeau V, Boe J, Chuine I, Delire C, Dufrêne E, François C, Gritti ES, Legay M, Pagé C, Thuiller W, Viovy N, Leadley P (2012) Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. *Ecology letters*, **15**, 533-544.

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024-1026.

Ciais P, Reichstein M, Viovy NN, Granier A, Ogée J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, de Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Cochard H, Bréda N, Granier A (1996) Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? *Annales des Sciences Forestières*, **53**, 197-206.

Cordell S, Goldstein G, Mueller-Dombois D, Webb D, Vitousek PM (1998) Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia*, **113**, 188-196.

Dai A, Fung IY, Del Genio AD (1997) Surface observed global land precipitation variations during 1900-88. *Journal of Climate*, **11**, 2943-2962.

Davis MB, Kabinski C (1992) Phenology of Ecosystem Processes: Applications in Global Change Research (eds. Peters RL, Lovejoy TE). *Global Warming and Biological Diversity*, 297–309, Yale University Press, Yale, USA.

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673-679.

Dewitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, **13**, 77-81.

Dittmar C, Elling W (1999) Jahrringbreite von Fichte und Buche in Abhängigkeit von Witterung und Höhenlage. *Forstwissenschaftliches Centralblatt vereinigt mit Tharandter forstliches Jahrbuch*, **118**, 251-270.

Dittmar C, Zech W, Elling W (2003) Growth variations of Common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe - A dendroecological study. *Forest Ecology and Management*, **173**, 63–78.

Dobbertin M (2005) Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *European Journal of Forest Research*, **124**, 319–333.

Döbbeler H, Spellmann H (2002) Methodological approach to simulate and evaluate silvicultural treatments under climate change. *Forstwissenschaftliches Centralblatt*, **121**, 52-69.

Dudley SA, Schmitt J (1996) Testing the adaptive plasticity hypothesis: Density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist*, **147**, 445-465

Eilmann B, Sterck F, Wegner L, de Vries SM, von Arx G, Mohren GM, den Ouden J, Sass-Klaassen U (2014) Wood structural differences between northern and southern beech provenances growing at a moderate site. *Tree Physiology*, **34**, 882–893.

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Hinsicht. Ulmer, Stuttgart, Germany.

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annual review of plant biology*, **40**, 503-537.

Folland CK, Colman AW, Rowell DP, Davey MK (2001) Predictability of northeast Brazil rainfall and real-time forecast skill, 1987-98. *Journal of Climate*, **14**, 1937-1958.

Fotelli MN, Geßler A, Peuke AD, Rennenberg H (2001) Drought affects the competitive interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*: responses of growth, water status and δ13C composition. *New Phytologist*, **151**, 427-435.

Fotelli MN, Nahm M, Heidenfelder A, Papen H, Rennenberg H, Geßler A (2002) Soluble nonprotein nitrogen compounds indicate changes in the nitrogen status of beech seedlings due to climate and thinning. *New Phytologist*, **154**, 85-97.

Fotelli MN, Rennenberg H, Holst T, Mayer H, Geßler A (2003) Carbon isotope composition of various tissues of beech (*Fagus sylvatica*) regeneration is indicative of recent environmental conditions within the forest understorey. *New Phytologist*, **159**, 229–244.

Fotelli MN, Rienks M, Rennenberg H, Geßler A (2004) Climate and forest management affect 15N-uptake, N balance and biomass of European beech seedlings. *Trees - Structure and Function*, **18**, 157–166.

Garland T, Kelly SA (2006) Phenotypic plasticity and experimental evolution. *Journal of Experimental Biology*, **209**, 2344-2361.

Gessler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees-Structure and Function*, **21**, 1–11.

Geßler A, Schrempp S, Matzarakis A, Mayer H, Rennenberg H, Adams MA (2001) Radiation modifies the effect of water availability on the carbon isotope composition of beech (F*agus sylvatica*). *New Phytologist*, **150**, 653-664.

Glaser R (2001) Klimageschichte Mitteleuropas: 1000 Jahre Wetter, Klima, Katastrophen. Primus, Darmstadt, Germany.

Gleason SM, Butler DW, Ziemińska K, Waryszak P, Westoby M (2012) Stem xylem conductivity is key to plant water balance across Australian angiosperm species. *Functional Ecology*, **26**, 343–352.

Granier A, Reichstein M, Bréda N, Janssens IA, Falge E, Ciais P, Grünwald T, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Facini O, Grassi G, Heinesch B, Ilvesniemi H, Keronen P, Knohl A, Köstner B, Lagergren F, Lindroth A, Longdoz B, Loustau D, Mateus J, Montagnani L, Nys C, Moors E, Papale D, Peiffer M, Pilegaard K, Pita G, Pumpanen J, Rambal S, Rebmann C, Rodrigues A, Seufert G, Tenhunen J, Vesala T, Wang Q (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, **143**, 123-145.

Gregorius H, Kleinschmit J (1999) The environmental dichotomy of adaptation and the role of genetic diversity. *Silvae Genetica*, **48**, 193-199.

Hacke U, Sauter JJ (1995) Vulnerability of Xylem to Embolism in Relation to Leaf Water Potential and Stomatal Conductance in *Fagus-Sylvatica f purpurea* and *Populus-Balsamifera*. *Journal of Experimental Botany*, **46**, 1177–1183.

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloch KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.

Halbritter AH, Alexander JM, Edwards PJ, Billeter R (2013) How comparable are species distributions along elevational and latitudinal climate gradients? *Global Ecology and Biogeography*, **22**, 1228–1237.

Hamrick JL, Godt MJW (1996) Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **351**, 1291–1298.

Hamrick JL (2004) Response of forest trees to global environmental changes. *Forest Ecology and Management*, **197**, 323–335.

Hartmann H (2011) Will a 385 million year-struggle for light become a struggle for water and for carbon?—How trees may cope with more frequent climate change-type drought events. *Global Change Biology*, **17**, 642–655.

Herbette S, Wortemann R, Awad H, Huc R, Cochard H, Barigah TS (2010) Insights into xylem vulnerability to cavitation in *Fagus sylvatica* L.: phenotypic and environmental sources of variability. *Tree physiology*, **30**, 1448–55.

Herrero A, Rigling A, Zamora R (2013) Varying climate sensitivity at the dry distribution edge of *Pinus sylvestris* and *P. nigra*. *Forest Ecology and Management*, **308**, 50-61.

Hertel D, Strecker T, Müller-Haubold H, Leuschner C (2013) Fine root biomass and dynamics in beech forests across a precipitation gradient - is optimal resource partitioning theory applicable to water-limited mature trees? *Journal of Ecology*, **101**, 1183–1200.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Huntington TG (2006) Evidence for intensification of the global water cycle: Review and synthesis. *Journal of Hydrology*, **319**, 83–95.

IPCC (2013) Summary for policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), PP. 1535. Cambridge University Press, Cambridge, UK.

Jacob D, Petersen J, Eggert B, Alias A, Christensen OB, Bouwer LM, Braun A, Colette A, Déqué M, Georgievski G, Georgopoulou E, Gobiet A, Menut L, Nikulin G, Haensler A, Hempelmann N, Jones C, Keuler K, Kovats S, Kröner N, Kotlarski S, Kriegsmann A, Martin E, Meijgaard E, Moseley C, Pfeifer S, Preuschmann S, Radermacher C, Radtke K, Rechid D, Rounsevell M, Samuelsson P, Somot S, Soussana J-F, Teichmann C, Valentini R, Vautard R, Weber B, Yiou P (2013) EURO-CORDEX: new high-resolution climate change projections for European impact research. *Regional Environmental Change*, **14**, 563-578.

Jacobsen AL, Pratt RB, Ewers FW, Davis SD (2007) Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs*, **77**, 99–115.

Jansen S, Choat B, Pletsers A (2009) Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. *American journal of botany*, **96**, 409–19.

Jantsch MC, Fischer A, Fischer HS, Winter S (2013) Shift in plant species composition reveals environmental changes during the last decades: a long-term study in beech (*Fagus sylvatica*) forests in Bavaria, Germany. *Folia Geobotanica*, **48**, 467–491.

Jones PD, Moberg A (2003) Hemispheric and large-scale surface air temperature variations: An extensive revision and an update to 2001. *Journal of Climate*, **16**, 206-223.

Joos F, Spahni RE (2008) Rates of change in natural and anthropogenic radiative forcing over the past 20,000 years. *Proceedings of the National Academy of Sciences*, **105**, 1425 - 1430.

Jump AS, Peñuelas J (2005) Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.

Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.

Kahle HP, Spiecker H, Unseld R, Pérez-Martínez PJ, Prietzel J, Mellert KH, Straussberger R, Rehfuess KE (2008) Short-, medium-, and long-term variation in radial growth, and the role of changes in the climatic water balance for the growth of three tree species in Europe. Causes and Consequences of Forest Growth Trends in Europe: Results of the Recognition Project, **169**.

Kint V, Aertsen W, Campioli M, Vansteenkiste D, Delcloo A, Muys B (2012) Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901-2008. *Climate Change*, **115**, 343-363.

Kjellström E, Thejll P, Rummukainen M, Christensen JH, Boberg F, Christensen OB, Maule CF (2013) Emerging regional climate change signals for Europe under varying large-scale circulation conditions. *Climate Research*, **56**, 103-119.

Knutti R, Sedláček J (2013) Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Climate Change*, **3**, 369-373.

Köcher P, Gebauer T, Hornbach V, Leuschner C (2009) Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies. *Annals of Forest Science*, **66**, 101.

Kölling C, Zimmermann L, Walentowski H (2007) Klimawandel: was geschieht mit Buche und Fichte. *AFZ-DerWald*, **11**, 584-588.

Kramer K, Degen B, Buschbom J, Hickler T, Thuiller W, Sykes MT, de Winter W (2010) Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change-Range, abundance, genetic diversity and adaptive response. *Forest Ecology and Management*, **259**, 2213–2222.

Lamb HH (2013) Climate: Present, Past and Future (Routledge Revivals): Volume 1: Fundamentals and Climate Now. Routledge, London, England.

Lauteri M, Scartazza A, Guido MC, Brugnoli E (1997) Genetic variation in photosynthetic capacity, carbon isotope discrimination and mesophyll conductance in provenances of *Castanea sativa* adapted to different environments. *Functional Ecology*, **11**, 675-683.

Lens F, Luteyn JL, Smets E, Jansen S (2004) Ecological trends in the wood anatomy of Vaccinioideae (Ericaceae s.l.). *Flora - Morphology, Distribution, Functional Ecology of Plants*, **199**, 309–319.

Leuschner C, Backes K, Hertel D, Schipka F, Schmidt U, Terborg O, Runge M (2001) Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *Forest Ecology and Management*, **149**, 33-46.

Linares JC, Delgado-Huertas A, Carreira JA (2011) Climatic trends and different drought adaptive capacity and vulnerability in a mixed *Abies pinsapo–Pinus halepensis* forest. *Climatic change*, **105**, 67-90.

Magri D (2008) Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). *Journal of Biogeography*, **35**, 450–463.

Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gömöry D, Latałowa M, Litt T, Paule L, Roure JM, Tantau I, van der Knaap WO, Petit RJ, de Beaulieu J-L (2006) A new scenario for the quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist*, **171**, 199-221.

Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB (2006) Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant Cell and Environment*, **29**, 571–583.

Markesteijn L, Poorter L, Paz H, Sack L, Bongers F (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment*, **34**, 137–48.

McDowell NG, Allen CD (2015) Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, **5**, 669–672.

Meier ES, Lischke H, Schmatz DR, Zimmermann NE (2012) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, **21**, 164–178.

Meier IC, Leuschner C (2008a) Leaf size and leaf area index in *Fagus sylvatica* forests: competing effects of precipitation, temperature, and nitrogen availability. *Ecosystems*, **11**, 655-669.

Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature*, **397**, 659–659.

Mette T, Dolos K, Meinardus C, Bräuning A, Reineking B, Blaschke M, Pretzsch H, Beierkuhnlein C, Gohlke A, Wellstein C (2013) Climatic turning point for beech and oak under climate change in Central Europe. *Ecosphere*, **4**, 1-19.

Montwé D, Spiecker H, Hamann A (2015) Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. *Tree Genetics and Genomes*, 11-29.

Moseley C, Panferov O, Döring C, Dietrich J, Haberlandt U, Ebermann V, Rechid D, Beese F, Jacob D (2012) Empfehlung für eine Niedersächsische Strategie zur Anpassung an die Folgen des Klimawandels. Niedersächsisches Ministerium für Umwelt, Energie und Klimaschutz, Regierungskommission Klimaschutz.

Müller-Haubold H, Hertel D, Seidel D, Knutzen F, Leuschner C (2013) Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. *Ecosystems*, **16**, 1498–1516.

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. *Trends in plant science*, **15**, 684-692.

Nielsen C, Jørgensen F (2003) Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and within provenances. *Forest Ecology and Management*, **174**, 233-249.

Nisbet EG, Dlugokencky EJ, Bousquet P (2014). Methane on the rise—again. *Science*, **343**, 493-495.

Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T. (2009) The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science*, **325**, 464-467.

Parmesan C (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637-669.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.

Penuelas J, Boada M (2003) A global change-induced biome shift in the Montseny Mountains (NE Spain). *Global Change Biology*, **9**, 131-140.

Peters GP, Andrew RM, Boden T, Canadell JG, Ciais P, Le Quéré C, Marland G, Raupach MR, Wilson C (2013) The challenge to keep global warming below 2° C. *Nature Climate Change*, **3**, 4-6.

Peters R (1997) Beech forests. Springer, Netherlands, 1997.

Petit RJ, Hampe A (2006) Some evolutionary consequences of being a tree. *Annual review of ecology, evolution, and systematics*, 187-214.

Peuke AD, Rennenberg H (2011) Impacts of drought on mineral macro-and microelements in provenances of beech (*Fagus sylvatica* L.) seedlings. *Tree physiology*, **31**, 196-207.

Peuke AD, Schraml C, Hartung W, Rennenberg H (2002) Identification of drought-sensitive beech ecotypes by physiological parameters. *New Phytologist*, **154**, 373–387.

Plavcová L, Jansen S, Klepsch M, Hacke UG (2013) Nobody's perfect: can irregularities in pit structure influence vulnerability to cavitation? *Frontiers in Plant Science*, **4**, 453.

Pócs T (2011) Signs of climate change in the bryoflora of Hungary. In: *Bryophyte Ecology and Climate Change* (eds Tuba Z, Slack NG, Stark LR), 359–370. Cambridge University Press, Cambridge, UK.

Pretzsch H, Uhl E, Biber P, Schütze G, Coates KD (2012) Change of allometry betweencoarse root and shoot of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia. *Scandinavian Journal of Forest Research*, **27**, 532–544.

Pretzsch H, Biber P, Schütze G, Uhl E, Rötzer T (2014) Forest stand dynamics in Central Europe has accelerated since 1870. *Nature Communications*, **5**, 1–10.

Rehfeldt GE, Tchebakova NM, Parfenova YI, Wykoff WR, Kuzmina NR, Milyutin LI (2002) Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology*, **8**, 912–929

Rennenberg H, Loreto F, Polle A, Brilli F, Fares S, Beniwal RS, Gessler A (2006) Physiological Responses of Forest Trees to Heat and Drought. *Plant Biology*, **8**, 556-571.

Rennenberg H, Seiler W, Matyssek R, Gessler A, Kreuzwieser J (2004) European beech (*Fagus sylvatica* L.) - a forest tree without future in the south of Central Europe. *Allgemeine Forst und Jagdzeitung*, **175**, 210–224.

Reusch TBH, Ehlers A, Hämmerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 2826–2831.

Rigling A, Bigler C, Eilmann B, Feldmeyer-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P, Vacchiano G, Weber P, Wolgemuth T, Zweifel R, Dobbertin M (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biology*, **19**, 229–240.

Rita A, Gentilesca T, Ripullone F, Todaro L, Borghetti M (2014). Differential climate–growth relationships in *Abies alba* Mill. and *Fagus sylvatica* L. in Mediterranean mountain forests. *Dendrochronologia*, **32**, 220-229.

Robson TM, Rodrguez-Calcerrada J, Snchez-Gmez D, Aranda I (2009) Summer drought impedes beech seedling performance more in a sub-Mediterranean forest understory than in small gaps. *Tree Physiology*, **29**, 249–259.

Robson TM, Sánchez-Gómez D, Cano FJ, Aranda I (2012) Variation in functional leaf traits among beech provenances during a Spanish summer reflects the differences in their origin. *Tree Genetics and Genomes*, **8**, 1111–1121.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-60.

Rose L, Leuschner C, Köckemann B, Buschmann H (2009) Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research*, **128**, 335-343.

Rowell DP, Jones RG (2006) Causes and uncertainty of future summer drying over Europe. *Climate Dynamics*, **27**, 281-299.

Ruffault J, Martin-StPaul NK, Rambal S, Mouillot F (2013) Differential regional responses in drought length, intensity and timing to recent climate changes in a Mediterranean forested ecosystem. *Climatic change*, **117**, 103-117.

Sabaté S, Gracia CA, Sánchez A (2002) Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *Forest Ecology and Management*, **162**, 23–37.

Saltré F, Saint-Amant R, Gritti ES, Brewer S, Gaucherel C, Davis BA, Chuine I (2013) Climate or migration: what limited European beech post-glacial colonization? *Global Ecology and Biogeography*, **22**, 1217-1227.

Sánchez-Salguero R, Navarro RM, Camarero JJ, Fernández-Cancio Á (2010) Drought-induced growth decline of Aleppo and maritime pine forests in south-eastern Spain. *Forest Systems*, **19**, 458-470.

Sánchez-Salguero R, Navarro-Cerrillo RM, Camarero JJ, Fernández-Cancio Á (2012) Selective drought-induced decline of pine species in southeastern Spain. *Climatic Change*, **113**, 767-785.

Seppälä J, Grönroos J, Koskela S, Holma A, Leskinen PJ, Liski J, Tuovinen JP, Laurila T, Turunen J, Lind S, Maljanen M, Matikainen P, Kilpeläinen A (2010) Climate impacts of peat fuel utilization chains–a critical review of the Finnish and Swedish life cycle assessments. *The Finnish Environment*, **16.**

Schall P, Lödige C, Beck M, Ammer C (2012) Biomass allocation to roots and shoots is more sensitive to shade and drought in European beech than in *Norway spruce* seedlings. *Forest Ecology and Management*, **266**, 246–253.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Scharnweber T, Manthey M, Criegee C, Bauwe A, Schröder C, Wilmking M (2011) Drought matters – declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management*, **262**, 947-961.

Schraml U, Volz KR (2004) Conversion of coniferous forests in social and political perspectives. Findings from selected countries with special respect to Germany. *Norway spruce* conversion–options and consequences. *EFI Research Report*, **18**, 97-119.

Spellmann H, Sutmöller J, Meeseburg H (2007) Risikovorsorge im Zeichen des Klimawandels. Vorläufige Empfehlungen der NW-FVA am Beispiel des Fichtenanbaus. *AFZ-Der Wald*, **23**, 1246-1249.

Sperry JS, Tyree MT (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiololgy*, **88**, 581–587.

Spiecker H, Mielikäinen K, Köhl M, Skovsgaard JP (1996) Growth Trends in European Forests. Studies from 12 Countries, European Forest Institute Research Report, **5**.

Spiecker H (1999) Overview of recent growth trends in European forests. *Water, Air, and Soil Pollution*, **116**, 33–46.

St. Clair JB, Howe GT (2007) Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Global Change Biology*, **13**, 1441–1454.

Sterck FJ, Zweifel R, Sass-Klaassen U, Chowdhury Q (2008) Persisting soil drought reduces leaf specific conductivity in Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*). *Tree Physiology*, **28**, 529–536.

Taeger S, Zang C, Liesebach M, Schneck V, Menzel A (2013) Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenances. *Forest Ecology and Management*, **307**, 30–42.

Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J (2008) Bergmann's rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences*, **105**, 13492-13496.

Thejll P, Lassen K (2000) Solar forcing of the Northern hemisphere land air temperature: New data. *Journal of Atmospheric and Solar-Terrestrial Physics*, **62**, 1207-1213.

Thiel D, Kreyling J, Backhaus S, Beierkuhnlein C, Buhk C, Egen K, Huber G, Konnert M, Nagy L, Jentsch A (2014) Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *European Journal of Forest Research*, **133**, 247-260.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL Williams SE (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.

Thomas CD, Hill JK, Anderson BJ, Bailey S, Beale CM, Bradbury RB, Bulman CR, Crick HQP, Eigenbrod F, Griffiths HM, Kunin WE, Oliver TH, Walmsley CA, Watts K, Worsfold NT, Yardley T (2011) A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution*, **2**, 125-142.

Tognetti R, Michelozzi M, Giovannelli A (1997) Geographical variation in water relations, hydraulic architecture and terpene composition of *Aleppo pine* seedlings from Italian provenances. *Tree Physiology*, **17**, 241-250.

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Berlin, Germany: Springer Verlag.

Tyree MT, Davis SD, Cochard H (1994) Biophysical Perspectives of Xylem Evolution - Is There A Tradeoff of Hydraulic Efficiency for Vulnerability to Dysfunction. *Iawa Journal*, **15**, 335–360.

Van der Werf GW, Sass-Klaassen UGW, Mohren GMJ (2007) The impact of the 2003 summer drought on the intra-annual growth pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on a dry site in the Netherlands. *Dendrochronologia*, **25**, 103–112.

Van Herk CV, Aptroot A, van Dobben HF (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *The Lichenologist*, **34**, 141-154.

Vicente-Serrano SM, Lasanta T, Gracia C (2010) Aridification determines changes in forest growth in *Pinus halepensis* forests under semiarid Mediterranean climate conditions. *Agricultural and Forest Meteorology*, **150**, 614-628

Weber P, Bugmann H, Pluess AR, Walthert L, Rigling A (2013) Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees - Structure and Function*, **27**, 171–181.

Yang F, Kumar A, Schlesinger ME, Wang W (2003) Intensity of hydrological cycles in warmer climates. *Journal of Climate*, **16**, 2419-2423.

Zimmermann J, Hauck M, Dulamsuren C, Leuschner C (2015) Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. *Ecosystems*, **18**, 560–572.

CHAPTER 2

Does reduced precipitation trigger physiological and morphological drought adaptations in European beech (*Fagus sylvatica* L.)? Comparing provenances across a precipitation gradient

---

Florian Knutzen · Ina Christin Meier · Christoph Leuschner

Published in Tree Physiology (2015),

Doi: 10.1093/treephys/tpv057

Abstract

Global warming and associated decreases in summer rainfall may threaten tree vitality and forest productivity in many regions of the temperate zone in the future. One option for forestry to reduce the risk of failure is to plant genotypes which combine high productivity with drought tolerance. Growth experiments with provenances from different climates indicate that drought exposure can trigger adaptive drought responses in temperate trees, but it is not well known as to whether and to what extent regional precipitation reduction can increase the drought resistance of a species. We conducted a common garden growth experiment with five European beech (*Fagus sylvatica* L.) populations from a limited region with pronounced precipitation heterogeneity (816 to 544 mm yr^{-1}), where phylogenetically related provenances grew under small to large water deficits. We grew saplings of the five provenances at four soil moisture levels (dry to moist) and measured about 30 morphological (leaf and root properties, root : shoot ratio), physiological (leaf water status parameters, leaf conductance) and growth-related traits (above- and belowground productivity) with the aim to examine provenance differences in the drought response of morphological and physiological traits and to relate the responsiveness to precipitation at origin. Physiological traits were more strongly influenced by provenance (1/3 of the studied traits), while structural traits were primarily affected by water availability in the experiment (2/3 of the traits). The modulus of leaf tissue elasticity ε reached much higher values late in summer in plants from moist origins resulting in more rapid turgor loss and a higher risk of hydraulic failure upon drought. While experimental water shortage affected the majority of morphological and productivity-related traits in the five provenances, most parameters related to leaf water status were insensitive to water shortage. Thus, plant morphology, and root growth in particular, did respond to reduced water availability with higher phenotypic plasticity than did physiology. We conclude that beech provenances exposed to different precipitation regimes have developed some genotypic differences with respect to leaf water status regulation, but these adaptations are associated with only minor adaptation in plant morphology and they do not affect the growth rate of the saplings.

Keywords: *Fagus sylvatica*, common garden experiment, leaf water relations, precipitation gradient, provenance effects, pressure-volume curves, saplings, $\delta^{13}C$ signature.

Introduction

Global warming is predicted to reduce summer rainfall and increase the frequency of heat waves in parts of Europe in the decades to come (Schär et al. 2004, Rowell and Jones 2006, IPCC 2013). Regionalized climate simulations for northern and eastern Germany based on the global atmosphere-ocean model system ECHAM5-MPIOM indicate rising mean annual temperatures by about 2.5 °C until the end of the 21st century and a decrease in summer rainfall (June-August) by 10-20 % (Moseley et al. 2012, Belli et al. 2013, Jacob et al. 2014). These predicted trends are consistent with the recorded past climate change in the region (Haberlandt et al. 2010). Forests will be particularly sensitive to these changes due to the trees' long lifespan.

Trees have the potential to adapt to adverse climatic conditions by different mechanisms. Important elements of adaptability are phenotypic plasticity and genotypic variability. In variable environments, phenotypic plasticity evolves to maximize fitness, i.e. the ability to modify the phenotype in response to environmental variation (Dudley and Schmit 1996); while in stable environments, specialization is favored over plasticity because of higher costs of the latter (DeWitt et al. 1998, Agrawal 2001). On longer time scales, the environment will select for genotypes with better adaptation to the actual stress regimes and/or for higher phenotypic plasticity of the individual. Adverse environments may also lead to higher genotypic variability at the population level (Hamrick 2004). In addition, considerable genotypic variation may exist at the species level, when populations of the same species are exposed to contrasting environmental conditions within the distribution range. Forestry has long experience in increasing yield by selecting provenances or preferred seed trees with higher growth rate and/or stress tolerance. However, the physiological basis for provenance or genotype differences in stress tolerance is poorly understood.

European beech (*Fagus sylvatica* L.) is an economically important and highly competitive species in Central European woodlands with a wide tolerance of contrasting soil chemical conditions (Leuschner et al. 2006, Ellenberg and Leuschner 2010). One reason for its competitive strength is the high plasticity in biomass partitioning to aboveground and belowground organs (e.g. Puhe 2001, Bolte et al. 2004, 2006). Crown dimensions and fine root system structure and size have been found to vary considerably in dependence on environmental conditions and neighborhood, both in mature stands (Bolte and Villanueva 2006, Meier and Leuschner 2008a, b, Seidel et al. 2011) and at the sapling stage (Löf et al. 2005, Meier and Leuschner 2008c, Hertel et al. 2013).

The distribution range of *F. sylvatica* shows affinity to oceanic and sub-oceanic climates and the species is rare or absent in Central European regions with sub-continental or continental climate where summer precipitation is relatively low (Bohn 2004). According to physiological and dendroecological research, beech responds more sensitively to drought than many other Central European broad-leaved tree species, as is reflected in the vulnerability to cavitation in the conducting system (Cochard et al. 2005, Bréda et al. 2006), pronounced reductions in pre-dawn leaf water potential in dry periods (Aranda et al. 2001, Backes and Leuschner 2000, Köcher et al. 2009), relatively high climate sensitivity of radial growth (Friedrichs et al. 2009, Michelot et al. 2012), recorded growth reductions in response to long-term precipitation decrease (Scharnweber et al. 2011, Zimmermann et al. 2015), increased fine root mortality and turnover at dry sites (Leuschner et al. 2001, Hertel et al. 2013), and pre-senescent leaf shedding and even death in drought periods (Granier et al. 2007, Jump 2006).

Under drought stress, plants have been hypothesized to invest preferentially in belowground organs and not in aboveground structures (optimal partitioning theory; Bloom 1985). This prediction has been confirmed for the beech trees of the precipitation gradient investigated here (Hertel et al. 2013). In a second precipitation gradient in Central Germany, fine root production apparently was stimulated by lower precipitation, but did not suffice for compensating increased fine root mortality. As a consequence, standing fine root biomass decreased from moister to drier stands (Meier and Leuschner 2008b). Leaf biomass was relatively insensitive to precipitation reduction in both gradients (Meier and Leuschner 2008a, Müller-Haubold et al. 2013). In addition to the response to soil water deficits, beech sapling growth was found to be also sensitive to dry air (Lendzion and Leuschner 2008). As a consequence, forest ecologists and foresters are debating on the future of Central European beech forests and the right choice of tree species for forestry under a drier and warmer climate (e.g. Rennenberg et al. 2004, Ammer et al. 2005, Mette et al. 2013).

The drought response of beech and other temperate broad-leaved tree species has been found to vary with genotype or provenance (Gregorius and Kleinschmitt 1999, Schraml and Rennenberg 2002, Rose et al. 2009, Wortemann et al. 2011). Provenances from moist origin responded to drought with higher ABA levels in leaf tissue (Bauerle et al. 2004), reduced photosynthetic rates and leaf stomatal conductance (Tognetti et al. 1997, Bauerle et al. 2003), lower hydraulic conductance (Tognetti et al. 1997), more negative $\delta^{13}C$ signatures in leaf mass (Lauteri et al. 1997), reduced tree growth (Matias et al. 2014), and slower recovery of photosynthetic rate and stomatal conductance upon stress relief (Ngugi et al. 2004). Thus, the right choice of seed material may help foresters to decrease the risk of failure of beech stands in a future drier and warmer climate. Most of the published common garden experiments on beech drought tolerance found better adaptation of drier than moister origins in relevant traits. However, the studies used plant origins from a wide range of climate types within the distribution range (e.g. Garcia-Plazaola and Becerril 2000a, b, Nielsen and Jørgensen 2003, Peuke et al. 2006, Rose et al. 2009), but they did not explicitly test for the influence of precipitation amount at tree origin on the drought response. Thus, any precipitation effect on drought adaptation may have partly or fully been obscured by co-variation in other site factors such as frost exposure, summer warmth and soil conditions. For understanding the drought adaptation potential of beech provenances in a more mechanistic way, a variety of traits characterizing the physiological drought response and plant fitness have to be examined in parallel and the drought intensity at origin must be defined more precisely while controlling for other site factors.

Here, we present the results of a common garden growth trial with five beech populations originating from a well-defined precipitation gradient (816 – 544 mm yr^{-1}) within a region of relatively small size, where other site factors (geology and soil, temperature regime) were relatively uniform. Earlier genetic analyses in beech stands from the region had shown that the different populations (termed provenances hereafter) were relatively closely related to each other. Thus, we expected that population differences in drought response must primarily reflect the outcome of adaptation and/or acclimation to the recent precipitation gradient and not be the result of genetic adaptation to climatic and edaphic factors experienced in the evolutionary past. Saplings were exposed to four levels of soil moisture availability (moist to dry) and nearly 30 physiological (leaf water status, stomatal conductance), leaf and root morphological and growth-related traits were measured.

Study aims were

(i) to examine provenance differences in drought response and to relate the response to precipitation at origin,

(ii) to compare above- and belowground responses to water shortage, and

(iii) to identify physiological and morphological traits with high or low drought sensitivity.

By referring to earlier beech provenance trials, we tested the hypotheses

(i) that provenances from drier climates reduce productivity under water shortage less than provenances from moister climates but are less productive under ample water supply,

(ii) root growth is more drought-sensitive than shoot growth,

(iii) adjustments in leaf conductance and leaf area, which reduce water consumption upon drought, are more pronounced in provenances from moister climates, and

(iv) physiological and morphological modifications suitable to maintain a favorable leaf water status and growth under drought, such as osmotic and cell elastic adjustments, are more pronounced in provenances from drier climates than from moister climates.

This investigation was complemented by a microsatellite marker study on the genetic variation and genetic relatedness of the five populations and an analysis of gene expression patterns under water shortage in the five provenances (Carsjens et al. 2014).

Material and methods

Field sites and investigated plants

We collected tree saplings from five *Fagus sylvatica* L. forests in the center of the species' distribution range in the German federal states Lower Saxony and Saxony-Anhalt (52°22' – 53°10' N, 9°57' – 11°17'E). The stands represent a 130-km-long NW-SE precipitation gradient from the Lüneburg Heath to the Altmark region in the North German Plain located on Pleistocene sandy deposits. Mean annual precipitation (MAP) decreased from the westernmost to the easternmost site from 816 mm yr^{-1} to 544 mm yr^{-1} (increasing continentality of the climate) and the corresponding mean summer precipitation (MGSP, May-Sep) from 352 to 255 mm yr^{-1} (Table 2.1). Study sites were carefully selected to minimize the variability of co-varying factors: all forest stands were comparable with respect to (1) mean annual temperature (mean: 8.7±0.1°C with a tendency for slightly higher temperatures in the eastern, more continental part of the gradient), (2) tree species composition (≥ 90 % cover of beech), (3) aboveground structure (closed canopy without major gaps), (4) tree age (100-130 yrs), and (5) soil chemical conditions (geological substrate: fluvioglacial sandy deposits from the penultimate Ice Age (Saalian), soil types: moderately to highly podzolic Umbrisols).

Table 2.1. Location, mean annual (MAP) and mean growing season precipitation (MGSP, May - September), as well as mean annual (MAT) and mean growing season temperature (MGST) at the five sites where the trees originated. Mean annual climate data are the average of 1971 – 2000 and were derived from weather station data provided by the National Climate Monitoring of Deutscher Wetterdienst (DWD) and were corrected for altitude. Federal states: SA – Saxony-Anhalt, LS – Lower Saxony.

Origin	Site code	Federal state	Latitude (N)	Longitude (E)	Elevation (m. a.s.l)	Precipitation (mm)		Temperature (°C)	
						MAP	MGSP	MAT	MGST
Sellhorn	Se	LS	53°10'	09°57'	130	820	350	8.5	14.6
Unterlüß	Un	LS	52°50'	10°19'	117	770	320	8.5	14.8
Göhrde	Go	LS	53°09'	10°52'	85	670	300	8.7	15.1
Klötze	Kl	SA	52°37'	11°15'	85	610	280	8.9	15.4
Calvörde	Ca	SA	52°22'	11°17'	105	540	260	9.1	15.6

In summer 2011, about 160 *F. sylvatica* saplings were excavated in each stand. The saplings were comparable in plant height (20 cm at most), corresponding to an age of about three years. The forest soil was carefully washed off the roots and the trees were planted individually in 5-L plastic pots filled with coarse unfertilized fluviatile sand (Oppermann, Hedemünden, Germany). The sand was relatively nutrient-rich with a pH (KCl) of 6.2, a C:N ratio of 7.4 mol mol^{-1}, 0.6 µmol P_t g^{-1}, and a base saturation of 99.5%. Thus, we refrained from the addition of fertilizer in the first year of cultivation (2011) and kept all saplings at ample soil moisture. The pots were positioned outdoors in the Experimental Botanical Garden of the University of Göttingen in a randomized set-up with mean air temperatures of ~18/12 °C (day/night) in the summers of 2011 and 2012. During winter 2011 / 12, the pots were transferred to a climate chamber with air temperatures of 4-7 °C and 70-80 % relative air humidity. In April 2012, the plants were moved back into the garden, where they were kept at ample soil moisture until the start of the soil moisture treatment in May (Figure 2.1).

Figure 2.1. Common garden experiment with 600 young beech trees from northwestern Germany in the Experimental Botanical Garden of the University of Göttingen.

Experimental set-up and harvest

We established a three-way factorial growth trial with the factors tree provenance (5 origins), soil moisture (4 levels), and time of the season (3 harvest dates). For all factors, a tenfold replication was established resulting in a total of 600 trees. In May 2012, planting pots were arranged in 10 blocks, with each block consisting of one tree per provenance (5), soil moisture level (4), and time of the season (planned harvests: 3), positioned randomly within the block. The experiment took place under a mobile Plexiglas roof equipped with a rain sensor (Eltako, Fellbach, Germany), which automatically covered the plants when it rained. This allowed controlling the water content of the soil while providing outdoor microclimatic conditions for the saplings. Shading net with a mesh width of 5 mm (Wunderlich, Osterode, Germany) reduced photosynthetically active radiation (PAR) by approximately 70 % which meets the light requirements of 3-yr-old beech saplings in the field (Ellenberg and Leuschner 2010).

The soil water treatment in the experiment began on May 25, 2012, after leaf expansion was completed. The treatment lasted until September 2012, simulating a period of reduced soil moisture of 17 weeks. Four different soil moisture regimes were established which simulate mean summer precipitation (May - September) at the five sites of plant origin: (i) a dry treatment with an equivalent of 160 mm of water added evenly over 17 weeks, resulting in average soil moisture of 2 % v/v SWC, (ii) a moderately dry treatment with 210 mm with average soil moisture of 4 % v/v SWC, (iii) a moderately moist treatment with 260 mm and average soil moisture of 6 % v/v SWC, and (iv) a moist treatment with 310 mm and average soil moisture of 10 % v/v SWC. Soil moisture was monitored every week to a soil depth of 0.16 m (total soil depth of the pots: 0.25 m) with a mobile time domain reflectometry probe (TRIME-FM2, IMKO GmbH, Ettlingen, Germany) in eight pots per treatment. Water loss through evapotranspiration was replaced every second day by dripping the missing amount of water evenly distributed on the soil surface using watering cans of four different sizes.

During the experimental phase from May to September 2012, air temperature in the culture was monitored with HOBO U10 data loggers (Onset, Cape Cod, MA, USA) and iButton Thermocron data loggers (Maxim, San Jose, CA, USA). In this 5-month period, mean air temperature was 17.5/12.0 °C at day/night and soil temperature in the pots was 16.9/11.6 °C at a depth of 0.1 m.

Each plant was treated once before the beginning of the experiment with 150 ml of a biocide solution composed of 0.025 % dimethoate (Perfekthion 40EC, BASF, Ludwigshafen, Germany), 0.04 % fenazaquin (Magister 10EC, Margarita Internacional, Funchal, Portugal) and 0.15 % tebuconazole (Folicur, Bayer AG, Monheim, Germany).

Each plant was fertilized thrice during the growing season with 200 ml of a 0.2 % fertilizer solution (Wuxal P profi NPK (5-20-5), AGLUKON, Düsseldorf, Germany). Each ten plants per provenance and soil moisture level were harvested completely on June 25 (early summer), July 30 (mid-summer) and September 17, 2012 (late summer), i.e. four, nine or sixteen weeks after the beginning of the soil moisture treatment. The sequential harvests allowed monitoring growth processes and the temporal development of plant water status during the 17-wk-long experimental phase.

Root and shoot biomass, and foliar and root surface araes

Tree saplings representing the four soil moisture treatments and five provenances were randomly assigned to the three harvests (n=200 trees per harvest in the 20 categories). At the time of harvest, all leaves were removed from the stem. Trees were carefully extracted from the soil and the shoot was cut off at the root collar. Maximum shoot and tap root length were determined. Leaf area measurements were conducted with a flatbed scanner, the images analyzed with WinFOLIA 2005b software (Régent Instruments Inc., Quebec, QC, Canada) and specific leaf area (SLA; in m^2kg^{-1}) was determined for all leaves of each tree. The roots were sorted according to diameter (fine roots < 2mm, coarse roots > 2mm). Four representative fine root strands were scanned and analyzed for root specific surface area (SRA; in m^2kg^{-1}) with WinRHIZO 2005c software (Régent Instruments Inc.). Afterwards, all fractions were dried (48 h, 70 °C) and weighed. Relative growth rate (RGR, in $g\ g^{-1}\ d^{-1}$) was calculated for both the above- and belowground compartments by subtracting the biomass at the experiment's beginning from the values at harvest and dividing by the experiment's duration.

Plant water relations

During the week before a harvest, i.e. on June 18, July 23, and September 10, 2012, leaf stomatal conductance (g_s) was measured and pressure-volume curves were established for the individuals selected for harvest. Stomatal conductance of the leaves (g_s) was measured with an AP4-UM-3 leaf porometer (Delta-T Devices Ltd., Cambridge, UK) in one terminal sun leaf per sapling at midday (12:00-14:00 solar time) under cloudless sky resulting in 10 replicate measurements per treatment, provenance and harvest date. Pressure-volume (P-V) relations were analyzed for four replicates per provenance, soil moisture treatment and harvest. In the P-V analyses, only four provenances were considered, the two driest and the two moistest origins (excluding the *Go* origin). The stems of the saplings were cut 1 cm above the stem base, re-cut under water and fully hydrated overnight. On the next morning, the stems were cut with a razor blade and weighed for determining fresh weight at full rehydration. Samples were put immediately into a pressure chamber to determine the corresponding leaf water potential (xylem pressure potential; $\Psi_{leaf(max)}$ at RWC = 100). Subsequently, the pressure was increased at steps of 0.3 MPa and the excised sap quantitatively collected with filter paper and weighed at a precision of 10 µg. Afterwards the corresponding xylem pressure potential in the stem segment was recorded. The measurement was finished when the accompanying documentation of the pressure-volume curves (the cumulative water volume expressed as the abscissa, and 1/P, the inverse of the equilibrium pressure as the ordinate) became linear.

Osmotic potential at full turgor (π_0), osmotic potential at the turgor loss point (π_{tlp}), and the relative symplastic water content at the turgor loss point (RWC_{tlp}) were read from the pressure–volume curves. Cell volume was calculated as saturated fresh weight divided by dry weight. The turgor potential at full hydration (Ψ_P) was calculated as the difference between π_0 and $\Psi_{leaf(max)}$, with $\Psi_{leaf(max)}$ being the bulk leaf water potential at full hydration. The bulk modulus of tissue elasticity near full hydration ε (in MPa) was calculated as

$$\varepsilon = \Delta\Psi_P / \Delta RWC_{symp} \qquad [1]$$

according to von Willert et al. (1995) and Bartlett et al. (2012), with $\Delta\Psi_P$ being the turgor loss and ΔRWC_{symp} the corresponding loss of symplastic water on the P-V curve. We took ε as the linear slope of the first four to six points of the pressure-volume curve.

Shifts in π_{tlp} from May to September 2012 within a provenance and treatment were interpreted as osmotic adjustment, shifts in ε as elastic adjustment. We further used the absolute difference in π_{tlp} means and ε means between the moist and dry treatments of a provenance at a given sampling date (denoted as $\Delta\pi_{tlp}$ (moist – dry) or $\Delta\varepsilon$ (moist – dry)) as an alternative measure of the capacity for osmotic or elastic adjustment within a provenance.

As a measure of long-term transpiration reductions, dried leaf samples were ground and analyzed for total C and N concentrations and the $\delta^{13}C$ signature using isotope ratio mass spectroscopy at the Centre for Stable Isotope Research and Analysis (KOSI) of the University of Göttingen.

Statistical analyses

The software SAS 9.3 (SAS Institute, Cary, NC, USA) was used for most statistical analyses. Probability of fit to normal distribution of the data was tested with a Shapiro-Wilk test. Normally distributed data was analyzed by a three-way analysis of variance for unbalanced data sets (general linear model, PROC GLM), treating all effects as fixed effects. A Tukey test was used to test for significant effects of experimental treatment, tree origin, time of season (harvest) and their interactions on structural and physiological properties of the investigated trees. Linear regression analyses were conducted for quantifying the influence of precipitation at tree origin or the amount of added water on the investigated traits. The phenotypic plasticity index PI was calculated as

$$\text{PI} = (\text{maximum median} - \text{minimum median}) / \text{maximum median}$$

(according to Valladares et al. 2006). A Mantel test (software Past 3.x) was used to analyze the relationship between morphological and physiological trait variance (first matrix) and genetic variance (second matrix). The genetic characterization of the provenances with microsatellite markers was adopted from Carsjens et al. (2014). In general, a significance level of $P < 0.05$ was used in the statistical procedures. In several cases, however, marginally significant effects ($0.1 > P > 0.05$) are also reported.

Results

Drought effects on morphological and physiological traits

The water supply during the growing season 2012 (May – September) affected morphology, biomass partitioning, and productivity of the beech saplings more than it affected physiological traits associated with leaf water relations. According to a three-way analysis of variance (general linear model), 10 out of the 16 investigated structural, morphological, and productivity-related traits (i.e. 63 %) were significantly altered by a reduction in water supply from 310 to 160 mm in the moisture manipulation experiment (Table 2.2), while only two of the 11 tested physiological traits were significantly influenced by soil water availability (i.e. 18%; Table 2.3). Water shortage significantly reduced leaf, fine and coarse root mass, and total biomass, as well as total leaf and root surface area, but increased SRA (Table 2.2).

Table 2.2. Significance of the effects of experimental treatment, tree origin, time of season (harvest) and their interaction on the variance of 16 structural parameters according to three-way analyses of variance, because of multiple comparisons *P*-values are adjusted by the Bonferroni correction (significance: *, $P \leq 0.05$; **, $P \leq 0.01$). The phenotypic plasticity index (PI) is also given for each parameter.

