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Effects of tree species diversity and soil drought on productivity, water consumption and hydraulic functioning of five temperate broad-leaved tree species

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Torben Lübbe

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Betreuungsausschuss

Prof. Dr. Christoph Leuschner, Abteilung Pflanzenökologie und Ökosystemforschung, Universität Göttingen

Prof. Dr. Dirk Hölscher, Abteilung Waldbau und Waldökologie der Tropen, Universität Göttingen

Dr. Bernhard Schuldt, Abteilung Pflanzenökologie und Ökosystemforschung, Universität Göttingen (Anleiter)

Mitglieder der Prüfungskommission

Referent: Prof. Dr. Christoph Leuschner, Abteilung Pflanzenökologie und Ökosystemforschung, Universität Göttingen

Korreferent: Prof. Dr. Dirk Hölscher, Abteilung Waldbau und Waldökologie der Tropen, Universität Göttingen

Weitere Mitglieder der Prüfungskommission

Prof. Dr. Hermann Behling, Abteilung Palynologie und Klimadynamik, Universität Göttingen

Prof. Dr. Erwin Bergmeier, Abteilung Vegetationsanalyse und Phytodiversität, Universität Göttingen

Prof. Dr. Christian Ammer, Abteilung Waldbau und Waldökologie der gemäßigten Zonen, Universität Göttingen

Prof. Dr. Alexander Knohl, Abteilung Bioklimatologie, Universität Göttingen

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Chapter 1

General Introduction

Biodiversity and Ecosystem Functioning (BEF)

During the last decades, the importance of biodiversity for ecosystems and their functionality has received increasing attention in ecological research (Hooper et al. 2005, Tilman et al. 2014). According to the convention on biological diversity (1992) biodiversity is defined as “the variability among living organisms from all sources including inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species, and of their habitats”. More comprehensively, it concerns all variety in life with respect to genes, species, communities, and processes (Cardinale et al. 2012). Most of the biomes and ecosystems worldwide are actual facing substantial losses in species richness and diversity (at least for the past 60 yrs.), as a consequence of human activities (Millennium Ecosystem Assessment 2005). At the global scale, climate and land use change, nitrogen deposition, increasing atmospheric CO_2, and biotic exchange and species invasion are presumably the most relevant drivers diminishing biodiversity (Sala et al. 2000). Due to the ecological, genetic, economic and recreational values of biodiversity, its loss is known to affect key processes for ecosystem functioning and services like productivity, element and energy fluxes, soil formation and retention (Loreau et al. 2002, Hooper et al. 2005, Naeem et al. 2009). In fact, there is mounting evidence that the impact of species loss on ecosystem functioning is even as severe as of other major determinants of global change, i.e. global warming (Hooper et al. 2012, Tilman et al. 2012).

A positive relation between biodiversity and ecosystem functioning (BEF) is usually known to be based on the interplay of three mechanisms: the selection effect, the complementarity effect, and facilitation (Vandermeer 1992, Loreau and Hector 2001). Through the selection effect (or sampling effect), a diverse community can be dominated by the most productive and/or strongest consumer species, which might enhance overall performance in comparison to the average of monocultures (overyielding). In case of species complementarity, niche differentiation (i.e. partitioning in root or crown space) and a more complete resource acquisition may provide reduced inter-specific competition in comparison to intra-specific competition, causing enhanced turnover rates and overyielding in growth. Furthermore, species in mixtures might be facilitated by others, like for instance by nitrogen fixation or hydraulic redistribution; such processes might be difficult to separate from complementary behavior (Forrester 2014).

BEF research arising in the 1990’s was primarily carried out in experimental grassland studies (Tilman et al. 1996, Hooper and Vitousek 1997, Hector et al. 1999), as community structures are less complex and determinants of nutrient cycling and productivity more easily distinguishable. Despite of preceding controversies on biased designs and hidden treatments (Huston et al. 1997, Doak et al. 1998) the results of numerous BEF studies conducted in terrestrial, aquatic and marine ecosystems provide reliable evidence for the general occurrence of positive diversity effects on primary production, resource use, decomposition, and ecosystem stability (Balvanera et al. 2006, Cardinale et al. 2006, 2011, Stachowicz et al. 2007, Quijas et al. 2010).

BEF research in forest ecosystems

During the last decade, the focus of functional biodiversity research has shifted toward forests (Kelty et al. 1992, Scherer-Lorenzen et al. 2005, Nadrowski et al. 2010, Bravo-Oviedo et al. 2014, Scherer-Lorenzen 2014) which are a key resource for humans with respect to their wood and fuel demand. Forests globally harbor about two thirds of the world's terrestrial biodiversity (e.g. Millennium Ecosystem Assessment 2005). While the species richness is extraordinary high in tropical regions (Gibson et al. 2011), temperate forests with fewer species though comprise a considerable grade of functional diversity regarding hydraulic architecture (vessel properties, diffuse- vs. ring-porous type), stomatal regulation (isohydric vs. anisohydric behavior), photosynthetic capacity, productivity, light demand, successional status, or sensitivity to drought (Körner et al. 2005, Köcher et al. 2009, 2013, Legner et al. 2013). Forests are additionally characterized by a rather complex structure considering the longevity of trees, enduring regeneration cycles and successional development of stands, versatility in vertical structure between deep burying tap roots and the canopy layer, and the acquirement of environmental interaction in the sense of ecosystem engineering (Chapin et al. 2002). As a consequence, only little is known about the validity and generality of a positive BEF-relationship within tree communities.

With