Parameter	Treatment	Origin	Time	Treatment x Origin	Treatment x Time	Origin x Time	PI
Number of leaves		**					0.68
Total leaf area (cm²)	*	*	**				0.82
Leaf size (cm²)	**	**	**				0.62
Leaf mass (g)	**		**				0.86
SLA (m^2 kg^{-1})							0.46
Shoot length (cm)		**					0.49
Fine root surface area (cm²)	**		**		**		0.85
Fine root diameter (mm)							0.80
Fine root mass (g)	**		**		**		0.88
SRA (m^2 kg^{-1})	**	**	**				0.68
Coarse root mass (g)	**		**		**		0.89
Total biomass (g)	**		**		**		0.43
Aboveground biomass (g)	**		**				0.66
Belowground biomass (g)	**		**		**		0.43
Fine root / leaf surface area ratio (m^2 m^{-2})						**	0.74
Root : shoot ratio (g g^{-1})						**	0.57

Table 2.3. Significance of the effects of experimental treatment, tree origin, time of season (harvest) and their interaction on the variance of 13 physiological parameters according to three-way analyses of variance, because of multiple comparisons *P*-values are adjusted by the Bonferroni correction (significance: *, $P < 0.05$; **, $P < 0.01$). Treatm. = moisture treatment; tlp = turgor loss point; n.a. = not applicable. The phenotypic plasticity index (PI) according to Valladares et al. (2006) is also given for each parameter.

Parameter	**Treatm.**	**Origin**	**Time**	**Treatm. x Origin**	**Treatm. x Time**	**Origin x Time**	**PI**
Osmotic potential at full hydration π_0 (MPa)			**				0.39
Osmotic potential at tlp π_{tlp} (MPa)			**				0.61
Rel. water content at tlp RWC_{tlp} (%)			**				0.12
Rel. symplastic water content at tlp RWC_{tlp} (%)			**				0.56
Modulus of elasticity ε (MPa)		**	**			*	0.91
Leaf water potential at full hydration $\Psi_{leaf(max)}$ (MPa)		**	**			**	0.98
Cell volume (g g^{-1})					*		0.91
Osmotic adjustment (MPa) $\Delta\pi_{tlp}$ (moist – dry)	n.a.		*	n.a.	n.a.		n.a.
Osmotic adjustment (MPa)$\Delta\pi_{tlp}$ (early – late)			n.a.	***	n.a.	n.a.	0.21
Elastic adjustment (MPa) Δε (moist – dry)	n.a.	**	**	n.a.	n.a.	**	n.a.
Elastic adjustment (MPa) Δε (early – late)		**	n.a.	*	n.a.	n.a.	1.00
Stomatal conductance at noon (mmol m^{-2} s^{-1})	**		**	**	**	**	0.75
$\delta^{13}C$ signature of leaf mass (‰)	**		n.a.		n.a.	n.a.	0.08

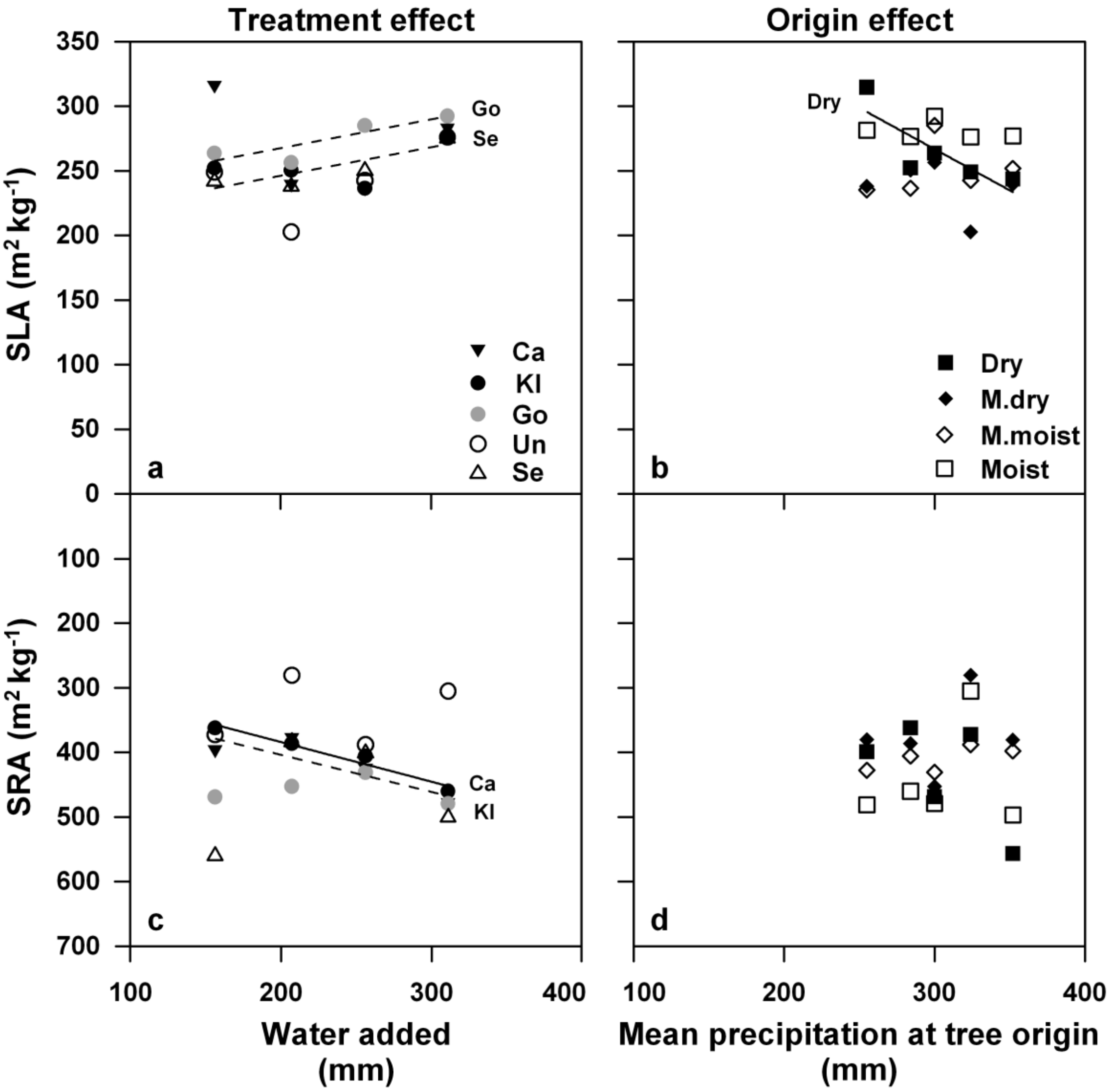

Figure 2.2. (a, b) Specific leaf area (SLA) and (c, d) specific fine root surface area (SRA) in relation to (a, c) the amount of water added during the experimental phase or to (b, d) mean precipitation at tree origin (May to September 1971-2001) (means of 10 beech trees per treatment and origin). Significant ($P < 0.05$) and marginally significant ($P < 0.1$) relationships are indicated by continuous and dashed lines, respectively. Tree provenances: *Se* = Sellhorn, *Un* = Unterlüß, *Go* = Göhrde, *Kl* = Klötze, *Ca* = Calvörde. Dry treatment: 160 mm, moderately dry treatment: 210 mm, moderately moist treatment: 260 mm, and moist treatment: 310 mm of water added between May and September 2012. Note different ordinate scaling for SLA and SRA. For parameters of linear regression equations see Table A. 2.1 in the Appendix.

Comparing soil moisture effects among the five provenances shows that SRA increased with decreasing soil moisture in the *Kl* provenance (significant) and in the *Ca* provenance (marginally significant), but not in the others (Figure 2.2c). In late summer, aboveground and belowground biomass decreased with decreasing soil moisture in the *Se* and *Kl* provenances (significant) as well as in the *Go* and *Ca* provenances (marginally significant; Figure 2.3). Belowground biomass exceeded aboveground biomass in all treatments. However, fine root surface : leaf area ratio increased with the amount of water added (significant in the *Kl* provenance; Figure A. 2.1) indicating that root growth was more sensitive to water shortage than shoot growth.

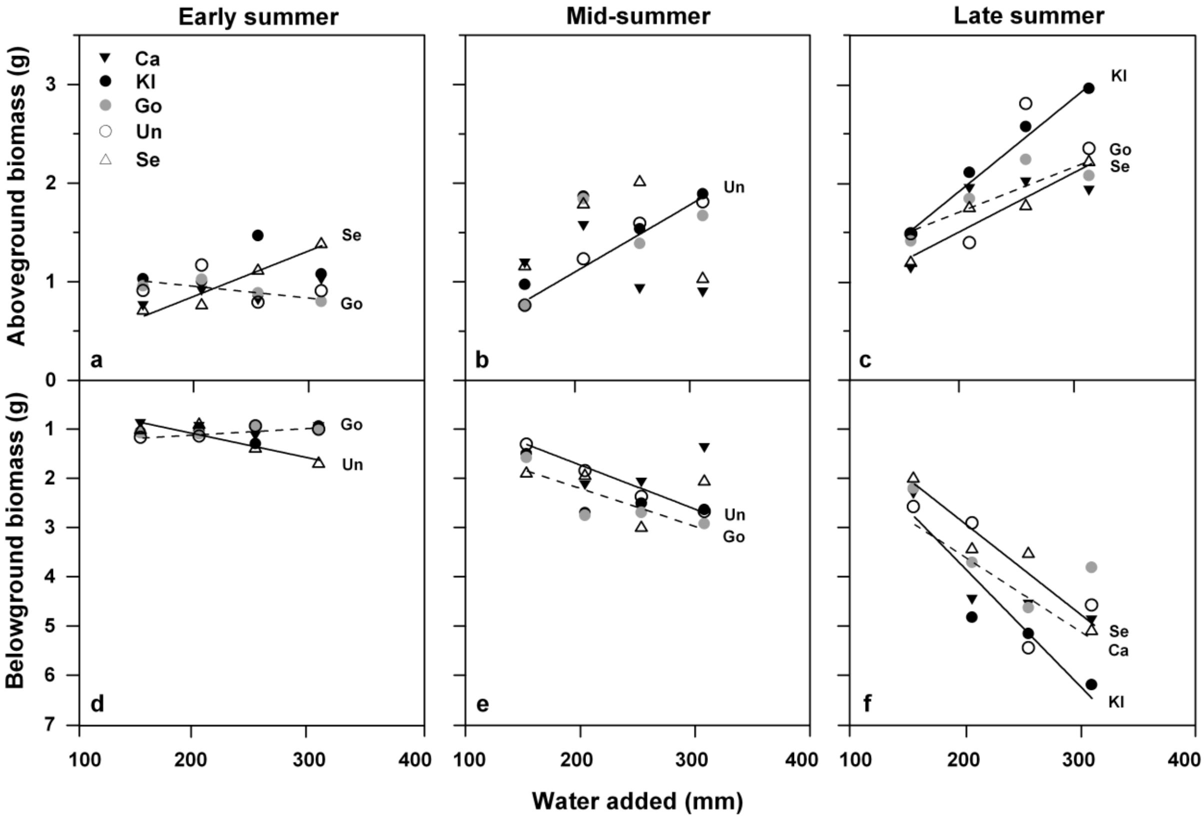

Figure 2.3. (a-c) Aboveground (leaves, shoot) and (d-f) belowground (fine roots, coarse roots) biomass in (a, d) early, (b, e) mid and (c, f) late summer 2012 in relation to the amount of added water during the experimental phase from May to September (means of 10 beech trees per treatment and origin). Significant and marginally significant relationships are indicated by continuous and dashed lines, respectively. Note different ordinate scaling for aboveground and belowground biomass. For tree provenances see Figure 2.2. For parameters of linear regression equations see Table A. 2.1 in the Appendix.

Surprisingly, none of the pressure-volume curve parameters (Ψ_P, π_0, π_{tlp}, RWC_{tlp}, ε) was influenced by the soil moisture treatment (Table 2.3), even though the reduction in water supply from 310 to 160 mm significantly reduced above- and belowground biomass (Figure 2.3). Invariance in the leaf water status parameters contrasted with decreases in stomatal conductance (significant or marginally significant in some provenances; Figure 2.4a) and increases in foliar $\delta^{13}C$ (significant in all provenances; Figure 2.4c) from the moist to the dry treatment.

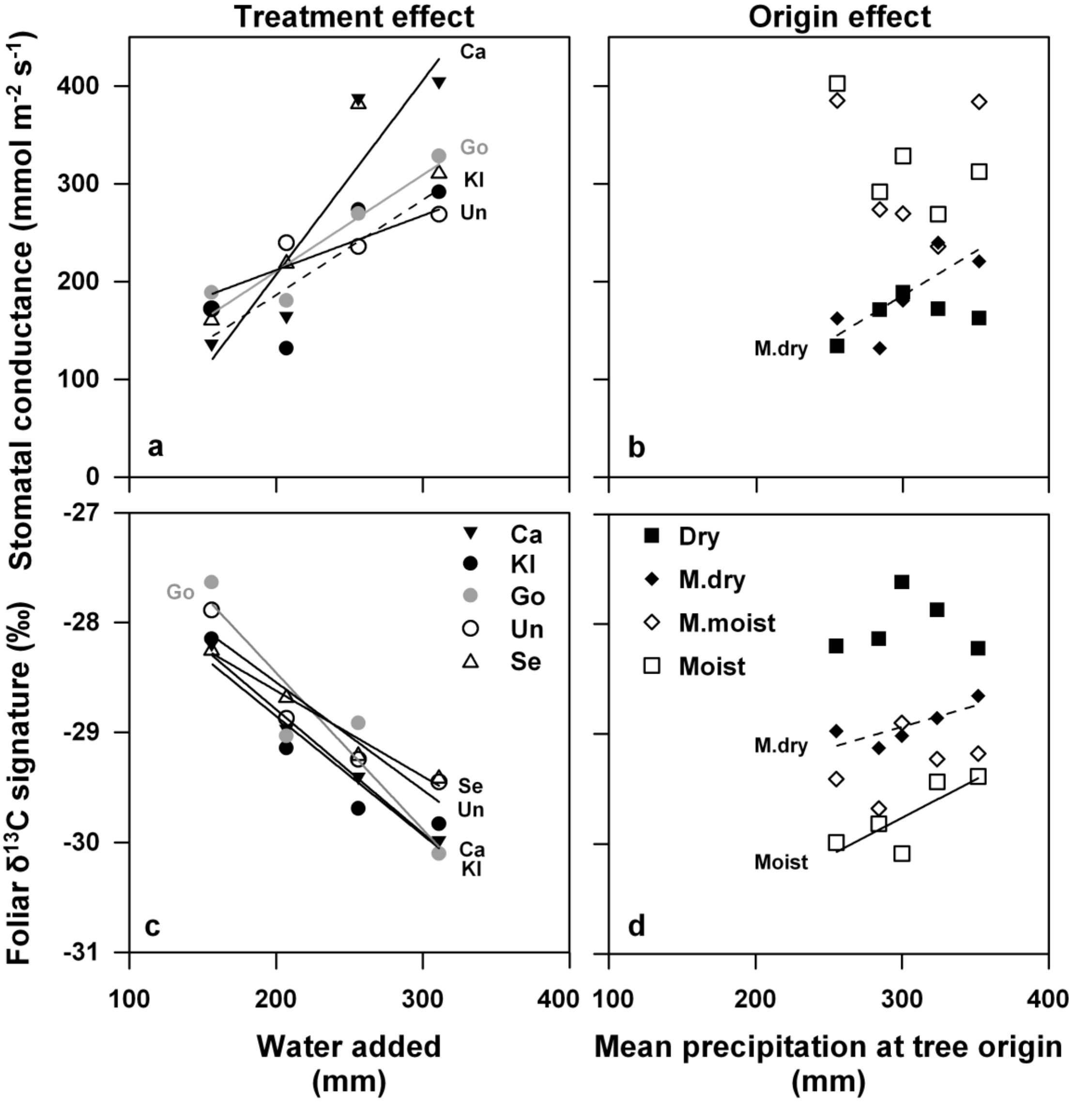

Figure 2.4. Relationship between (a, b) foliar $\delta^{13}C$ signature or (c, d) stomatal conductance at noon in late summer 2012 and (a, c) the amount of water added during May to September or (b, d) mean precipitation at tree origin (May to September 1971-2001) (means of 8 beech trees per treatment and origin for $\delta^{13}C$, or of 20 trees per treatment and origin for stomatal conductance). Significant and marginally significant relationships are indicated by continuous and dashed lines, respectively. For parameters of linear regression equations see Table A. 2.1 in the Appendix.

As expected, most (19 out of 26; i.e. 73%) of the studied morphological and physiological traits were significantly influenced by time, i.e. varied between the three harvest dates in June, July, and September. The seasonal variation in the traits added to the variation caused by the moisture treatment; the overall trait variation is reflected by the phenotypic plasticity index PI. Leaf and fine root mass and the related surface areas were the most plastic structural traits (PI: 0.82-0.89; Table 2.2), while SLA and SRA behaved more conservatively (0.46 and 0.68, respectively) as did root : shoot mass ratio (0.57) and total biomass (0.43). Interestingly, the plasticity of total aboveground biomass (0.66) was greater than that of total belowground biomass (0.43). Among the physiological parameters, highest PI indices were found for the leaf water potential at full hydration, cell volume, cell wall elastic modulus ε, and elastic adjustment $\Delta\varepsilon$ (0.91-1.0), intermediate values for stomatal conductance at noon (0.75) and π_{tlp} (0.61), and low values (< 0.4) for RWC_{tlp}, osmotic adjustment $\Delta\pi_{tlp}$ (early – late), and π_0 (Table 2.3).

Provenance effects on the drought response

Genotypic variation, i.e. the genetic differences between the five provenances, influenced a smaller number of structural, morphological or productivity-related traits (5 of 16 traits; i.e. 31%) than the moisture treatment (Table 2.2). We observed highly significant genotype effects on the number and size of leaves, total leaf area, shoot length, and SRA. Leaf size increased in the dry, moderately dry, and moist treatments with decreasing precipitation at origin, i.e. the provenances from the drier climates formed larger leaves than the moister provenances when exposed to water shortage (Figure 2.5b; significant in the moderately dry treatment, marginally significant in the dry and moist treatment).

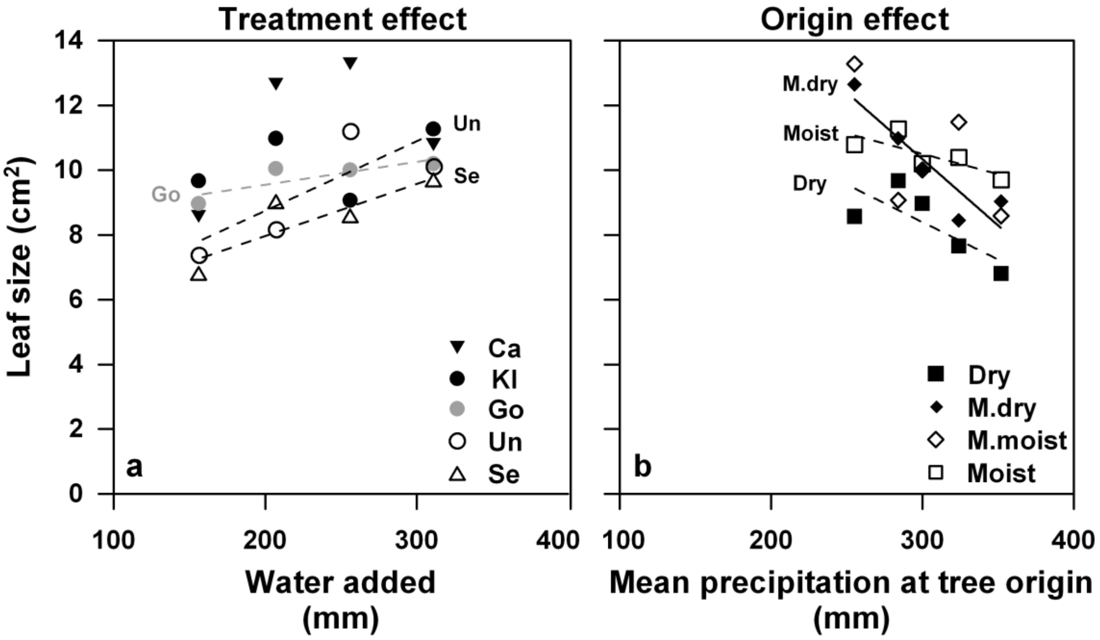

Figure 2.5. Leaf size in relation to (a) the amount of water added during the experimental phase, or to (b) mean precipitation at tree origin (May to September 1971-2001) (means of 10 beech trees per treatment and origin). Significant and marginally significant relationships are indicated by continuous and dashed lines, respectively. For tree provenances and treatment details see Figure 2.2. For parameters of linear regression equations see Table A. 2.1 in the Appendix.

In contrast, SLA was independent from provenance in the three-way ANOVA (even though SLA decreased significantly with increasing precipitation at tree origin in the dry treatment according to the regression analysis; Figure 2.2b). Similarly, there was no genotype effect on aboveground, belowground, and total biomass, even though aboveground biomass increased in the moderately moist treatment with decreasing precipitation at the origin in mid-summer (see Figure A. 2.2 in the Appendix). Provenance had no effect on root : leaf area (see Figure A. 2.1 in the Appendix) or root : shoot mass ratios.

Four of the 13 physiological parameters (cell wall elastic modulus ε, $\Delta\varepsilon$ (moist – dry), $\Delta\varepsilon$ (early – late), and leaf water potential at full hydration $\Psi_{leaf(max)}$) showed a significant influence of genotype in the analyses of variance (equaling 31% of the traits; Table 2.3), which is a stronger influence than exerted by the soil moisture treatment (two out of 11 physiological parameters; i.e. 18%). $\delta^{13}C$ tended to decrease from the moister to the drier provenances (more negative values in the latter; significant in the moist treatment, marginally significant in the moderately dry treatment; Figure 2.4d), while midday stomatal conductance measured in September did not differ significantly among the provenances (Figure 2.4b).

The turgor potential at full hydration Ψ_P was similar in all treatments and origins during early (1.3 to 1.9 MPa) and mid-summer (1.7 to 2.1 MPa; see Figure A. 2.3 in the Appendix). Towards the end of summer, Ψ_P remained low in trees originating from drier climates (*Kl*, *Ca*) (1.7 - 2.2 MPa) and increased in trees originating from moist climates (*Se*, *Un*) (3.1-5.1 MPa). No consistent genotype effect on osmotic adjustment was detected at the leaf level (measured either as temporal shift in π_{tlp} or as π_{tlp} difference between moist and dry treatments; Figures 2.5b and A. 2.4 in the Appendix), while the moisture treatment effect was significant in the analyses of variance (Table 2.3). Only in the moderately moist treatment, $\Delta\pi_{tlp}$ (early – late) decreased significantly with decreasing precipitation at tree origin, while it increased in the moderately dry treatment (marginally significant; Figure 2.6b).

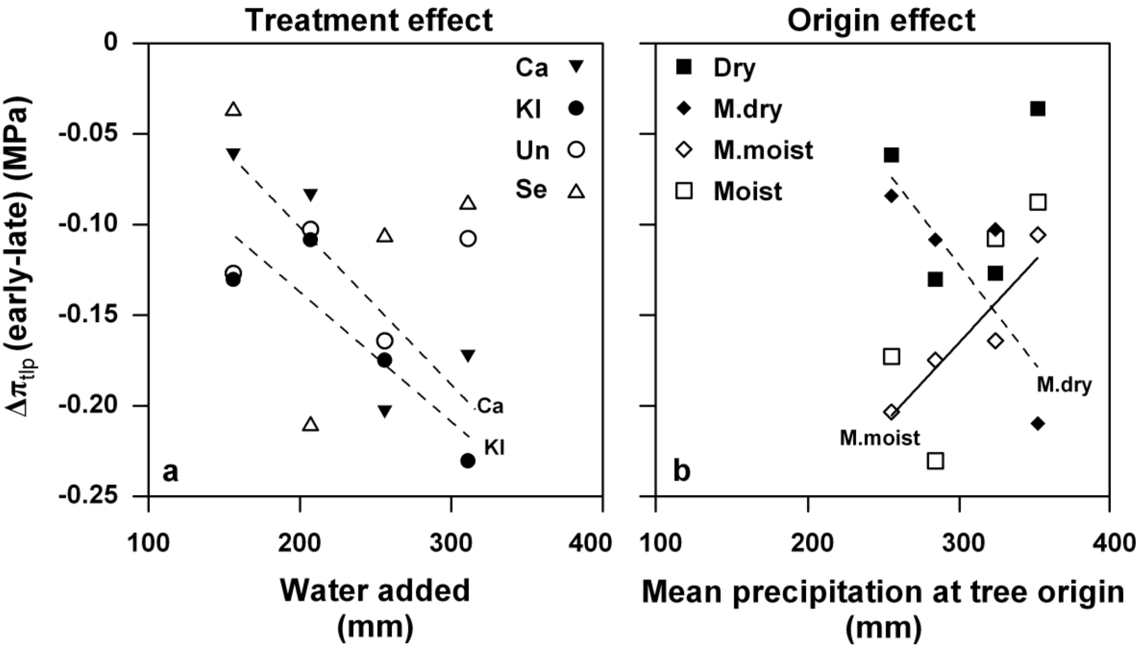

Figure 2.6. Osmotic adjustment from May to September 2012 in the shoots in relation to (a) the amount of water added during May to September or to (b) mean precipitation at tree origin (May to September 1971-2001). Significant and marginally significant relationships are indicated by continuous and dashed lines, respectively. For tree provenances and treatment details see Figure 2.2. For parameters of linear regression equations see Table A. 2.1 in the Appendix.

Early in summer (May and July), the modulus of cell wall elasticity ε remained fairly stable (7 – 12 MPa) and was similar among the provenances (see Figure A. 2.5a, b in the Appendix). Late in summer, the one-way linear regression showed – in agreement with the three-way analyses of variance - that ε was significantly higher in the moister provenances *Se* and *Un* in late summer (11.3 – 20.7 MPa) than in the drier provenances *Kl* and *Ca* (6.7 – 13.0 MPa) (Figures 2.6a and A. 2.5c in the Appendix). The effect of soil moisture treatment on ε was only significant in the *Se* provenance. Similarly, elastic adjustment Δε was significantly influenced by genotype in the three-way analyses of variance, but not influenced by the soil moisture treatment (Table 2.3). Elastic adjustment measured as temporal shift (Δε (early-late)) was significantly larger in the moister provenances *Se* and *Un* (0.27 - 10.29 MPa) than in the drier provenances *Kl* and *Ca* (-4.31 - 1.59 MPa) (Figure A. 2.6a in the Appendix) and decreased with decreasing precipitation at tree origin (Figure A. 2.6b in the Appendix). Elastic adjustment measured as the difference between moist and dry treatment (Δε (moist-dry)) increased in early summer with increasing precipitation at tree origin, but showed no consistent trend in mid and late summer (Figure A. 2.7 in the Appendix). Yet, the results of the Mantel test (*cf.* Table A. 2.2 in the Appendix) revealed no relationship between the genetic variation between provenances based on microsatellite markers and the variation in elastic adjustment.

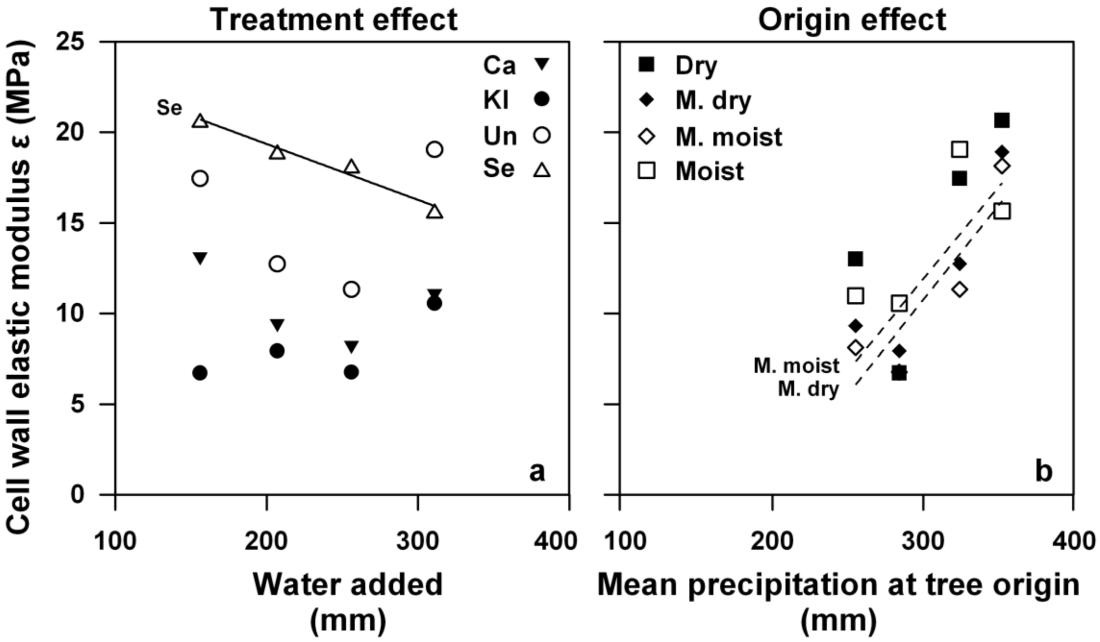

Figure 2.7. Modulus of elasticity of cell walls in late summer in relation to (a) the amount of water added during the experimental phase, or to (b) mean precipitation at tree origin (May to September 1971-2001) (means of 4 beech trees per treatment and origin). Significant and marginally significant relationships are indicated by continuous and dashed lines, respectively. For parameters of linear regression equations see Table A. 2.1.

Discussion

Provenance effects on physiological drought response

A main finding of this study is that provenance and thus precipitation at origin had a larger effect on leaf water status than the moisture treatment itself, even though the plants in the dry treatment received only half the water supply of the moist treatment. We detected a strong provenance effect for tissue elasticity (ε) and the extent of elastic adjustment (Δε) but not for parameters characterizing cellular osmotic relations and leaf conductance. As expected, stomatal conductance (measured at noon on the days before harvest) was increasingly reduced from the moist (310 mm water added) to the dry treatment (160 mm), corresponding to a significant increase in foliar $\delta^{13}C$, but such sensitive stomatal control of transpiration in the drier treatments was observed in all provenances irrespective of precipitation at origin. We obtained no evidence in support of our hypothesis (3) that the plants from moist origins reduced their leaf conductance under water shortage to a greater extent than plants from dry origins.

The pressure-volume curve analyses in June, July and September revealed that the concentration of osmolytes in the cytosol was remarkably invariant over time. Moreover, it differed barely with moisture treatment and provenance. Osmotic adjustment in response to water shortage, i.e. the active net accumulation of osmotic substances in the cell sap of leaf tissue, was observed in none of the treatments and provenances at relevant intensities: π_{tlp} dropped (more negative values) by not more than 0.25 MPa from June to September in any of the beech plants, and it differed by less than 0.15 MPa between the driest and the corresponding moistest treatment. Drought-exposed *Betula pendula* saplings achieved by 0.7 MPa lower (more negative) π_{tlp} values than plants in moist soil, and the extent of osmotic adjustment differed largely between genotypes (Aspelmeier and Leuschner 2004). Seasonal osmotic adjustment was even larger in other temperate broad-leaved trees (e.g. European *Acer* species), for which π_{tlp} drops by up to 3 MPa were observed (Alder et al. 1996). Lack of significant osmotic adjustment in desiccated *F. sylvatica* plants has been reported earlier from both mature trees (Aranda et al. 1996, Schipka 2002) and saplings (Lendzion and Leuschner 2008). The apparently low capability for osmotic adjustment in beech contrasts with the observation of pronounced elastic adjustment in the plants from moist origins (provenances Sellhorn and Unterlüß) and the significant genotypic variation in ε. In the Sellhorn and Unterlüss plants, ε increased by 3 to 10 MPa between July and September, i.e. the cell walls of the leaf tissue stiffened with proceeding drought. In these provenances, water loss results in larger drops of leaf water potential and turgor than in plants from drier origin. This modification may be helpful for securing water absorption from desiccating soil, but at the same time it increases the risk for cavitation. Thus, the beech saplings from the moister provenances may face a higher risk of hydraulic failure due to more rigid cell walls in leaf tissue than plants from drier origins when exposed to similar levels of water shortage.

Our findings seem to contradict Bartlett et al. (2012) who concluded from a theoretical consideration of plant water relations that plants should adapt to water shortage mainly through modification of π_{tlp} while adaptations of cell wall elastic properties play only an indirect role. Our findings are not in agreement with this assumption because none of the leaf water status parameters (π_0, π_{tlp}, RWC_{tlp}, cell volume) except elastic adjustment was influenced by the large experimental reduction in water supply and soil moisture. This seems to indicate that the adjustment of cell wall elastic properties is of higher relevance for the drought adaptation strategy of beech than modifications in π_{tlp}.

Provenance and treatment effects on plant morphology and growth

Surprisingly, provenance had only a weak and non-consistent influence on the morphology and growth of the beech saplings despite some genotype differences in physiology. From the results of published growth trials with different beech provenances (e.g. Peuke et al. 2002, Meier and Leuschner 2008c, Rose et al. 2009, Robson et al. 2012), we had expected that the drier provenances would develop specific morphological and physiological adaptations and a superior growth performance in the drier treatments as compared to the moister provenances. In our experiment, neither productivity nor total leaf area, SLA and SRA were significantly smaller in the drier than in the moister provenances in a given moisture treatment, as one would expect as an adaptive response to increase drought resistance. The only exception was leaf size in the moderately dry treatment with the largest leaves produced by the provenances from drier climates. This may point at an adaptive response of leaf growth to drought experienced in the past, resulting in better maintenance of leaf growth under conditions of water shortage. However, total plant leaf area and productivity apparently did not profit from this response. Saplings originating from drier climates did not develop deeper roots or a higher fine root biomass than provenances from moister climates.

Even more astonishing is that neither aboveground nor belowground productivity differed consistently among the provenances from dry or moist origin. This suggests that, in the more drought-exposed beech populations, no selection for traits promoting sapling growth under dry conditions has occurred in our study region. In fact, we found a significant increase in aboveground RGR from the driest to the moistest provenance in the dry treatment, and not a decrease (data not shown). This seems to conflict with results of an accompanying study on the expression of seven genes for abscisic acid (ABA)-related drought signaling in the same plants (Carsjens et al. 2014). The transcript levels of four genes (superoxide dismutase SOD, aldehyde dehydrogenase ALDH, glutamine amidotransferase GAT, and a gene encoding for proteins associated with the early response to dehydration ERD) were related to the precipitation amount at the origin of the beech populations, suggesting that physiological drought stress-compensating mechanisms differed among the populations and were apparently subject to climate selection. Our results on growth rate and morphology do not reflect these population differences in transcript levels indicating that intra-specific differences in the constitutive expression of the four genes must only be of secondary importance for maintaining growth under drought in beech saplings.

Our results on lacking growth differentiation also contradict several earlier reports about pronounced growth differences between different *F. sylvatica* provenances (e.g., Tognetti et al. 1995, Schraml and Rennenberg 2000, Meier and Leuschner 2008c, Rose et al. 2009). We can only speculate why the growth rate of the beech saplings was so invariant across the 130-km-long precipitation gradient in our study. First, the genetic characterization of the five *F. sylvatica* populations through nine highly polymorphic microsatellite markers revealed only small genetic differences at the population level for the adult trees (Carsjens et al. 2014). Accordingly, the genetic distance after Nei (1972) was in the range of 0.017 - 0.053 for any pair of the five populations and thus only small (see Table A. 2.3 in the Appendix). In fact, more than 97 % of the genetic variation was detected within the populations and less than 3 % was contributed by genetic differences between populations according to an AMOVA (Carsjens et al. 2014). Genetic differentiation between European beech stands has generally been found to be low, whereas genetic variation within autochthonous populations is high (Comps et al. 1990, Konnert 1995, Belletti and Lanteri 1996, Wang 2003, Meier and Leuschner 2008c). Even on a cross-continental scale, genetic differences in *F. sylvatica* were found to be located mainly within stands and not between them (Buiteveld et al. 2007). This may partly be a result of the dramatic shrinkage of the *F. sylvatica* distribution range during the last glaciation (Comps et al. 2001) and subsequent founding events (Hewitt 2000), which must have reduced the differentiation between provenances and stands. Despite the impoverishment of the beech gene pool, limited gene flow has promoted local genetic differentiation in recent time (Cuguen et al. 1988, Müller-Stark 1996, Wang 2001). Nevertheless, such local genetic differences between beech populations have been decreased by foresters through the distribution of preferred seed material over long distances. This may explain why Nei’s genetic distance was much smaller between the most distant populations Sellhorn and Calvörde (0.025; 130 km distance) than between the Sellhorn and nearby Unterlüß populations (0.050; 40 km). It should be noted, however that Carsjens et al. (2014) used neutral markers and not adaptive genes; the latter are under higher selection pressures and thus might better reflect any genetic differentiation between forest stands along a precipitation gradient. In addition, provenance studies with beech saplings or seeds collected in the forest (as done in our study and elsewhere) lead to considerable genetic variation at the sample level, which may hinder the detection of provenance differences in trait means. In a species with low differentiation between populations as in *F. sylvatica*, this problem may be more serious than in other tree species with higher genetic variation on the regional scale.

A second possible explanation for the small growth differentiation among the investigated provenances relates to the selection of the provenances. The environmental gradient covered by the five provenances was comparably short (precipitation difference: 280 mm yr^{-1}, only minor temperature and soil differences) since our study aim was to restrict environmental variation mostly to precipitation. This contrasts with most other common garden growth trials, where the provenances represented much longer precipitation, temperature, and soil chemical gradients. It is possible that marked provenance differences in growth rate and drought tolerance do only manifest when longer precipitation (and drought intensity) gradients are covered. It could be that the growth differences reported from other common garden studies are only in part resulting from precipitation differences at the origin, while differences in temperature and soil nutrient availability are acting as significant co-varying factors in these studies. The higher the variability of these co-varying factors, the more difficult it is to disentangle precipitation effects from effects of other influential factors.

A third possible explanation for the small growth differentiation among our provenances is that additional long-term structural drought responses of beech saplings develop only with longer duration of the experiment. This should be at the attention of future research. In pronounced contrast to the minor provenance differences, the moisture treatment significantly affected leaf area, SRA and growth (but not SLA). This result corroborates earlier reports about high phenotypic plasticity in the morphology and growth of beech saplings in the aboveground (e.g. Valladares et al. 2002) or belowground compartment (Meier and Leuschner 2008c). As in several other studies with *F. sylvatica* saplings (Fotelli et al. 2001, Löf et al. 2005, Rose et al. 2009), increasing drought reduced root growth more than shoot growth in our study which resulted in a large decrease of root : shoot ratio. The greater importance of phenotypic plasticity in root than shoot growth of beech saplings may be explained by the greater spatial and temporal heterogeneity of the soil environment. However, our results contrast with biomass inventories in the mature stands along our precipitation gradient, where an increase in the root : shoot ratio with decreasing precipitation and soil moisture was observed (Hertel et al. 2013). This discrepancy might be caused by different allocation priorities and carbohydrate reserves of juvenile and mature trees.

Conclusions

Our growth trial with examination of nearly 30 morphological, physiological and growth-related parameters indicates that *F. sylvatica* saplings occurring in a limited region of the northern German lowlands seem to have achieved only a limited number of specific drought adaptations when exposed to low summer rainfall (<600 mm yr^{-1}). Small genetic differences between the populations of this region, high within-population genetic variation, a relatively small environmental gradient, and a rather short presence of *F. sylvatica* in the region (since only 4-5 kya, i.e., since not more than 30-40 tree generations; Magri et al. 2006) may all have contributed to this unexpected result. Nevertheless, high phenotypic plasticity in terms of biomass partitioning and leaf and root system morphology is apparently a key strategy of beech saplings to cope with water shortage, irrespective of the drought intensity that has been experienced at the origin. With respect to sapling survival under a future warmer and drier climate, our results seem to indicate no clear advantage of selecting provenances in this study region which experienced drought in the past, because their saplings may not perform better than other provenances, at least in the short term. Genotypes from more distant regions such as southern Europe may be more drought resistant (e.g. Nielsen and Jørgensen 2003, Thiel et al. 2014), but they could possess other adaptations that are disadvantageous under a Central European climate. In any case, it has to be considered that mature trees likely are differing from juveniles in their drought adaptation; thus, corresponding studies with mature trees are needed. The separation of adaptive from non-heritable modifying drought responses would require common garden experiments with mature trees which have rarely been conducted so far.

Acknowledgments

We thank Regina Helbig and Gabi Kuchenbuch for plant nurture, Heiko Eichner for help in constructing the experimental set-up and Jutta Czernitzki, Irmgard Gerstmann, Ute Nüsse-Hahne, and Ute Schlonsog for excellent technical assistance. We are grateful to Dietrich Hertel, Hilmar Müller-Haubold and Julia Juchheim for valuable comments. This work was supported by grants provided by the Ministry for Science and Culture of Lower Saxony (Germany) in the context of the program "Klimafolgenforschung in Niedersachsen" (KLIFF).

Conflict of interest

None declared.

References

Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. *Science*, **294**, 321-326.

Alder N, Sperry J, Pockman W (1996) Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia*, **105**, 293-301.

Ammer C, Albrecht L, Borchert H, Brosinger F, Dittmar C, Elling W, Ewald J, Felbermayer B, Gilsa VH, Huss J, Kenk J, Kölling C, Kohnle U, Meyer P, Mosandl R, Moosmayer HU, Palmer S, Reif A, Refuss KE, Stimm B (2005) Zur Zukunft der Buche (*Fagus sylvatica* L.) in Mitteleuropa–kritische Anmerkungen zu einem Beitrag von Rennenberg et al. (2004) *Allgemeine Forst und Jagdzeitung*, **176**, 60-67.

Aranda I, Gil L, Pardos J (1996) Seasonal water relations of three broadleaved species (*Fagus sylvatica* L., *Quercus petraea* (Mattuschka) Liebl. and *Quercus pyrenaica* Willd.) in a mixed stand in the centre of the Iberian Peninsula. *Forest Ecology and Management*, **84**, 219-229.

Aranda I, Gil L, Pardos J (2001) Effects of thinning in a *Pinus sylvestris* L. stand on foliar water relations of *Fagus sylvatica* L. seedlings planted within the pinewood. *Trees – Structure and Function*, **15**, 358-364.

Aspelmeier S, Leuschner C (2004) Genotypic variation in drought response of silver birch (*Betula pendula*): leaf water status and carbon gain. *Tree Physiology*, **24**, 517-528.

Backes K, Leuschner C (2000) Leaf water relations of competitive *Fagus sylvatica* and *Quercus petraea* trees during 4 years differing in soil drought. *Canadian Journal of Forest Research*, **30**, 335-346.

Bartlett MK, Scoffoni C, Sack L (2012) The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters*, **15**, 393-405.

Bauerle WL, Whitlow TH, Setter TL, Bauerle TL, Vermeylen FM (2003) Ecophysiology of *Acer rubrum* seedlings from contrasting hydrologic habitats: growth, gas exchange, tissue water relations, abscisic acid and carbon isotope discrimination. *Tree Physiololgy*, **23**, 841-850.

Bauerle WL, Whitlow TH, Setter TL, Vermeylen FM (2004) Abscisic acid synthesis in *Acer rubrum* L. leaves - A vapor-pressure-deficit-mediated response. *Journal of the American Society for Horticultural Science*, **129**, 182-187.

Beck W, Heußner KU (2012) Increased sensitivity in ring width series of common beech after 1990 – climatic impact or normal patterns due to ageing ? *Dendrosymposium*, **10**, 13–19.

Belletti P, Lanteri S (1996) Allozyme variation among European beech (*Fagus sylvatica* L.) stands in Piedmont, north-western Italy. *Silvae Genetica*, **45**, 33-37.

Belli R, Frisia S, Borsato A, Drysdale R, Hellstrom J, Zhao JX, Spotl C (2013) Regional climate variability and ecosystem responses to the last deglaciation in the northern hemisphere from stable isotope data and calcite fabrics in two northern Adriatic stalagmites. *Quaternary Science Reviews*, **72**, 146-158.

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363-392.

Bohn U (2004) Karte der natürlichen Vegetation Europas. Map of the Natural Vegetation of Europe. Landesamt für Umweltschutz Sachsen-Anhalt, Halle.

Bolte A, Czajkowski T, Kompa T (2007) The north-eastern distribution range of European beech - a review. *Forestry*, **80**, 413-429.

Bolte A, Rahmann T, Kuhr M, Pogoda P, Murach D, Gadow KV (2004) Relationships between tree dimension and coarse root biomass in mixed stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst.). *Plant and Soil*, **264**, 1-11.

Bolte A, Villanueva I (2006) Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.). *European Journal of Forest Research*, **125**, 15-26.

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625-644.

Buiteveld J, Vendramin GG, Leonardi S, Kamer K, Geburek T (2007) Genetic diversity and differentiation in European beech (*Fagus sylvatica* L.) stands varying in management history. *Forest Ecology and Management*, **247**, 98-106.

Carsjens C, Ngoc QN, Guzy J, Knutzen F, Meier IC, Müller M, Finkeldey R, Leuschner C, Polle A (2014) Intra-specific variations of the expression of stress-related genes in beech progenies are stronger than drought-induced responses. *Tree Physiology*, **34**, 1348-1361.

Cochard H, Coste S, Chanson B, Guehl JM, Nicolini E (2005) Hydraulic architecture correlates with bud organogenesis and primary shoot growth in beech (*Fagus sylvatica*). *Tree Physiology*, **25**, 1545-1552.

Comps B, Thiebaut B, Paule L, Merzeau D, Letouzey J (1990) Allozymic variability in beechwoods (*Fagus sylvatica* L.) over Central Europe: spatial differentiation among and within populations. *Heredity*, **65**, 407-417.

Cuguen J, Merzeau D, Thiebaut B (1988) Genetic structure of the European beech stands (*Fagus sylvatica* L.): F-statistics and importance of mating system characteristics in their evolution. *Heredity*, **60**, 91-100.

Dewitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends Ecology Evolution*, **13**, 77-81.

Dudley SA, Schmit J (1996) Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *The American Naturalist*, **147**, 445-465.

Ellenberg H, Leuschner C (2010): Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht. 6th edn. Ulmer UTB, Stuttgart.

Fotelli MN, Geßler A, Peuke AD, Rennenberg H (2001) Drought affects the competitive interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*: responses of growth, water status and δ^{13}C composition. *New Phytologist*, **151**, 427-435.

Friedrichs DA, Trouet V, Büntgen U, Frank DC, Esper J, Neuwirth B, Löffler J (2009) Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees - Structure and Function*, **23**, 729-739.

García-Plazaola JI, Becerril JM (2000a) Photoprotection mechanisms in European beech (*Fagus sylvatica* L.) seedlings from diverse climatic origins. *Trees - Structure and Function*, **14,** 339-343.

García-Plazaola JI, Becerril JM (2000b) Effects of drought on photoprotective mechanisms in European beech (*Fagus sylvatica* L.) seedlings from different provenances. *Trees - Structure and Function,* **14**, 485-490.

Granier A, Reichstein M, Bréda N, Janssens IA, Falge E, Ciais P, Grünwald T, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Facini O, Grassi G, Heinesch B, Ilvesniemi H, Keronen P, Knohl A, Köstner B, Lagergren F, Lindroth A, Longdoz B, Loustau D, Mateus J, Montagnani L, Nys C, Moors E, Papale D, Peiffer M, Pilegaard K, Pita G, Pumpanen J, Rambal S, Rebmann C, Rodrigues A, Seufert G, Tenhunen J, Vesala T, Wang Q (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology,* **143**, 123-145.

Gregorius H, Kleinschmit J (1999) The environmental dichotomy of adaptation and the role of genetic diversity. *Silvae Genetica,* **48**, 193-199.

Haberlandt U, Belli A, Hölscher J (2010) Trends in beobachteten Zeitreihen von Temperatur und Niederschlag in Niedersachsen. *Hydrologie Und Wasserbewirtschaftung*, **54**, 28-36.

Hamrick J (2004) Response of forest trees to global environmental changes. *Forest Ecology and Management*, **197**, 323-335.

Hertel D, Strecker T, Müller-Haubold H, Leuschner C (2013) Fine root biomass and dynamics in beech forests across a precipitation gradient - is optimal resource partitioning theory applicable to water-limited mature trees? *Journal of Ecology*, **101**, 1183-1200.

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907-913.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University press, Cambridge. 1535 pp.

Jacob D, Petersen J, Eggert B, Alias A, Christensen OB, Bouwer LM, Braun A, Colette A, Déqué M, Georgievski G, Georgopoulou E, Gobiet A, Menut L, Nikulin G, Haensler A, Hempelmann N, Jones C, Keuler K, Kovats S, Kröner N, Kotlarski S, Kriegsmann A, Martin E, Meijgaard E, Moseley C, Pfeifer S, Preuschmann S, Radermacher C, Radtke K, Rechid D, Rounsevell M, Samuelsson P, Somot S, Soussana J-F, Teichmann C, Valentini R, Vautard R, Weber B, Yiou P (2013) EURO-CORDEX: new high-resolution climate change projections for European impact research. *Regional Environmental Change*, **14**, 563-578.

Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163-2174.

Köcher P, Gebauer T, Hornbach V, Leuschner C (2009) Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies. *Annals of Forest Science,* **66**, 101.

Konnert M (1995) Investigations on the genetic variation of beech (*Fagus sylvatica* L.) in Bavaria. *Silvae Genetica*, **44**, 346-351.

Lauteri M, Scartazza A, Guido MC, Brugnoli E (1997) Genetic variation in photosynthetic capacity, carbon isotope discrimination and mesophyll conductance in provenances of *Castanea sativa* adapted to different environments. *Functional Ecology*, **11**, 675-683.

Lendzion J, Leuschner C (2008) Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits. *Forest Ecology and Management*, **256**, 648-655.

Leuschner C, Meier IC, Hertel D (2006) On the niche breadth of *Fagus sylvatica*: soil nutrient status in 50 Central European beech stands on a broad range of bedrock types. *Annals of Forest Science*, **63**, 355-368.

Leuschner C, Backes K, Hertel D, Schipka F, Schmidt U, Terborg O, Runge M (2001) Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and

Quercus petraea (Matt.) Liebl. trees in dry and wet years. *Forest Ecology and Management*, **149**, 33-46.

Löf M, Bolte A, Welander NT (2005) Interacting effects of irradiance and water stress on dry weight and biomass partitioning in *Fagus sylvatica* seedlings. *Scandinavian Journal of Forest Research*, **20**, 322-328.

Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gömöry D, Latałowa M, Litt T, Paule L, Roure JM, Tantau I, van der Knaap WO, Petit RJ, de Beaulieu J-L (2006) A new scenario for the quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist*, **171**, 199-221.

Matias L, Gonzalez-Diaz P, Jump AS (2014) Larger investment in roots in southern range-edge populations of Scots pine is associated with increased growth and seedling resistance to extreme drought in response to simulated climate change. *Environmental and Experimental Botany*, **105**, 32-38.

Meier IC, Leuschner C (2008a) Leaf size and leaf area index in *Fagus sylvatica* forests: competing effects of precipitation, temperature, and nitrogen availability. *Ecosystems*, **11**, 655-669.

Meier IC, Leuschner C (2008b) Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biology*, **14**, 2081-2095.

Meier IC, Leuschner C (2008c) Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. *Tree Physiology*, **28**, 297-309.

Mette T, Dolos K, Meinardus C, Bräuning A, Reineking B, Blaschke M, Pretzsch H, Beierkuhnlein C, Gohlke A, Wellstein C (2013) Climatic turning point for beech and oak under climate change in Central Europe. *Ecosphere*, **4**, 1-19.

Michelot A, Simard S, Rathgeber C, Dufrêne E, Damesin C (2012) Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiology*, **32**, 1033-1045.

Moseley C, Panferov O, Döring C, Dietrich J, Haberlandt U, Ebermann V, Rechid D, Beese F, Jacob D (2012) Empfehlung für eine Niedersächsische Strategie zur Anpassung an die Folgen des Klimawandels. Niedersächsisches Ministerium für Umwelt, Energie und Klimaschutz, Regierungskommission Klimaschutz.

Müller-Haubold H, Hertel D, Seidel D, Knutzen F, Leuschner C (2013) Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. *Ecosystems*, **16**,1498-1516.

Müller-Stark R (1996) Genetische Aspekte der Reproduktion der Buche (*Fagus sylvatica* L.) unter Berücksichtigung waldbaulicher Gegebenheiten. *Berichte des Forschungszentrums Waldökosysteme A135*, Göttingen, Germany, 103 p.

Nielsen C, Jørgensen F (2003) Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and within provenances. *Forest Ecology and Management*, **174**, 233-249.

Nei M (1972) Genetic distance between populations. *American Naturalist*, **106**, 283-292.

Ngugi MR, Doley D, Hunt MA, Ryan P, Dart P (2004) Physiological responses to water stress in *Eucalyptus cloeziana* and *E. argophloia* seedlings. *Trees - Structure and Function*, **18**, 381-389.

Peuke AD, Geßler A, Rennenberg H (2006) The effect of drought on C and N stable isotopes in different fractions of leaves, stems and roots of sensitive and tolerant beech ecotypes. *Plant Cell and Environment***, 29**, 823-835.

Peuke AD, Schraml C, Hartung W, Rennenberg H (2002) Identification of drought-sensitive beech ecotypes by physiological parameters. *New Phytologist*, **154**, 373-387.

Puhe J (2001) Global climate change and human impacts on forest ecosystems. *Ecological Studies*, **143**, 463-476.

Rennenberg H, Seiler W, Matyssek R, Gessler A, Kreuzwieser J (2004) Die Buche (*Fagus sylvatica* L.) – ein Waldbaum ohne Zukunft im südlichen Mitteleuropa? *Allgemeine Forst und Jagdzeitung*, **175**, 210-224.

Robson TM, Sánchez-Gómez D, Cano FJ, Aranda I (2012) Variation in functional leaf traits among beech provenances during a Spanish summer reflects the differences in their origin. *Tree Genetics and Genomes*, **8**, 1111-1121.

Rose L, Leuschner C, Köckemann B, Buschmann H (2009) Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research*, **128**, 335-343.

Rowell DP, Jones RG (2006) Causes and uncertainty of future summer drying over Europe. *Climate Dynamics*, **27**, 281-299.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332-336.

Scharnweber T, Manthey M, Criegee C, Bauwe A, Schröder C, Wilmking M (2011) Drought matters – declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management*, **262**, 947-961.

Schipka F (2002) Blattwasserzustand und Wasserumsatz von vier Buchenwäldern entlang eines Niederschlagsgradienten in Mitteldeutschland. Ph.D. thesis, University of Göttingen.

Schraml C, Rennenberg H (2000) Sensitivität von Ökotypen der Buche (*Fagus sylvatica* L.) gegenüber Trockenstreß. *Forstwissenschaftliches Centralblatt*, **119**, 51-61.

Schraml C, Rennenberg H (2002) Ökotypen der Rotbuche (*Fagus sylvatica* L.) zeigen unterschiedliche Reaktionen auf Trockenstreß. *Forstwissenschaftliches Centralblatt*, **121**, 59-72.

Seidel D, Leuschner C, Müller A, Krause B (2011) Crown plasticity in mixed forests—quantifying asymmetry as a measure of competition using terrestrial laser scanning. *Forest Ecology and Management*, **261**, 2123-2132.

Thiel D, Kreyling J, Backhaus S, Beierkuhnlein C, Buhk C, Egen K, Huber G, Konnert M, Nagy L, Jentsch A (2014) Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *European Journal of Forest Research*, **133**, 247-260.

Tognetti R, Johnson J, Michelozzi M (1995) The response of European beech (*Fagus sylvatica* L.) seedlings from two Italian populations to drought and recovery. *Trees - Structure and Function*, **9**, 348-354.

Tognetti R, Michelozzi M, Giovannelli A (1997) Geographical variation in water relations, hydraulic architecture and terpene composition of Aleppo pine seedlings from Italian provenances. *Tree Physiology*, **17**, 241-250.

Valladares F, Manuel J, Aranda I, Balaguer L, Dizengremel P (2002) The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees - Structure and Function*, **16**, 395-403.

Valladares F, Sanchez-Gomez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology*, **94**, 1103-1116.

Von Willert DJ, Matyssek R., Herppich W (1995) Experimentelle Pflanzenökologie: Grundlagen und Anwendungen. Thieme, Stuttgart, New York.

Wang K (2001) Gene flow and mating system in European beech (*Fagus sylvatica* L.). Cuvillier-Verlag, Göttingen, Germany, 159 p.

Wang KS (2003) Genetic diversity and temporal genetic structure in European beech (*Fagus sylvatica* L.). *Silvae Genetica*, **52**, 100-106.

Wortemann R, Herbette S, Barigah TS, Fumanal B, Alia R, Ducousso A, Gomory D, Roeckel-Drevet P, Cochard H (2011) Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiology*, **31**, 1175-1182.

Zimmermmann J, Hauck M, Dulamsuren Ch, Leuschner C (2015) Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. *Ecosystems*, in press.

Appendix

Table A. 2.1. Results of linear regression analyses for significant (in bold) and marginal significant relationships between soil moisture or precipitation and various morphological or physiological parameters.

Figure	Panel	Origin /Treatment	Linear regression
2.1	a	Se	y=201.74+0.22x; R^2=0.76; P=0.07
		Go	y=222.64+0.22x; R^2=0.75; P=0.07
	b	**Dry**	**y=-458.07-0.64x; R^2=0.67; P=0.04**
	c	**Kl**	**y=260.96+0.61x; R^2=0.95; P=0.01**
		Ca	y=288.73+0.57x; R^2=0.75; P=0.07
2.2	a	**Se**	**y=-0.07+0.003x; R^2=0.94; P=0.03**
		Go	y=1.20-0.001x; R^2=0.68; P=0.09
	b	**Un**	**y=-0.23+0.007x; R^2=0.97; P=0.01**
	c	**Se**	**y=0.34+0.006x; R^2=0.91; P=0.04**
		Kl	**y=0.08+0.009x; R^2=0.98; P=0.006**
		Go	Y=0.83+0.005x; R^2=0.72; P=0.08
	d	**Se**	**y=0.08+0.005x; R^2=0.82; P=0.04**
		Un	y=1.37-0.001x; R^2=0.65; P=0.09
	e	**Un**	**y=-0.04+0.009x; R^2=0.98; P=0.008**
		Go	y=0.69+0.008x; R^2=0.69; P=0.09
	f	**Se**	**y=-0.77+0.02x; R^2=0.93; P=0.003**
		Kl	**y=-0.95+0.02x; R^2=0.87; P=0.03**
		Ca	y=0.56+0.02x; R^2=0.73; P=0.08
2.3	a	**Un**	**y=99.54+0.56x; R^2=0.82; P=0.04**
		Go	**y=12.03+0.99x; R^2=0.87; P=0.03**
		Ca	**y=-190.75+1.99x; R^2=0.86; P=0.03**
		Kl	y=-9.19+0.97x; R^2=0.69; P=0.09
	b	Mod. dry	y=-88.29+0.91x; R^2=0.60; P=0.06
	c	**Se**	**y=-27.05-0.008x; R^2=0.97; P=0.01**
		Un	**y=-26.57-0.01x; R^2=0.88; P=0.03**
		Go	**y=-25.59-0.01x; R^2=0.87; P=0.03**
		Kl	**y=-26.67-0.01x; R^2=0.88; P=0.03**
		Ca	**y=-6.52-0.01x; R^2=0.99; P=0.02**
	d	**Moist**	**y=-31.83+0.007x; R^2=0.65; P=0.04**
		Mod. dry	y=-30.09+0.004x; R^2=0.63; P=0.06
2.4	a	Se	y=4.80+0.02x; R^2=0.74; P=0.07
		Un	y=4.50+0.02x; R^2=0.66; P=0.09
		Go	y=8.16+0.007x; R^2=0.69; P=0.08
	b	**Mod. dry**	**y=22.65-0.04x; R^2=0.84; P=0.02**
		Dry	y=15.34-0.02x; R^2=0.59; P=0.07
		moist	y=14.27-0.01x; R^2=0.61; P=0.06
2.5	a	Kl	y=0.005-0.0007x; R^2=0.77; P=0.06
		Ca	y=0.07-0.0009x; R^2=0.71; P=0.08
	b	**Mod.moist**	**y=0.0008-0.41x; R^2=0.90; P=0.04**
		Mod.dry	y=0.20-0.001x; R^2=0.67; P=0.09
2.6	a	**Se**	**y=25.51-0.03x; R^2=0.97; P=0.006**
	b	Mod. dry	y=-18.64+0.10x; R^2=0.79; P=0.06
		Mod. moist	y=-20.65+0.10x; R^2=0.78; P=0.06

Table A. 2.2. Results of a Mantel test conducted to analyze the relationship between morphological or physiological trait variance (first matrix) and genetic variance based on microsatellite markers (second matrix). Genetic data after Carsjens et al. (2014).

Parameter	**Mantel`s *R***	**Probability *P***
Number of leaves	-0.17	0.64
Total leaf area (cm^2)	0.11	0.33
Leaf size (cm^2)	-0.42	0.93
Leaf mass (g)	0.36	0.22
SLA (m^2 kg^{-1})	-0.15	0.67
Shoot mass (g)	0.28	0.28
Shoot length (cm)	-0.11	0.55
Fine root surface area (cm^2)	0.58	0.06
Fine root diameter (mm)	-0.09	0.54
Fine root mass (g)	0.62	0.13
SRA (m^2 kg^{-1})	0.2	0.27
Coarse root mass (g)	0.35	0.23
Taproot length (cm)	0.48	0.17
Total biomass (g)	0.05	0.35
Aboveground biomass (g)	0.001	0.54
Belowground biomass (g)	0.11	0.4
Fine root : leaf surface area ratio (m^2 m^{-2})	0.78	0.09
Fine root : leaf biomass ratio (g g^{-1})	0.09	0.39
Root : shoot ratio (g g^{-1})	0.66	0.1
Osmotic potential at full hydration π_0 (MPa)	0.09	0.5
Osmotic potential at turgor loss point π_{tlp} (MPa)	-0.34	0.75
Rel. water content at turgor loss point RWC_{tlp} (%)	0.31	0.42
Rel. symplastic water content at turgor loss point RWC_{tlp} (%)	-0.47	0.75
Modulus of elasticity ε (MPa)	-0.51	0.96
Cell volume (g g^{-1})	-0.34	0.79
Leaf water potential at full hydration $\Psi_{leaf(max)}$ (MPa)	-0.47	0.88
Turgor potential at full hydration Ψ_P (MPa)	-0.51	0.92
Osmotic adjustment (MPa) $\Delta\pi_{tlp}$ (moist – dry)	0.36	0.25
Osmotic adjustment (MPa) $\Delta\pi_{tlp}$ (early – late)	-0.53	0.84
Elastic adjustment (MPa) $\Delta\varepsilon$ (moist – dry)	-0.54	0.96
Elastic adjustment (MPa) $\Delta\varepsilon$ (early – late)	-0.32	0.79
Stomatal conductance at noon (mmol m^{-2} s^{-1})	0.40	0.16
Foliar δ^{13}C signature (‰)	-0.16	0.63

Table A. 2.3. Nei's genetic distance (Nei 1972) between the five stands according to microsatellite analyses in the mature trees of the five stands (after Carsjens et al. 2014).

	Sellhorn **Se**	**Unterlüß** **Un**	**Göhrde** **Go**	**Klötze** **Kl**	**Calvörde** **Ca**
Sellhorn	0.000				
Unterlüß	0.050	0.000			
Göhrde	0.027	0.053	0.000		
Klötze	0.035	0.041	0.048	0.000	
Calvörde	0.025	0.043	0.015	0.037	0.000

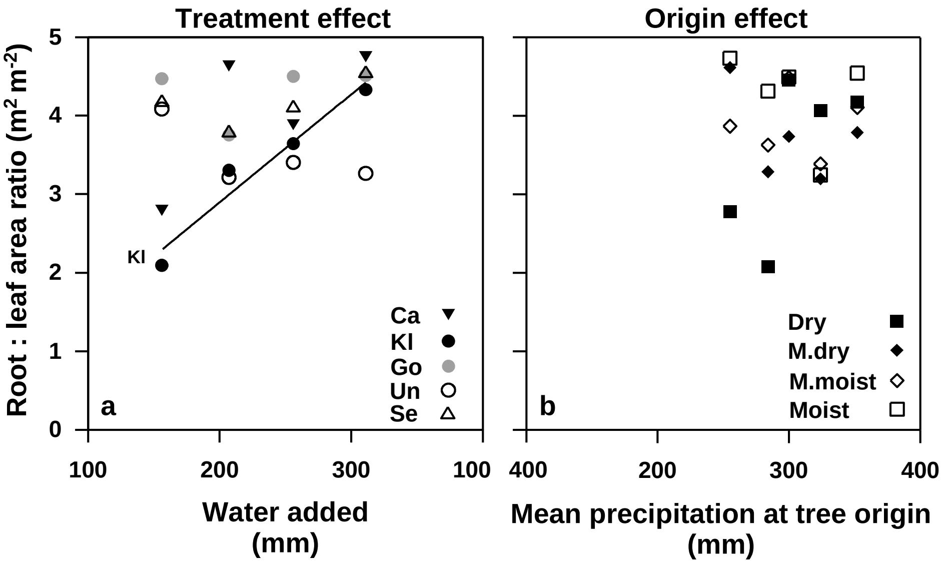

Figure A. 2.1. Ratio of fine root surface to leaf surface area in its dependence on (a) the amount of water added, or to (b) mean precipitation at tree origin (May to September 1971-2001) (means of 10 beech trees per treatment and origin). A significant relation existed for the *Kl* plants: y=0.14+0.01x, R^2=0.95, *P*=0.02 (panel a). For tree provenances and treatment details see Figure 2.2.

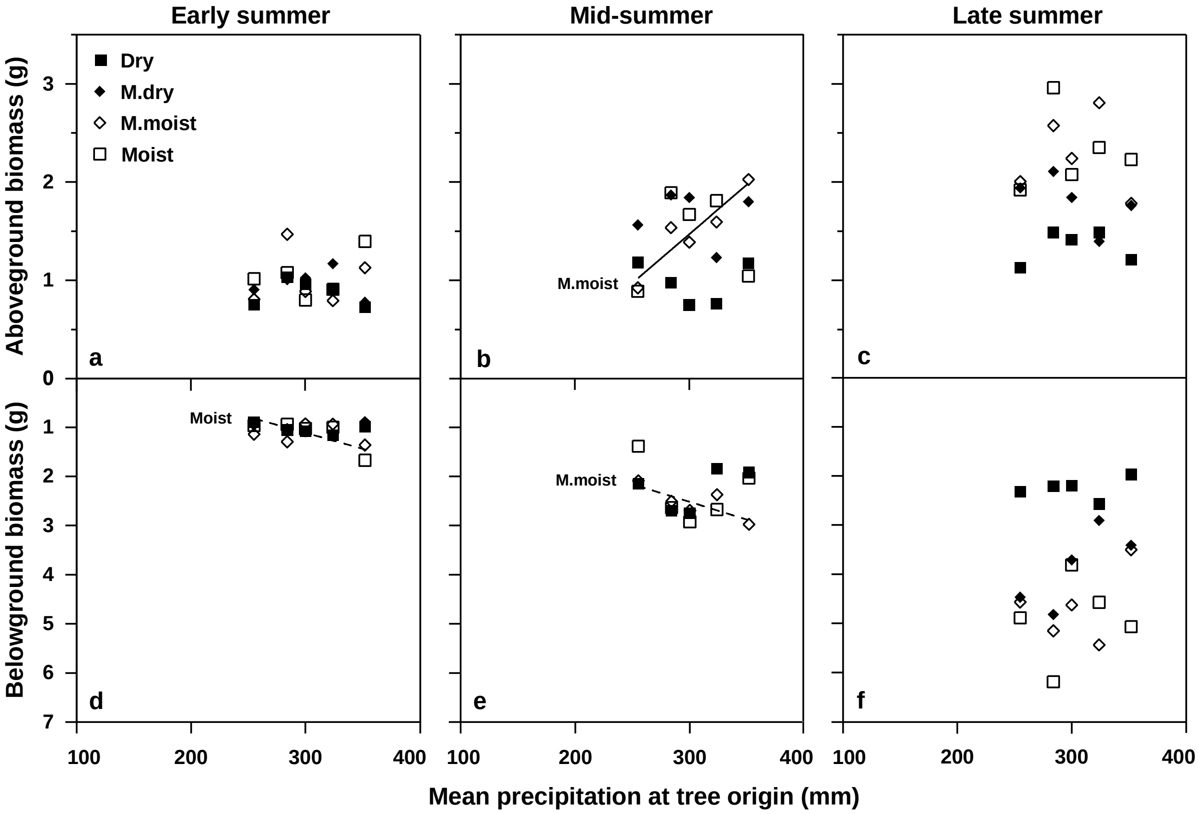

Figure A. 2.2. (a-c) Aboveground (leaves, shoot) and (d-f) belowground (fine roots, coarse roots) biomass in (a, d) early, (b, e) mid and (c, f) late summer 2012 in relation to precipitation (May – September) at tree origin (means of 10 beech trees per treatment and origin). The relation was significant for aboveground biomass in mid-summer (moderately moist treatment only): y=-1.53+0.01x, R^2=0.87, P=0.02. Note different ordinate scaling for aboveground and belowground biomass. For treatment details see Figure 2.2. Marginally significant relations are depicted by dashed lines.

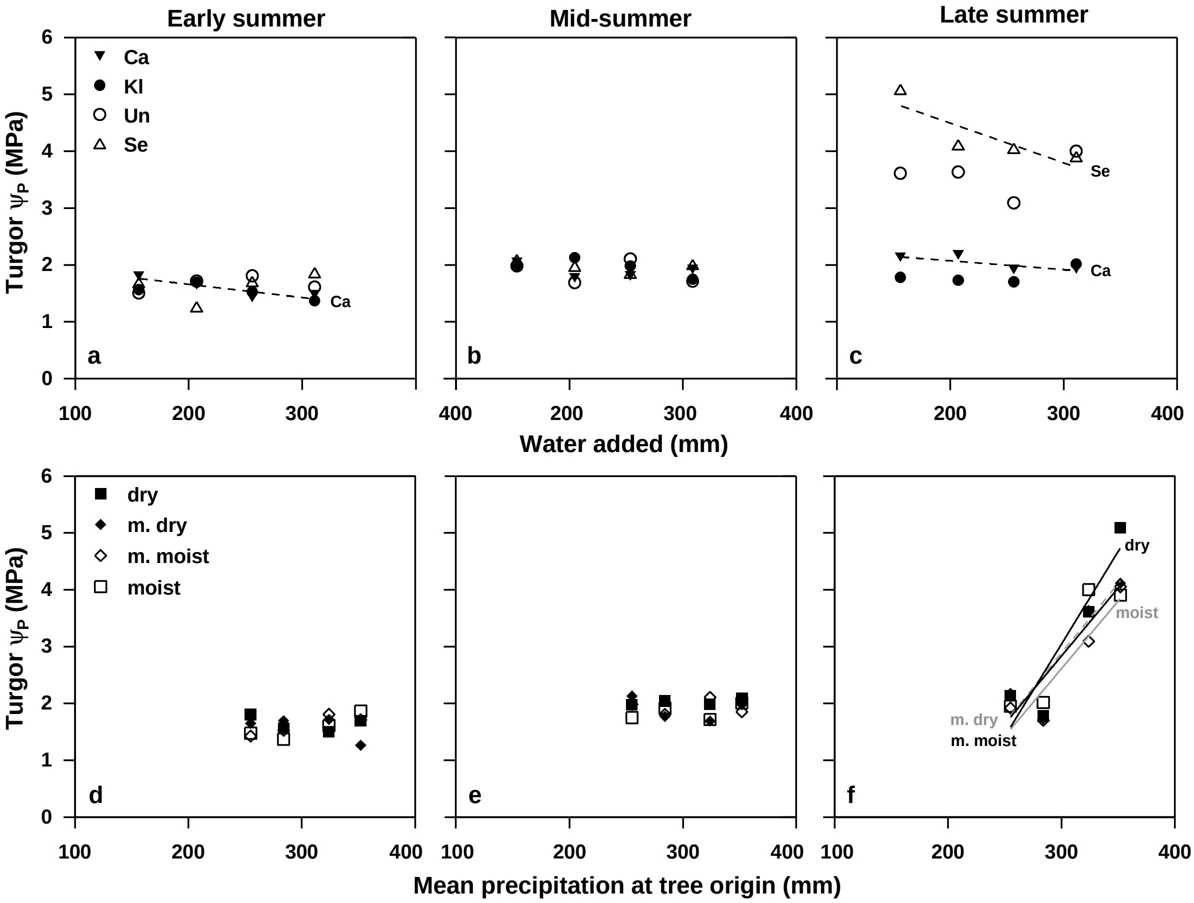

Figure A. 2.3. Turgor at full hydration in (a,d) early, (b,e) mid and (c, f) late summer 2012 in relation to (a-c) the amount of water added during the experimental phase, or to (d-f) mean precipitation at tree origin (May to September 1971-2001) (means of 4 beech trees per treatment and origin). Significant relations existed at late summer in the dry treatment: y=-6.74+0.03x; R^2=0.85, P=0.04, moderately moist treatment: y= -4.53+0.02x, R^2=0.87, P=0.03 and the moist treatment: y=-4.46+0.02x, R^2=0.85, P=0.04; in panel f. Marginally significant relations are depicted by dashed lines. For tree provenances and treatment details see Figure 2.2.

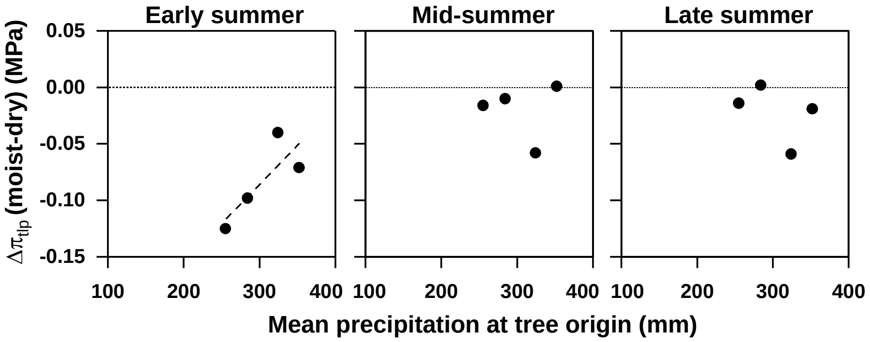

Figure A. 2.4. Osmotic potential at turgor loss point in the plants of the driest treatment relative to the plants of the moistest treatment (drought-induced change in π_{tlp}) as dependent on the precipitation at tree origin in summer 2012 (means of each four PV-curves). Dry treatment: 160 mm, moist treatment: 310 mm of water added from May to September 2012. Marginally significant relations are depicted as dashed line.

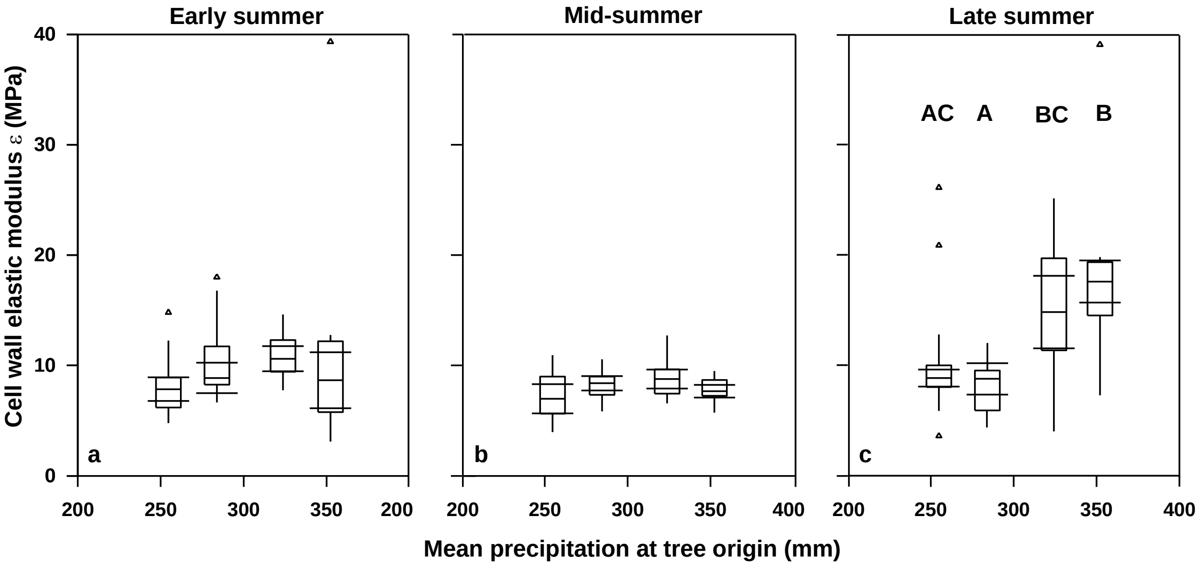

Figure A. 2.5. Modulus of elasticity of leaf tissue in summer 2012 of plants from four origins along the precipitation gradient (means of 16 beech trees per origin; box-whisker plots with median, 25 and 75 percent quartiles, maximum and minimum values (bars) and outliers (triangles)).

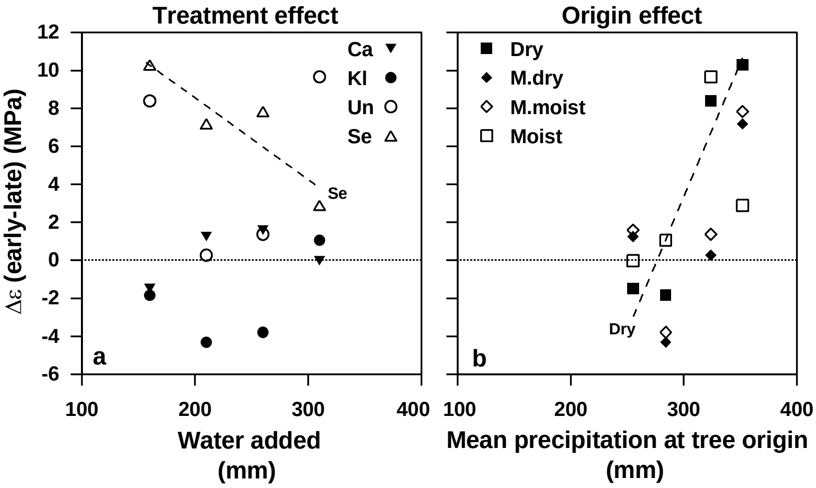

Figure A. 2.6. Elastic adjustment from May to September 2012 in the shoots in relation to (a) the amount of water added during May to September or to (b) mean precipitation at tree origin (May to September 1971-2001). For tree provenances and treatment details see Figure 2.2. Marginally significant relations (for *Se* in panel a and the dry treatment in panel b) are depicted as dashed line.

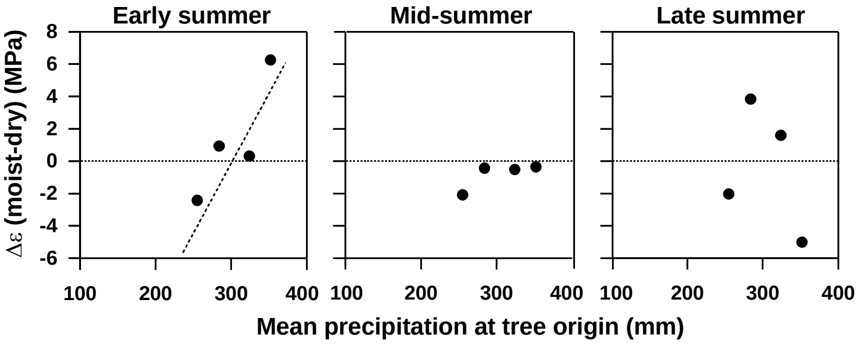

Figure A. 2.7. Modulus of elasticity ε in the plants of the dry treatment relative to the plants of the moist treatment (drought-induced change in ε) as dependent on the precipitation at tree origin in summer 2012 (means of each four PV-curves). Dry treatment: 160 mm, moist treatment: 310 mm of water added from May to September 2012. Marginally significant relations are depicted as dashed line.

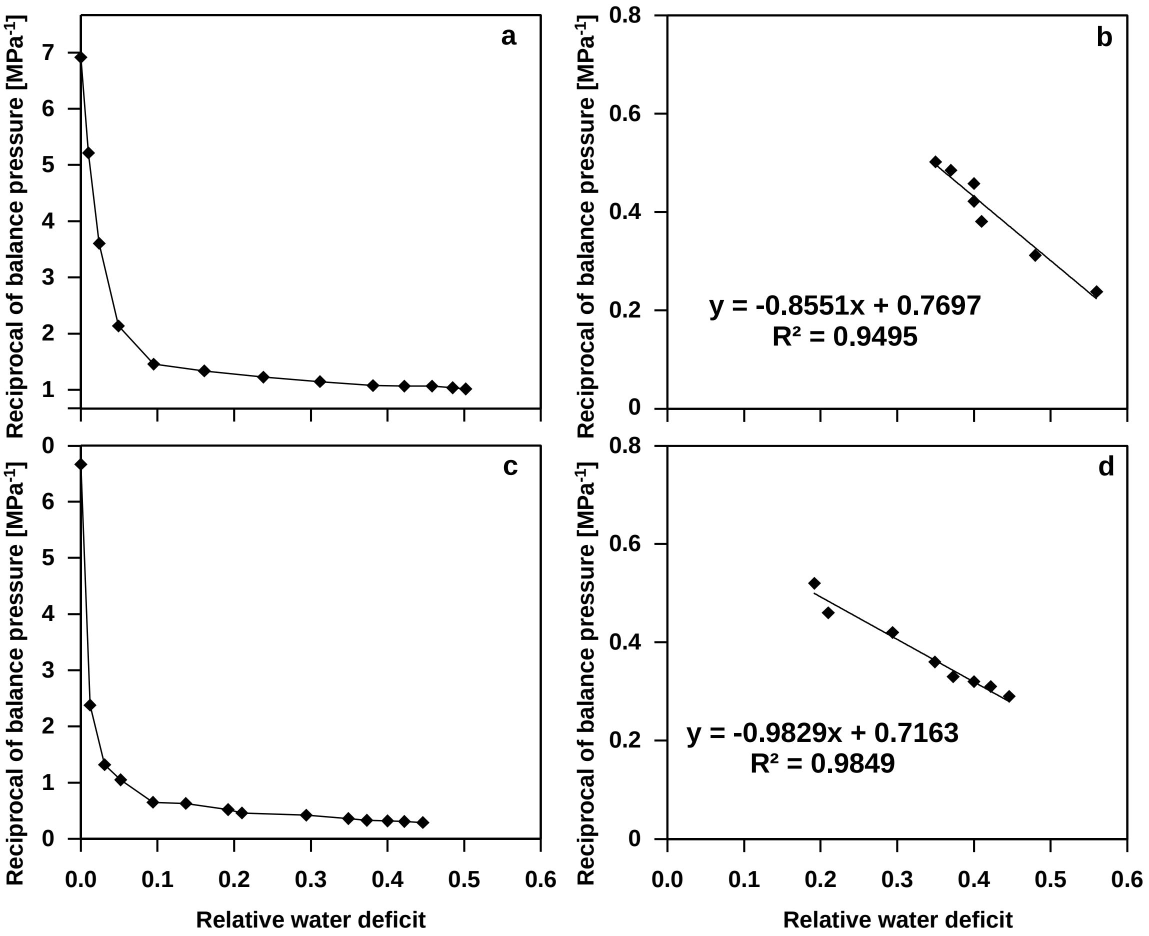

Figure A. 2.8. Two example P-V curves. Sample *Kl*_022 (a, b) from the dry treatment and sample *Kl*_108 (c, d) from the moist treatment at late season (September). Panels a and c: P-V curves, b and d: linear range of the curves with equations.

CHAPTER 3

Recent climate warming-related growth decline impairs European beech in the center of its distribution range

Florian Knutzen · Choimaa Dulamsuren · Ina Christin Meier
Christoph Leuschner

Submitted to Ecosystems

Abstract

Global warming-related decreases in summer precipitation represent a major threat for the vitality and productivity of forests in large parts of the temperate zone. *Fagus sylvatica* (European beech), the most important tree species of Central Europe's natural forest vegetation, is known to suffer from increased drought intensity at its southern distribution limits, but it is not well known how increasing summer drought is affecting this species in the center of its distribution range in a sub-oceanic climate. We compared tree ring chronologies and the climate sensitivity of growth (MS) in 11 mature beech stands (6 sites along a precipitation gradient (855-576 mm yr^{-1}) on two soil types (sandy-loamy vs. sandy soil) with contrasting water storage capacity (WSC) in the northwest German lowlands to test the hypotheses that recent warming is impacting on beech growth also in the center of the distribution range below a certain precipitation limit, and stands with low soil WSC are more susceptible. We found a threshold of *c.* 350 mm of mean growing season precipitation (MGSP) (or of ~660 mm mean annual precipitation, MAP) below which basal area increment (BAI) showed a consistent decline since the 1960s or 1970s. The frequency of negative pointer years and MS were highest in low-precipitation stands on sandy soil, but both parameters have increased during the last decades also in the moister stands. The factor with largest impact on BAI was precipitation in June, but high mid-summer temperatures additionally reduced growth at the drier sites. Contrary to our hypothesis, the edaphic effect on growth dynamics was surprisingly small, as the BAI decrease was more pronounced in stands on sandy-loamy soil with higher WSC. We conclude that global warming-related growth decline is affecting *F.sylvatica* even in the center of its distribution below a hydrological threshold that is mainly determined by mid-summer rainfall.

Keywords: Basal area increment, Climatic drought, Edaphic drought, European beech, Growth decline, Mean sensitivity, Negative pointer years, Precipitation gradient, Tree ring chronology

Introduction

Due to their longevity, trees are facing global warming and associated longer, hotter and often drier summers (Parry et al. 2007, Allen et al. 2010). Regional climate models such as ECHAM5-MPIOM (Max-Planck Institute for Meteorology, Hamburg) project declining summer precipitation by up to 40% in certain regions of Germany in conjunction with a temperature increase by up to 3°C (scenario A1B) until the end of this century (Jacob et al. 2014). Even more relevant for biological systems are meteorological extremes such as summer heat waves that may increase in frequency and severity (Schär et al. 2004, IPCC 2013). Rising temperatures have, on the one hand, extended the growing season length of European forests (Menzel and Fabian 1999), increased forest productivity (Spiecker 1999, Pretzsch et al. 2014), and promoted the spread of thermophilic forest plants with more southerly distribution (van Herk et al. 2002, Pócs 2011, Jantsch et al. 2013). On the other hand, climate warming has reduced the vitality and productivity of various tree species, notably Scots pine (*Pinus sylvestris* L.; Rebetez and Dobbertin 2004) and European beech (*Fagus sylvatica* L.).

In particular beech, the most important tree species of the natural forest vegetation of Central Europe, has been found to be affected by severe droughts as that in 2003 (Rennenberg et al. 2004, Ciais et al. 2005, Bréda et al. 2006). Pre-senescent leaf abscission and growth decline have been observed at the southern and eastern limits of the beech range in Spain, Italy and Hungary (e.g., Jump et al. 2006, Piovesan et al. 2005, 2008, Garamszegi and Kern 2014). More alarming is that recent growth decline has been observed in dendrochronological studies also in the center of beech distribution, i.e. in Switzerland and Germany (Scharnweber et al. 2011, Weber et al. 2013, Zimmermann et al. 2015). Otherwise, there are reports that wood formation in beech is relatively insensitive to droughts (van der Werf et al. 2007). In fact, *F. sylvatica* occurs in Europe at a wide range of precipitation amounts (*c.* 2000 to less than 450 mm yr^{-1}, Ellenberg and Leuschner 2010). Moreover, various authors have emphasized the adaptation potential of beech to a drier climate (e.g. Meier and Leuschner 2008, Rose et al. 2009, Weber et al. 2013, Carsjens et al. 2014), but the bulk of adaptation studies were conducted with saplings, the results of which cannot simply be extrapolated to mature trees. Thus, considerable uncertainty remains with respect to the drought sensitivity of European beech. No doubt, more precise information on precipitation and soil moisture limits of *F. sylvatica* is urgently needed, given the typical production cycle of beech in managed forests of 100 years (Weber et al. 2013).

One reason for the partly contradicting observations on the drought response of *F. sylvatica* is that water shortage can arise from low precipitation, a small WSC of the soil, or a combination of both factors. Moreover, the timing of drought is of paramount importance for its biological significance (Zimmermann et al. 2015). Further, Köcher et al. (2013) could show for a beech stand in central Germany that the most important environmental factor controlling stem cambial activity was not precipitation or soil moisture but air humidity. It appears that the precipitation and atmospheric moisture regimes are interacting with soil texture in their control of stem water status in a complex way. It will be difficult to disentangle these three hydrological factors when attempting to define precise drought limits of vital radial growth in beech. While many earlier studies have produced empirical evidence that the drought limit of trees depends to a considerable extent on soil properties (e.g., Rigling et al. 2001, Lebourgeois et al. 2005, Weber et al. 2007), synchronous variation in precipitation and soil WSC and its impact on tree growth has not been investigated in detail so far.

Climate change and new forest management goals render a deeper understanding of beech drought limits even more urgent. Before man began to reduce forest cover from Neolithic times onwards, beech covered roughly 75% of Germany’s land surface area (BMEL 2014). Until recent time, this area has been reduced to 7%, which represents *c.* 17% of the current forest area (BMU 2011, BMEL 2014). In a move to more natural forest management, in many regions of Central Europe, forestry has begun to convert conifer plantations into beech forests or mixed broad-leaved conifer forests (Tarp et al. 2000, Metz et al. 2013). However, especially in more sub-continental regions with relatively low summer precipitation, this goal may conflict with the assumed drought sensitivity of *F. sylvatica*. The tendency for decreasing summer precipitation in various regions of Central Europe (Schönwiese et al. 2003) will further increase the drought risk in future time.

With a comparative dendrochronological study in mature beech stands along a precipitation gradient (855-577 mm MAP), we aimed to characterize climatic and edaphic drought effects on the radial growth of *F. sylvatica* in the center of its distribution range. As hydrological variables, we considered mid-summer (June, July), summer and annual precipitation as well as two levels of soil WSC (sandy and sandy-loamy soil) to assess the influence of climatic and edaphic drought on radial growth in a 60-yr investigation period (1951-2010).

We had four main study goals,

(i) to identify precipitation thresholds beyond of which long-term negative growth trends are realized,

(ii) to analyze the patterns of growth decline (continuous decline or abrupt decrease triggered by certain drought events),

(iii) to examine what precipitation component (mid-summer vs. late-summer or spring precipitation) has the largest influence on radial growth, and

(iv) to compare the effects of reduced precipitation with those of lowered soil WSC on growth.

The comparison of six sites along a precipitation gradient allowed to examine long-term adaptive responses to a permanent reduction in precipitation by nearly 300mm and contrast it with short- to medium-term growth responses (years to a few decades) as visible in annual ring chronologies. Based on earlier research by our group and other authors, we hypothesized that

(i) increases in summer drought and/or temperaturereduce the radial growth of *F. sylvatica* below a yet to be defined precipitation threshold,

(ii) the climatic impact on *F. sylvatica* has increased since about the 1970s, and

(iii) the growth decline is stronger on sandy soil with lower WSC than on loam richer soil.

Material and methods

Forest site selection

Eleven mature beech forests with comparable stand structure were selected for study in the center of the distribution range of *F. sylvatica* between 52 and 53°N and 9 and 11° E in the lowlands of northwestern Germany. The forests are located along a 130-km long NW-SE precipitation gradient in the Lüneburg Heath (federal states of Lower Saxony and Saxony-Anhalt). Apart from the climate influence (precipitation, temperature) on tree growth, we examined the effect of soil texture by selecting each one stand with a sandy or a sandy-loamy soil texture at six locations along the gradient (except for the locations *Oe* and *Go*: only one stand with sandy texture, and the location *Ca*: one stand with sandy-loamy and two stands with sandy textures; Table 3.1).

Table 3.1. Location and climatic data of the 11 investigated beech stands in northwestern Germany. Climate data refer to the period 1981-2010 and were derived from weather station data provided by the National Climate Monitoring of Deutscher Wetterdienst (DWD) which were corrected for elevation. Soil water: soil water storage capacity in the profile to 1.2 m depth. For additional edaphic and stand structural properties of the 11 beech stands see Müller-Haubold et al. (2013). Climatic data: MAP, mean annual precipitation; MGSP, mean growing season precipitation (April – September); MSP, mean summer precipitation (June – August); MAT = mean annual temperature; Sites: *Se* = Sellhorn; *Un* = Unterlüß; *Oe* = Oerrel; *Go* = Göhrde; *Kl* = Klötze; *Ca* = Calvörde. Code for textures: L = sandy-loamy; S = sandy.

Site	**Texture**	**Code**	**Latitude** (N)	**Longitude** (E)	**Elevation** (m a.s.l.)	**MAP** (mm)	**MGSP** (mm)	**MSP** (mm)	**MAT** (°C)	**Soil water** (mm 120 cm^{-1})
Se	Loamy	Se L	53°10'	09°57'	127	855	419	237	8.7	111
	Sandy	Se S	53°10'	09°57'	130	855	419	237	8.7	90
Un	Loamy	Un L	52°50'	10°19'	120	816	394	223	8.7	95
	Sandy	Un S	52°50'	10°19'	117	816	394	223	8.7	79
Oe	Sandy	Oe S	52°59'	10°14'	90	786	384	217	8.9	59
Go	Sandy	Go S	53°09'	10°52'	85	707	365	212	9.0	78
Kl	Loamy	Kl L	52°37'	11°14'	102	656	343	195	9.0	124
	Sandy	Kl S	52°37'	11°15'	85	655	344	196	9.1	90
Ca	Loamy	Ca L	52°24'	11°16'	72	577	308	175	9.3	140
	Sandy	Ca S	52°23'	11°17'	75	576	307	174	9.4	81
	Sandy	Ca S II	52°22’	11°16’	105	594	315	179	9.3	46

The stands on sandy-loamy soil are mostly located on sandy moraine deposits with elevated silt and clay content and thus in general higher water storage capacity (WSC). The stands on sandy soil grow on more coarse-grained meltwater sands with low silt and clay content and a smaller WSC. Additional stand selection criteria were: canopy closure (canopy cover >0.9 in the upper layer, additional tree or shrub layers mostly absent), mature and even-aged stand structure (85-125 years old; Table 3.2), no or low admixture of other tree species (*Se*S, *Un*S, *Kl*S, *Ca*L: 3–19% *Quercuspetraea*, *Oe*S 39%, *Go*S: 6% *Pseudotsugamenziesii*), last forest management activities at least ten years ago, and tree origin from natural regeneration (with the exception of *Oe*). For the sake of comparability with respect to soil chemical conditions, all stands were elected on similar geological substrate, Pleistocene glacial or fluvioglacial sandy deposits from the penultimate (Saalian) Ice Age. Soil types ranged from haplic Arenosols to stagnicPodzols, with 4-9 cm-thick organic layers.

Table 3.2. Descriptive statistics for unstandardized tree ring data and chronologies of 11 mature beech stands located along a precipitation gradient in northwestern Germany. Tree age refers to the mean age at breast height (1.3 m). Mean ring width (MRW), mean sensitivity (MS), and first-order autocorrelation (AC1) were calculated for the period 1951-2010. Significant differences between means were tested with Ryan-Einot-Gabriel-Welsch multiple Range-Test. n = number of sampled trees; DBH = mean diameter at breast height; EPS = expressed population signal.

Site code	n	Age (years)	DBH (cm)	MRW (mm)	MS	AC1	EPS > 0.85 since
Se L	20	106 ± 15^{c}	40.6 ± 3.7^{ab}	1.59 ± 0.13^{f}	0.34 ± 0.01^{bcd}	0.51 ± 0.03^{abc}	1930
Se S	20	108 ± 13^{c}	34.6 ± 2.3^{abc}	1.72 ± 0.13^{e}	0.28 ± 0.01^{d}	0.65 ± 0.03^{a}	1930
Un L	21	103 ± 15^{cd}	34.6 ± 2.6^{abc}	2.28 ± 0.19^{b}	0.32 ± 0.01^{cd}	0.45 ± 0.04^{abc}	1940
Un S	21	100 ± 11^{cd}	26.7 ± 2.1^{cd}	1.50 ± 0.16^{f}	0.32 ± 0.01^{cd}	0.57 ± 0.04^{ab}	1940
Oe S	35	82 ± 13^{e}	20.3 ± 2.0^{d}	1.50 ± 0.10^{f}	0.35 ± 0.01^{bcd}	0.56 ± 0.03^{abc}	1950
Go S	21	124 ± 12^{b}	32.8 ± 2.4^{bc}	1.33 ± 0.12^{g}	0.37 ± 0.01^{cb}	0.59 ± 0.03^{abc}	1920
Kl L	20	128 ± 10^{b}	46.7 ± 2.5^{a}	1.55 ± 0.10^{f}	0.38 ± 0.01^{cbd}	0.50 ± 0.05^{abcd}	1920
Kl S	21	108 ± 8^{c}	38.9 ± 3.1^{abc}	1.72 ± 0.19^{e}	0.32 ± 0.01^{cd}	0.59 ± 0.03^{ab}	1940
Ca L	12	99 ± 11^{cd}	40.1 ± 2.9^{ab}	2.11 ± 0.16^{c}	0.32 ± 0.02^{cbd}	0.62 ± 0.04^{d}	1950
Ca S	12	82 ± 4^{e}	31.2 ± 1.4^{bcd}	1.95 ± 0.13^{d}	0.45 ± 0.02^{a}	0.35 ± 0.05^{dc}	1970
Ca S II	12	83 ± 3^{e}	36.1 ± 1.5^{abc}	2.44 ± 0.13^{a}	0.39 ± 0.02^{b}	0.35 ± 0.04^{bcd}	1970

The nutrient-poor sandy soils had a pH(KCl) of 4.0-4.3 (mean: 4.2), a C:N ratio of 13-26 mol mol^{-1} (mean: 20), and a base saturation of 3-13% (mean: 8) in the top mineral soil (data from Müller-Haubold et al. 2013). The stands on sandy-loamy soil had a similar stand basal area as those on sandy soil but were slightly older (13 years) and taller (4 m); while stem density was slightly higher in the latter (Table A.3.1).

Climate conditions and meteorological data

Mean annual temperature (averaged from climate data of the years 1981-2010) along the gradient was 9.0°C, with a tendency of slightly higher temperatures at the drier southeastern end of the gradient (Table 3.1). MAP decreased from 855 mm yr^{-1} in the more sub-oceanic northwest to 575 mm yr^{-1} in the more sub-continental southeast. The corresponding summer rainfall (April to September) decreased from 405 to 295 mm yr^{-1}.

For the analysis of the response of tree ring width to monthly or yearly climate conditions, we used climate data (precipitation, temperature, sunshine duration) from the 1 x 1 km^2 grid data set provided by the German Meteorological Service (DeutscherWetterdienst DWD, Offenbach, Germany). This data was regionalized by averaging climate data of the nine nearest grid fields of a study site and correcting for altitude. The DWD data were available from 1951 onwards. The close relation between the precipitation gradient and an associated soil moisture gradient was demonstrated by the measurement of volumetric soil water content with time domain reflectometry probes (TDR CS616; Campbell Scientific Inc., Logan, UT) installed at 20 cm soil depth in the center of each study site. The volumetric water content during the summer months (April to September) decreased from 11.5 to 6.0% v/v in the sandy-loamy soils and from 8.7 to 6.5% v/v in the sandy soils from the moistest to the driest study site (data from Müller-Haubold, unpubl.).

Increment core sampling and analyses of tree ring chronologies

The sampling of increment cores took place in a 30 x 30 m plot in the center of each forest stand. In December 2011, wood cores (5 mm in diameter) were taken with an increment corer (Suunto, Vantaa, Finland, 400 mm length) from 20 randomly selected trees per site (exceptions due to permission constraints: each twelve at the three sites in Calvörde, 35 at the single site in Oerrel), with at least ten dominant trees, resulting in 237 wood cores in total. All sampled trees had canopy access and diameters at breast height (DBH) ≥15 cm. Permissions were granted for one increment core per tree only. Wood cores were taken at 1.3 m height at the northern side of the trunk, except for trees with reaction wood in this sector. The DBH of every cored tree was recorded. Cores with rotten segments or knobs were excluded from further analyses. Subsequently, the wood cores were air-dried, mounted on grooved boards, sanded, and polished (Figure 3.1). Every sample was scanned with an Epson perfection A4 or A3 scanner at a resolution of 1200 dpi and analyzed for tree ring widths with the software LignoVision (version 1.38m; Rinntech, Heidelberg, Germany). In case of questionable measurements, the increment cores were recut with a scalpel and reanalyzed using a movable object table (Lintab 6; Rinntech) and the software TSAP-Win (version 4.69h; Rinntech). All measurements had a precision of 10 µm.

Figure 3.1 Example of an increment core, mounted on a wooden groove board (from the loamy field site in Calvörde).

Tree ring chronologies were derived for the 60-yr period 1951 to 2010 by averaging annual ring width over all analyzed trees per stand. In a first step, the ring widths were cross-dated with TSAP-Win software based on three parameters, the coefficient of agreement (‘Gleichläufigkeit’ GL; Eckstein and Bauch 1969), the cross-dating-index (CDI; Dobbertin&Grissino-Mayer 2004), and Student’s t-value (TVBP; Baillie and Pilcher 1973). Tree ring series used for the calculation of mean tree ring chronologies had a GL ≥65%, a CDI ≥20, and a TVBP ≥3.5. For the determination of tree age, ten years were added to the age determined by coring at 1.3 m height. The coherence within the tree ring chronologies was examined with the expressed population signal (EPS; Wigley et al. 1984), using the software ARSTAN (version 41d; Cook, 1985). Chronologies were split into 30-year intervals with a running window overlap of 15 years. EPS was calculated for each interval. Chronologies were considered reliable if EPS exceeded the 0.85-threshold. Longer time series were also plotted for inspecting the age-related growth trend but data prior to 1951 was not analyzed for climate sensitivity.

Analysis of climate-growth relationships

For eliminating long-term age-related growth trends from the climate signal on radial growth, tree ring series were standardized with $z_i = (x_i - \mu)/\sigma$, where x_i is the tree ring width of year i, μ is the mean of the time series, and σ is the standard deviation of the time series. Standardized tree-ring indices were used to quantify the influence of temperature, precipitation and sunshine duration in individual months on tree ring width in the climate-response analysis.

The mean sensitivity (MS) of a tree ring width series was calculated from the year-to-year variability in unstandardized tree ring widths with $\mathrm{MS} = \frac{200}{N}\sum_{1}^{N}\left|\frac{a_n - a_{n-1}}{a_n + a_{n-1}}\right|$, where N is the length of the series (years), a is the tree ring width and n is the year. MS characterizes the interannual fluctuation of stem increment in a forest stand. The first-order autocorrelation (AC1, autocorrelation lag of 1 year) was calculated from the influence of the increment of the previous year on the increment of the current year. Autocorrelation can be seen as the degree of similarity between a time series and a lagged version of itself. Both MS and AC1 were calculated for different time periods within the period 1951-2010.

For identifying pointer years, we quantified the extent of growth deviation from the mean with $\delta p_i = (p_i - m_i)/\sigma_c \times 100$, where p_i is the tree ring width of year i, m_i is the 5-year moving average of year i, and σ_c the standard deviation (SD) of the whole chronology. A year was defined as pointer year if the difference between p_i and m_i was larger than one SD of the chronology and if 85% of the trees of a chronology showed the same growth trend (*cf.* Zimmermann et al. 2015). Because of the focus on drought effects on increment in this study, only negative pointer years were considered ($\delta p_i \leq -50$).

We calculated three coefficients that characterize the tolerance of a tree’s radial increment, (1) resistance Rt (the ratio between BAI during a drought year and the pre-drought period), (2) recovery Rc, which expresses the ability to recover growth relative to the increment reduction experienced during drought (i.e. the ratio between the BAI in the post-drought period and in the drought year), and (3) resilience Rs, i.e. the ability to reach after the drought the performance level observed prior to drought (the ratio between the BAI of the post-drought period and the pre-drought period), following Lloret et al. (2011) and Zang et al. (2014). A two-year period was chosen for the post-drought and pre-drought periods in order to avoid interference when investigating the two pan-European drought years 2000 and 2003.

The de-trending of ring widths into normalized ring width indices for eliminating growth trends largely removes information on long-term climate change influences on growth (Cook et al. 1990, Briffa et al. 1996, 2001, Jump et al. 2006). Thus, we also calculated mean unstandardized basal area increment (BAI) for the stands, because this parameter is less affected than ring width by uneven stem geometry (Biondi and Qeadan 2008, Weber et al. 2008) and differences in tree age and stem diameter (Biondi 1999, Hogg et al. 2005, Nakawatase and Peterson 2006). The BAI of dominant trees can be seen as an indicator of forest productivity and a negative trend in BAI as strong indication of a true decline in radial growth (Jump et al. 2006).

Competition and also social position may alter the climate response of trees (e.g. Piutti and Cescatti 1997) and the strongest climate signals are expected in dominant trees. Thus, we considered only the each ten sampled dominant trees of the stands for the investigation of the climate response, while all sampled trees entered the pointer year analysis conducted for the climate response analysis to the extremely dry years 2000 and 2003.

Statistical analyses

Arithmetic means and standard errors (SE) were calculated either for the ten investigated dominant trees or for all twenty sampled trees per stand. Probability of fit to normal distribution was tested with a Shapiro-Wilk test using the software SAS, version 9.3 (SAS Institute, Cary, NC, USA). The stand means were compared with the Ryan-Einot-Gabriel-Welsch multiple rangetest. The number of climatic, edaphic, and stand structural parameters to be considered in subsequent analyses was reduced by three independent principal components analyses (PCA; Table A.3.2), using the package CANOCO, version 5.03 (Biometris, Wageningen University and Research Centre, The Netherlands). Those PCA axes that were explaining ≥75% of the cumulative variance were used as independent variables in subsequent multiple regression analyses with forward variable selection to test whether the PCA-derived variables were significant predictors for BAI, using SAS software (Table 3.3). Subsequently, we analyzed for covariance of tree age (covariate) on the influence of annually resolved precipitation amounts (main effect) on BAI. We further calculated multiple regression analyses with forward variable elimination to test the influence of different monthly climate variables (precipitation, temperature, and sunshine duration) of the year before ring production and during the year of ring production on standardized tree ring width. Finally, linear regression analyses were conducted for quantifying the influence of precipitation on BAI, AC1, and MS using the software Xact, version 8.03 (SciLab, Hamburg, Germany). Significance was determined at $P \leq 0.05$; in one case a marginal significant effect at $P \leq 0.10$ was also reported (Table 3.4).

Results

Precipitation and temperature trends

The climate record evidences significant change during the last decades (Figure 3.2). The amount of precipitation in mid-season (June) decreased during the last 60 years especially in the drier part of the transect (Figure 3.2a). At the moistest location Se, the amount of June precipitation remained almost unchanged with about 78-79 mm while at the driest location Ca, the amount decreased from 76 mm in 1950 to 51 mm in 2010, i.e. by about 30%. By contrast, the amount of precipitation in the late season (September) increased from 1950 to 2010 in particular at the moister sites (Figure 3.2b) with the result that the September precipitation changed only little in the driest forest stand but increased from 67 to 75 mm in the moistest stand. Similar to the trend for September precipitation, MAP also showed a larger increase at the moister than the drier sites (Figure 3.2c), with the result that the absolute difference in MAP was only *c.* 200 mm along the transect in the 1950s, but nearly 300 mm in the 2010s. Consequently, the slope of the precipitation gradient has increased during the lifetime of the trees.

Mean temperature increased in all forest stands in both June and September as well as during the whole year from the 1950s to the 2010s (Figure 3.2d-f). The average temperature increase during the last 60 years was 0.5°C in June and 0.8°C in September. Mean annual temperature even increased by 1.4°C in 1950-2010.

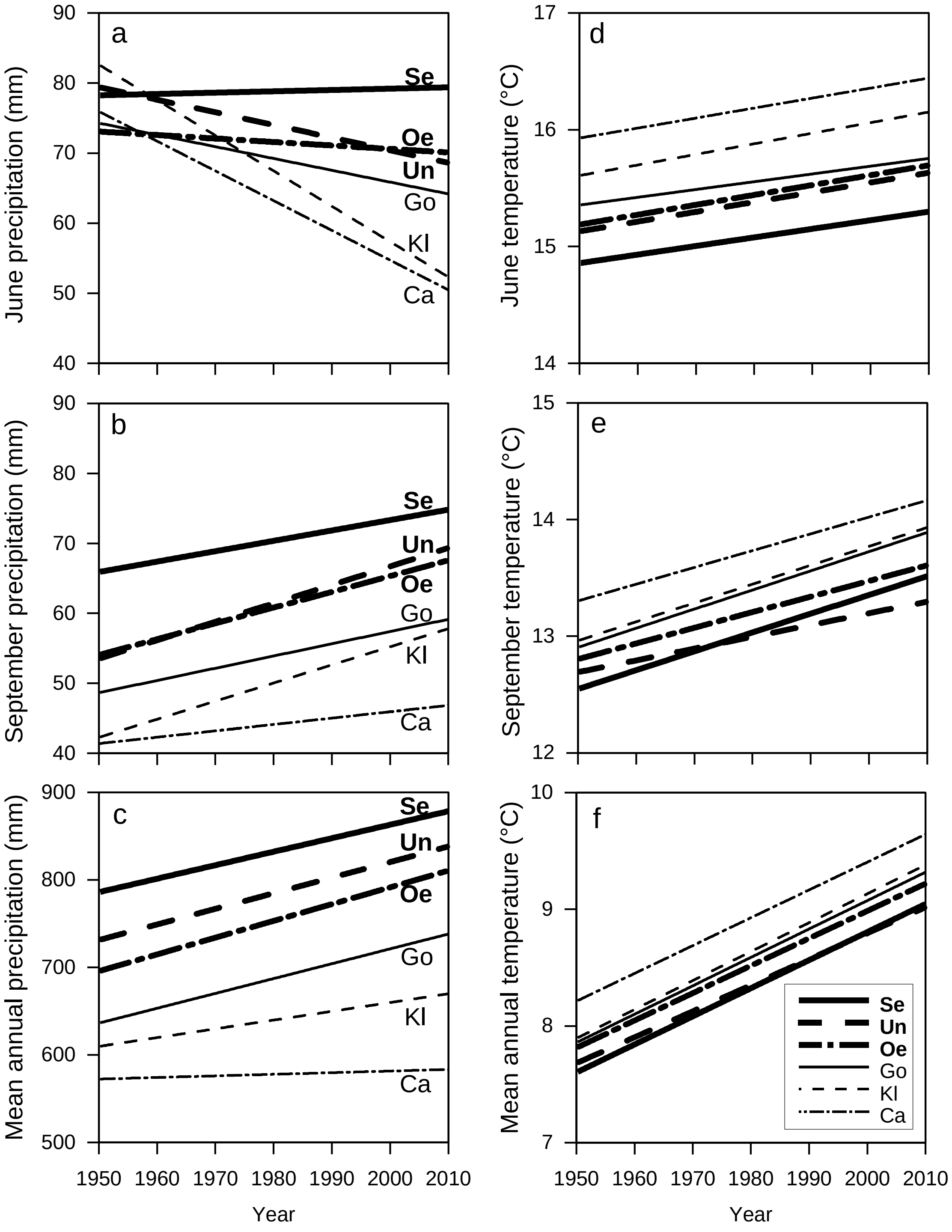

Figure 3.2. Trends in (a) precipitation in June, (b) precipitation in September, and (c) mean annual precipitation, as well as (d) temperature in June, (e) temperature in September, and (f) mean annual temperature from 1951 to 2010 in 11 mature beech stands at six locations along the investigated precipitation gradient in northwestern Germany.

Variability of stem increment during the last decades

Mean tree ring width varied between 1.3 and 2.4 mm per year among the 11 mature beech stands investigated (Table 3.2), and decadal means of BAI derived from the tree ring chronologies varied between 12 and 33 cm^{2}yr^{-1} (Figure 3.3). BAI remained relatively constant (sites: *Se*L, *Un*L, *Un*S) or increased (sites: *Se*S, *Oe*, *Go*S) in the moister beech stands (>700 mm yr^{-1}, or >345 mm from April to September) over the last six decades (Figure 3.3a), while it decreased in all five drier beech stands (<660 mm yr^{-1}, or <345 mm from April to September) since the 1960s and 1970s from about 24 to 16 cm^2 yr^{-1} (Figure 3.3b and A3.3 in the Appendix).

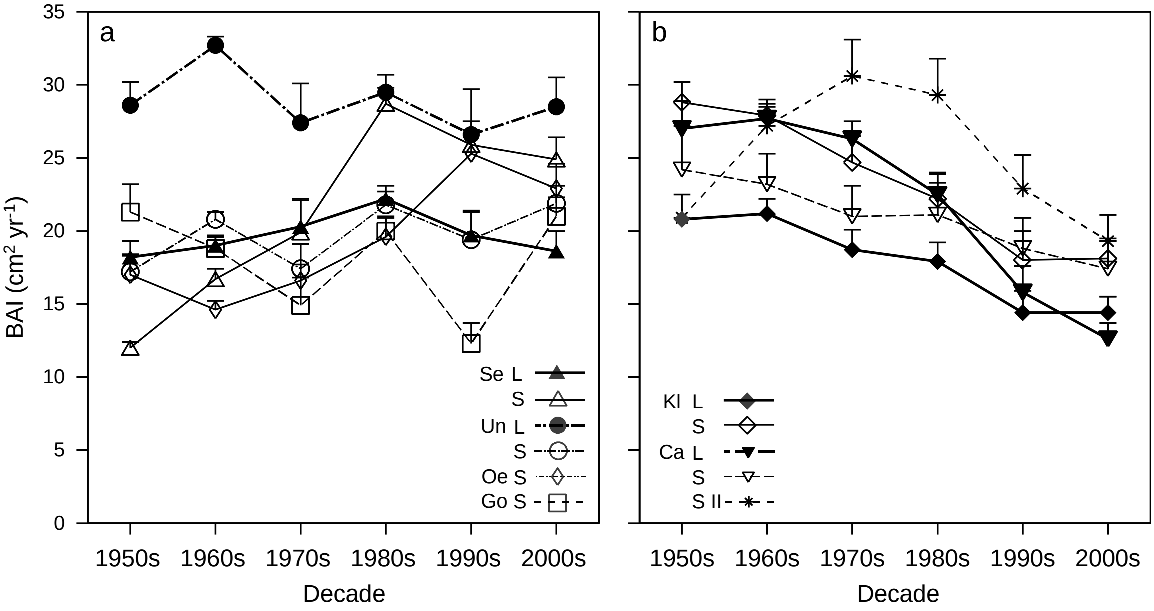

Figure 3.3. Basal area increment (BAI) of the each ten dominant beech trees per stand from 1951 to 2010 (decadal means and SE over the each 10 trees) in (a) the 6 stands with MGSP >350 mm (or MSP >200 mm) and (b) the 5 stands with MGSP <350 mm (or MSP <200 mm).

According to a multiple regression analysis, the main factors influencing BAI were PCA Climate 1 (which is related to precipitation and temperature) and PCA Climate 2 (related to WSC), but not any other PCA axes, which were related to parameters of nutrient availability, tree age or stand structure (Table 3.3).

Table 3.3. Multiple regression analysis with forward variable selection on the effects of the parameter groups climate, soil, and stand structure (as derived from principal components analyses; cf. Table A.3.2) on mean basal area increment (BAI) of 110 dominant beech trees from 11 mature beech stands located along a precipitation gradient in northwestern Germany. Values given are the determination coefficient R^2 and the probability of error *P* for the model and the *F* value and probability of error *P* for the selected predictors. The + or – signs at the predictor variables indicate positive or negative relationships.

	Model					
Y	R^2	*P*		**Predictor**	*F*	*P*
BAI	0.46	0.08	+	Climate 1	6.5	0.03
			-	Climate 2	0.7	0.44

The trend of a decline in BAI at the drier sites started in the 1970s at the latest, when the underlying age effect on the variance of BAI became insignificant and the climate signal dominated the variation in BAI (Table 3.4; Figures A.3.1- A.3.3).

Table 3.4. General linear model (proc GLM) analyzing the influence of annually resolved precipitation amounts and tree age on the variance of mean basal area increment (BAI) of 110 dominant beech trees from 11 mature beech stands located along the investigated precipitation gradient. The ANCOVAs were conducted separately for each decade between 1951 and 2010. Values given are the *F* value and probability of error *P*. Significance is indicated at $P \leq 0.05$ and ≤ 0.001 as * and ***, respectively.

		Predictor			
		Precipitation		Age	
Y	**Period**	*F*	*P*	*F*	*P*
BAI	1951-1960	64.0	***	409.5	***
	1961-1970	0.3		5.9	*
	1971-1980	14.8	***	1.3	
	1981-1990	0.1		3.9	
	1991-2000	5.2	*	0.1	
	2001-2010	6.1	*	0.5	

Negative growth deviations in pointer years appeared until the 1973-pointer year mainly at the driest forest site with MAP of less than 600 mm yr^{-1}, while from the 1976-pointer year onwards, growth was depressed at all sites simultaneously in the strong pointer years 1976 and 2000 (Table 3.5, Figure A.3.5). In addition, the frequency of pointer years increased at the moister sites of the precipitation gradient. While in the forest stands with a MGSP >345 mm, the number of negative pointer years increased from one event during the period 1951-1970 to three during the 1971-1990 interval, and to seven between 1991 and 2010, the number of negative pointer years in stands with a MGSP <345 mm remained more or less constant with four to six events during all three 20-year intervals.

Table 3.5. Negative growth deviations δ*pi* in pointer years between 1951 and 2010 in 11 mature beech stands at six locations along a precipitation gradient in northwestern Germany. Masting year in ^{LS} Lower Saxony and ^{SA} Saxony-Anhalt with at least 40 % fruiting beech trees (according to Niedersächsische Landesforsten, data available from 1991).

Site	**Se**	**Un**	**Oe**	**Go**	**Kl**	**Ca**
MGSP (mm)	**419**	**394**	**384**	**367**	**344**	**310**
1954						-121
1957						-51
1959						-108
1960		-105		-63		
1963						-70
1973						-51
1976	-94	-97	-58	-75	-85	-71
1983	-78				-59	
1989					-55	-92
1992 $^{NS\ SA}$	-59	-79				-85
1995 $^{NS\ SA}$		-70			-56	
1996						-73
1998 $^{NS\ SA}$						
2000 $^{NS\ SA}$	-101	-159	-95	-119	-119	-108
2002^{SA}						
2004$^{NS\ SA}$	-70	-98	-93		-69	
2006 $^{NS\ SA}$						
2009 $^{NS\ SA}$						

Climate response of radial growth

The multiple regression models for the effect of precipitation, temperature and sunshine duration on the ring width of dominant trees were statistically significant for the amount of precipitation in June of the current year as well as for the amount of precipitation and heat intensity in September of the preceding year (Figure 3.4). In all stands except for *Ca*, the positive influence of June precipitation was larger than that of other months or of summer (June-August) or growing season precipitation (April-September).

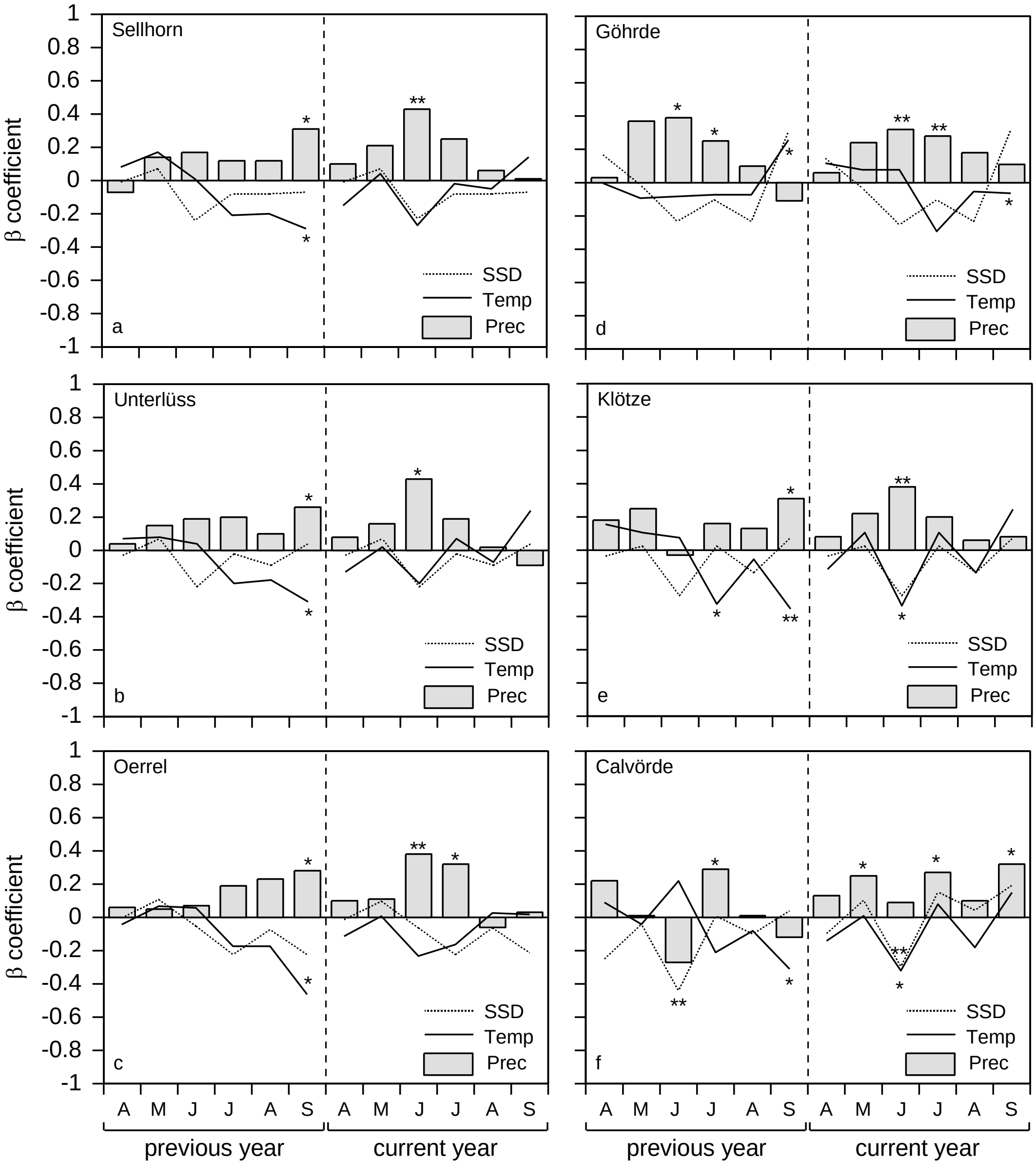

Figure 3.4 Standardized coefficients of the response of tree ring width of 20 (in Calvörde 30) dominant trees to monthly precipitation (Prec), temperature (Temp), and sunshine duration (SSD) of the year before ring production and during the year of tree ring production for (a) Sellhorn (MGSP: 419 mm), (b) Unterlüss (MGSP: 394 mm), (c) Oerrel (MGSP: 384 mm), (d) Göhrde (MGSP: 365 mm), (e) Klötze (MGSP: 344 mm) and (f) Calvörde (MGSP: 310 mm). The trees on the sandy and sandy-loamy plots of a site were pooled. Significance is indicated at P ≤ 0.05, ≤ 0.01, and ≤ 0.001 as *, **, and ***, respectively.

The multiple regression analyses also revealed for the year of ring production, that the radial growth of trees on sandy soil is mostly influenced by June precipitation, while the growth of trees on sandy-loamy soil is not only affected by June precipitation but additionally by other climatic factors like June temperature as well. Generally, sunshine duration had only a minor influence on radial growth. A remarkable finding is that the negative influence of temperature both in June and in September of the last year on ring width became increasingly important toward the driest sites (*Kl* and *Ca*), while June temperature had no effect in the moister stands (*Se*, *Un*, and *Oe*).

Climate change responses of ring width and BAI across the precipitation gradient

Apart from radial growth responses to climate at the monthly or annual time scales, we also investigated decade-long growth trends in their relation to climate warming and summer drying for the trees along the precipitation gradient. Across the gradient, mean June precipitation had a significant positive effect on mean BAI in the 1990s ($R^2 = 0.24$, $P = 0.03$) and in the 2000s ($R^2 = 0.45$, $P = 0.005$; Figure 3.5). In the latter period, mean BAI increased by 6 cm^2 yr^{-1} with an increase in MGSP by 100 mm.

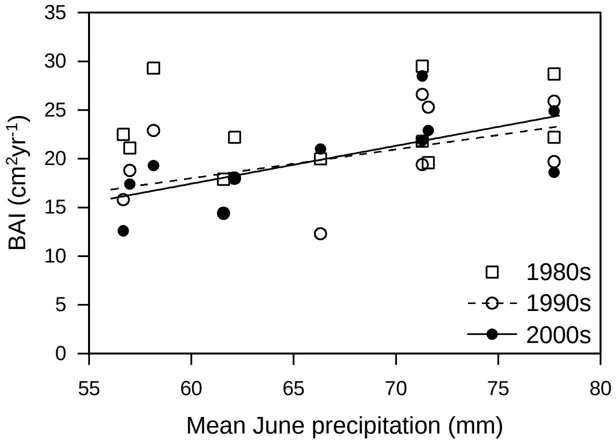

Figure 3.5. Relationship of mean basal area increment (BAI) of each ten dominant beech trees per stand with mean June precipitation in the11 mature beech stands along the precipitation gradient in northwestern Germany for the periods 1981-1990, 1991-2000 and 2001-2010. The relationship between mean BAI and MGSP was not significant in the period 1981-1990, significant in the periods 1991-2000 (y= 0.29-0.30x, R^2=0.24, P=0.03), and 2001-2010 (y=-5.9+0.39x, R^2=0.45, P=0.005). Similar relationships existed for mean summer (June-August) and mean growing season precipitation (April – September).

On sandy soil, the level of autocorrelation in the beech tree ring chronologies for the period 1951-2010 increased significantly from the dry to the moist stands (Figure 3.6a), indicating decreasing growth dependence on precipitation and other external factors. Correspondingly, the sensitivity of radial growth increased from the moister to the drier stands (Figure 3.6b).

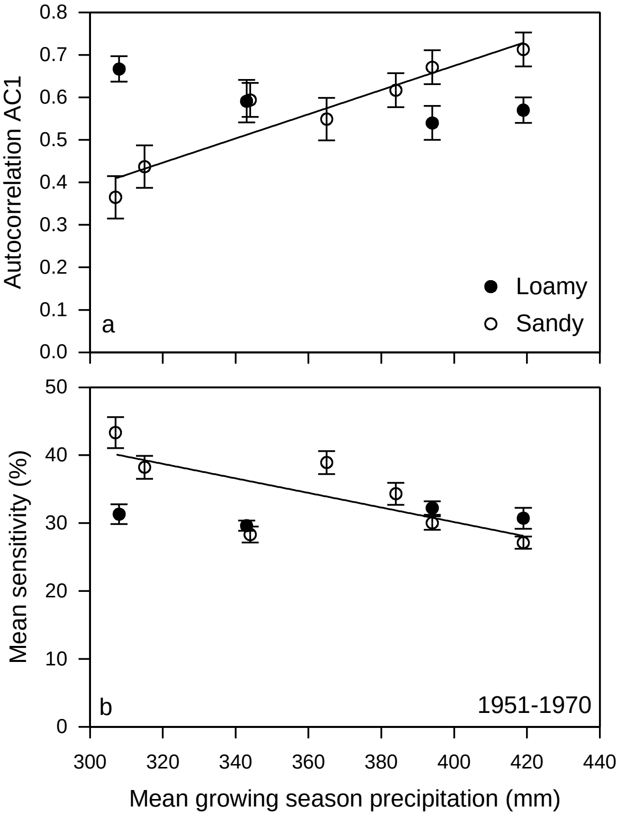

Figure 3.6. Relationship of (a) first-order autocorrelation (AC1) and (b) mean sensitivity of each ten dominant beech trees with mean growing season precipitation (MGSP, April - September) in 11 stands on sandy-loamy or sandy soil in the period 1951-2010. At the sandy sites, the correlations of both AC (y= -0.47-0.003x, R^2=0.90, P<0.001) and MS (y= 73.0-0.11x, R^2=0.53, P=0.03) with MGSP were significant.

Splitting the considered 60-yr period into three 20-yr intervals shows that AC1 from 1951 to 1970 had an average for all stands of 0.32± 0.05. This was comparable to the period from 1971 to 1990 (mean 0.4 ± 0.03), but in the most recent period from 1991 to 2010, mean AC1 dropped to 0.2 ± 0.03 (Figure 3.7a-c). Mean sensitivity (MS) increased from 29.5% (± 2.5) across all stands in 1951-1970 to 32.3± 1.2% in 1971-1990 and to 40.3± 1.9% in 1991-2010. MS was negatively related to MGSP in the 1951-1970 and 1991-2010 intervals (steeper slope in the first period), but no relation existed in the 1971-1990 interval (Figure 3.7d-f).

Nearly all sites showed an increase in MS during the last decades (Figures A.3.1-A.3.3). The relationship of first order autocorrelation (AC1) with MGSP was highly significant before the 1970s with a slope of 0.003 showing low AC1 values in beech stands with <320 mm MGSP (Figure 3.7a). In the subsequent time period (1971-1990), the relationship was not significant (Figure 3.7b). In the most recent period from 1991-2010, the relationship between MAP and AC1 was significant, but with a smaller slope (0.002) than in the 1951-1970 period and smaller AC1 values across the whole precipitation gradient (Figures 3.7c).

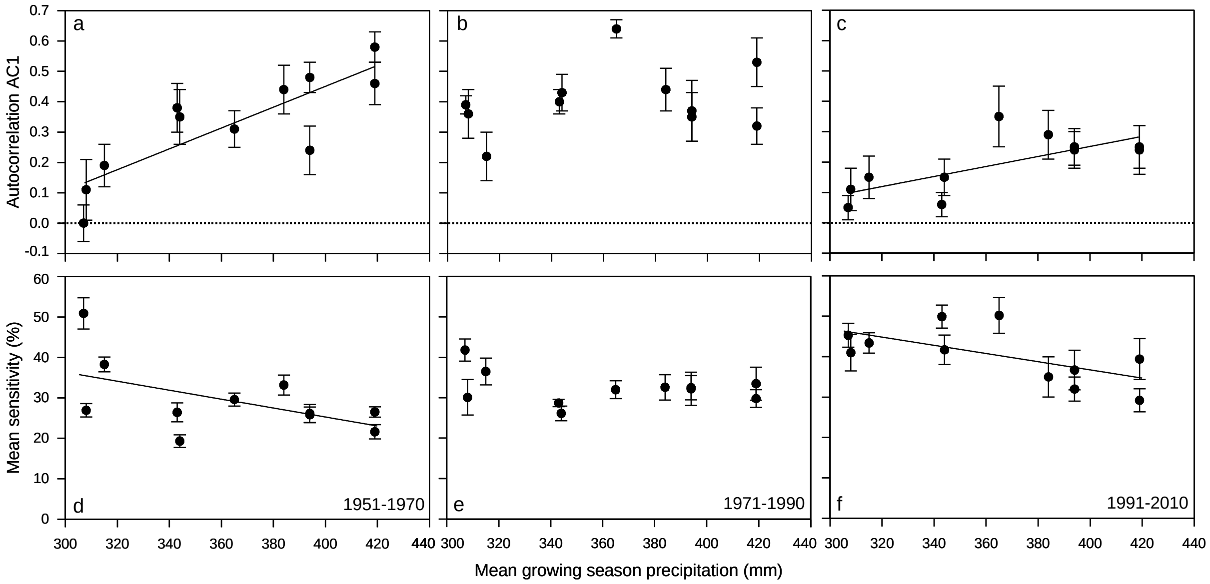

Figure 3.7. Relationship of (a-c) first-order autocorrelation (AC1) and (d-f) mean sensitivity of each ten dominant beech trees with mean growing season precipitation (MGSP, April - September) in 11 mature beech stands for the periods (a, d) 1951-1970, (b, e) 1971-1990, and (c, f) 1991-2010. The correlations of both AC1 and MS with MGSP were significant in the earliest (AC1: y= -0.9-0.003x, R^2=0.71, P<0.001; MS: y= 72.7-0.12x, R^2=0.33, P=0.02) and latest period (AC1: y= -0.41-0.002x, R^2=0.52, P<0.006; MS: y= 77.3-0.10x, R^2=0.40, P=0.02).

In the three pan-European drought summers 1976, 2000 and 2003, the drought tolerance indices Rt, Rc and Rs showed significant growth decreases (negative Rt values) at all sites during the three events (Figure 3.8). However, a much higher recovery (Rc index) in 2000 and 1976 than in 2003 and a reduction in Rs values (resilience) was observed. This reflects the growth decline in the last decades, while in 1976 moister stands suffered more but recovered faster after drought than drier stands. This relation had disappeared in the 2000 and 2003 events.

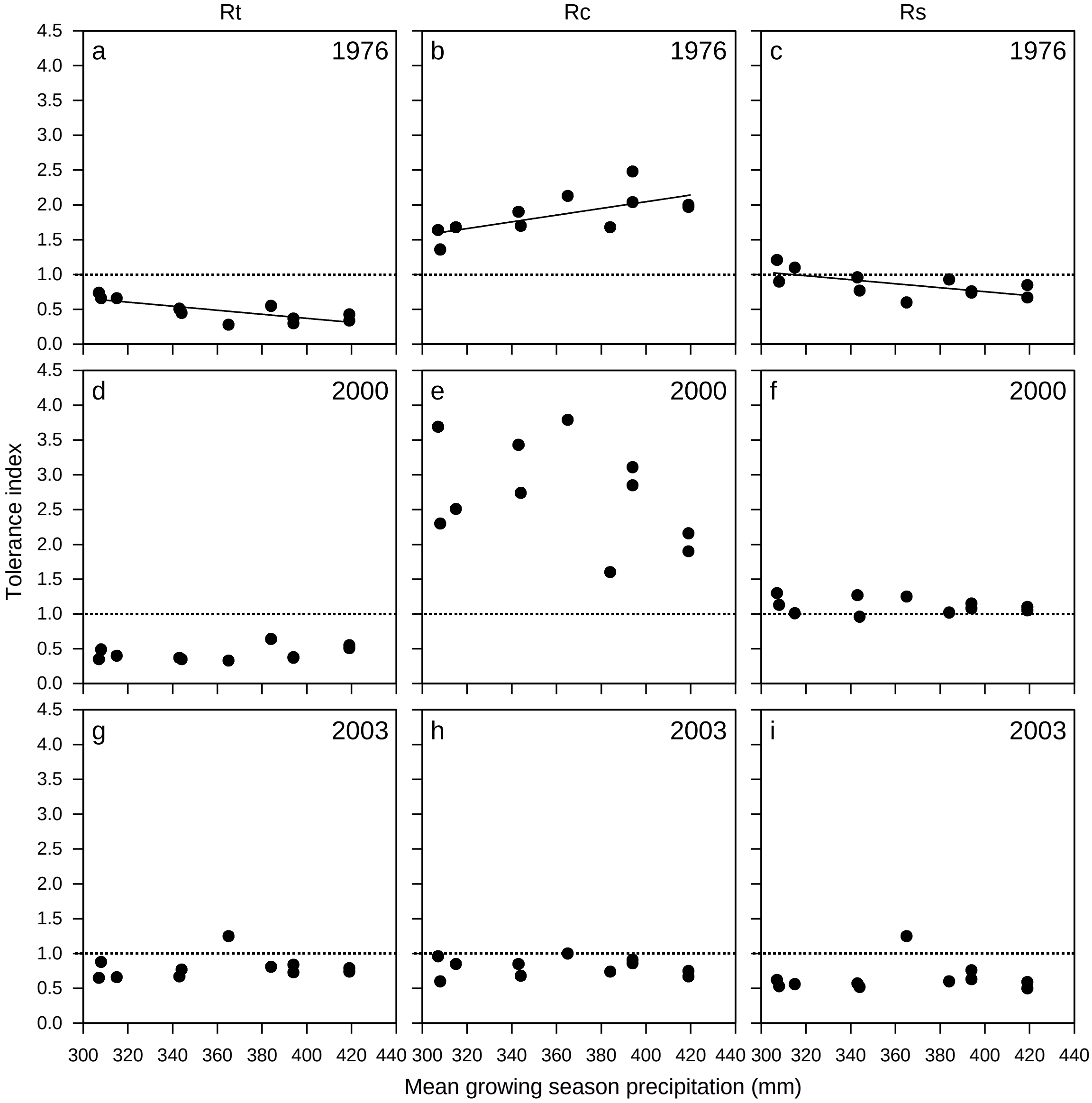

Figure 3.8. Relationship of the tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) with mean growing season precipitation (MGSP, April – September) in each ten dominant beech trees per stand in 11 mature forest stands during the pan-European drought years 1976 (a-c), 2000 (d-f),and 2003 (g-i). A two-year period was chosen for the pre-drought and post-drought periods. The relationships between the tolerance indices Rt (y= 1.53 0.003x, R^2=0.61, P=0.002), Rc (y= 0.12-0.005x, R^2=0.46, P=0.01), and Rs (y= 1.89-0.003x, R^2=0.43, P=0.01) with MGSP were significant for the drought year 1976 ($P \leq 0.05$) but not significant for the drought years 2000 and 2003. The dashed lines indicate unity.

Discussion

Global warming effects on beech radial growth

The results of this study indicate that recent global warming causes a radial growth decline in *F. sylvatica* even in the center of the species' distribution range when water supply is less favorable. We found a consistent decrease in BAI since the 1980s in the five stands with MGSP (April – September) of less than 345 mm (Figure 3.3). This growth decline in the eastern part of the transect was more pronounced on sandy-loamy than on sandy soil and cannot be explained by a tree age effect because the multiple regression analysis showed precipitation and soil WSC to be the only determinants of BAI variation but detected no tree age or stand structure effect (Table 3.3). An age-dependent growth decline can be excluded also because any age effect visible on radial growth disappeared after the 1970s according to the general linear model which was calculated separately for the decades since 1950 (Table 3.4). Finally, most trees of our study were 80-120 years old which is younger than the age when a senescence-driven BAI decrease may begin in *F. sylvatica* (Jump et al. 2006).

Our results match earlier findings on a recent growth decline in central European *F. sylvatica* populations as reported from northern Switzerland (Weber et al. 2013: on shallow soil at ~1100 mm yr^{-1} precipitation), in the lowlands of north-east Germany (Scharnweber et al. 2011: on sandy soil at <595 mm yr^{1}) and in the uplands of central Germany (Zimmermann et al. 2015: 600-640 mm yr^{-1}). Summer precipitation thresholds (June –August) in central and northern Germany were in this present study identified with ~200 mm, and in central Germany with 190 mm (Zimmermann et al. 2015) beyond which a negative growth trend was observed. Thus, the turning point is found in a relatively narrow precipitation range given that the edaphic conditions are quite diverse, and the climate ranges from sub-oceanic to sub-continental in the three studies.

Our study has produced convincing evidence that climate warming gains increasing importance as a stressor in *F. sylvatica* stands in the lowlands of northwestern Germany. Apart from the long-term growth reduction in the east of the gradient, we found (1) since the 1950s increasing mean sensitivity of radial growth to climate variationat four of the six sites, while the (2) degree of autocorrelation decreased. This finding is in line with other studies that reported a marked increase in mean sensitivity of growth of *F. sylvatica* since *c.* 1990 (e.g., Beck 2009, Scharnweber et al. 2011, Beck and Heußner 2012). Even though some controversy exists with respect to the interpretation of sensitivity data (e.g., Bunn et al. 2013), the increase in this parameter at most of our sites is obvious. The picture of an increasing climate warming impact is further supported by the observation that (3) a dependence of BAI on growing season precipitation across our gradient was absent before 1990 but developed only since then with a marginally significant relation in the 1990s and a significant one since 2000. Strong indication of increased climate stress is also (4) the more frequent occurrence of negative pointer years since 1976 at all sites except for the driest one (Ca) where they were relatively frequent already before 1976 (Table 3.5). Today, stands in moister climates are showing symptoms of climate sensitivity that were characteristic for the driest stands 40 years ago. One future scenario for the moister stands can be that the more frequent negative pointer years are leading to a similar growth decline as observed in the drier stands since the 1980s.

Extreme summer droughts like in 1976, 2000 and 2003 will probably occur with increasing frequency in the decades to come (e.g., Schär et al. 2004, Bréda and Badeau 2008). In 1976, all major tree species in Central Europe were affected by a cold and long winter and cool spring, which was followed by a hot and dry summer. These two harmful events resulted in an outstanding negative pointer year in all our stands and elsewhere (Beck 2011). The drought years 2000 and 2003 also impacted on all stands irrespective of the mean precipitation level, but the two events differed strongly in their index of beech growth recovery (Rc). In 2003, the index was particularly low (0.5-1.0). We speculate that this may either be caused by the short time interval between the 2000 and 2003 events, or related to the fact that both 2000 and the year after the 2003 drought were masting years.

Climatic factors likely driving the growth decline

It is likely that declining summer precipitation is one driver of the observed growth decline at the drier sites of our study region. This is suggested by the marked decrease in mid-summer precipitation especially at the sites *Ca* and *Kl*, where radial growth declined since about the 1960s and 1970s. The response analysis in Figure 3.4 indicates that June rainfall exerts the largest influence on radial growth of beech in our study region. At five of the six sites, the effect of June rainfall was more relevant than that of summer (June-August) or growing season precipitation (April-September). Only at the driest site (*Ca*), the April-September rainfall was more influential than June rainfall (Figure 3.4f). The outstanding role of mid-summer precipitation is in accordance with other studies on the climate-growth relation in temperate trees (e.g.,Bouriaud et al. 2005, Lebourgeois et al. 2005, Hacket-Pain et al. 2015, Zimmermann et al. 2015). According to Čufaret al. (2008), June can be considered as the most important month for tree-ring formation in *F. sylvatica* in Central Europe, where up to 35% of the entire tree ring is normally formed. By the end of June, 75% of the tree ring is typically completed followed by cambial cell division stagnation until mid-August.

Scharnweber et al. (2011) found for northeastern Germany also the closest correlation between seasonal climatic parameters and ring width for current year's June. Other studies on the cambial activity and xylogenesis of *F. sylvatica* from stands all over Europe showed in accordance that drought in April and June had the strongest negative effect on growth (e.g. Michelot et al. 2012, Prislan et al. 2013; Vavrčík et al. 2013, Rozas et al. 2015) which is explained by the onset of cambial activity in April and highest radial growth rates in June. This has important implications for the likely future of beech forests in the lowlands of central-northern Germany: June rainfall is the precipitation component with largest decrease in the past decades at four of the six sites, implying further growth decline when this trend is continuing in the 21st century as predicted by regional climate scenarios. Our finding that warmer temperatures in previous year's September have a negative effect on radial growth can perhaps be explained with the observed latewood cell wall thickening in this month (Lebourgeois et al. 2005) which consumes resources that are not available for next year's radial growth.

However, a mid-summer precipitation decrease was also recorded at the site *Un* with relatively high annual precipitation, where no recent growth decline occurred. This indicates that either the marked increase in mid-summer temperature (by ~0.5°C since 1950) or the associated increased in atmospheric water vapor saturation deficit must have contributed to the growth decline at the sites *Kl* and *Ca*. In fact, the response analysis evidences a negative effect of elevated mid-summer temperatures (in particular of current year's June) and of previous year's autumn (September) on radial growth, and this effect was more pronounced at the driest sites *Kl* and *Ca* (Figures 3.3a, b and 3.4). A direct negative effect of elevated summer temperatures on the photosynthesis or growth of temperate trees has only rarely been proven so far (e.g., García-Plazaola and Becceril 2000, Alvarez-Uria and Körner 2007). Köcher et al. (2013) could show that elevated air humidity is a main driver of higher radial growth in beech. Drier air in a warmer summer could therefore negatively impact on cambial growth. The effects of higher temperatures and elevated vpd will be difficult to disentangle. In any case, correlative analyses have proven similarly strong negative effects of higher summer temperatures and of reduced summer precipitation on the radial growth of beech (e.g. Zimmermann et al. 2015) indicating that precipitation reduction may not be the only factor impeding growth.

In other regions of Europe, different climate-growth relationships may exist in *F. sylvatica* than found in this study. In southwestern Europe, water availability in summer is also a major driver of radial growth, but other than in Central Europe, May temperature and precipitation during winter are playing important roles as well (e.g., Biondi 1993, Piovesan et al. 2005, Lebourgeois et al. 2005). In colder regions, low winter temperatures often affect tree growth through freezing embolism (Lemoine et al. 1999) which was not detectable in our study. At higher elevation, the temperature dependence of growth turns into a positive relation and cloudiness is often an important factor limiting photosynthesis (e.g., Dittmar et al. 2003, Graham et al. 2003, Di Fillipo 2007, Peñuelas et al. 2008, Rozas et al. 2015).

Another factor that may influence radial growth is mast fruiting of beech which is influenced in a complicate manner by climate warming (Müller-Haubold et al. 2015). Full mast in *F. sylvatica* greatly reduces stem radial growth and thus is often responsible for negative pointer years (Schweingruber 1996, Mund et al. 2010, Hacket-Pain et al. 2015). Since the frequency of beech masting has increased during the last decades in Central Europe (Hilton and Packham 2003, Övergaard et al. 2007), long-term growth decline could in theory also result from a tree-internal allocation shift from stem growth to fruit production. In our study region, information on masting events was available for the last 20 years (1991-2010), i.e. a third of the observation period (Table 3.5). In this period, eight mast years occurred, four of which were negative pointer years. Since only one negative pointer year was not a masting year, it seems that masting plays an important role in the explanation of growth reductions in pointer years and probably for long-term growth trends as well. Müller-Haubold et al. (2015) could show that masting likely is triggered by an extraordinarily high radiation input (and probably high temperatures) in the year prior to a mast, while drought itself is not influential. Climate warming with reduced precipitation and elevated temperatures and sunshine duration during mid-summer thus may act on stem growth through at least two pathways, (i) directly via reduced soil moisture availability (and possibly increased VPD), and (ii) indirectly through a higher masting frequency. This could explain why both reduced precipitation and elevated temperature in mid-summer (which is related to higher sunshine duration) are negatively influencing radial growth in recent time.

The role of edaphic factors

A remarkable result of our study is that the stands on sandy-loamy soil did not differ significantly from those on sandy soil with respect to mean annual ring width and also mean sensitivity of growth (Table A.3.1), even though the former have a higher soil WSC. Even more astonishing is that the sandy-loamy sites had an on average stronger growth decline since the 1980s at the drier sites than the corresponding sandy sites; this is mainly caused by the strong growth decline of the sandy-loamy *Ca* stand at the dry end of the gradient.

However, the stands on sandy soil at the dry *Kl* and *Ca* sites had the highest mean sensitivity and lowest autocorrelation of all 11stands and thus may be particularly vulnerable to climate warming. In contrast, no relation between growing season precipitation and mean sensitivity (and autocorrelation) existed across the loamy sites. When interpreting differences between the two substrate categories, some structural differences between sandy and sandy-loamy sites must be considered. The sandy stands were on average 13years younger than the sandy-loamy stands which may perhaps be an explanation of the stronger recent growth decline of the loamy sites. Yet, stem density was higher in the sandy stands which might have increased the intensity of competition for water in these stands (Table A.3.1). In any case, the rather similar growth performance of stands on sandy and more loam-rich substrate is remarkable because it seems to indicate that the effect of soil WSC is relatively minor in our study region. This could result from the fact that all investigated Pleistocene substrates have similar profile depths (>1 m) and that the soil texture differences between sandy and sandy-loamy profiles are only moderate. A comparison of sites with largely different soil profile depths as done by Weber et al. (2013) should detect more pronounced effects of soil WSC.

Conclusions

Our study produced convincing evidence that global warming is already acting as a major stressor in *F. sylvatica* stands even in the center of the species' distribution range. Our first hypothesis that recent global warming is locally causing a growth decline in *F. sylvatica* in northwestern Germany was confirmed. The results of this gradient study and other published dendrochronological studies in *F. sylvatica* in central and northern Germany allow for the first time to define a minimum summer precipitation level which seems to be necessary for vital beech growth in the center and north of its distribution range. This threshold is located close to 660 mm of annual precipitation, 350 mm of growing season precipitation (April – September) or 200 mm of summer precipitation (June-August).

Our second hypothesis of an increasing climatic impact on the growth of *F. sylvatica* since about the 1970s was also supported but different criteria revealed different time frames of response. Mean ring width sensitivity seems to have increased (and first-order autocorrelation decreased) in several stands already since the 1950s; however, we cannot exclude that the trees have improved their demographic position in the canopy by achieving greater dominance since the 1950s. If so, this may have exposed them to a more stressful atmospheric environment with growing age, which could have increased ring width sensitivity. Both the

BAI decrease and the increased frequency of negative pointer years became visible from the 1960s and 1970s onwards, which is somewhat earlier than the onset of declining growth observed since about the 1980s in central German beech stands by Zimmermann et al. (2015).

Unexpected is that our third hypothesis of a soil moisture effect on the extent of growth decline was not supported. Although mean sensitivity showed a dependence on precipitation only on the sandy, but not on the loam-richer sites, the BAI decline at the drier sites was stronger on the loam-richer than the sandy soils indicating clear priority for the climatic over the edaphic effect. The role of soil water storage for the growth dynamics of beech requires further study by considering other geologic substrates and soil types.

Given that regional climate change scenarios predict a further decrease in summer precipitation for parts of central and eastern Germany and beyond (Jacob et al. 2014); the above-defined summer precipitation thresholds for vital beech growth may even be too low for safeguarding *F. sylvatica* stands until the time of harvest in 100-120 years. It is likely that not only beech stands in regions with actually <200 mm of summer precipitation will face growth decline in the future but stands in currently moister regions as well. The results of our study call for careful tree species selection by foresters in all those central European beech forest regions where precipitation is already below the precipitation thresholds elaborated here. *F. sylvatica* may lose part of its range in the managed and natural forest area of Central Europe upon climate warming. These findings suggest that other mesophytic tree species of the temperate forests in North America and Eurasia might also be at drought risk, even though the climate is oceanic or sub-oceanic, notably other *Fagus* or *Acer* species which dominate large forest areas in the eastern U.S., in Japan, south-western Asia and elsewhere.

Acknowledgements

We are grateful to Hanns-Hubert Leuschner, Hilmar Müller-Haubold and Jorma Zimmermann for valuable comments on the results. This work was supported by grants provided by the Ministry for Science and Culture of Lower Saxony (Germany) in the context of the program “Klimafolgenforschung in Niedersachsen” (KLIFF; climate response research in Lower Saxony).

Conflict of interest

None declared.

References

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EHT, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Alvarez-Uria P, Körner C (2007) Low temperature limits of root growth in deciduous and evergreen temperate tree species. *Functional Ecology*, **21**, 211–218.

Baillie MGL, Pilcher JR (1973) A simple crossdating program for tree-ring research. *Tree-Ring Bulletin*, **33**, 7–11.

Beck W (2009) Growth patterns of forest stands - the response towards pollutants and climatic impact. *iForest-Biogeosciences and Forestry*, **2**, 4–6.

Beck W (2011) Impact of drought and heat on tree and stand vitality – results of the study commissioned by the Federal Ministry of Food, Agriculture and Consumer Protection. In: *TRACE - Tree Rings in Archaeology, Climatology and Ecology* (eds Maaten-Theunissen M, Spiecker H, Gärtner H, Helle G, Heinrich I), PP. 20–27, GFZ Potsdam, Germany.

Beck W, Heußner KU (2012) Increased sensitivity in ring width series of common beech after 1990 – climatic impact or normal patterns due to ageing ? *Dendrosymposium*, **10**, 13–19.

Biondi F (1993) Climatic signals in tree rings of *Fagus sylvatica* L. from the central Apennines, Italy. *Acta Oecologica*, **14**, 57–71.

Biondi F (1999) Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecological Applications*, **9**, 216–227.

Biondi F, Qeadan F (2008) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research*, **64**, 81–96.

BMEL (2014) *Der Wald in Deutschland – Ausgewählte Ergebnisse der dritten Bundeswaldinventur*. Berlin: Bundesministerium für Ernährung und Landwirtschaft.

BMU (2011) *Beech forests – UNESCO world natural heritage*. Bundesministerium für Umwelt, Naturschutz, Bau und Reaktorsicherheit, Berlin, Germany.

Bouriaud O, Bréda N, Dupouey JL, Granier A (2005) Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. *Canadian Journal of Forest Research*, **35**, 2920–2933.

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625–644.

Bréda N, Badeau V (2008) Forest tree responses to extreme drought and some biotic events: towards a selection according to hazard tolerance? *Comptes Rendus Geoscience*, **340**, 651–662.

Briffa KR, Jones PD, Schweingruber FH, Karlén W, Shiyatov SG (1996) Tree-ring variables as proxy-climate indicators: problems with low-frequency signals. In: *Climatic Variations and Forcing Mechanisms of the Last 2000 Years* (eds Jones PD, Bradley RS, Jouzel J), PP. 9–41, Springer, Heidelberg, Germany.

Briffa KR, Osborn TJ, Schweingruber FH, Harris IC, Jones PD, Shiyatov SG, Vaganov EA (2001) Low-frequency temperature variations from a northern tree ring density network. *Journal of Geophysical Research*, **106**, 2929–2941.

Bunn AG, Jansma E, Korpela M, Westfall RD, Baldwin J (2013) Using simulations and data to evaluate mean sensitivity (ζ) as a useful statistic in dendrochronology. *Dendrochronologia*, **31**, 250–254.

Carsjens C, Ngoc QN, Guzy J, Knutzen F, Meier IC, Müller M, Finkeldey R, Leuschner C, Polle A (2014) Intra-specific variations of the expression of stress-related genes in beech progenies are stronger than drought-induced responses. *Tree Physiology*, **34**, 1348–1361.

Ciais P, Reichstein M, Viovy NN, Granier A, Ogée J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, de Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze

ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Cook ER (1985) A time series analysis approach to tree ring standardization. PhD Thesis. University of Arizona, USA.

Cook ER, Briffa KR, Shiyatov S (1990) Tree-ring standardization and growth-trend estimation. In: Cook ER, Kairiukstis LA, Eds. Methods of Dendrochronology: Applications in the Environmental Sciences. Dordrecht: Kluwer. Pp. 104–124.

Čufar K, Prislan P, de Luis M, Gričar J (2008) Tree-ring variation, wood formation and phenology of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees - Structure and Function*, **22**, 749–758.

Di Filippo A, Biondi F, Čufar K, de Luis M, Grabner M, Maugeri M, Presutti Saba E, Schirone B, Piovesan G (2007) Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: Spatial and altitudinal climatic signals identified through a tree-ring network. *Journal of Biogeography*, **34**, 1873–1892.

Dittmar C, Zech W, Elling W (2003) Growth variations of Common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe - A dendroecological study. *Forest Ecology and Management*, **173**, 63–78.

Dobbertin MK, Grissino-Mayer HD (2004) The online bibliography of dendrochronology. *Dendrochronologia*, **21**, 85–90.

Eckstein D, Bauch J (1969) Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. *Forstwissenschaftliches Centralblatt*, **88**, 230–250.

Ellenberg H, Leuschner C (2010) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Hinsicht*. Ulmer, Stuttgart, Germany.

Garamszegi B, Kern Z (2014) Climate influence on radial growth of *Fagus sylvatica* growing near the edge of its distribution in Bükk Mts., Hungary. *Dendrobiology*, **72**, 93–102.

García-Plazaola JI, Becerril JM (2000) Effects of drought on photoprotective mechanisms in European beech (*Fagus sylvatica* L.) seedlings from different provenances. *Trees - Structure and Function*, **14**, 485–490.

Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2003) Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 572–576.

Hacket-Pain AJ, Friend AD, Lageard JGA, Thomas PA (2015) The influence of masting phenomenon on growth-climate relationships in trees: explaining the influence of previous summers' climate on ring width. Tree Physiology, **35**, 319–330.

Hilton GM, Packham JR (2003) Variation in the masting of common beech (*Fagus sylvatica* L.) in northern Europe over two centuries (1800-2001). *Forestry*, **76**, 319–328.

Hogg E, Brandt JP, Kochtubajda B (2005) Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. *Canadian Journal of Forest Research*, **35**, 610–622.

IPCC (2013) Summary for policymakers. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), PP. 1535. Cambridge University Press, Cambridge, UK.

Jacob D, Petersen J, Eggert B, Alias A, Christensen OB, Bouwer LM, Braun A, Colette A, Déqué M, Georgievski G, Georgopoulou E, Gobiet A, Menut L, Nikulin G, Haensler A, Hempelmann N, Jones C, Keuler K, Kovats S, Kröner N, Kotlarski S, Kriegsmann A, Martin E, Meijgaard E, Moseley C, Pfeifer S, Preuschmann S, Radermacher C, Radtke K, Rechid D, Rounsevell M, Samuelsson P, Somot S, Soussana J-F, Teichmann C, Valentini R, Vautard R, Weber B, Yiou P (2013) EURO-CORDEX: new high-resolution climate change projections for European impact research. *Regional Environmental Change*, **14**, 563-578.

Jantsch MC, Fischer A, Fischer HS, Winter S (2013) Shift in plant species composition reveals environmental changes during the last decades: a long-term study in beech (*Fagus sylvatica*) forests in Bavaria, Germany. *Folia Geobotanica*, **48**, 467–491.

Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.

Köcher P, Horna V, Leuschner C (2013) Stem water storage in five coexisting temperate broad-leaved tree species: Significance, temporal dynamics and dependence on tree functional traits. *Tree Physiology*, **33**, 817–832.

Lebourgeois F, Bréda N, Ulrich E, Granier A (2005) Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees - Structure and Function*, **19**, 385–401.

Lemoine D, Granier A, Cochard H (1999) Mechanism of freeze-induced embolism in *Fagus sylvatica* L. *Trees - Structure and Function*, **13**, 206–210.

Lloret F, Keeling EG, Sala A (2011) Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, **120**, 1909–1920.

Meier IC, Leuschner C (2008) Genotypic variation and phenotypic plasticity in the drought responseof fine roots of European beech. *Tree Physiology*, **28**, 297-309.

Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature*, **397**, 659–659.

Metz J, Seidel D, Schall P, Scheffer D, Schulze ED, Ammer C (2013) Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra- and interspecific competition on tree growth. *Forest Ecology and Management*, **310**, 275–288.

Michelot A, Bréda N, Damesin C, Dufrêne E (2012) Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *Forest Ecology and Management*, **265**, 161–171.

Müller-Haubold H, Hertel D, Seidel D, Knutzen F, Leuschner C (2013) Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. *Ecosystems*, **16**, 1498–1516.

Müller-Haubold H, Hertel D, Leuschner C (2015) Climatic drivers of mast fruiting in European beech and resulting C and N allocation shifts. *Ecosystems*, doi: 10.1007/s10021-015-9885-6.

Mund M, Kutsch WL, Wirth C, Kahl T, Knohl A, Skomarkova MV, Schulze ED (2010) The influence of climate and fructification on the inter-annual variability of stem growth and netprimary productivity in an old-growth, mixed beech forest. *Tree Physiology*, **30**, 689–704.

Nakawatase JM, Peterson DL (2006) Spatial variability in forest growth – climate relationships in the Olympic Mountains, Washington. *Canadian Journal of Forest Research*, **36**, 77–91.

Övergaard R, Gemmel P, Karlsson M (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry*, **80**, 555–565.

Parry ML (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability: Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Peñuelas J, Hunt JM, Ogaya R, Jump AS (2008) Twentieth century changes of tree-ring δ^{13}C at the southern range-edge of *Fagus sylvatica*: Increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. *Global Change Biology*, **14**, 1076–1088.

Piovesan G, Bernabei M (1997) Influence of summer precipitation on growth and reproduction of beech in a southern site of the range. *Italia Forestale e Montana*, **6**, 444–459.

Piovesan G, di Filippo A, Alessandrini A, Biondi F, Schirone B (2005) Structure, dynamics and dendroecology of an old-growth *Fagus* forest in the Apennines. *Journal of Vegetation Science*, **16**, 13–28.

Piutti E, Cescatti A (1997) A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. *Canadian Journal of Forest Research*, **27**, 277–284.

Pócs T (2011) Signs of climate change in the bryoflora of Hungary. In: *Bryophyte Ecology and Climate Change* (eds Tuba Z, Slack NG, Stark LR), PP. 359–370. Cambridge University Press, Cambridge, UK.

Pretzsch H, Biber P, Schütze G, Uhl E, Rötzer T (2014) Forest stand dynamics in Central Europe has accelerated since 1870. *Nature Communications*, **5**, 1–10.

Prislan P, Gričar J, de Luis M, Smith KT, Čufar K (2013) Phenological variation in xylem and phloem formation in *Fagus* from two contrasting sites. *Agricultural and Forest Meteorology*, **180**, 142–151.

Rebetez M, Dobbertin M (2004) Climate change may already threaten Scots pine stands in the Swiss Alps. *Theoretical and Applied Climatology*, **79**, 1–9.

Rennenberg H, Seiler W, Matyssek R, Gessler A, Kreuzwieser J (2004) European beech (*Fagus sylvatica* L.) - a forest tree without future in the south of Central Europe. *Allgemeine Forst und Jagdzeitung*, **175**, 210–224.

Rigling A, Waldner PO, Forster T, Bräker OU, Pouttu A (2001) Ecological interpretation of tree-ring width and intraannual density fluctuations in *Pinus sylvestris* on dry sites in the central Alps and Siberia. *Canadian Journal of Forest Research*, **31**, 18–31.

Rose L, Leuschner C, Köckemann B, Buschmann H (2009) Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research*, **128**, 335-343.

Rozas V, Camarero JJ, Sangüesa-Barreda G, Souto M, García-González I (2015) Summer drought and ENSO-related cloudiness distinctly drive *Fagus sylvatica* growth near the species rear-edge in northern Spain. *Agricultural and Forest Meteorology*, **201**, 153–164.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Scharnweber T, Manthey M, Criegee C, Bauwe A, Schröder C, Wilmking M (2011) Drought matters - Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management*, **262**, 947–961.

Schönwiese CD, Grieser J, Trömel S (2003) Secular change of extreme monthly precipitation in Europe. *Theoretical and Applied Climatology*, **75**, 245–250.

Schweingruber FH (1996) Tree rings and environment: dendroecology. Paul Haupt AG, Bern, Switzerland.

Spiecker H (1999) Overview of recent growth trends in European forests. *Water, Air, and Soil Pollution*, **116**, 33–46.

Tarp P, Helles F, Holten-Andersen P, Bo Larsen J, Strange N (2000) Modelling near-natural silvicultural regimes for beech - An economic sensitivity analysis. *Forest Ecology and Management*, **130**, 187–198.

Van der Werf GW, Sass-Klaassen UGW, Mohren GMJ (2007) The impact of the 2003 summer drought on the intra-annual growth pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on a dry site in the Netherlands. *Dendrochronologia*, **25**, 103–112.

Van Herk CV, Aptroot A, van Dobben HF (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist*, **34**, 141–154.

Vavrčík H, Gryc V, Menšík L, Baar J (2013) Xylem formation in *Fagus sylvatica* during one growing season. *Dendrobiology*, **69**, 69–75.

Weber P, Bugmann H, Fonti P, Rigling A (2008) Using a retrospective dynamic competition index to reconstruct forest succession. *Forest Ecology and Management*, **254**, 96–106.

Weber P, Bugmann H, Rigling A (2007) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. *Journal of Vegetation Science*, **18**, 777–792.

Weber P, Bugmann H, Pluess AR, Walthert L, Rigling A (2013) Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees - Structure and Function*, **27**, 171–181.

Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, **23**, 201–213.

Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A (2014) Patterns of drought tolerance in major European temperate forest trees: Climatic drivers and levels of variability. *Global Change Biology*, **20**, 3767–3779.

Zimmermann J, Hauck M, Dulamsuren C, Leuschner C (2015) Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. *Ecosystems*, **18**, 560–572.

Appendix

Table A. 3.1. Means of stand structural properties and tree ring data for the four sandy-loamy and the seven sandy beech stands in northwestern Germany. Mean diameter at breast height refers to the 20 sampled beech trees. NPP_a data after Müller-Haubold et al. (2013). DBH, mean diameter at breast height; MRW, mean ring width; NPPa, aboveground net primary production (wood growth, leaf and fruit production); MS, mean sensitivity.

Site code	Age (years)	Stem density (no. ha^{-1})	DBH (cm)	MRW (mm)	Mean tree height (m)	Stand basal area (m^2 ha^{-1})	Timber volume (m^3 ha^{-1})	NPP_a (g m^{-2} yr^{-1})	MS
Sandy-loamy sites									
Se L	106	156	40.6	1.59	31.4	31.0	490	795	0.34
Un L	103	411	34.6	2.28	28.4	28.5	378	1103	0.32
Kl L	128	267	46.7	1.55	33.8	44.9	758	922	0.38
Ca L	99	300	40.1	2.11	28.3	33.3	454	903	0.32
Mean	**109**	**283**	**40.5**	**1.88**	**30.6**	**34.4**	**520**	**930.8**	**0.34**
Sandy sites									
Se S	108	367	34.6	1.72	28.0	37.0	395	918	0.28
Un S	100	611	26.7	1.50	25.3	24.3	227	788	0.32
Oe S	82	500	20.3	1.48	27.2	32.3	287	828	0.35
Go S	124	289	32.8	1.33	24.6	24.4	289	843	0.37
Kl S	108	478	38.9	1.72	30.2	40.8	516	938	0.32
Ca S	82	711	31.2	1.95	23.8	33.2	374	786	0.45
Ca S II	83	578	36.1	2.44	25.5	32.6	402	763	0.39
Mean	**96**	**511**	**31.9**	**1.78**	**26.3**	**32.7**	**374**	**838**	**0.38**

Table A. 3.2 Principal components analysis (PCA) on the importance of various biogeochemical, stand structural and climatic parameters in the 11 mature beech stands located along a precipitation gradient in northwestern Germany. The most characteristic variables (according to their loading) of each PCA axis are in bold. P_{resin}, plant-available (resin-extractable) phosphorus; CEC, cation exchange capacity; DBH, diameter at breast height; MGSP, mean growing season precipitation; MGST, mean growing season temperature.

	PCA		
	Axis 1	Axis 2	Axis 3
Biogeochemical parameters	Soil 1	Soil 2	Soil 3
Eigenvalue	0.40	0.22	0.13
pH(KCl)	0.45	0.54	**-0.64**
C:N	0.57	**0.61**	0.39
Net N mineralization	-0.63	0.37	-0.53
Amino acids	0.61	**-0.59**	-0.33
N:P	**0.79**	0.41	-0.07
P_{resin}	**0.76**	-0.43	-0.25
CEC	0.71	0.25	0.22
Base saturation	-0.41	0.43	-0.06
Stand structural parameters	Structure 1	Structure 2	
Eigenvalue	0.62	0.29	
Tree age	0.69	0.58	
Tree height	**0.92**	-0.21	
Stem density	-0.83	-0.46	
DBH	**0.92**	0.28	
Stem basal area	0.47	**-0.86**	
Timber volume	0.81	-0.55	
Climatic parameters	Climate 1	Climate 2	
Eigenvalue	0.56	0.29	
Altitude	0.83	-0.28	
MGSP	**0.95**	-0.21	
Volumetric water content	0.79	0.06	
Water storage capacity	0.17	**0.93**	
Fraction of sand particles	0.47	0.83	
MGST	**-0.94**	0.19	

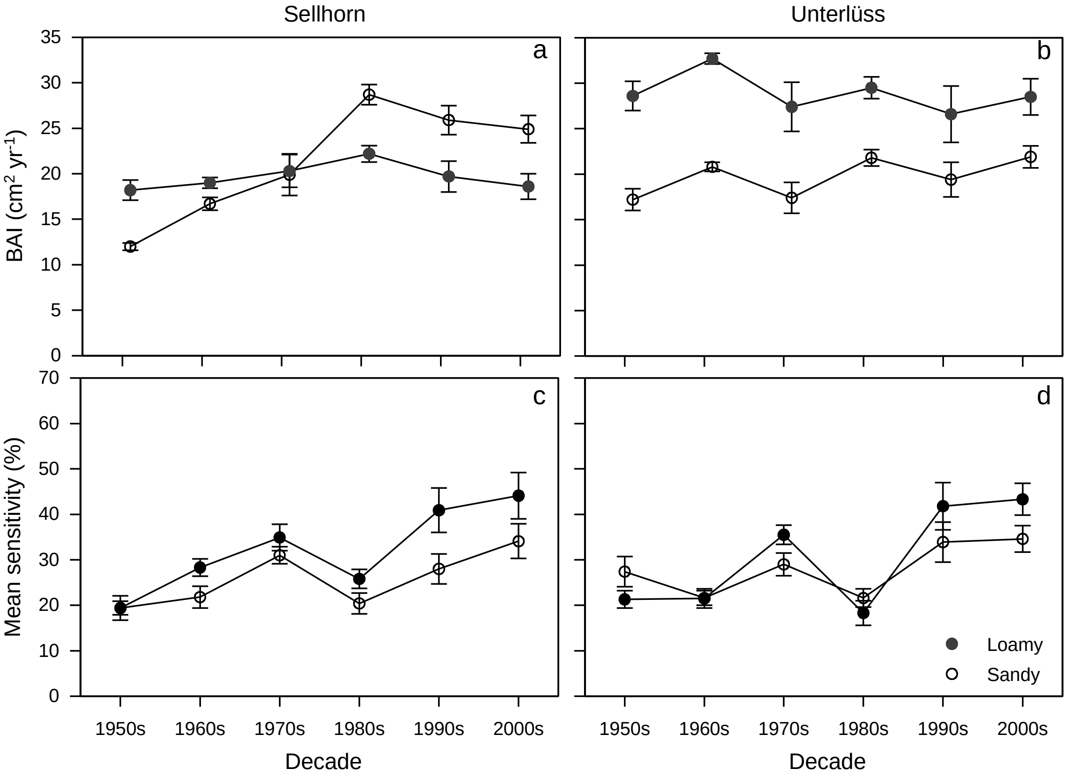

Figure A. 3.1. Change in (a-b) mean basal increment (BAI) and in (c-d) mean sensitivity of ring width of each 10 dominant trees in the 6 decades since the 1950s for the stands on sandy-loamy soil and on sandy soil in Sellhorn (MGSP: 419 mm) and Unterlüß (MGSP: 394 mm).

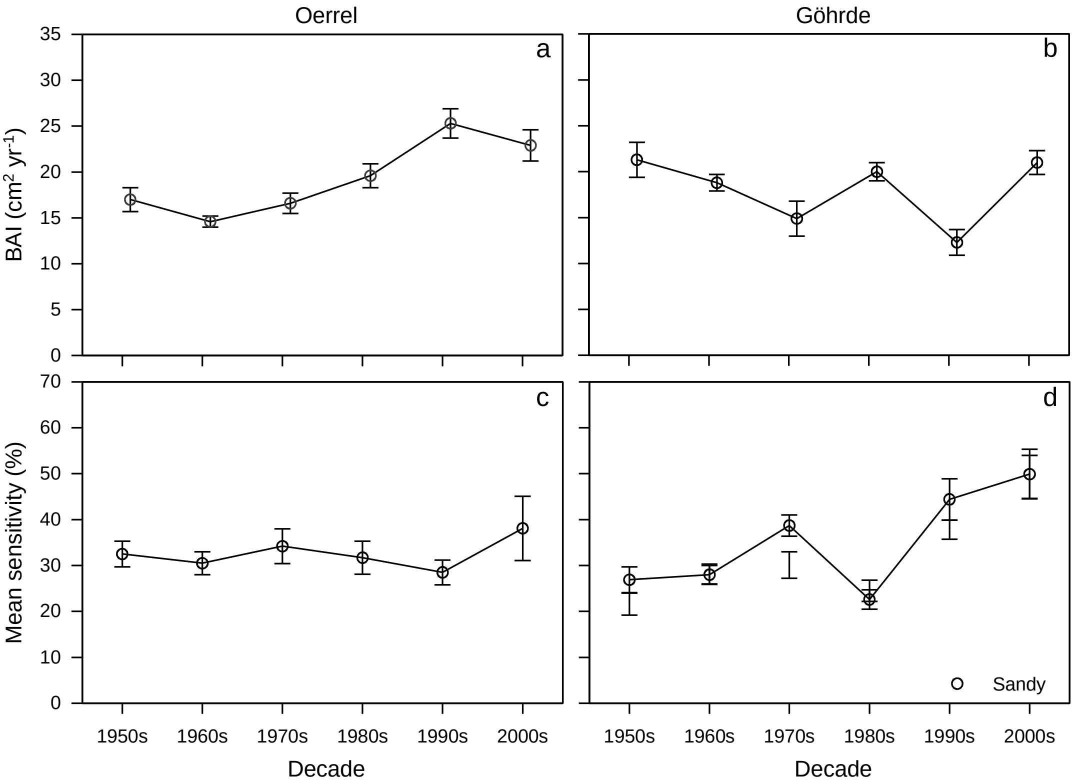

Figure A. 3.2. Change in (a-b) mean basal increment (BAI) and in (c-d) mean sensitivity of ring width of each 10 dominant trees in the 6 decades since the 1950s for the stands on sandy soil in Oerrel (MGSP: 384 mm) and Göhrde (MGSP: 365 mm).

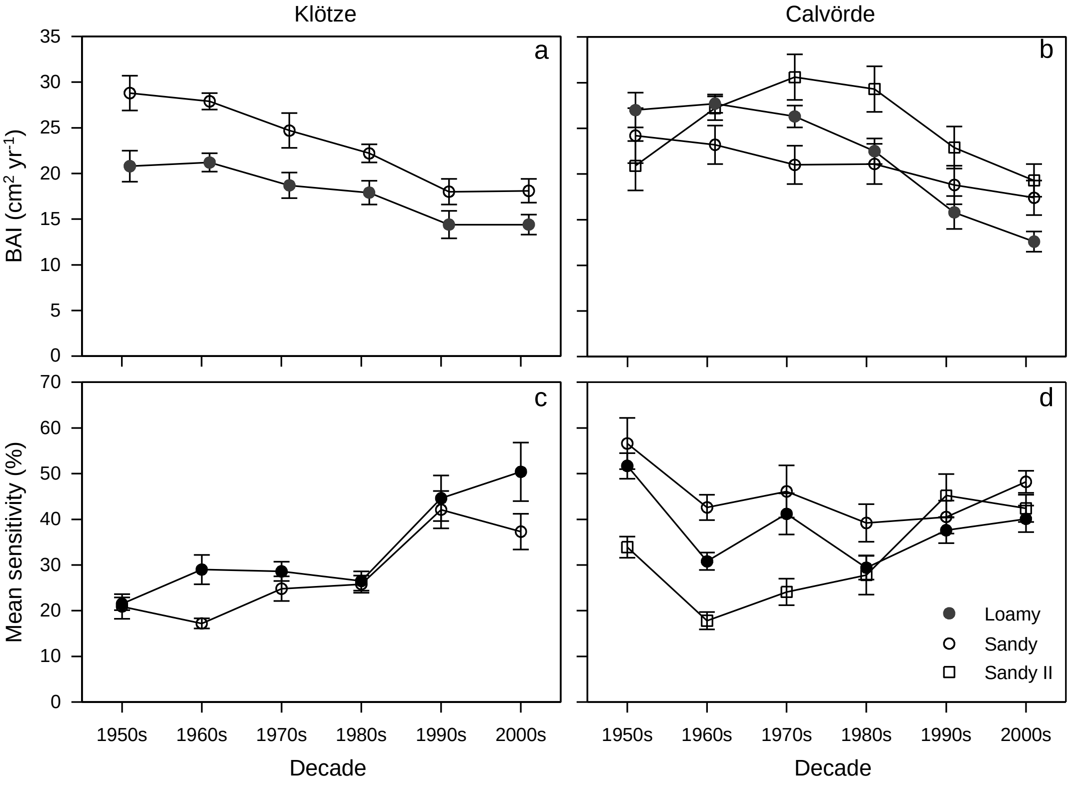

Figure A. 3.3 Change in (a-b) mean basal increment (BAI) and in (c-d) mean sensitivity of ring width of each 10 dominant trees in the 6 decades since the 1950s for the stands on sandy-loamy soil and on sandy soil in Klötze (MGSP: 344 mm) and Calvörde (MGSP: 310).

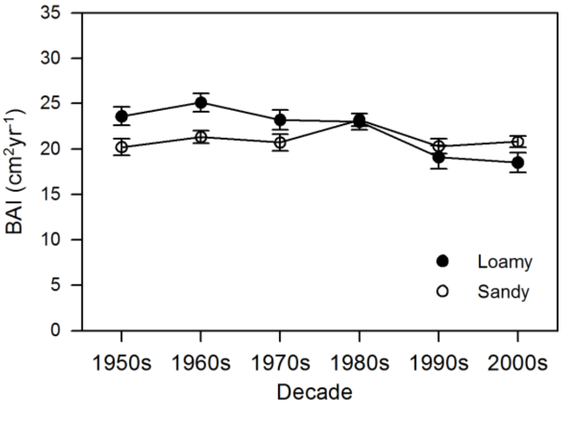

Figure A. 3.4. Change in mean basal area increment in the 6 decades since the 1950s in the 5 stands on sandy-loamy soil and the 7 stands on sandy soil. Given are means and SE over the 5 or 7 stands.

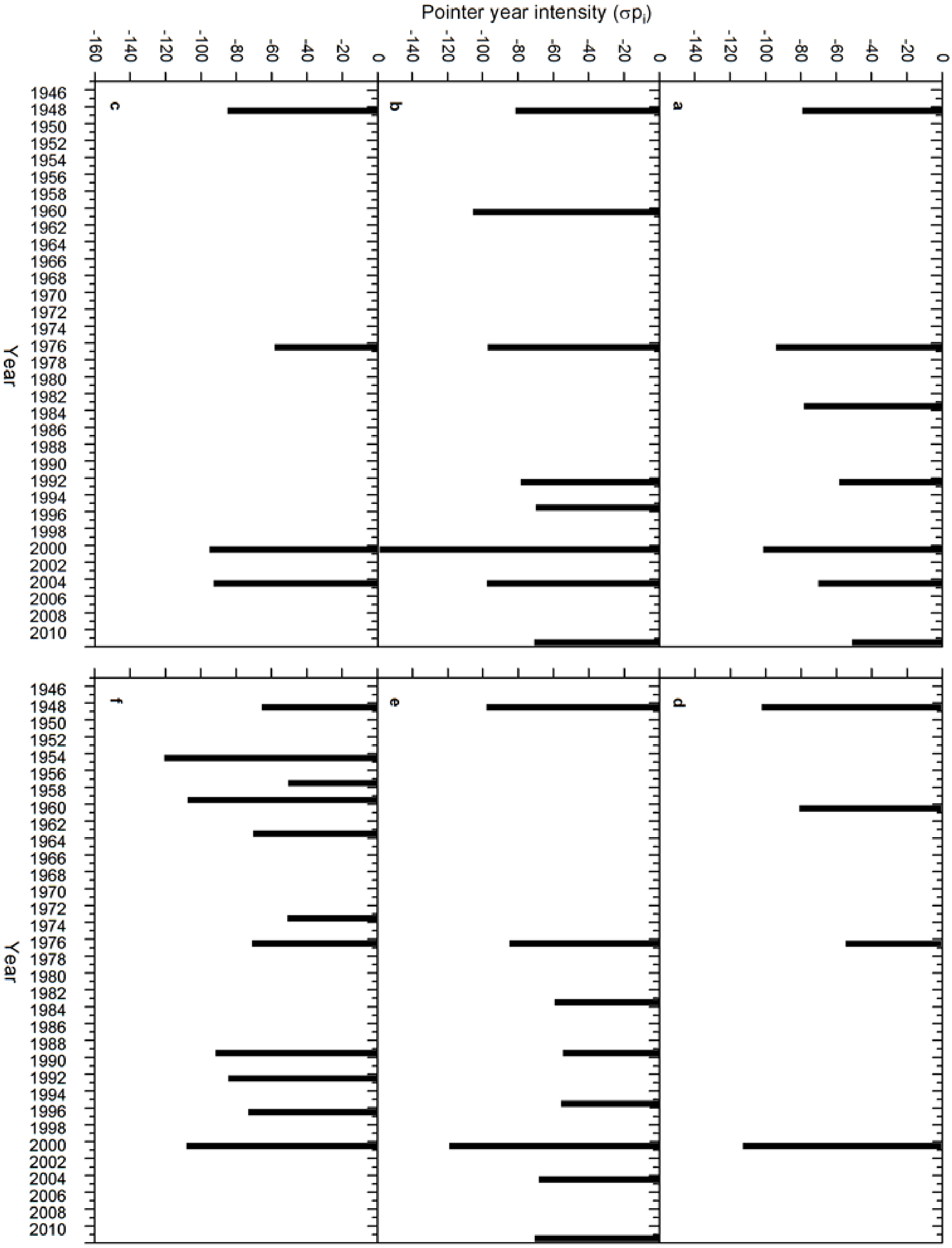

Figure A. 3.5. Negative growth deviations δp*i* in pointer years between 1946 and 2011 in 11 mature beech stands at (a) Sellhorn (MGSP: 419 mm), (b) Unterlüß (MGSP: 394 mm), (c) Oerrel (MGSP: 384 mm), (d) Göhrde (MGSP: 365 mm), (e) Klötze (MGSP: 344 mm), and (f) Calvörde (MGSP: 310 mm).

CHAPTER 4

How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction?

**Bernhard Schuldt · Florian Knutzen · Sylvain Delzon · Steven Jansen ·
Hilmar Müller-Haubold · Regis Burlett · Yann Clough
Christoph Leuschner**

Published in New Phytologist (2016),

Doi: 10.1111/nph.13798

First and second author equally contributed to this work.

Abstract

Climate warming will increase the drought exposure of many forests worldwide. It is not well understood how trees adapt their hydraulic architecture to a long-term decrease in water availability.

We examined 23 traits characterizing the hydraulic architecture and growth rate of branches and the dependent foliage of mature European beech (*Fagus sylvatica* L.) trees along a precipitation gradient (855 to 594 mm yr^{-1}) on uniform soil. A main goal was to identify traits which are associated with xylem efficiency, safety and growth.

Our data evidence for the first time a linear increase in embolism resistance with climatic aridity (by 10%) across populations within a species. Simultaneously, vessel diameter declined by 7% and pit membrane thickness (T_m) increased by 15%. Although specific conductivity did not change, leaf-specific conductivity declined by 40% with decreasing precipitation. Of eight plant traits commonly associated with embolism resistance, only vessel density in combination with pathway redundancy and T_m were related.

We did not confirm the widely assumed trade-off between xylem safety and efficiency but obtained evidence in support of a positive relation between hydraulic efficiency and growth. We conclude that the branch hydraulic system of beech has a distinct adaptive potential to respond to a precipitation reduction due to the environmental control of embolism resistance.

Key words: drought stress, functional trait, hydraulic conductivity, leaf morphology, pit membrane, precipitation gradient, vulnerability to cavitation, wood anatomy.

Introduction

Most climate change scenarios for Central Europe predict a rise in mean annual temperature by 2.5 to 3.5 °C for the end of the 21st century (Rowell and Jones, 2006; Jacob *et al.*, 2008), an increasing frequency and raised intensity of summer heat waves (Schär *et al.*, 2004; Fischer and Schär, 2008) and a regional decrease in summer precipitation by up to 25% (Meinke *et al.*, 2010). These changes will most likely affect forest productivity, which in many regions of Central Europe largely depends on water availability (Bréda *et al.*, 2006; Weber *et al.*, 2013). In regions with a rising frequency and severity of summer drought, the dependence of tree growth and vitality on water supply is therefore likely to increase in the future. Such a trend can also increase tree mortality through hydraulic failure (Anderegg *et al.*, 2015; McDowell and Allen, 2015), and it may eventually change tree species composition in natural forests due to differential species responses (Rigling *et al.*, 2013). A better understanding of drought effects on the vitality and productivity of important tree species is urgently needed.

The natural forest vegetation of Central Europe is dominated by a single species, European beech (*Fagus sylvatica* L., Ellenberg and Leuschner, 2010), which would naturally cover almost 66% of the area of Germany (Bohn *et al.*, 2003). Although this species preferentially grows on well-drained, moist soils in oceanic to sub-oceanic climates, it occurs under largely different precipitation regimes (Ellenberg and Leuschner, 2010). Such a wide spectrum of hydrological site conditions can be colonized by a species if it maintains a high degree of genetic variability at the meta-population level by producing genotypes with adaptation to moist or relatively dry habitats, or if a high phenotypic plasticity does exist which allows the individual to acclimatize to a broad range of hydrological conditions (Kremer *et al.*, 2014). However, it remains a matter of controversial debate to what extent beech is threatened by increasing drought in future, especially at its distributional margins (Jump *et al.*, 2006; Herbette *et al.*, 2010). In fact, the genotypic variation of drought tolerance and the drought acclimation potential are not sufficiently known for mature beech trees (Bolte *et al.*, 2007; Gessler *et al.*, 2007; Leuschner, 2009).

In beech, several traits have been identified that indicate a considerable sensitivity to drought, including a marked precipitation sensitivity of radial growth (Weber *et al.*, 2013; Zimmermann *et al.*, 2015). Common-garden experiments with seedlings from several European beech provenances, on the other hand, evidence a pronounced adaptability of the hydraulic system. While wood anatomical traits partly seem to be under genetic control

(Eilmann *et al.*, 2014), embolism resistance was uncoupled from genetic differentiation and appears to be mainly under environmental control building on phenotypic plasticity (Wortemann *et al.*, 2011; Aranda *et al.*, 2015). However, the degree of phenotypic variability in hydraulic traits has never been quantified in European beech and corresponding information is needed in particular for adult trees across gradients of water availability.

So far, only few studies have investigated the synchronous variation of xylem anatomy, hydraulic properties and leaf traits within a single tree species across environmental gradients (Anderegg and Meinzer, 2015). Consequently, less is known about intra-specific variation in hydraulic traits than inter-specific variation, despite the importance of the former for predicting tree responses to climate change (Anderegg, 2014). This is somewhat surprising given the long-standing understanding that wood anatomical diversity is induced by environmental factors and influenced by the capacity to withstand drought (Vesque, 1876; Carlquist, 1966). Several studies on intraspecific variation in hydraulic properties have evidenced a strong precipitation effect on conduit traits (e.g. Chenlemuge *et al.*, 2015; Schreiber *et al.*, 2015) as a consequence of either genetic variability or phenotypic plasticity. Consequently, a central role in hydraulic efficiency and safety is played by average vessel size and vessel size distribution (Tyree *et al.*, 1994). Furthermore, wood anatomical and derived hydraulic properties are directly related to growth (Hajek *et al.*, 2014; Hoeber *et al.*, 2014; Kotowska *et al.*, 2015), demonstrating the close relation between plant hydraulic conductance and productivity (Tyree, 2003). However, it has repeatedly been demonstrated that decreasing precipitation causes narrower conduits and higher conduit densities, both across and within species (Carlquist, 1977; Lens *et al.*, 2004; Sterck *et al.*, 2008; Gleason *et al.*, 2012; Chenlemuge *et al.*, 2015). When comparing various species, this pattern generally leads to increased embolism resistance, while within-species comparisons yielded mixed results (Martinez-Vilalta *et al.*, 2009; Herbette *et al.*, 2010; Wortemann *et al.*, 2011; Sterck *et al.*, 2012). It is generally accepted that air-seeding is the primary cause of cavitation and thus embolism formation, subsequently rupturing the water column and causing water transport failure (Tyree and Zimmermann, 2002). The consequences are stomatal closure and reduced carbon assimilation. In the past, several traits have been found to be related to embolism resistance, among them wood density (Hacke *et al.*, 2001; Jacobsen *et al.*, 2007; Martinez-Vilalta *et al.*, 2009; Gleason *et al.*, 2015), vessel size (Carlquist, 1977; Tyree *et al.*, 1994; Maherali *et al.*, 2006; Hajek *et al.*, 2014), vessel density (Lens *et al.*, 2011; Ogasa *et al.*, 2013), hydraulic conductivity (Maherali *et al.*, 2006; Markesteijn *et al.*, 2011; Gleason *et al.*, 2015), vessel grouping (Loepfe *et al.*, 2007; Lens *et al.*, 2011; Carlquist, 2012), pit structure

(Wheeler *et al.*, 2005; Jansen *et al.*, 2009; Plavcová *et al.*, 2013; Bouche *et al.*, 2014), sapwood-to-leaf area ratio (Wilson *et al.*, 2008; Sterck *et al.*, 2012; Schreiber *et al.*, 2015) and specific leaf area (Maherali *et al.*, 2006; Fan *et al.*, 2011; Markesteijn *et al.*, 2011); a number of these traits are at least partly interrelated.

Precipitation gradients represent a valuable tool for investigating the short-term acclimation (plasticity) of mature trees to a decrease in rainfall when the edaphic conditions and stand structure are sufficiently uniform across the stands. Here, we investigate acclimation in the branch hydraulic system of mature beech trees in five stands on uniform sandy soil across a 130-km long gradient of ~260 mm yr^{-1} difference in mean annual precipitation. The low end of the gradient was close to the known drought limit of beech. We combined anatomical and hydraulic measurements in sun-canopy branches with the examination of foliar properties addressing 20 parameters in total and related these traits to three common measures of embolism resistance.

The main goal of this study in mature European beech trees was to identify morphological and physiological traits which are associated with xylem efficiency, safety and growth in trees of comparable age and size growing along a precipitation gradient on uniform soil. The main hypotheses tested were that

- (i) vessel diameter and hydraulic efficiency decrease with a lasting reduction in precipitation while
- (ii) embolism resistance increases, and
- (iii) that branch growth rate trades off with both hydraulic efficiency and safety.

Material and methods

Study sites and microclimatic conditions

The study was carried out in five mature beech (*Fagus sylvatica* L.) stands of similar age and structure along a precipitation gradient in the Pleistocene lowlands of north-western Germany in 2011. The precipitation gradient covers a 130 km-long NW-SE transect from the East of the state Lower Saxony to the western part of Saxony-Anhalt and includes a climatic gradient from a sub-oceanic to a sub-continental climate with a continuous long-term (1981-2010) mean annual precipitation (MAP) decrease from 855 to 594 mm yr^{-1} and a temperature (MAT) increase from 8.5 to 9.1 °C (Table 4.1). Climatic data were obtained from a 1 × 1 km^2 grid data set (Deutscher Wetterdienst, Offenbach, Germany). We additionally calculated a simplified forest aridity index (FAI) according to Führer *et al.* (2011) as $FAI = 100 \times T_{Jul\text{-}Aug} / (P_{May\text{-}Jul} + P_{Jul\text{-}Aug})$, where T is the temperature and P the precipitation of the associated interval. Since the atmospheric evaporative demand in the growing season is highest in mid-summer (July and August), the July precipitation was weighted by a factor of two in the denominator. This index has been developed for the comparison of different beech stands in southeast Europe; FAI values in the distribution range of beech are generally <4.75 (Führer *et al.*, 2011).

Table 4.1. Stand characteristics of the five investigated beech forests along a precipitation gradient in north-west Germany. Given are the site code and symbol colour, mean annual precipitation (MAP, mm yr^{-1}) and mean early summer growing season (April – June) precipitation (MSP, mm) for the period 1981-2010, mean annual temperature (MAT, °C), the forest aridity index (FAI), average diameter at breast height (DBH, cm), tree height (H, m) and number of tree individuals measured (ntree) and samples per site (including pseudo-replicates, nsample). Given are means ± SE. The sample numbers for wood density and TEM measurements are not given here; see corresponding Material and Methods section.

Site	**Code**	**Symbol**	**MAP**	**MSP**	**MAT**	**FAI**	**DBH**	***H***	n_{tree}	n_{sample}
Calvörde	Ca	🟥	593.91	146.75	9.3 ± 1.9	6.19	37.42 ± 2.47	25.82 ± 0.18	5	13 - 17
Klötze	Kl	🟨	654.76	157.30	9.1 ± 1.9	5.60	42.36 ± 3.65	29.71 ± 0.29	5	14 - 16
Göhrde	Go	🟫	707.11	164.57	9.0 ± 1.8	5.15	40.13 ± 2.00	24.20 ± 1.14	5	16 - 19
Unterlüß	Un	🟦	816.06	175.96	8.7 ± 1.8	4.86	40.83 ± 3.07	22.27 ± 1.10	5	16 - 18
Sellhorn	Se	🟦	855.37	188.14	8.7 ± 1.8	4.53	39.79 ± 2.43	28.93 ± 1.04	5	14 - 17

All five sites were situated on highly acidic and nutrient-poor sandy soils developed in fluvio-glacial sands or moraine deposits of the penultimate Ice Age (Saalian) covered by periglacial drift sand. Mean tree age was 104.6 ± 6.7 years (mean ± SE). For detailed information on stand structure and climatic parameters at the five study sites see Müller-Haubold *et al.* (2013) and Hertel *et al.* (2013). Some structural data on the beech individuals investigated are given in Table 4.1.

Tree selection and plant material

Five mature beech trees of similar size and canopy position within a particular stand were selected at the five sites and branch and twig samples collected from the uppermost sun-exposed crown with tree-climbing equipment in August 2011 (Figure 4.1). Per tree, 5 twigs with c. 50 cm length were air-cut and immediately transferred to polyethylene tubes filled with water containing a sodium-silver-chloride complex (16 µg l^{-1} Ag, 8 mg l^{-1} NaCl, Micropur katadyn, Wallisellen, Switzerland) to prevent microbial growth and stored at 4 °C. Across the gradient, all branches were more or less of comparable size and age although a certain variation in sapwood area at a given branch age was not avoidable (Figure A. 4.1).

Figure 4.1. Tree climber on the way to the sun canopy using rope technique in order to sample branches from the uppermost sun-exposed crown.

Additionally, all leaves distal to the sampled twig segments were harvested. For wood density determination, three large branch wood samples were collected from the uppermost canopy of a tree. A list of all traits measured, the corresponding acronyms and units is given in Table 4.2.

Table 4.2. List of variables with definition and units studied.

Abbreviation	**Unit**	**Definition**
Environmental conditions		
MAP	mm yr^{-1}	Long-term mean annual precipitation
MSP	mm yr^{-1}	Long-term mean annual early summer growing season precipitation
MAT	°C	Long-term mean annual temperature
FAI		Forest aridity index
Structural parameters		
H	m	Tree height
DBH	cm	Diameter at breast height
BA	yr	Branch age
Hydraulic traits		
K_{S}	kg m^{-1} MPa^{-1} s^{-1}	Specific conductivity
K_{P}	kg m^{-1} MPa^{-1} s^{-1}	Potential conductivity
K_{L}	10^{-4} kg m^{-1} MPa^{-1} s^{-1}	Leaf-specific conductivity
P_{12}	MPa	Xylem pressure at 12% loss of hydraulic conductance
P_{50}	MPa	Xylem pressure at 50% loss of hydraulic conductance
P_{88}	MPa	Xylem pressure at 88% loss of hydraulic conductance
Wood properties		
WD	g cm^{-3}	Branch wood density
D	µm	Vessel diameter
D_{h}	µm	Hydraulically-weighted vessel diameter
VD	n mm^{-2}	Vessel density
VI	mm m^{-2}	Carlquist's vulnerability index
V_{G}		Vessel grouping index
V_{S}		Solitary vessel index
T_{m}	nm	Intervessel pit membrane thickness
T_w	µm	Intervessel wall thickness
A_{xylem}	mm^2	Branch sapwood area
A_{xylem}:A_{leaf}	10^{-4} m^2 m^{-2}	Sapwood to leaf area ratio (Huber value)
A_{lumen}:A_{xylem}	%	Relative vessel lumen area (lumen to sapwood area ratio)
G_{dw}	mg m^{-1} yr^{-1}	Branch growth rate
Foliar traits		
LS	cm^2	Mean leaf size
SLA	cm^2 g^{-1}	Specific leaf area
δ^{13}C	‰	Carbon isotope signature

Wood density

Wood density (WD, g cm^{-3}) was determined for three branch wood samples per tree (mean diameter ± SE: 3.09 ± 0.07 cm; mean length ± SE: 15.15 ± 0.43 cm), yielding 64 samples in total. Fresh volume was gravimetrically measured at a precision of 10 mg after removing pith and bark by water displacement according to Archimedes' principle and branch samples subsequently oven-dried at 105 °C for 72h.

Hydraulic conductivity and vulnerability curves

Hydraulic properties were measured for 3-5 samples per tree, yielding 78 samples in total. Branch segments were shortened to c. 28 cm length (mean basipetal diameter ± SE: 8.04 ± 0.11 mm), lateral branches cut off, scars sealed with quick-drying superglue (Loctite 431, Henkel, Düsseldorf, Germany) and the segments connected to the Xyl'em apparatus (Bronkhorst, Montigny les Cormeilles, France). Segments were flushed three times for 10 min at a pressure of 120 kPa with filtered (0.2 µm) and degased demineralized water (10 mM KCl, 1 mM $CaCl_2$) and maximum hydraulic conductivity (K_h, kg m MPa^{-1} s^{-1}) recorded along a 6 kPa pressure difference. The diameter of each segment was measured twice at the basipetal and distal end, and at four positions along the segment. In order to calculate specific conductivity (K_S, kg m^{-1} MPa^{-1} s^{-1}) normalized by sapwood area, a regression analysis between total cross-sectional (A_{cross}, mm^2) and corresponding xylem cross-sectional area (A_{xylem}, mm^2) was carried out assuming that all rings were still functional. From each segment, high-quality top-view images from the planed thick and thin end were analysed for A_{cross} and A_{xylem} with the software ImageJ (v1.44p, http://rsb.info.nih.gov/ij). The following regression coefficients were used to calculate sapwood area without pith and bark for a given segment diameter: $A_{xylem} = -3.715 + 0.770\ A_{cross}$ ($P<0.001$, $r^2 = 0.98$, n = 238). According to linear regression analyses, K_h divided by the maximal basipetal sapwood area revealed the strongest relationships (Table A.4.1). This pattern was documented in Hajek *et al.* (2014) and Hoeber *et al.* (2014). Leaf -specific conductivity (K_L, kg m^{-1} MPa^{-1} s^{-1}) was calculated by dividing K_h by the total supported leaf area distal to the branch segment (A_{leaf}, cm^2).

Subsequently, branch segments were inserted into a honeycomb custom-made rotor (Delzon *et al.*, 2010) of the Cavitron (Cochard *et al.*, 2005) attached to a commercially available centrifuge (Sorvall RC-5C, Thermo Fisher Scientific, Waltham, MA, USA). Conductivity measurements started at 1.0 MPa and were stepwise repeated at intervals of 0.2 to 0.3 MPa until the percent loss of conductivity (PLC) reached at least 90%. Vulnerability curves were generated by plotting PLC against xylem pressure (Figure 4.2), and the pressure causing 50% loss of conductivity (P_{50}) was calculated according to a sigmoidal function (Pammenter and van der Willigen, 1998) as PLC = 100 / (1 + exp(s / 25 × ($P_{\mathrm{i}} - P_{50}$)), where s (% MPa^{-1}) is the negative slope of the curve at the inflexion point and P_{i} the xylem pressure. The xylem pressures causing 12% (P_{12}, air entry point) and 88% (P_{88}) loss of conductivity were calculated as well following Domec and Gartner (2001) as $P_{12} = 2 / (s / 25) + P_{50}$ and $P_{88} = -2 / (s / 25) + P_{50}$.

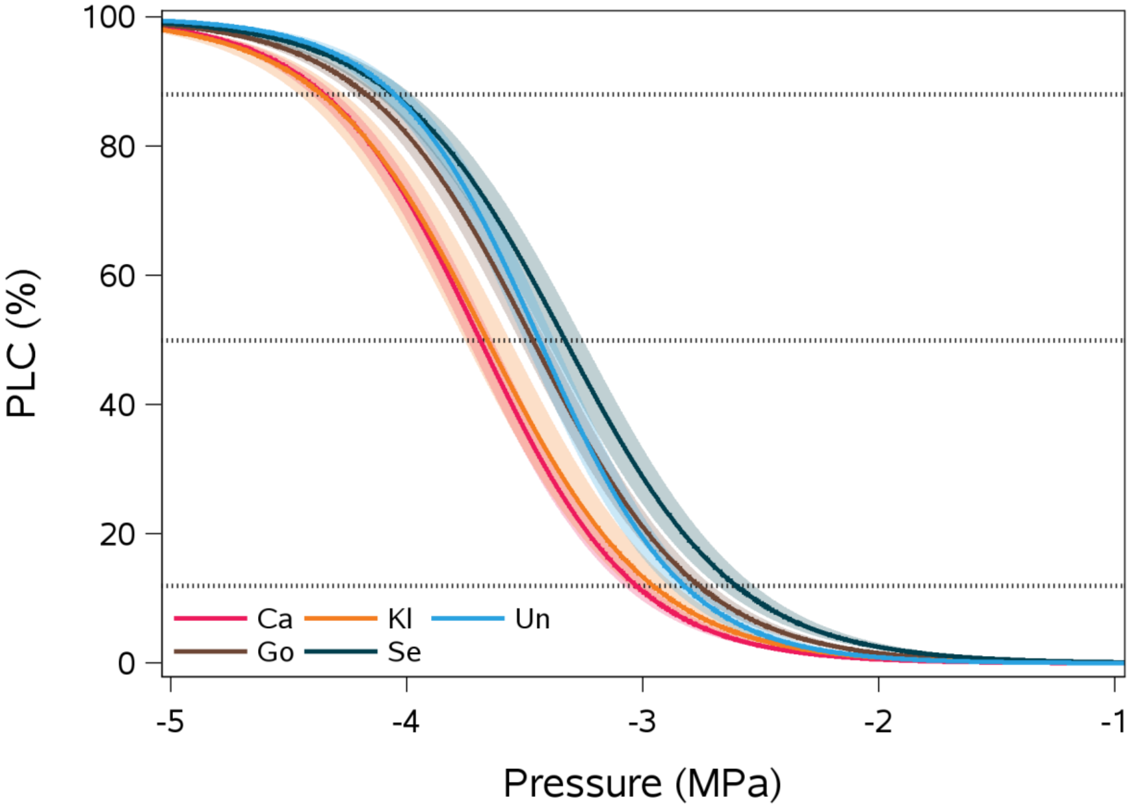

Figure 4.2. Mean vulnerability curves for the five sites differing in water availability showing xylem pressure in relation to percentage loss of hydraulic conductance (PLC). Shown curves have been averaged for all samples per tree and subsequently across the five trees per site, for site abbreviations see Table 4.1. The shaded band represents the standard deviation. Different colours indicate differences in water availability.

Wood anatomy, potential conductivity and branch growth rate

Branch segments from the basipetal end were used for wood anatomical investigation, yielding 77 samples in total. Transverse sections cut with a sliding microtome (G.S.L.1, Schenkung Dapples, Zurich, Switzerland) were digitalized at 100x magnification using a stereo-microscope equipped with a digital camera (SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany). Image processing was done with the software Adobe Photoshop CS6 (Version 13.0.1, Adobe Systems Incorporated, USA) and ImageJ (v1.44p, http://rsb.info.nih.gov/ij) using the particle analysis function to estimate single and cumulative vessel lumen area (A_{lumen}, m^2), vessel density (VD, $\mathrm{n\,mm}^{-2}$) and vessel diameters (D, µm) from major (a) and minor (b) vessel radii according to the equation given by Lewis and Boose (1995) as $D = ((32 \times (a \times b)^3) / (a^2 + b^2))^{¼}$ and used to calculate the hydraulically-weighted diameter (D_{h}, µm) according to Sperry *et al.* (1994) as $D_{\mathrm{h}} = \Sigma D^5 / \Sigma D^4$. Relative vessel lumen area (A_{lumen}:A_{xylem}, %) was calculated by dividing cumulative vessel lumen area (A_{lumen}, m^2) by the corresponding sapwood area (A_{xylem}, m^2). Carlquist's vulnerability index (Carlquist, 1977), which is commonly used to indicate a species' adaptation to xeric or mesic conditions (e.g. De Micco *et al.*, 2008), was calculated as $\mathrm{VI} = (D / 1{,}000) / (\mathrm{VD} / 1{,}000{,}000)$. The vessel grouping index (V_{G}) was estimated by dividing the total number of vessels by the number of grouped vessels, and the solitary vessel index (V_{S}) by dividing the number of solitary vessels by the total number of vessels; for these calculations a subsample of 216.4 ± 5.6 vessels (mean ± SE) were measured per branch sample, with both solitary vessels and grouped vessels considered as a vessel group (Scholz *et al.*, 2013).

For all calculations (except for V_{G} and V_{S}), the complete cross-section was analysed, yielding 3,537 to 30,989 measured vessels per branch sample. For V_{G} and V_{S}, pie slices from the cross-section were used, yielding 110 to 379 measured vessels per sample. Potential conductivity (K_{P}, $\mathrm{kg\,m^{-1}\,MPa^{-1}\,s^{-1}}$) was calculated according to the Hagen-Poiseuille equation as $K_{\mathrm{P}} = (((\pi \times \Sigma D^4) / 128\ \eta) \times \rho) / A_{\mathrm{xylem}}$, where η is the viscosity ($1.002\ 10^{-9}$ MPa s) and ρ the density of water (998.2 $\mathrm{kg\,m^{-3}}$), both at 20 °C, and A_{xylem} (m^2) the analysed sapwood area. Additionally, the relative abundance of vessels in five vessels size classes was calculated by dividing the number of vessels in a class by total vessel number.

We further calculated branch growth rate (G_{dw}, $\mathrm{mg\,m^{-1}\,yr^{-1}}$) according to Sterck *et al.* (2012) as $G_{\mathrm{dw}} = \mathrm{BAI} \times \mathrm{WD} \times 10^{-6}$, where BAI is the average annual basal area increment ($\mathrm{m^2\,yr^{-1}}$) and WD the corresponding wood density ($\mathrm{kg\,m^{-3}}$). BAI was calculated by analysing the area of each growth ring separately, yielding 451 analysed growth rings in total.

Transmission light microscopy (TEM)

A subsample of three to four branch segments from each three trees per site was used for TEM observations of intervessel pit membrane thickness (T_{m}, nm) and intervessel wall thickness (T_{w}, nm), yielding 18 samples in total. Samples were stored in 70% ethanol, and were from the same branches that were used to construct vulnerability curves and for wood anatomical measurements. Samples were prefixed in a standard solution (2.5% glutaraldehyde, 0.1 mol phosphate, 1% saccharose, pH 7.3) and prepared according to a standard TEM protocol (Jansen *et al.*, 2009a). Ultra-thin, transverse sections were observed with a JEOL 1400 TEM (JEOL USA, Inc., MA, USA). The conduit size and general morphology of bordered pits was used to distinguish intervessel pit membranes from vessel-tracheid or tracheid-tracheid pit membranes. Given the morphological continuum between vessel elements and tracheids, the exact nature of conduits could not always be distinguished. Therefore, TEM measurements were only included in our analyses when the vessel identity was clear.

Leaf morphology

All leaves distal to the twig segments used for hydraulic conductivity measurements were stripped off and scanned for determination of single and cumulative leaf area (WinFolia 2005, Régent Instruments, Quebec, Canada). Per branch segment, 8 to 132 leaves were scanned, yielding 5,464 leaves in total. Average leaf size (LS, cm^2) was determined by dividing total leaf area by the number of leaves per branch, and the Huber value, i.e. sapwood-to-leaf-area ratio (A_{xylem}:A_{leaf}, 10^{-4} m^2 m^{-2}), by dividing sapwood area determined according to the linear regression analysis mentioned above by the corresponding total leaf area (A_{leaf}, cm^2). Subsequently, leaves were oven-dried at 70 °C for 48h in order to determine specific leaf area (SLA, cm^2 g^{-1}). The carbon isotope signature ($\delta^{13}C$) of the leaf dry mass was analysed by mass ratio spectroscopy (Deltaplus, ThermoFinnigan, Bremen, Germany) at the Centre for Stable Isotope Research and Analysis (KOSI), University of Göttingen.

Statistical analyses

The trait variables investigated are summarized in Table 4.2. Our approach and the labour-demanding access to the upper-most canopy by tree climbing equipment forced us to apply a nested design, i.e. three to five samples were taken per tree, but only five trees analysed per site.

All statistical analyses were done with the software package R (R Development Core Team 2013, version 3.0.0) except for linear regression analyses that were executed with the software Xact 8.03 (SciLab, Hamburg, Germany). All variables were tested for normality with a Shapiro-Wilk Normality Test and log transformed if required. Linear mixed effect models (LME) with FAI, MAP or MSP as a fixed variable were used to test for significant differences in all trait variables along the rainfall gradient. We assumed non-independence of different samples within a tree and of different trees within a plot in the models by adding plot and tree nested in plot as random effects. For investigating relationships between trait variables, Pearson correlation analyses were carried out on the tree level.

To search for patterns of inter-relationships among the examined 23 traits, a Principle Components Analysis (PCA) was conducted with plot-level means using the package CANOCO (Version 5.02, Biometris, Wageningen, The Netherlands) with all functional traits centered and standardized before analysis. Although our number of variables exceeded the number of plots by far, the first few eigenvectors are little affected when the matrix is not of full rank and do not lead to incorrect interpretations of ordinations in reduced space (Legendre and Legendre, 1998).

Results

Variation in functional traits along the precipitation gradient

Across our gradient, mean annual precipitation (MAP) declined by 261 mm yr^{-1} while mean early growing season precipitation (MSP) from April to June was reduced by 41 mm. Changes in precipitation and the increase in mean annual temperature (MAT) by 0.4 °C from the wet to the dry end are additionally mirrored in the forest aridity index (FAI), which increased by 1.66 (Table 4.1).

According to linear mixed effect models (LME), only five of the 23 structural, hydraulic, wood anatomical and foliar traits were significantly related to the three measures of water availability MAP, MSP and FAI (Table 4.3).

Table 4.3. Results of linear mixed effect models examining the influence of FAI, MAP and MSP as fixed variable on the 23 measured parameters in European beech. Given are the delta Akaike information criterion (Δ_i), the likelihood ratio (LR) and probability of error (P-value); for abbreviations see Table 4.2. Significant correlations (P<0.05) are printed in bold, marginally significant correlations (P<0.10) in italic bold letters.

Variable	**FAI**			**MAP**			**MSP**		
	Δ_i	**LR**	**p**	**Δ_i**	**LR**	**p**	**Δ_i**	**LR**	**p**
Structural parameters									
BA	1.95	0.05	0.81	1.75	0.25	0.62	1.65	0.35	0.55
Hydraulic traits									
K_S	1.41	0.59	0.44	1.04	0.96	0.33	0.72	1.28	0.26
K_P	1.35	0.65	0.42	1.64	0.36	0.55	1.28	0.72	0.39
K_L	2.99	4.99	**0.03**	2.91	4.91	**0.03**	1.83	3.83	**0.05**
P_{12}	5.02	7.02	**0.01**	4.10	6.10	**0.01**	4.97	6.97	**0.01**
P_{50}	4.72	6.72	**0.01**	4.60	6.60	**0.01**	4.57	6.57	**0.01**
P_{88}	2.19	4.19	**0.04**	2.65	4.65	**0.03**	2.03	4.03	**0.04**
Wood properties									
WD	1.87	0.13	0.72	1.69	0.31	0.58	1.58	0.42	0.51
D	1.84	3.84	**0.05**	1.55	3.55	***0.06***	2.48	4.48	**0.03**
D_h	1.73	0.27	0.60	1.87	0.13	0.72	1.63	0.37	0.55
VD	0.20	1.80	0.18	0.19	2.19	0.14	0.51	2.51	0.11
VI	0.56	2.56	0.11	0.98	2.98	***0.08***	1.46	3.46	***0.06***
V_G	1.24	0.76	0.38	1.55	0.45	0.50	1.15	0.85	0.36
V_S	1.24	0.76	0.38	1.59	0.41	0.52	1.21	0.79	0.37
T_m	0.27	1.73	0.19	0.20	1.63	0.20	0.30	1.70	0.19
T_w	1.97	0.03	0.87	0.20	0.04	0.84	1.95	0.05	0.82
A_{xylem}	1.84	0.16	0.69	1.96	0.04	0.83	1.98	0.02	0.90
$A_{xylem} : A_{leaf}$	0.36	1.64	0.20	0.09	2.09	0.15	0.74	1.26	0.26
$A_{lumen} : A_{xylem}$	1.77	0.23	0.63	1.94	0.06	0.80	1.87	0.13	0.72
G_{dw}	1.78	0.22	0.64	1.97	0.03	0.86	1.98	0.02	0.88
Foliar traits									
LS	1.50	3.50	***0.06***	1.24	3.24	***0.07***	0.42	2.42	0.12
SLA	0.92	1.08	0.30	0.74	1.26	0.26	0.83	1.17	0.28
$\delta^{13}C$	1.09	0.91	0.34	0.31	1.69	0.19	0.44	1.56	0.21

A key result is that xylem safety increased linearly with an increase in climatic aridity (Figure 4.3a). The three measures of embolism resistance (P_{12}, P_{50} and P_{88}) differed in their response with P_{12} showing the strongest decrease with a reduction in MAP (by 15% or 0.44 MPa), followed by P_{50} (by 10% or 0.33 MPa) while P_{88} was the least modified traits (by 5% or 0.23 MPa; Figure 4.3, Table A. 4.2).

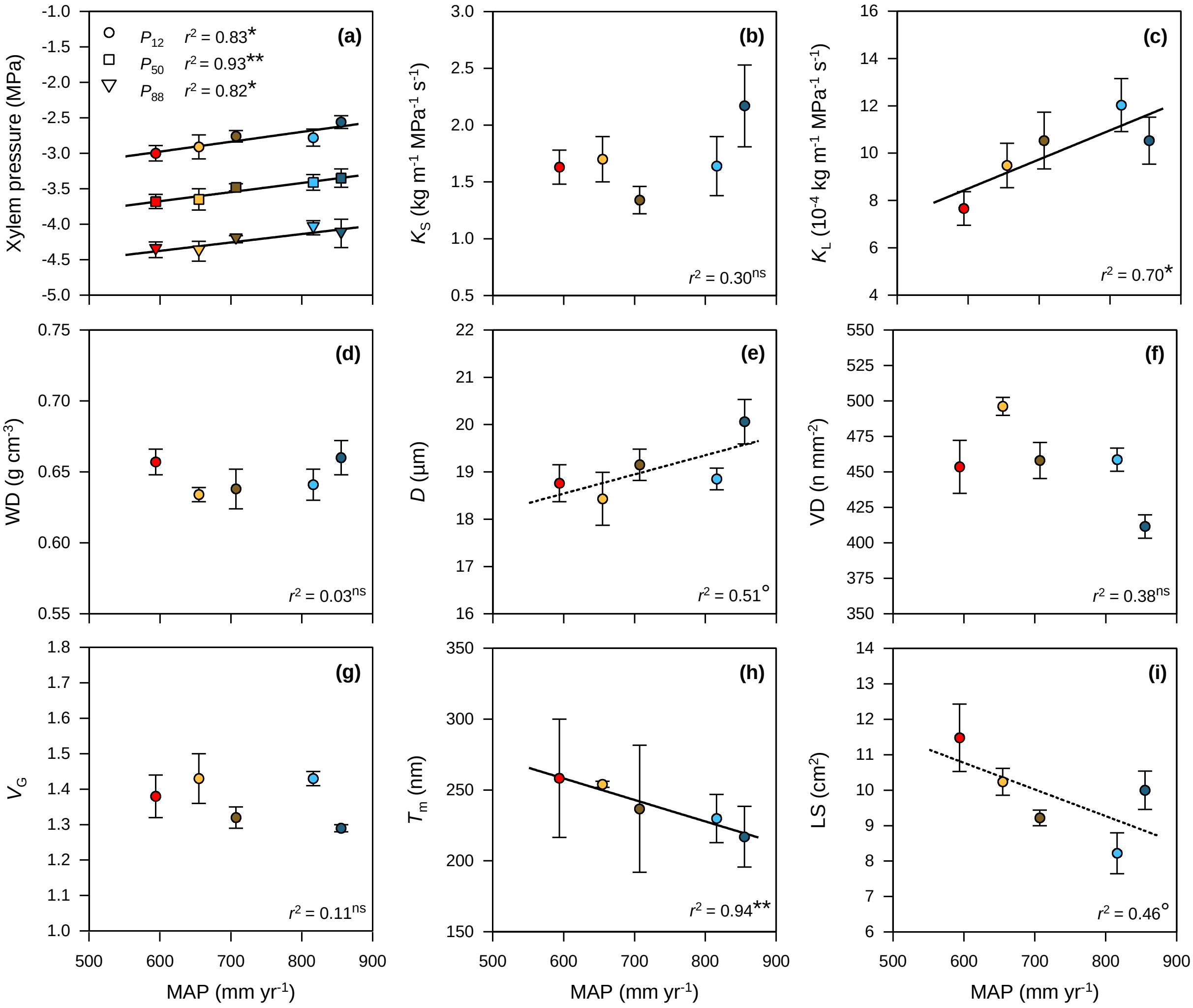

Figure 4.3. Mean annual precipitation (MAP) in relation to the xylem pressure causing 12, 50 or 88% loss of hydraulic conductance (a, P_{12}, $P_{50,}$ P_{88}), specific conductivity (b, K_S), leaf-specific conductivity (c, K_L), wood density (d, WD), vessel diameter (e, D), vessel density (f, VD), vessel grouping index (g, V_G), intervessel pit membrane thickness (h, T_m) and mean leaf size (i, LS) in European beech. Values are means ± SE per site, asterisk indicate the level of significance (° $P<0.10$; * $P<0.05$; ** $P<0.01$), non-significant relationships are indicated by ns. For symbol colour see Table 4.1.

The increase in hydraulic safety toward the drier sites was not associated with a decline in xylem efficiency measured as specific (K_S, Figure 4.3b) or potential conductivity (K_P, Table 4.3), even though the highest conductivities were observed at the wettest site Sellhorn (Se, Table A.4.2). In contrast to K_S, leaf-specific conductivity (K_L) was strongly influenced by changes in MAP and declined by 40% towards the dry end of the gradient (Figure 4.3c).

Wood density (WD) did not vary significantly along the gradient (Figure 4.3d), and of all wood properties examined only vessel diameter (*D*) was significantly related to both FAI and MSP (and at marginal significance to MAP, $P<0.10$; Table 4.3). From the wet to the dry end of the gradient, average vessel diameter *D* declined by 7% (i.e. by 1.3 µm) (Figures 4.3e and 4.4a) due to changes in the abundance of vessels in the two size classes 10-20 µm ($D_{10\text{-}20\ \mu m}$, increase by 10%) and 20-30 µm ($D_{20\text{-}30\ \mu m}$, decline by 10%, Figure 4.4b), while the abundance of vessels in the other three size classes was unaffected by the precipitation level (Table A.4.3). As a consequence, the hydraulically-weighted vessel diameter (D_h) did not vary across the gradient (Table 4.3, Table A.4.2), which contrasts with the decrease in *D*.

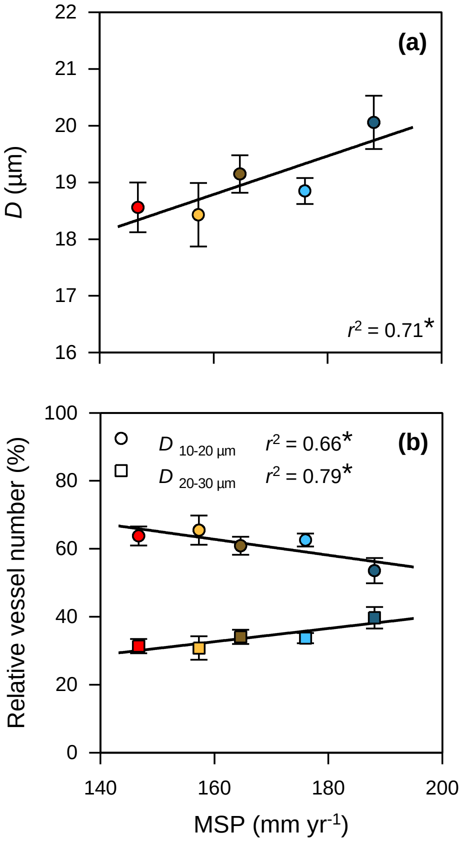

Figure 4.4. Vessel diameter (a, *D*) and percentage of vessels in the vessel diameter classes 10-20 µm and 20-30 µm of total vessel number (b) in dependence on mean early summer growing season precipitation (MSP) in European beech. Values are means ± SE per site. Asterisk indicate the level of significance (* $P<0.05$). For symbol colour see Table 4.1.

None of the parameters related to vessel distribution, i.e. vessel density (VD, Figure 4.3f), vessel grouping index (V_G, Figure 4.3g), solitary vessel index (V_S) and vulnerability index (VI), were altered in response to the precipitation decrease (Table 4.3). In contrast, intervessel pit membrane thickness (T_m) increased by 15% with increasing climatic aridity (Figure 4.3h) while intervessel wall thickness (T_w) remained unchanged (Table 4.3). The strong negative relationship between MAP and T_m according to the linear regression analysis could, however, not be confirmed by the LME (Table 4.3), presumably due to the low sample number and thus high variation within two of the five sites (Table A.4.2). Neither branch growth rate (G_{dw}) nor the lumen to sapwood area ratio (A_{lumen}:A_{xylem}) or the sapwood to leaf area ratio (A_{xylem}:A_{leaf}) were significantly related to the precipitation decrease.

The precipitation gradient had a surprisingly small effect on the sun canopy leaves of the beech trees: neither SLA nor the foliar carbon isotope signature (δ^{13}C) did change along the gradient suggesting that higher climatic aridity did not lead to stomatal closure. However, we found a trend to a larger leaf sizes at the drier sites, contrary to expectation ($P<0.10$, Figure 4.3i).

Determinants of hydraulic efficiency and branch growth

On the tree level, the variation in leaf -specific conductivity (K_L) was caused by alteration of the A_{xylem}:A_{leaf} ratio ($P<0.001$, $r = 0.60$) and partly by modification of D ($P<0.05$, $r = 0.41$), but K_L showed no relationship neither to VD, D_h nor K_S (Table 4.4). Differences in specific conductivity (K_S), in contrast, were mainly driven by changes in D (Figure 4.5a) but not by VD (Figure 4.5d). Contrary to K_S, wood density was unrelated to D (Figure 4.5b) but closely associated with VD (Figure 4.5e). We further could confirm the commonly assumed trade-off between hydraulic efficiency and growth; fast-growing branches possessed a more efficient hydraulic system composed of larger (Figure 4.5c) but fewer vessels (Figure 4.5f) as compared to slower growing branches, and a significant positive relationship existed with both K_S and K_P ($P<0.05$, $r = 0.44$) but also negatively with WD ($P<0.05$, $r = 0.40$; Table 4.4). Furthermore, G_{dw} was negatively related to branch age (BA, $P<0.001$, $r = 0.64$) and leaf size (LS, $P<0.01$, $r = 0.48$), and positively to δ^{13}C ($P<0.05$, $r = 0.35$), indicating that younger branches grew faster at the cost of a more frequent stomatal closure. This finding is further supported by the negative relationship between BA and K_S ($P<0.01$, $r = 0.52$), and the absence of any relation between BA and WD (Table 4.4).

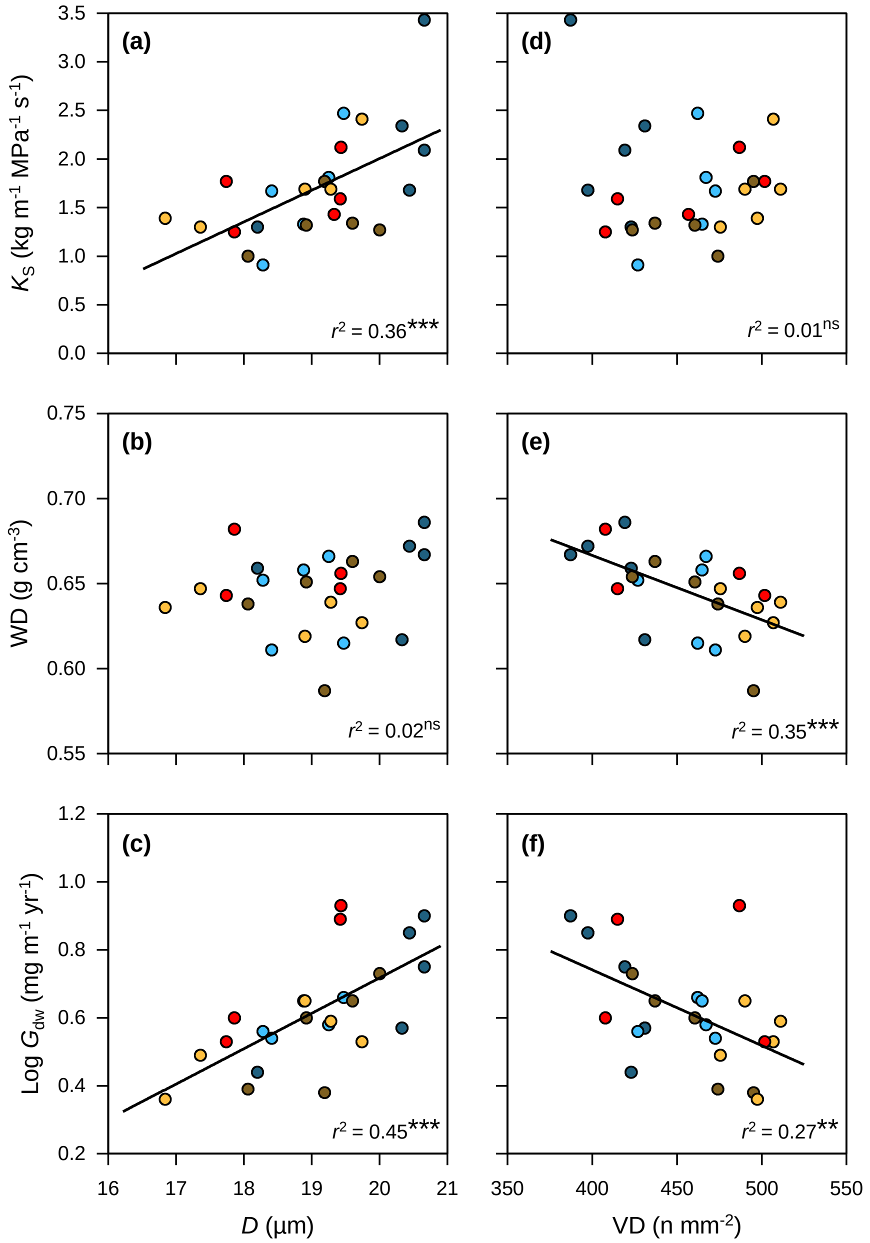

Figure 4.5. Vessel diameter (*D*, left) and vessel density (VD, right) in relation to specific conductivity (a, d, K_S), wood density (b, e, WD) and branch growth rate (c, f, G_{dw}) in European beech. Values are means per tree (n = 25), asterisk indicate the level of significance (** P<0.01; *** P<0.001), non-significant relationships are indicated by ns. For symbol colour see Table 4.1.

Determinants of embolism resistance

At the tree level, only two of eight examined traits commonly associated with embolism resistance (K_S or K_L, WD, D, VD, V_G, T_m, A_{xylem}:A_{leaf} and SLA) were found to be related with embolism resistance in our study (Table 4.4). Contrary to expectation, neither hydraulic efficiency (K_S, K_L) nor D decreased with embolism resistance, indicating that a clear trade-off between hydraulic efficiency and safety does not exist in European beech. However, both VD and T_m were negatively related to embolism resistance with VD showing a closer relation to the air-entry point at high pressure ($P_{12;}$ $P<0.01$, $r = 0.46$) than to the P_{50} value ($P<0.05$, $r = 0.34$), while T_m was most strongly associated with P_{88} ($P<0.05$, $r = 0.56$), i.e. the full embolism point at low pressure, and less tightly to P_{50} ($P<0.10$, $r = 0.40$). Increased embolism resistance is achieved by the beech trees along the gradient by producing more vessels arranged in distinct groups but not necessarily by reducing vessel diameter (Figure 4.6a); this is indicated by the positive relation between VD and V_G (Figure 4.6b). This finding is supported by a negative relation between V_G and P_{12} at marginal significance ($P<0.10$, $r = 0.28$). These adjustments in the vascular system apparently allowed to maintain a favourable leaf water status at the drier sites as indicated by the negative relation between VD and $\delta^{13}C$ (Figure 4.6c), i.e. a higher vessel density decreased the need to reduce leaf conductance.

The Pearson correlation analysis revealed several relationships between embolism resistance and morphological and growth-related parameters that were partly unexpected: BA was positively related to P_{50} ($P<0.05$, $r = 0.34$; Table 4.4, Figure A.4.2b) and P_{88} ($P<0.01$, $r = 0.49$), and branch size (A_{xylem}) was positively associated with P_{12} ($P<0.05$, $r = 0.37$), P_{50} ($P<0.01$, $r = 0.47$) and P_{88} ($P<0.01$, $r = 0.49$; Table 4.4). G_{dw} as a measure of productivity was negatively related to P_{88} ($P<0.05$, $r = 0.34$) but not P_{12} and P_{50}.

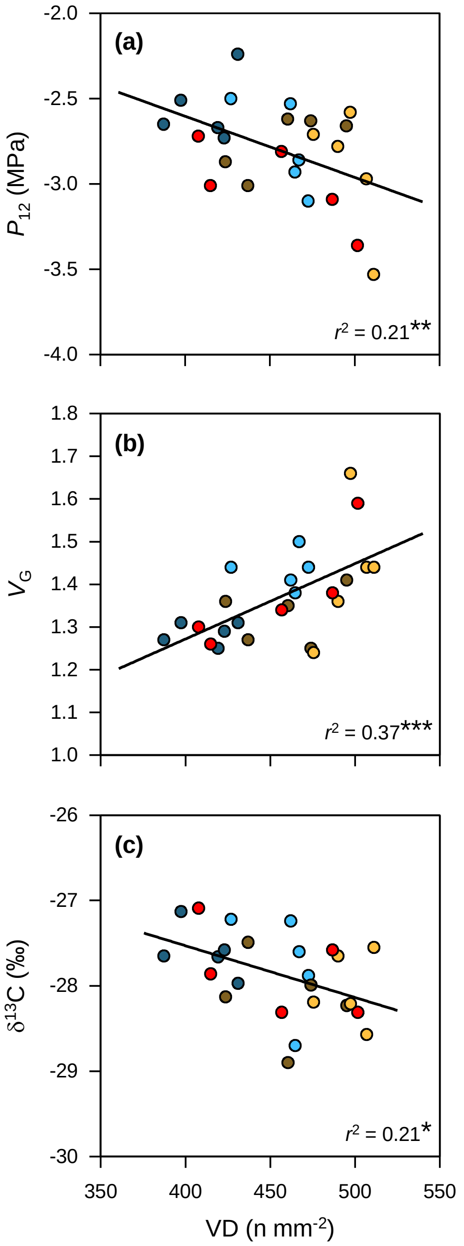

Figure 4.6. Xylem pressure causing 12% loss of hydraulic conductance (a, P_{12}), vessel grouping index (b, V_G) and the carbon isotope signature (c, $\delta^{13}C$) in relation to vessel density (VD) in European beech. Values are means per tree (n = 25), asterisk indicate the level of significance (* $P<0.05$; ** $P<0.01$; *** $P<0.001$). For symbol colour see Table 4.1.

Influence of branch age on embolism resistance across the gradient

Although we carefully sampled branches of similar size across the gradient, a certain variation in BA per given A_{xylem} was observed (Figure A.4.1). This variation was unrelated to changes in MAP and thus not site-specific (Table 4.3). According to a LME with BA added as co-variable or as third random effect, MAP was still significantly related to all three measures of embolism resistance (co-variable: $P<0.01$; random effect: $P<0.05$). We further removed the youngest and oldest branches from the dataset, i.e. the 15% extreme ages younger than four years and older than nine years; this linear regression analysis confirmed the LME with BA included as co-variable or random effect (Figure A.4.2a). Consequently, BA can be excluded as principal driver of embolism resistance along the gradient.

Mutual inter-relationships between traits

The inter-relationships between hydraulic, wood anatomical and foliar traits revealed by the tree-level Pearson correlation analysis (Table 4.4) principally match the results of a Principle Components Analysis conducted with plot-level means. The first two principle components together explained 72% of the variance (Table 4.5). Axis 1 (eigenvalue 0.44) was strongly associated with MAP and all hydraulic and wood anatomical traits including foliar δ^{13}C, but showed no relation to K_L, P_{88} and the traits depending on sapwood area. These parameters and the foliar traits SLA and leaf size (LS) as well as branch growth rate (G_{dw}) were associated with axis 2. The plot-level analysis thus reveals relationships between climatic aridity, branch wood anatomical properties, hydraulic efficiency and embolism resistance that are closer than found in the tree-level analysis in Table 4.4: neither hydraulic efficiency nor vessel diameter were related to embolism resistance at the tree level but such relationships became visible at the plot level (Figure A.4.3).

Our differential analyses at the branch, tree and plot (stand) levels revealed that, for most functional traits, the largest variation existed among the branches within a tree, followed by the variance between the trees of a plot, while a much lower variation was detected between the five plots along the precipitation gradient (see Table A.4.4). This suggested selecting the tree as the focal object of analysis and pooling over the replicate branches, while examining differences between plots in a second step.

Table 4.4. Pearson correlation coefficients for linear relationships between 23 functional trait variables across trees in European beech. Significance levels: ^{ns}: non-significant; bold italic letters: P<0.05; bold letters: P<0.01; bold underlined letters: P<0.001. See Table 4.2 for definition of abbreviations.

	BA	K_S	K_P	K_L	P_{12}	P_{50}	P_{88}	WD	D	D_h	VD	VI	V_G	V_S	T_m	T_w	A_{xylem}	$A_{xylem}:A_{leaf}$	$A_{lumen}:A_{xylem}$	G_{dw}	LS	SLA
K_S	**-0.52**																					
K_P	ns	**0.62**																				
K_L	ns	**0.47**	ns																			
P_{12}	ns	ns	ns	ns																		
P_{50}	***0.34***	ns	ns	ns	**0.91**																	
P_{88}	**0.49**	ns	ns	ns	**0.66**	**0.92**																
WD	ns	ns	ns	ns	ns	ns	ns															
D	ns	**0.60**	**0.87**	***0.41***	ns	ns	ns	ns														
D_h	ns	**0.56**	**0.90**	ns	ns	ns	ns	ns	**0.83**													
VD	ns	ns	ns	ns	**-0.46**	***-0.34***	ns	**-0.59**	***-0.43***	ns												
VI	***-0.41***	***0.36***	***0.39***	ns	***0.40***	ns	ns	***0.44***	**0.77**	**0.50**	**-0.87**											
V_G	ns	ns	ns	ns	ns	ns	ns	ns	***-0.35***	ns	**0.60**	**-0.57**										
V_S	ns	ns	ns	ns	ns	ns	ns	ns	0.31	ns	**-0.58**	**0.54**	**-0.95**									
T_m	ns	ns	ns	ns	ns	ns	***-0.56***	ns	ns	ns	ns	ns	ns	ns								
T_w	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	***0.44***							
A_{xylem}	***0.37***	***-0.39***	ns	ns	***0.37***	**0.47**	**0.49**	ns	ns	ns	ns	ns	ns	ns	ns	ns						
$A_{xylem}:A_{leaf}$	ns	ns	***-0.40***	**0.60**	ns	ns	ns	ns	ns	**-0.55**	ns	ns	ns	ns	ns	ns	***0.34***					
$A_{lumen}:A_{xylem}$	ns	**0.48**	**0.91**	ns	ns	ns	ns	ns	**0.67**	**0.71**	ns	ns	ns	ns	ns	ns	ns	ns				
G_{dw}	**-0.64**	***0.44***	***0.44***	ns	ns	ns	***-0.34***	***0.40***	**0.65**	***0.44***	**-0.49**	**0.70**	ns	ns	ns	ns	ns	ns	ns			
LS	ns	ns	ns	***-0.40***	ns	ns	ns	ns	ns	***0.34***	ns	ns	ns	ns	ns	ns	ns	**-0.68**	ns	**0.48**		
SLA	ns	ns	ns	***-0.37***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	***-0.44***	ns	ns	**0.55**	
$\delta^{13}C$	***-0.34***	ns	ns	ns	ns	ns	ns	ns	ns	ns	**-0.45**	***0.42***	ns	ns	ns	ns	ns	ns	ns	***0.35***	ns	ns

Table 4.5 Results of a Principle Components Analysis (PCA) on the relationships between various climatic, hydraulic, woody and foliar traits (means of the five investigated study sites) and the eigenvalues of the four main axes in European beech. The cumulative coefficient of determination is given in parentheses. Numbers in bold mark the variable with the closest correlation to the respective axis. See Table 4.2 for definition of abbreviations.

Variables	**Axis 1**		**Axis 2**		**Axis 3**		**Axis 4**	
	EV 0.44		**EV 0.28**		**EV 0.18**		**EV 0.10**	
Environmental conditions								
MAP	**0.75**	**(0.56)**	0.64	(0.97)	-0.14	(0.99)	0.08	(1.00)
Structural parameters								
BA	-0.51	(0.26)	0.34	(0.38)	**0.77**	**(0.97)**	-0.18	(1.00)
Hydraulic traits								
K_S	**0.73**	**(0.53)**	-0.17	(0.56)	-0.58	(0.89)	0.32	(1.00)
K_P	**0.78**	**(0.61)**	-0.36	(0.74)	0.40	(0.91)	0.30	(1.00)
K_L	0.30	(0.09)	**0.95**	**(0.99)**	0.05	(1.00)	0.07	(1.00)
P_{12}	**0.88**	**(0.77)**	0.39	(0.92)	0.17	(0.95)	0.22	(1.00)
P_{50}	**0.79**	**(0.62)**	0.61	(0.99)	0.09	(1.00)	-0.02	(1.00)
P_{88}	0.57	(0.32)	**0.77**	**(0.91)**	-0.01	(0.91)	-0.29	(1.00)
Wood properties								
WD	**0.70**	**(0.49)**	-0.58	(0.82)	-0.23	(0.88)	-0.35	(1.00)
D	**0.99**	**(0.97)**	0.00	(0.97)	0.16	(1.00)	0.02	(1.00)
D_h	**0.76**	**(0.57)**	-0.51	(0.83)	0.41	(1.00)	-0.02	(1.00)
VD	**-0.95**	**(0.90)**	0.11	(0.91)	-0.01	(0.91)	0.30	(1.00)
VI	**0.98**	**(0.96)**	-0.03	(0.96)	0.01	(0.96)	-0.19	(1.00)
V_G	**-0.81**	**(0.65)**	0.34	(0.77)	-0.48	(1.00)	-0.03	(1.00)
V_S	**0.73**	**(0.54)**	-0.35	(0.66)	0.58	(1.00)	0.05	(1.00)
T_m	**-0.84**	**(0.71)**	-0.53	(0.99)	-0.06	(1.00)	-0.04	(1.00)
T_w	0.45	(0.20)	-0.23	(0.25)	**-0.84**	**(0.96)**	0.21	(1.00)
A_{xylem}	-0.04	(0.00)	0.44	(0.20)	**0.73**	**(0.73)**	-0.52	(1.00)
$A_{xylem} : A_{leaf}$	-0.17	(0.03)	**0.86**	**(0.78)**	-0.32	(0.88)	-0.34	(1.00)
$A_{lumen} : A_{xylem}$	0.21	(0.04)	-0.17	(0.07)	0.66	(0.51)	**0.70**	(1.00)
G_{dw}	0.55	(0.30)	**-0.62**	**(0.68)**	-0.19	(0.72)	-0.53	(1.00)
Foliar traits								(1.00)
LS	-0.09	(0.01)	**-0.99**	**(0.98)**	-0.14	(1.00)	0.04	(1.00)
SLA	-0.13	(0.02)	**-0.66**	**(0.45)**	0.34	(0.57)	-0.66	(1.00)
$\delta^{13}C$	**0.68**	**(0.47)**	0.04	(0.47)	-0.69	(0.94)	-0.24	(1.00)

Discussion

Climatic influences on wood anatomical, hydraulic and foliar traits

We observed a close relation between mean early growing season precipitation (MSP) and vessel diameter (D) in similarly-sized branches from the uppermost canopy of mature beech trees, partly supporting our first hypothesis which postulated that vessel diameter and hydraulic efficiency decrease with a lasting reduction in precipitation. The decline in D by 7% from the wet to the dry end of the gradient was nearly exclusively caused by shifts in the relative abundance of vessels with a diameter between 10 to 30 µm. On the other hand, the three larger vessel diameter classes, which primarily consist of early-wood vessels and are of great importance for the calculation of the hydraulically-weighted vessel diameter (D_h), were unaffected. As a consequence, D_h did not change across our precipitation gradient. The altered diameter pattern is also mirrored in the absence of any relationship between either mean annual precipitation (MAP) or MSP and potential (K_P) or specific conductivity (K_S), because hydraulic conductivity increases with diameter raised to the fourth power according to the Hagen-Poiseuille law, and the diameter alteration in the 10-30 µm class is of low importance for K_P.

The functionality of the vascular system is best analysed in conjunction with the dependent foliage for understanding wood anatomical modifications in response to the environment (Carlquist, 2012). Both tissues related to water transport might have co-evolved with respect to traits governing xylem vulnerability to embolism (Brodribb *et al.*, 2003; Nolf *et al.*, 2015). Although K_P and K_S remained more or less constant, leaf-specific conductivity (K_L) decreased unexpectedly by 40% with a MAP decrease by 260 mm yr^{-1}. Generally, K_L is supposed to increase in plants that are frequently exposed to drought in order to maintain a favourable leaf water status (Mencuccini & Grace, 1995; Sterck *et al.*, 2008). This is either achieved by an increase in K_S, or more likely by adjustment of the sapwood-to-leaf area ratio (A_{xylem}:A_{leaf}). In Scots pine, for example, both K_L and A_{xylem}:A_{leaf} increased with climate dryness across Europe, while K_S and D remained unchanged (Martinez-Vilalta *et al.*, 2009; Sterck *et al.*, 2012). This indicates that this coniferous species responds to increasing drought exposure mainly by reducing the supported leaf area per unit sapwood area. In beech, the decrease in K_L with a reduction in MAP along the gradient was likewise caused by an increase in dependent leaf area toward the drier stands. In contrast, most other studies found an increase in A_{xylem}:A_{leaf} with increasing climatic aridity, both within and between species (e.g. Poyatos *et al.*, 2007; Gleason *et al.*, 2013). Along our gradient, however, mean leaf size tended to increase, and not decrease, toward the drier eastern stands as also observed by Meier &

Leuschner (2008) in a precipitation gradient of beech forests on sandstone in Central Germany.

A major finding of this study is that embolism resistance increased in parallel with declining *D* with increasing climatic aridity across our gradient supporting our second hypothesis. To our knowledge, this is the first study evidencing a linear intra-specific increase in embolism resistance with increasing drought stress. This finding provides additional support for the assumption that *F. sylvatica* is highly plastic with respect to the embolism resistance (Herbette *et al.*, 2010), and that embolism resistance is under environmental rather than genetic control in this angiosperm tree species (Wortemann *et al.*, 2011). In *Pinus sylvestris* and *Pinus pinaster*, in contrast, P_{50} was unrelated to climatic aridity (Martinez-Vilalta *et al.*, 2009; Lamy *et al.*, 2014). These contradicting results might be attributed to the observation that populations of angiosperm tree species generally possess a higher intra-specific variation in hydraulic traits than conifers (Anderegg, 2015). However, one has to keep in mind that vessel diameter, hydraulic properties and embolism resistance are not only influenced by the moisture regime but certainly by other biotic and environmental factors as well, which complicates the interpretation of results obtained from climatic gradients. It has been shown that tree size and sampling height (Anfodillo *et al.*, 2013; Lintunen & Kalliokoski, 2010), as well as soil properties, in particular nutrient availability (Goldstein *et al.*, 2013) and water storage capacity (Tukomoto *et al.*, 2014), are strongly influencing the hydraulic architecture of plants. In cross-regional comparisons, it is therefore mandatory to keep tree size (or age) and soil properties as constant as possible in order to detect effects of environmental factors.

The observed modification of the hydraulic system across our precipitation gradient indicates that trees growing at the dry end tolerate more negative stem water potentials before the water transport to the canopy is impeded. This hydraulic adaptation was effective with respect to the maintenance of leaf gas exchange under drier conditions is suggested by the invariance of leaf $\delta^{13}C$ across the precipitation gradient.

Relationships between wood properties and embolism resistance

One of the principal hypotheses of plant hydraulics postulates a general trade-off between hydraulic safety and efficiency. This hypothesis is not confirmed by our data, which is in line with the majority of studies recently summarized by Gleason *et al.* (2015). Although both *D* and the three measures of embolism vulnerability decreased with climatic aridity and a close relation between *D* and hydraulic efficiency was observed, neither *D* nor K_S were related to xylem safety. Tyree and Sperry (1989) argued that *D* is not directly related to the mechanism of embolism formation but rather results from a correlation with pit membrane pore size. Nevertheless, several studies have evidenced this close, albeit presumably indirect, relation among and across species (Wheeler *et al.*, 2005; Maherali *et al.*, 2006; Domec *et al.*, 2010; Hajek *et al.*, 2014). We assume that the range of variation in D and P_{50} was too small to confirm this relation across the trees in our intraspecific study. Instead, vessel density (VD) was closely related to the air-entry point of embolism formation (P_{12}) but not to hydraulic efficiency. The vessel grouping index (V_G) was likewise associated with P_{12} (although at marginal significance only) and closely related to VD as observed by Lens *et al.* (2011). These results are in line with Carlquist's (1966) assumption that vessels should group to a larger degree in species adapted to water-limited environments with a xylem tissue composed of nonconductive fibres and no vasicentric tracheids; this would enable the maintenance of the conductive flow path by pathway redundancy if the largest vessel of the group embolizes. Through such vascular modification with more and to a higher degree grouped vessels in order to lower the xylem pressure at the onset of embolism formation, trees are presumably able to tolerate more negative leaf water potentials before stomata have to be closed. This assumption is supported by our negative relation between VD and foliar $\delta^{13}C$. It has further been shown that stomatal closure correlates with the entry point of embolism formation in angiosperms, i.e. the P_{12} value (Nardini *et al.*, 2001; Cochard *et al.*, 2002).

Contrary to VD and V_G, intervessel pit membrane thickness (T_m) correlated best with the xylem pressure inducing 88% of loss of hydraulic conductance (P_{88}), although a marginally significant relation also existed with P_{50}. It has been shown that the thickness of the membrane in angiosperm xylem is directly related to its maximum pore diameter (Jansen *et al.*, 2009b), making air-seeding more likely for thin membranes (Wheeler *et al.*, 2005). However, this does not explain why in our sample the closest relation existed to the most negative pressure at P_{88}. It is likely that there are still serious gaps in our mechanistic understanding of air-seeding in plants (Schenk *et al.*, 2015).

For three other traits often associated with embolism resistance, namely wood density (WD), A_{xylem}:A_{leaf} and specific leaf area, we were not able to confirm such a relationship in our data set. Such relations may become visible only in data sets spanning different species or in intra-specific studies with much greater site and trait variation than is encountered in our precipitation gradient. Other biological properties may also influence embolism resistance, notably branch age, as we found older branches to be most vulnerable to cavitation in agreement with Domec *et al.* (2009). However, we believe that this effect is primarily caused by cavitation fatigue, i.e. the reduction of cavitation pressure as a consequence of previous cavitation in older xylem elements (Hacke *et al.*, 2001), even though we corrected for the potential bias of fatigue by applying a certain pressure before the onset of conductivity measurements (Jacobsen *et al.*, 2007). Future research has to show how many growth rings of older branches remain conductive in angiosperm trees (but see Christensen-Dalsgaard & Tyree, 2014) and it has to clarify whether sample flushing prior to the construction of vulnerability curves introduces measuring artefacts.

Relationship between hydraulic efficiency and branch growth

Similar to Sterck *et al.* (2012) we use sun-canopy branch growth rate (G_{dw}) as a measure of productivity because a dependence of growth on branch hydraulics is more likely at this level than for stem wood or total aboveground productivity. In our study, faster growing younger branches of similar size as older ones possessed a more efficient hydraulic system and supported larger leaves, which subsequently caused a more frequent stomatal closure. This finding is in agreement with our third hypothesis assuming a close relation between hydraulic efficiency and growth, which might trade-off with embolism resistance (Cochard *et al.*, 2007). Unexpected is our finding that older slower-growing branches in a given diameter class were more vulnerable than younger faster-growing branches as is indicated by the negative relation between G_{dw} and P_{88}. Generally, fast growth is associated with larger vessels that cause higher hydraulic efficiency, which should result in a relatively vulnerable xylem (e.g. Hajek *et al.*, 2014). Although all branches investigated originate from the uppermost sun-exposed canopy, we assume that the older and the slower-growing branches of similar size have not been exposed to full sunlight and thus to high atmospheric demand in the last years, presumably because they were shaded by younger fast growing branches. A similar pattern was observed by Herbette *et al.* (2010) when comparing sun-exposed and deeply shaded beech branches; the latter were on average 50% more vulnerable. This high variability in xylem embolism resistance, even at the same canopy position, is strong support for the frequently claimed high phenotypic plasticity in the morphology and physiology of European beech (Herbette *et al.*, 2010; Bresson *et al.*, 2011; Wortemann *et al.*, 2011). Shade-tolerant beech trees produce leaves that tolerate either full sunlight or deep shade and it can be assumed that this great plasticity in leaf function is also reflected in the hydraulic system of branches and petioles. However, given that G_{dw} was not related to any other parameter of embolism resistance in our study, it is premature to conclude that a trade-off between embolism resistance and branch growth does exist in the beech trees of our study. In agreement with this assumption, several other studies failed to detect relationships between vulnerability and growth (Sterck *et al.*, 2012; Hajek *et al.*, 2014; Guet *et al.*, 2015), indicating that embolism resistance is partly decoupled from hydraulic efficiency and biomass production (Fichot *et al.*, 2015).

Conclusion

In the sun canopy of beech trees, morphological adjustment to permanently reduced precipitation seems to occur primarily through the development of more cavitation-resistant branch wood, and not through reduction of the supported leaf area. Due to this modification, trees at the dry end of the gradient are capable of tolerating 15% more negative stem water potentials before the onset of cavitation. Our results show that the branch hydraulic system of beech has a considerable adaptive potential to respond to the local climatic conditions. This finding is strong evidence in support of the assumption that embolism resistance is largely under environmental control in this angiosperm tree species. It remains unclear, however, whether the observed hydraulic variability at the branch level can fully buffer against constraints imposed on growth and vitality by a warming and drying climate. Over the last three to four decades, a radial growth decline has been observed in those beech stands of our study region that are exposed to less than ~635 mm yr^{-1} precipitation. This casts doubt on the capability of *F. sylvatica* to withstand increased drought and warming stress in future time solely by its flexible hydraulic response.

Acknowledgements

We thank Julia Juchheim for strong support in field and lab, Andre Meier and Tobias Fochler (BaumDirekt) for sample collection from the uppermost canopy with tree climbing equipment, Claus Döring for providing meteorological data, and Ina Meier for support with data on leaf morphology as well as all involved technical and student assistants for their invaluable help in collecting and processing this dataset. This study is part of the research program ‘Climate Impact and Adaptation Research in Lower Saxony (KLIFF)’. Financial support granted by the Ministry of Science and Culture of Lower Saxony to C.L. is gratefully acknowledged. S.J. acknowledges technical support from the Electron Microscopy Section (Ulm University) for the preparation of TEM samples. Constructive and helpful comments from three anonymous reviewers and the handling editor helped to improve the manuscript.

Conflict of interest

None declared.

References

Anderegg WRL, Flint A, Huang C, Flint L; Berry JA, Davis FW, Sperry JS, Field CB (2015) Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience*, **8**, 367–371.

Anderegg WRL (2015) Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* **205**, 1008–1014.

Anderegg WRL, Meinzer FC (2015) Wood anatomy and plant hydraulics in a changing climate. *Functional and Ecological Xylem Anatomy*. Springer International Publishing, Switzerland, 235–253.

Anfodillo T, Petit G, Crivellaro A (2013) Axial conduit widening in woody species: a still neglected anatomical pattern. *IAWA Journal*, **34**, 352–364.

Aranda I, Cano FJ, Gascó A, Cochard H, Nardini A, Mancha JA, López R, Sánchez-Gómez D (2015) Variation in photosynthetic performance and hydraulic architecture across European beech (*Fagus sylvatica* L.) populations supports the case for local adaptation to water stress. *Tree Physiology*, **35**, 34–46.

Bohn U, Neuhäusl R, Mitarbeit U. 2003. Map of the Natural Vegetation of Europe. Scale 1:2500000. Bundesamt für Naturschutz (BfN)/Federal Agency for Nature Conservation, Bonn.

Bolte A, Czajkowski T, Kompa T (2007) The north-eastern distribution range of European beech a review. *Forestry*, **80**, 413–429.

Bouche PS, Larter M, Domec JC, Burlett R, Gasson P, Jansen S, Delzon S (2014) A broad survey of hydraulic and mechanical safety in the xylem of conifers. *Journal of Experimental Botany*, **65**, 4419–4431.

Breda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625–644.

Bresson CC, Vitasse Y, Kremer A, Delzon S. (2011) To what extent is altitudinal variation of functional traits driven by genetic adaptation in European oak and beech? *Tree Physiology*, **31,** 1164–1174.

Brodribb TJ, Holbrook NM, Edwards EJ, Gutierrez M V (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant Cell and Environment*, **26**, 443–450.

Carlquist S (1966) Wood anatomy of compositae: a summary, with comments on factors controlling wood evolution. *Aliso*, **6**, 25–44.

Carlquist S (1977) Ecological Factors in Wood Evolution - Floristic Approach. *American Journal of Botany*, **64**, 887–896.

Carlquist S (2012) How wood evolves: a new synthesis. *Botany*, **90**, 901–940.

Chenlemuge T, Schuldt B, Dulamsuren C, Hertel D, Leuschner C, Hauck M (2015) Stem increment and hydraulic architecture of a boreal conifer (*Larix sibirica*) under contrasting macroclimates. *Trees-Structure and Function*, **29**, 623–636.

Christensen-Dalsgaard KK, Tyree MT (2014) Frost fatigue and spring recovery of xylem vessels in three diffuse-porous trees in situ. *Plant, Cell and Environment*, **37**, 1074–85.

Cochard H, Casella E, Mencuccini M (2007) Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. *Tree Physiology*, **27**, 1761–1767.

Cochard H, Damour G, Bodet C, Tharwat I, Poirier M, Ameglio T (2005) Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiologia Plantarum*, **124**, 410–418.

De Micco V, Aronne G, Baas P (2008) Wood anatomy and hydraulic architecture of stems and twigs of some Mediterranean trees and shrubs along a mesic-xeric gradient. *Trees-Structure and Function*, **22**, 643–655.

Delzon S, Douthe C, Sala A, Cochard H (2010) Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell and Environment*, **33**, 2101–11.

Domec J-C, Gartner BL (2001) Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees*, **15**, 204–214.

Domec JC, Schafer K, Oren R, Kim HS, McCarthy HR (2010) Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO2 concentration. *Tree Physiology*, **30**, 1001–1015.

Domec JC, Warren JM, Meinzer FC, Lachenbruch B (2009) Safety factors for xylem failure by implosion and air-seeding within roots, trunks and branches of young and old conifer trees. *International Association of Wood Anatomists Journal*, **30**, 101–120.

Eilmann B, Sterck F, Wegner L, de Vries SM, von Arx G, Mohren GM, den Ouden J, Sass-Klaassen U (2014) Wood structural differences between northern and southern beech provenances growing at a moderate site. *Tree Physiology*, **34**, 882–893.

Ellenberg H, Leuschner C (2010) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Hinsicht*. Ulmer, Stuttgart, Germany.

Fan DY, Jie SL, Liu CC, Zhang XY, Xu XW, Zhang SR, Xie ZQ (2011) The trade-off between safety and efficiency in hydraulic architecture in 31 woody species in a karst area. *Tree Physiology*, **31**, 865–877.

Fichot R, Brignolas F, Cochard H, Ceulemans R (2015) Vulnerability to drought-induced cavitation in poplars: synthesis and future opportunities. *Plant, Cell and Environment*, **38**, 1233–1251.

Fischer EM, Schär C (2008) Future changes in daily summer temperature variability: driving processes and role for temperature extremes. *Climate Dynamics*, **33**, 917–935.

Führer E, Horváth L, Jagodics A, Machon A, Szabados I (2011) Application of a new aridity index in Hungarian forestry practice. *Idojaras*, **115**, 205–216.

Gessler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees-Structure and Function*, **21**, 1–11.

Gleason SM, Butler DW, Waryszak P (2013) Shifts in Leaf and Stem Hydraulic Traits across Aridity Gradients in Eastern Australia. *International Journal of Plant Sciences*, **174**, 1292–1301.

Gleason SM, Butler DW, Ziemińska K, Waryszak P, Westoby M (2012) Stem xylem conductivity is key to plant water balance across Australian angiosperm species. *Functional Ecology*, **26**, 343–352.

Goldstein G, Bucci SJ, Scholz FG (2013) Why do trees adjust water relations and hydraulic architecture in response to nutrient availability? *Tree Physiology*, **33**, 238–240.

Guet J, Fichot R, Ledee C, Laurans F, Cochard H, Delzon S, Bastien C, Brignolas F (2015) Stem xylem resistance to cavitation is related to xylem structure but not to growth and water-use efficiency at the within-population level in *Populus nigra* L. *Journal of Experimental Botany*, **66**, 4643-4652.

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloch KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.

Hajek P, Leuschner C, Hertel D, Delzon S, Schuldt B (2014) Trade-offs between xylem hydraulic properties, wood anatomy and yield in Populus. *Tree Physiology*, **34**, 744–756.

Herbette S, Wortemann R, Awad H, Huc R, Cochard H, Barigah TS (2010) Insights into xylem vulnerability to cavitation in Fagus sylvatica L.: phenotypic and environmental sources of variability. *Tree physiology*, **30**, 1448–55.

Hertel D, Strecker T, Müller-Haubold H, Leuschner C (2013) Fine root biomass and dynamics in beech forests across a precipitation gradient - is optimal resource partitioning theory applicable to water-limited mature trees? (ed Guo D). *Journal of Ecology*, **101**, 1183–1200.

Hoeber S, Leuschner C, Köhler L, Arias-Aguilar D, Schuldt B (2014) The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate. *Forest Ecology and Management*, **330**, 126–136.

Jacob D, Göttel H, Kotlarski S, Lorenz P, Sieck K (2008) Klimaauswirkungen und Anpassung in Deutschland – Phase 1: Erstellung regionaler Klimaszenarien für Deutschland. *Climate Change*, **11**.

Jacobsen AL, Pratt RB, Ewers FW, Davis SD (2007) Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs*, **77**, 99–115.

Jansen S, Choat B, Pletsers A (2009) Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. *American journal of botany*, **96**, 409–19.

Jansen S, Dute RR, Plavcová L, Choat B (2009) Preparation of material for TEM examination. Prometheus Wiki, CSIRO Publishing.

Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.

Kotowska MM, Hertel D, Abou Rajab Y, Barus H, Schuldt B (2015) Patterns in hydraulic architecture from roots to branches in six tropical tree species from cacao agroforestry and their relation to wood density and stem growth. *Frontiers in Plant Science*, **6**, 1–16.

Kremer A, Potts BM, Delzon S (2014) Genetic divergence in forest trees: Understanding the consequences of climate change. *Functional Ecology*, **28**, 22–36.

Lamy JB, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, Plomion C (2014) Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *New Phytologist*, **201**, 874–886.

Legendre P, Legendre L (1998) Numerical ecology. 2nd English edn. Elsevier Science B.V., Amsterdam, The Netherlands.

Lens F, Luteyn JL, Smets E, Jansen S (2004) Ecological trends in the wood anatomy of Vaccinioideae (Ericaceae s.l.). *Flora - Morphology, Distribution, Functional Ecology of Plants*, **199**, 309–319.

Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S (2011) Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. *New Phytologist*, **190**, 709–23.

Leuschner C. 2009. Die Trockenheitsempfindlichkeit der Rotbuche vor dem Hintergrund des prognostizierten Klimawandels. Jahrbuch der Akademie der Wissenschaften zu Göttingen. Walter de Gruyter, Berlin, pp 281–296, adw-digital.sub.uni-goettingen.de/bitstream/handle/11858/00-001S-0000-0007-371C-7/Article-1.pdf?sequence=1.

Lewis AM, Boose ER (2011) Estimating flow rates through xylem conduits. *American Journal of Botany*, **82**, 1112–1116.

Lintunen A, Kalliokoski T (2010) The effect of tree architecture on conduit diameter and frequency from small distal roots to branch tips in *Betula pendula*, *Picea abies* and *Pinus sylvestris*. *Tree physiology*, **30**, 1433–47.

Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB (2006) Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant Cell and Environment*, **29**, 571–583.

Markesteijn L, Poorter L, Paz H, Sack L, Bongers F (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment*, **34**, 137–48.

Martinez-Vilalta J, Cochard H, Mencuccini M, Sterck F, Herrero A, Korhonen JFJ, Llorens P, Nikinmaa E, Nolè A, Poyatos R, Ripullone F, Sass-Klaassen U, Zweifel R (2009) Hydraulic adjustment of Scots pine across Europe. *New Phytologist*, **184**, 353–364.

McDowell NG, Allen CD (2015) Darcy’s law predicts widespread forest mortality under climate warming. *Nature Climate Change*, **5**, 669–672.

Meier IC, Leuschner C (2008) Leaf size and leaf area index in Fagus sylvatica forests: Competing effects of precipitation, temperature, and nitrogen availability. *Ecosystems*, **11**, 655–669.

Meinke I, Gerstner E, von Storch H, Marx A, Schipper H, Kottmeier C, Treffeisen R, Lemke, P (2010) Regionaler Klimaatlas Deutschland der Helmholtz-Gemeinschaft informiert im Internet über möglichen künftigen Klimawandel. *DMG Mitteilungen*, **2**, 7–9.

Mencuccini M, Grace J (1995) Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology*, **15**, 1–10.

Müller-Haubold H, Hertel D, Seidel D, Knutzen F, Leuschner C (2013) Climate Responses of Aboveground Productivity and Allocation in *Fagus sylvatica*: A Transect Study in Mature Forests. Ecosystems, **16**: 1498–1516.

Nardini A, Tyree MT, Salleo S. 2001. Xylem cavitation in the leaf of Prunus laurocerasus and its impact on leaf hydraulics. *Plant Physiology*, **125**, 1700–1709.

Nolf M, Creek D, Duursma R, Holtum J, Mayr S, Choat B (2015) Stem and leaf hydraulic properties are finely coordinated in three tropical rainforest tree species. *Plant, Cell and Environment*.

Ogasa M, Miki NH, Murakami Y, Yoshikawa K (2013) Recovery performance in xylem hydraulic conductivity is correlated with cavitation resistance for temperate deciduous tree species. *Tree Physiology*, **33**, 335–344.

Pammenter NW, Vander Willigen C (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology*, **18**, 589–593.

Plavcová L, Jansen S, Klepsch M, Hacke UG (2013) Nobody’s perfect: can irregularities in pit structure influence vulnerability to cavitation? *Frontiers in Plant Science*, **4**, 453.

Poyatos R, Martínez-Vilalta J, Cermák J, Ceulemans R, Granier A, Irvine J, Köstner B, Lagergreen F, Meiresonne L, Nadezhdina N, Zimmermann R, Llorens P, Mencuccini M (2007) Plasticity in hydraulic architecture of Scots pine across Eurasia. *Oecologia*, **153**, 245–59.

Rigling A, Bigler C, Eilmann B, Feldmeyer-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P, Vacchiano G, Weber P, Wolgemuth T, Zweifel R, Dobbertin, M (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biology*, **19**, 229–240.

Rowell DP, Jones RG (2006) Causes and uncertainty of future summer drying over Europe. *Climate Dynamics*, **27**, 281–299.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–6.

Schenk HJ, Steppe K, Jansen S (2015) Nanobubbles: a new paradigm for air-seeding in xylem. *Trends in Plant Science*, **20**, 199–205.

Scholz A, Klepsch M, Karimi Z, Jansen S (2013) How to quantify conduits in wood? *Frontiers in Plant Science*, **4**, 56.

Schreiber SG, Hacke UG, Hamann A (2015) Variation of xylem vessel diameters across a climate gradient: insight from a reciprocal transplant experiment with a widespread boreal tree. *Functional Ecology*.

Sperry JS, Nichols KL, Sullivan JEM, Eastlack SE (1994) Xylem Embolism in Ring-Porous, Diffuse-Porous, and Coniferous Trees of Northern Utah and Interior Alaska. *Ecology*, **75**, 1736–1752.

Sterck FJ, Martínez-Vilalta J, Mencuccini M, Cochard H, Gerrits P, Zweifel R, Herrero A, Korhonen FJF, Llorens P, Nikinmaa E, Nolè A, Poyatos R, Ripullone F, Sass-Klaassen U (2012) Understanding trait interactions and their impacts on growth in Scots pine branches across Europe. *Functional Ecology*, **26**, 541–549.

Sterck FJ, Zweifel R, Sass-Klaassen U, Chowdhury Q (2008) Persisting soil drought reduces leaf specific conductivity in Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*). *Tree Physiology*, **28**, 529–536.

Tokumoto I, Heilman JL, Schwinning S, McInnes KJ, Litvak ME, Morgan CLS, Kamps RH (2014) Small-scale variability in water storage and plant available water in shallow, rocky soils. *Plant and Soil*, **385**, 193–204.

Tyree MT (2003) Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. *Trees-Structure and Function*, **17**, 95–100.

Tyree MT, Davis SD, Cochard H (1994) Biophysical Perspectives of Xylem Evolution - Is There A Tradeoff of Hydraulic Efficiency for Vulnerability to Dysfunction. *Iawa Journal*, **15**, 335–360.

Tyree MT, Sperry JS (1989) Vulnerability of Xylem to Cavitation and Embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 19–38.

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Berlin, Germany: Springer Verlag.

Vesque J. (1876) Note sur l’anatomie du Goodenia ovate. Annales des Sciences Naturalles-Botanique et Biologie Vegetale, **6**, 312-326.

Weber P, Bugmann H, Pluess AR, Walthert L, Rigling A (2013) Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees - Structure and Function*, **27**, 171–181.

Wheeler JK, Sperry JS, Hacke UG, Hoang N (2005) Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant Cell and Environment*, **28**, 800–812.

Willson CJ, Manos PS, Jackson RB (2008) Hydraulic Traits Are Influenced By Phylogenetic History in the Drought-Resistant, Invasive Genus Juniperus (Cupressaceae). *American Journal of Botany*, **95**, 299–314.

Wortemann R, Herbette S, Barigah TS, Fumanal B, Alia R, Ducousso A, Gomory D, Roeckel-Drevert P, Cochard H (2011) Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiology*, **31**, 1175–82.

Zimmermann J, Hauck M, Dulamsuren C, Leuschner C (2015) Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. *Ecosystems*, **18**, 560–572.

Appendix

Table A. 4.1. Pearson correlation coefficient (r) and level of significance (P) for the relationship between specific conductivity (K_S) at the sample level, normalized to different positions along the branch segments (maximum, mean or minimum segment diameter), on the predictor vessel diameter (D), hydraulically-weighted diameter (D_h), potential conductivity (K_P) as well as three measures of specific conductivity as determined with the Cavitron device. Acronyms follow Table 4.2.

Variable	$K_S A_{xylem}^{max}$		$K_S A_{xylem}^{mean}$		$K_S A_{xylem}^{min}$	
	r	P	r	P	r	P
D	0.50	<0.001	0.45	<0.001	0.34	0.001
D_h	0.42	<0.001	0.41	<0.001	0.33	0.001
K_P	0.47	<0.001	0.46	<0.001	0.34	0.001
$K_S^{cavi} A_{xylem}^{max}$	0.73	<0.001	0.56	<0.001	0.30	0.002
$K_S^{cavi} A_{xylem}^{mean}$	0.69	<0.001	0.62	<0.001	0.44	<0.001
$K_S^{cavi} A_{xylem}^{min}$	0.59	<0.001	0.66	<0.001	0.59	<0.001

Table A. 4.2. Summary of all major variables explored. Values were averaged for every tree (two to five samples per tree) and subsequently averaged for a site (five tree individuals per site). Given values are means ± SE, for definition of abbreviations see Table 4.2**.**

Variable	Ca	Kl	Go	Un	Se
Structural parameters					
BA	6.07 ± 1.23	6.37 ± 0.46	8.73 ± 0.83	6.76 ± 0.79	4.73 ± 0.69
Hydraulic traits					
K_{S}	1.63 ± 0.15	1.70 ± 0.20	1.34 ± 0.12	1.64 ± 0.26	2.17 ± 0.36
K_{P}	2.38 ± 0.23	2.35 ± 0.34	2.54 ± 0.10	2.21 ± 0.12	2.73 ± 0.18
K_{L}	7.66 ± 0.71	9.48 ± 0.94	10.53 ± 1.20	12.03 ± 1.12	10.53 ± 0.99
P_{12}	-3.00 ± 0.11	-2.91 ± 0.17	-2.76 ± 0.08	-2.78 ± 0.12	-2.56 ± 0.09
P_{50}	-3.68 ± 0.10	-3.65 ± 0.15	-3.48 ± 0.05	-3.41 ± 0.11	-3.35 ± 0.13
P_{88}	-4.36 ± 0.11	-4.38 ± 0.14	-4.21 ± 0.05	-4.05 ± 0.10	-4.13 ± 0.20
Wood properties					
WD	0.657 ± 0.009	0.634 ± 0.005	0.638 ± 0.014	0.641 ± 0.011	0.660 ± 0.012
D	18.76 ± 0.39	18.43 ± 0.56	19.15 ± 0.33	18.85 ± 0.23	20.06 ± 0.47
D_{h}	26.39 ± 0.62	25.32 ± 0.93	26.62 ± 0.57	25.07 ± 0.39	27.34 ± 0.31
VD	453.54 ± 18.73	496.15 ± 6.34	458.03 ± 12.77	458.64 ± 8.12	411.54 ± 8.24
VI	41.89 ± 2.00	37.63 ± 0.96	42.16 ± 1.74	42.26 ± 1.27	48.61 ± 2.10
V_{G}	1.38 ± 0.06	1.43 ± 0.07	1.32 ± 0.03	1.43 ± 0.02	1.29 ± 0.01
V_{S}	0.76 ± 0.03	0.75 ± 0.03	0.79 ± 0.01	0.74 ± 0.01	0.80 ± 0.01
T_{m}	258.27 ± 41.66	254.00 ± 2.15	236.74 ± 44.80	229.99 ± 17.00	217.04 ± 21.46
T_{w}	2.29 ± 0.06	2.29 ± 0.15	2.16 ± 0.20	2.28 ± 0.19	2.35 ± 0.32
A_{xylem}	33.83 ± 2.48	32.22 ± 2.98	39.71 ± 3.35	36.47 ± 2.49	32.69 ± 1.89
$A_{\mathrm{xylem}} : A_{\mathrm{leaf}}$	3.12 ± 0.44	3.66 ± 0.29	3.68 ± 0.53	7.13 ± 1.14	3.19 ± 0.18
$A_{\mathrm{lumen}} : A_{\mathrm{xylem}}$	14.27 ± 0.83	14.94 ± 1.18	15.17 ± 0.30	14.44 ± 0.22	14.88 ± 0.49
G_{dw}	6.15 ± 1.20	3.63 ± 0.37	3.82 ± 0.58	4.27 ± 0.38	5.46 ± 0.98
Foliar traits					
LS	11.48 ± 0.95	10.24 ± 0.38	9.22 ± 0.22	8.22 ± 0.58	10.00 ± 0.54
SLA	151.10 ± 20.44	111.84 ± 7.55	134.65 ± 3.97	115.04 ± 3.86	117.96 ± 3.56
δ^{13}C	-27.83 ± 0.23	-28.03 ± 0.19	-28.15 ± 0.23	-27.73 ± 0.27	-27.60 ± 0.14

Table A. 4.3. Results of linear mixed effects models (delta AIC, likelihood ratio and probability of error) on the influence of FAI, MAP and MSP on the relative abundance of vessels of five different vessel diameter classes.

Variable	**FAI**			**MAP**			**MSP**		
	Δ_i	**LR**	**p**	**Δ_i**	**LR**	**p**	**Δ_i**	**LR**	**p**
$D_{10\text{-}20\ \mu m}$	2.22	4.22	**0.04**	1.95	3.95	**0.05**	3.30	5.30	**0.02**
$D_{20\text{-}30\ \mu m}$	3.70	5.70	**0.02**	3.50	5.50	**0.02**	4.71	6.71	**0.01**
$D_{30\text{-}40\ \mu m}$	0.83	1.17	0.28	0.99	1.01	0.32	0.42	1.58	0.21
$D_{40\text{-}50\ \mu m}$	1.97	0.03	0.85	1.84	0.16	0.69	1.99	0.01	0.94
$D_{>50\ \mu m}$	1.00	1.00	0.32	0.78	1.22	0.27	0.83	1.17	0.28

Table A. 4.4. : Coefficient of variation (*s* in % of mean) of all traits measured for the variance between plots, between trees within a plot, and within a given tree.

Parameter	**Between plots**	**Between trees**	**Within-tree**
Hydraulic traits			
K_S	8.12	35.10	56.78
K_P	0.00	57.56	42.44
K_L	11.98	10.90	77.12
P_{12}	12.95	48.44	38.61
P_{50}	9.51	54.86	35.63
P_{88}	3.91	53.66	42.44
Average	***7.74***	***43.42***	***48.84***
Structural parameters and wood properties			
BA	18.56	28.39	53.04
D	13.70	43.90	42.40
D_h	15.37	35.67	48.96
VD	35.86	14.90	49.24
VI	31.91	16.68	51.41
V_G	13.70	46.47	39.84
V_S	7.55	33.36	59.09
T_m	0.00	48.52	51.48
T_w	0.00	25.66	74.34
A_{xylem}	4.92	12.57	82.52
$A_{lumen} : A_{xylem}$	0.00	56.80	43.20
$A_{xylem} : A_{leaf}$	39.02	14.74	46.24
G_{dw}	10.91	38.17	50.92
Average	***14.73***	***31.99***	***53.28***
Foliar traits			
LS	38.96	32.19	28.85
SLA	14.46	0.00	85.54
$\delta^{13}C$	1.15	63.64	35.22
Average	***18.19***	***31.94***	***49.87***
Grand average	***13.30***	***35.10***	***51.60***

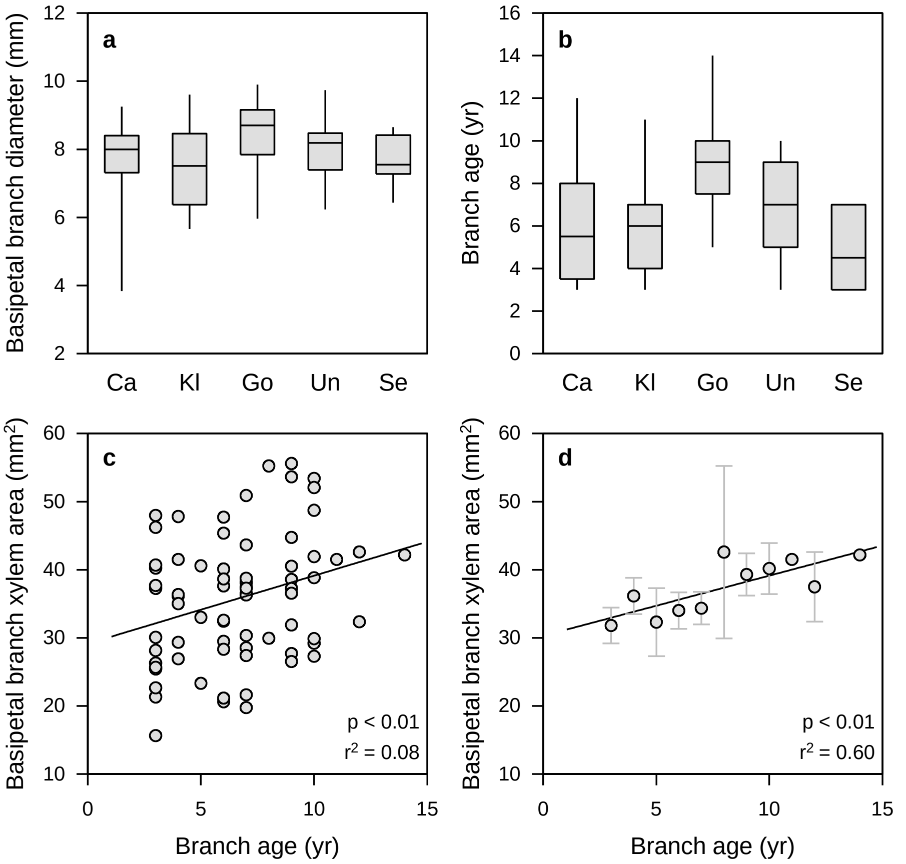

Figure A. 4.1. Box-whisker plots on the variation in basipetal maximal diameter (a) and age (b) of the sampled branches from the uppermost sun-exposed canopy along the precipitation gradient, and relation between branch age and basipetal xylem area (A_{xylem}, c) examined at the sample level as well as averaged per age class (d, means ± SE). For site abbreviations see Table 4.1.

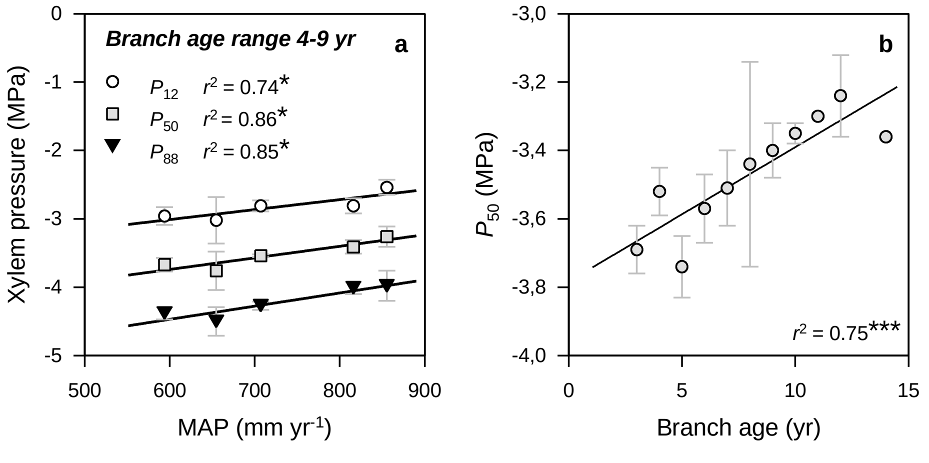

Figure A. 4.2. Mean annual precipitation (MAP) in relation to the xylem pressure causing 12%, 50% or 88% loss of hydraulic conductivity; for this linear regression analysis, all branches younger than 4 years and older than 9 years have been removed (a), and branch age (BA) in relation to P_{50}; for this analysis, values were averaged for a given branch age class (b). Given values are means ± SE. Asterisk indicate the level of significance (* $P<0.05$; *** $P<0.001$).

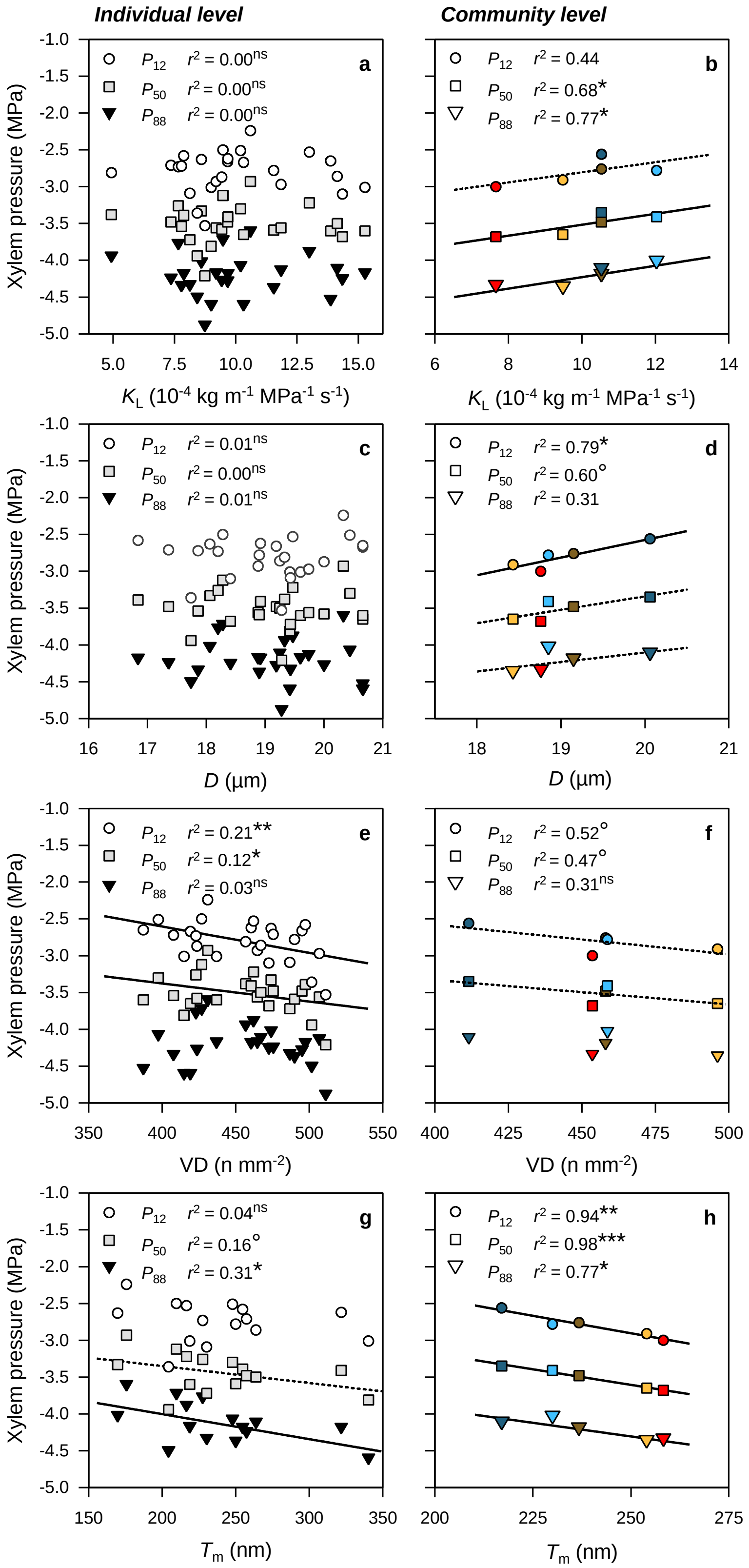

Figure A. 4.3. Relation between P_{12}, P_{50} and P_{88} in European beech branches and four traits commonly associated with embolism resistance at the individual (tree, left) and community (plot, right) level; these are leaf-specific conductivity (a, b, K_L), vessel diameter (c, d, D), vessel density (e, f, VD) and pit membrane thickness (g, h, T_m). Values are means per tree (n = 25, left) or plot (n = 5, right), asterisk indicate the level of significance (° $P<0.10$; * $P<0.05$; ** $P<0.01$), non-significant relationships are indicated by ns. For symbol colour see Table 4.1.

CHAPTER 5

Synopsis

Drought response of young beech trees

With the objective to investigate variances in provenances of young beech trees regarding morphological and physiological traits in response to environmental precipitation amounts we implemented a common garden experiment. A pivotal result of this experimental approach is that provenance and thus precipitation at tree origin showed a stronger influence on leaf water status than the given irrigation.

This study shows that for tissue elasticity and the extent of elastic adjustment a strong provenance effect existed. In the plants originating from moister forest stands, cell walls of leaf tissue hardened with decreasing water availability. This result might be supportive for safeguarding water absorption from the soil, but it also lowers the safety from cavitation. Accordingly, young beech trees from more humid origins may be exposed to higher risks of hydraulic failure under drought due to more stiffened cell walls in leaf tissue than beech saplings from forest sites with lower precipitation amounts. It is known that in European beech osmotic adjustment is nearly absent (e.g. Schipka 2002, Lendzion and Leuschner 2008). This could be confirmed in our study: osmolyte concentration in the cytosol was invariant during the growing season and showed no relation to soil moisture or origin. This seems to point to the fact that cell wall elastic properties are more important for the drought adaptation strategy of young beech trees than variations in osmotic adjustment. Unexpectedly, provenance had only a minor effect on the morphology and growth of young beech trees. Specific leaf and root areas, aboveground and belowground productivity did not differ consistently among the provenances originating from drier or moister origins.

Genetic differentiation between *F. sylvatica* stands is known to be comparably small, whereas genetic variability within autochthonous populations is high (Comps et al. 1990, Belletti and Lanteri 1996, Buiteveld et al. 2007). In order to investigate the plasticity and adaption of the investigated beech trees on a molecular scale, an accompanying study on gene expression for drought signaling linked to abscisic acid (ABA) was conducted (Carsjens et al. 2014). The results of this study reveal that phosphatase-mediated signalling shows aclimatization to environmental conditions, while stress compensatory measures exhibit genotypic variation. The responses to drought treatments were less distinct than modifications related to tree origin. Hence, it is likely that the selection for drought adaption might have already occured in local populations. Although the investigated beech trees originated from five different forest sites, they showed only very small variation between and high variation within populations. The applied neutral markers had the ability to differ between the populations, but the genetic distances did not mirror the precipitation gradient of the forest stands. Genetic differences between more or less vicinal beech populations declined through forest management activites like spreading of presumably better seeds from somewhere else. This may explain the relatively low values of Nei’s genetic distance (Nei 1972) and their lacking relatedness to geographic distances or mean precipitation amounts of the forest stands (Figure 5.1). The results of an AMOVA revealed that only 3% of the molecular variance was detected among and 97% within populations. Young *F. sylvatica* trees originating from the investigated region in northwestern Germany seemed to have achieved only slight adaptions to drought. The main reason might be found in a shorter presence of European beech in northwestern Germany, namely since about 5,000 years, which is equivalent to 40 tree-generations at the most (Magri et al. 2006). In addition, only little genetic differences between populations and high genetic variation within populations may have contributed to this finding. However, drought affected most morphological and productivity-related traits and root growth in particular. Here, *F. sylvatica* saplings did respond with high phenotypic plasticity to drought. Provenances of young beech trees developed genotypic differences in their leaf water status regulation by cell wall elastic adjustment, while biomass partitioning as well as leaf and root system morphology was driven by phenotypic plasticity.

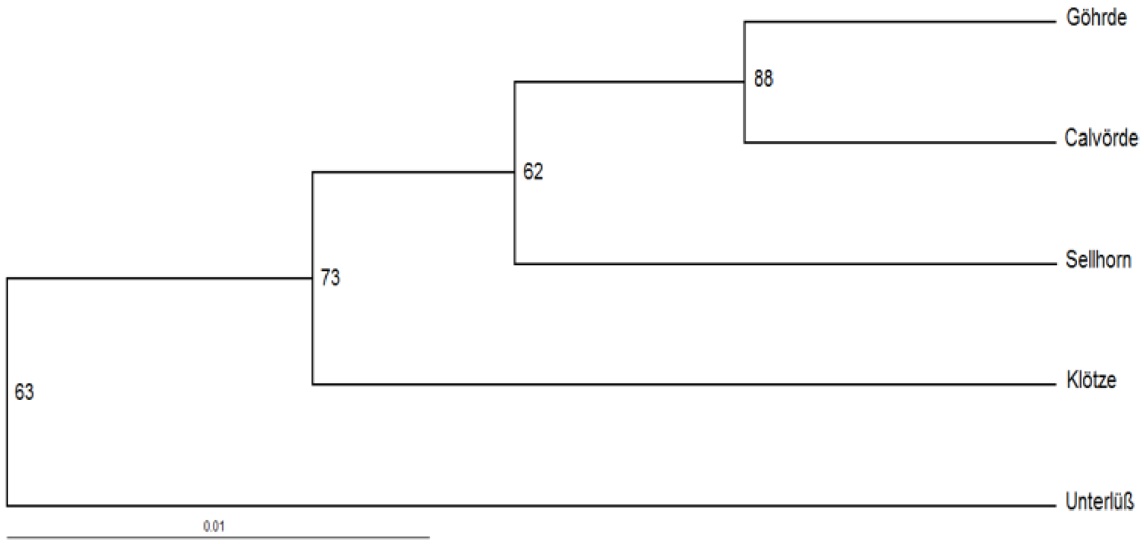

Figure 5.1. Dendrogram of five populations of *F. sylvatica* from the investigated forest sites in northwestern Germany along a precipitation gradient according to Carsjens et al. (2014). The dendrogram was calculated with Nei’s genetic distance based on the analysis of nine microsatellite markers. Bootstrap values (1000 permutations) are indicated.

Global warming-related effects on mature beech forests

With a comparative dendrochronological approach in beech forest stands along a precipitation gradient we focused on climatic and edaphic drought effects on the radial growth of European beech in the center of its natural distribution. The obtained results showed that climate warming gains increasing importance as a stressor in *F. sylvatica* stands in northwestern Germany.

This study allowed us to define a precipitation threshold beyond which a negative stem growth trend was observed, i.e. MAP < ~660 mm, MGSP (April – September) < ~360 mm and MSP (June – August) < ~200 mm, respectively, which is in line with other studies in Central Europe (Scharnweber et al. 2011, Weber et al. 2013, Zimmermann et al. 2015). The relationship between mean long term precipitation amounts at tree origins with basal area increment (BAI) of the stems was absent until the 1980s and developed afterwards. This supports the assumption that the global warming impact on beech forests is increasing during the last decades. At the drier sites of the investigated gradient a radial growth decline since the 1960s or 1970s was observed. Since the 1950s there is a marked increase in mean sensitivity of growth of *F. sylvatica* at most of the investigated sites, whereas the degree of autocorrelation decreased. This finding is in agreement with other studies that reported increasing mean sensitivity of radial growth to climate variation during the last decades (e.g. Beck 2009, Scharnweber et al. 2011, Beck and Heußner 2012). Another indication for increasing impact of global warming on beech forests is the more frequent appearance of negative pointer years since 1976 at nearly all sites; at the driest site they used to be relatively frequent even before (Table 3.5).

At five of the six investigated sites, the largest influence on beech radial growth in our study region was by precipitation during June, only at the driest site precipitation from May to July was more relevant. This outstanding role of mid-summer precipitation is in line with other studies on the climate-growth relation in temperate trees (e.g. Čufar et al. 2008, Zang et al. 2011, Zimmermann et al. 2015). Warmer temperatures in September of the year before ring-formation had a negative effect on radial growth. This can be due to the observed latewood cell wall thickening in this month (Lebourgeois et al. 2005) which consumes carbon resources lacking next year, or with an inhibitory effect on the survival of herbivorous insects.

The comparison of the drought effects on forest stands of two different soil types with different soil water storage capacities did not show clear results. Although mean sensitivity showed a relation on precipitation only in the sandy sites, the BAI decline at the drier sites was more pronounced on the loam-richer soils. This surprising result might occur due to structural parameters of the stands or the differences between the soils were distinct enough.

Hydraulic adaption potential of European beech to global warming

In order to improve the understanding how mature European beech trees adapt their hydraulic architecture in response to long-term drought exposure, different parameters were investigated that characterize the hydraulic architecture and thus xylem safety and embolism resistance of branches in the upper sun canopy. A main finding of this cooperative study is that the branch hydraulic system of beech has a distinct adaptive potential to respond to long-term reductions in summer precipitation.

We observed a close relation between long-term mean precipitation of early summer (April – June) and vessel diameter in similarly-sized branches from the sun canopy of *F. sylvatica*. Mean vessel diameter declined by 7% across the gradient with increasing drought. A closer look revealed that this fact could be explained with modifications in the relative abundance of vessels sized between 10 µm and 30 µm in diameter.

Supposing that vessels and tracheids are functionally and morphologically homologous (Jansen and Nardini, 2014), it is likely that the number of tracheids in beech trees at drier sites also increases. However, the larger vessel diameter classes did not alter. This can be seen as evidence for an adaptive process in the conductive system and excludes the possibility that the reduction in mean vessel diameter results passively from a drought-induced growth reduction of the whole branch wood. The absence of relations between long-term mean annual precipitation or precipitation of early summer and potential (K_P) or specific conductivity (K_S) also reflects the altered diameter pattern. According to the Hagen-Poiseuille law, hydraulic conductivity increases with diameter raised to the fourth power, and the diameter alteration in the vessel group from 10 to 30 µm is of minor relevance for K_P.

Parallel with declining mean vessel diameter, the embolism resistance increased with decreasing water availability across the investigated gradient. Embolism resistance, even at the same location in the canopy, showed a high variability. This supports the assumption that *F. sylvatica* is plastic in its embolism resistance (Herbette et al. 2010, Wortemann et al. 2011). The variability between sites was low in our study, which indicates the possibility of limited adaptive capacities, but the observed high variability of traits within populations could be seen as a valuable tool for drought adaption in European beech.

A close relation between intervessel pit membrane thickness and embolism resistance was also detected: pit membrane thickness linearly increased by 15% toward the drier stands and, thus, is also dependent on precipitation experiences. An interesting result was that faster growing younger branches showed more effectivity in their hydraulic system and owned larger leaves then older branches of comparable size.

Main conclusion

From the present work on the drought response of European beech under global warming, the following main conclusions can be drawn:

- *F. sylvatica* saplings seem to have achieved only a limited number of specific drought adaptations when exposed to reduced rainfall during summer (<600 mm yr^{-1}).
- Physiological traits of beech saplings are more strongly influenced by provenance and, hence, are under genotypic control, while biomass partinionig and morphology are influenced by water availability and, thus, are under phenotypic control.
- Adjustment of cell wall elastic properties is of high importance for drought adaption of beech saplings. The young trees originating from moister forests face a higher risk of hydraulic failure due to more rigid cell walls in leaf tissue then saplings from drier forest sites.
- Climate warming gains increasing importance as a stressor in *F. sylvatica* stands in the Pleistocene lowlands of northwestern Germany.
- A minimum summer precipitation level which seems to be necessary for vital beech growth in the center and north of its distribution range is located close to 660 mm of annual precipitation, 350 mm of growing season precipitation (April – September) or 200 mm of summer precipitation (June-August).
- Since the 1950s, there is a long-term growth reduction in the drier forest stands, increasing mean sensitivity of radial growth to climate variation, while the degree of autocorrelation decreased.
- The branch hydraulic system of beech has a distinct adaptive potential to respond to long-term drought exposure.
- Vulnerability to cavitation, vessel diameter and hydraulic conductivity decreased, while pit membrane thickness increased with decreasing long-term precipitation at tree origin.
- Due to branch wood modification, trees originating from drier field sites can tolerate more negative leaf water potentials (15%).

Future threats by global warming on European beech

According to the regional climate models REMO and CLM, climate change in Lower Saxony will cause a reduction of 10% of summer precipitation until the period 2071-2100. The discussed global warming-related climatic changes are also mirrored in our study area (Figure 5.2). If we focus on June precipitation, the strongest effector on stem growth, the climate record evidences that the amount of precipitation in June decreased during the last 60 years especially in the drier part of the investigated transect (Figure 5.1). At the moistest location Sellhorn (*Se*), the amount of June precipitation remained almost unchanged, while at the driest location Calvörde (*Ca*), the amount decreased by about one third from 1950 to 51 mm to 2010. Global warming is also reflected in the increasing temperatures in all forest stands in June and for all other observed periods as well. In the period from 1950 to 2010, mean temperature increased by 0.5°C in June and mean annual temperature increased even by 1.4°C in 1950-2010.

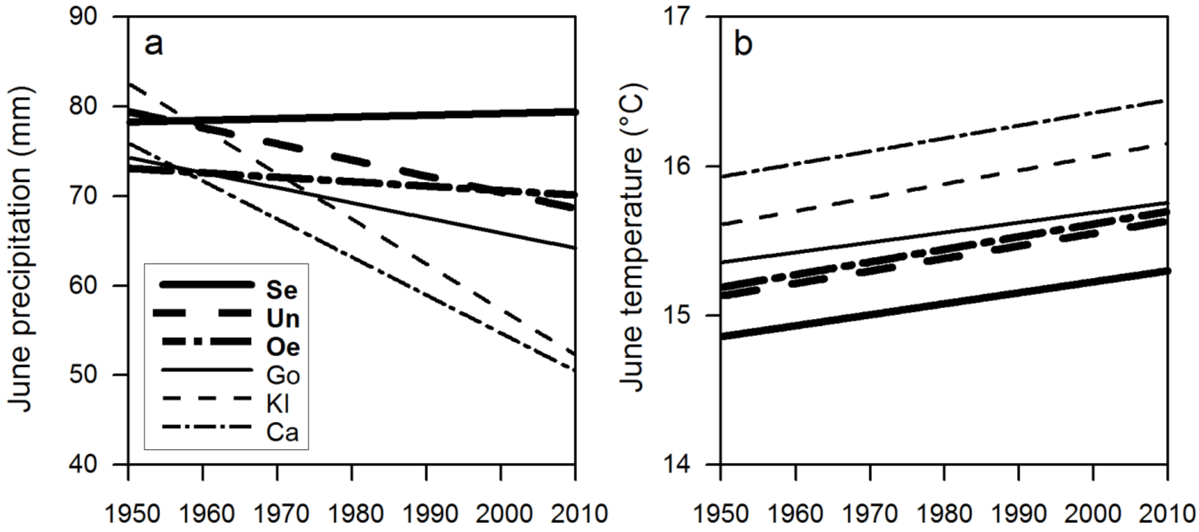

Figure 5.2. Trends in (a) precipitation and (b) temperature in June from 1950 to 2010 in 12 mature beech stands at six locations along the investigated precipitation gradient in northwestern Germany.

This probably has strong impacts on the future of beech forests in Northern and Central Europe, because June is known as the month where more than a third of an entire tree-ring is normally formed (Čufar et al. 2008). Also in our study region, June precipitation exerts the largest positive influence on radial growth of beech. Particularly, this month showed strongest precipitation reduction in the current past at four of the six sites. If this trend is continuing in the 21st century as it is predicted by regional climate scenarios, it implies further growth decline of European beech trees or it can even threaten its survival in some parts of Central

Europe. It is also expected that pan-European summer droughts like in 1976, 2000 and 2003 will appear with increasing frequency in the future (e.g. Schär et al. 2004, Bréda and Badeau 2008). At present, the investigated stands from moister regions show symptoms of climate sensitivity which are comparable to the drier forest stands about 40 years ago. Hence, it is likely that the increasing frequency of negative pointer years will lead to decreasing stem increment as detected in the drier stands since the 1980s.

Through the present dendroecological study and comparison with other studies (e.g. Scharnweber et al. 2011), we were able to define a minimum precipitation amount, which seems to be necessary for vital beech growth in the center and north of its distribution range. This threshold is located close to 660 mm of annual precipitation, 350 mm of growing season precipitation (April – September), and more importantly, 200 mm of summer precipitation (June-August). Trees have long generation times and grow for about 100 years until harvest. In less than hundred years, only the moistest investigation site Sellhorn might be slightly above the here defined precipitation threshold. That might threaten the safeguarding of most of the investigated stands. At least, it is likely that forest stands in regions with actually <200 mm of summer precipitation will face growth decline in the future, but stands in currently moister regions as well. The results of our study call for careful tree species selection by foresters in all those Central European beech forest regions where precipitation is already below the precipitation thresholds elaborated here.

The investigated beech trees originating from drier forest stands already showed growth reductions during the last decades. According to Leblanc (1990) and Pedersen (1998), “a negative trend in BAI is a strong indication of a true decline in tree growth”. However, this growth decline implies also slower growth rates of the wooden compartments of the tree. On the one hand, faster growth is accompanied with larger vessels, what allows a higher hydraulic efficiency; on the other hand, smaller cells tolerate more negative sap pressure without cavitation (Hacke et al. 2001). Martínez-Vilalta et al. (2012) showed on Scots pine a connection between high growth performance prior to drought and high-drought susceptibility. Also within populations, fast growing trees show higher susceptibility to drought stress (Morán-López et al. 2014). By investigating the branch hydraulic system of *F. sylvatica*, we detected slower-growing branches being more vulnerable than comparable younger faster-growing branches. Accordingly, it is difficult to decide whether growth reductions in dry beech stands should be interpreted as global-warming induced growth and vitality decline or as already occurring adaption to a changing environment. In the provenance trial with beech seedlings, no relation between lower growth rate and higher drought adaption was detectable. Those beech trees have developed some genotypic differences regarding the regulation of leaf water status. However, these adaptations are accompanied by a limited number of adaptations in morphology and they do not clearly affect the growth performance of *F. sylvatica*. With respect to improve growth performance, vigour or survival of beech saplings under an increasing occurrence of summer drought periods, it doesn´t seem to be advantageous to translocate provenances across the investigated region.

We must conclude that global warming is already acting as a major stressor in *F. sylvatica* forest stands even in the center of the species’ distribution range. Current growth-reductions were detected in regions, where precipitation in summer is below 200 mm. In future, growth reductions will also occur in today’s moderately moist habitats. But it is not clear if growth limitations are contributed to investments into safety mechanisms or should be seen as loss of vitality. Beech showed high plasticity in most of the investigated morphological, physiological and growth-related traits. Changes in vessel diameter, hydraulic properties and embolism resistance in mature beech trees and adjustment of cell wall elasticity in beech saplings show that beech has a substantial adaptive potential to respond to environmental climatic conditions. Also the high trait variability within populations could represent a valuable source for adaptation in *F. sylvatica*. All this can be advantageous for the future wellbeing of *F. sylvatica* in Central Europe. However, it is doubtful whether these careful and slow evolving drought adaptions are enough to safeguard growth and vitality of *F. sylvatica* against the challenges by a rapidly warming and drying climate.

Further research recommendations

European beech forests are a valuable ecosystem and of high economic importance in large parts of Europe (Figure 5.3). For a better understanding of the ability to cope with future challenges under predicted global warming and to help establishing a base for a future wellbeing of this important and beautiful forest tree, I would like recommend the following approaches:

Seedlings and saplings likely differ from mature trees in their response to drought. Accordingly, corresponding studies on the drought response of mature trees are required. Despite the difficult realizability, the separation of adaptive from non-heritable modifying drought responses would call for common garden experiments with mature trees.

The role of soil water storage for the growth dynamics of beech requires further study by considering other geologic substrates and soil types. A comparison of sites with largely different soil profile depths as done by Weber et al. (2013) should detect more pronounced effects of soil water storage capacity.

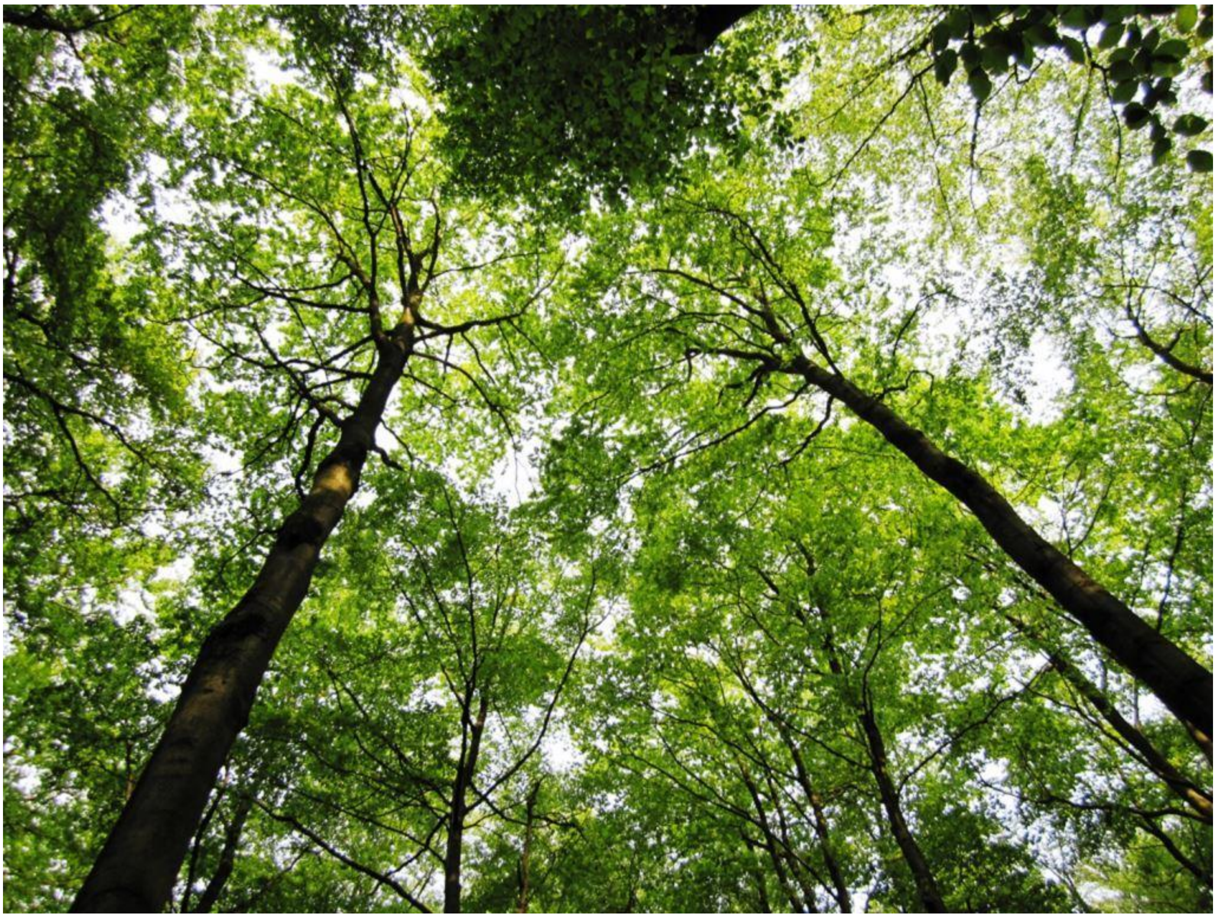

Figure 5.3. Mature beech forest in the north-western German Lowlands.

References

Beck W (2009) Growth patterns of forest stands - the response towards pollutants and climatic impact. *iForest-Biogeosciences and Forestry*, **2**, 4–6.

Beck W, Heußner KU (2012) Increased sensitivity in ring width series of common beech after 1990 – climatic impact or normal patterns due to ageing? *Dendrosymposium*, **10**, 13–19.

Belletti P, Lanteri S (1996) Allozyme variation among European beech (*Fagus sylvatica* L.) stands in Piedmont, north-western Italy. *Silvae Genetica*, **45**, 33-37.

Bolte A, Czajkowski T, Kompa T (2007) The north-eastern distribution range of European beech - a review. *Forestry*, **80**, 413–429.

Bréda N, Badeau V (2008) Forest tree responses to extreme drought and some biotic events: towards a selection according to hazard tolerance? *Comptes Rendus Geoscience*, **340**, 651–662.

Buiteveld J, Vendramin GG, Leonardi S, Kamer K, Geburek T (2007) Genetic diversity and differentiation in European beech (*Fagus sylvatica* L.) stands varying in management history. *Forest Ecology and Management*, **247**, 98–106.

Carsjens C, Nguyen Ngoc Q, Guzy J et al. (2014) Intra-specific variations in expression of stress-related genes in beech progenies are stronger than drought-induced responses. *Tree Physiology*, **34**, 1348–1361.

Comps B, Thiebaut B, Paule L, Merzeau D, Letouzey J (1990) Allozymic variability in beechwoods (*Fagus sylvatica* L.) over Central Europe: spatial differentiation among and within populations. *Heredity*, **65**, 407–417.

Čufar K, Prislan P, de Luis M, Gričar J (2008) Tree-ring variation, wood formation and phenology of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees - Structure and Function*, **22**, 749–758.

Herbette S, Wortemann R, Awad H, Huc R, Cochard H, Barigah TS (2010) Insights into xylem vulnerability to cavitation in *Fagus sylvatica* L.: phenotypic and environmental sources of variability. *Tree physiology,* **30**, 1448–55.

IPCC (2013) Summary for policymakers. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), PP. 1535. Cambridge University Press, Cambridge, UK.

Jansen S, Nardini A (2014) From systematic to ecological wood anatomy and finally plant hydraulics: Are we making progress in understanding xylem evolution? *New Phytologist*, **203**, 12–15.

Leblanc DC (1990) Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface mountain, New York. *Canadian Journal of Forest Research*, **20**, 1399–1407.

Lebourgeois F, Bréda N, Ulrich E, Granier A (2005) Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees - Structure and Function*, **19**, 385–401.

Lendzion J, Leuschner C (2008) Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits. *Forest Ecology and Management*, **256**, 648–655.

Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gömöry D, Latałowa M, Litt T, Paule L, Roure JM, Tantau I, van der Knaap WO, Petit RJ, de Beaulieu J-L (2006) A new scenario for the quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist*, **171**, 199–221.

Martínez-Vilalta J, Lopez BC, Loepfe L, Lloret F (2012) Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia*, **168**, 877–888.

Moran-Lopez T, Poyatos R, Llorens P, Sabate S (2014) Effects of past growth trends and current water use strategies on Scots pine and pubescent oak drought sensitivity. *European Journal of Forest Research*, **133**, 369–382.

Nei M (1972) Genetic distance between populations. *American Naturalist*, **106**, 283–292.

Nielsen C, Jørgensen F (2003) Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and within provenances. *Forest Ecology and Management*, **174,** 233–249.

Pedersen BS (1998) The role of stress in the mortality of Mid-western oaks as indicated by growth prior to death. *Ecology*, **79**, 79–93.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Scharnweber T, Manthey M, Criegee C, Bauwe A, Schröder C, Wilmking M (2011) Drought matters - Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management*, **262**, 947–961.

Schipka F (2002) Blattwasserzustand und Wasserumsatz von vier Buchenwäldern entlang eines Niederschlagsgradienten in Mitteldeutschland. Ph.D. thesis, University of Göttingen.

Thiel D, Kreyling J, Backhaus S, Beierkuhnlein C, Buhk C, Egen K, Huber G, Konnert M, Nagy L, Jentsch A (2014) Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *European Journal of Forest Research*, **133**, 247–260.

Weber P, Bugmann H, Pluess AR, Walthert L, Rigling A (2013) Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees - Structure and Function*, **27**, 171–181.

Wortemann R, Herbette S, Barigah TS, Fumanal B, Alia R, Ducousso A, Gomory D, Roeckel-Drevet P, Cochard H (2011) Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiology*, **31**, 1175–1182.

Zang C, Rothe A, Weis W, Pretzsch H (2011) Zur Baumarteneignung bei Klimawandel: Ableitung der Trockenstress-Anfälligkeit wichtiger Waldbaumarten aus Jahrringbreiten. *Allgemeine Forst- und Jagdzeitung*, **182**, 98–112.

Zimmermann J, Hauck M, Dulamsuren C, Leuschner C (2015) Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. *Ecosystems*, **18**, 560–572.

General Appendix

Index of Figures

Index of Tables

Curriculum Vitae

Personal Details

Name: Florian Knutzen
Date of birth: 03.09.1976
Place of birth: Hamburg, Germany

2011-2015	PhD study in Biological Diversity and Ecology at Georg-August-Universität Göttingen, Germany
2009-2011	Research associate at the Authority for Urban Development and Environment Hamburg; Landschafts und Grünplanung, Referat Stadtbäume.
2002-2009	Study of biology, at University of Hamburg; Degree obtained: Diplom-Biologe
1996-2002	Various positions in concert lighting, sound and stage techniques.
1987-1996	Gymansium Lerchenfeld, Hamburg. High school graduation.

Danksagung

Ich danke Prof. Christoph Leuschner für die Bereitstellung des Themas und die fachliche Betreuung sowie Prof. Markus Hauck für die Übernahme des Korreferats und den weiteren Mitgliedern der Prüfungskommission. Ich danke meiner Betreuerin Ina C. Meier, auf die ich mich jederzeit verlassen konnte. Bernhard Schuldt und Duja Dulamsuren sei gedankt für interessante Kooperationen.

Dank geht an Dietrich Hertel für viele kompetente Ratschläge, Heinz Coners für technische Unterstützung, unsere TAs, insbesondere Mechthild Stange, Jutta Cternizki, Marianne Gscheidlen und Irmgard Gerstmann, den Gärtnern des Experimentellen Botanischen Gartens, insbesondere Regina Helbig, Gaby Kuchenbuch, Reinhard Schomberg-Klee und Heiko Eichner. Ich danke Hilmar Müller-Haubold vor allem für die guten Gespräche und all den lieben Kollegen, insbesondere Petra, Robin, Bettina, Yasmin, Carola, Rebecca, Kristina, Fabi, Stefan, Kaufi, Jonas, Eike, Jorma, Martyna und der Spinne.

Herzlicher Dank an Monica-Elena Stoian für sprachliche Korrekturen und die tolle Unterstützung in der Endphase dieser Arbeit. Ein ‘Danke Digger‘ geht an Ollie Marquardt nicht nur für Formatierungshilfen. Persönlicher Dank geht an Fridolin Knutzen und Pesci Knutzen-Marquardt sowie Emil und Kristina Reinelt. Felix ‚Pönty‘ Beyer sei gedankt für Hilfe bei mathematisch-physikalischen und anderen Fragestellungen.

Tiefer Dank geht an Julia Juchheim für den langen gemeinsamen Weg in der Biologie und darüber hinaus.

Ich danke meinen Eltern und meiner Schwester Sonja herzlich dafür, dass sie immer zu mir standen.

In Gedenken an meinen Freund Sven Kaak.

Declaration of originality and certificate of ownership

I, Florian Knutzen, hereby declare that I am the sole author of this dissertation entitled ‘RESPONSE OF EUROPEAN BEECH TO DECREASING SUMMER PRECIPITATION UNDER GLOBAL CLIMATE CHANGE’. All references and data sources that were used in the dissertation have been appropriately acknowledged. I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure.

(Florian Knutzen)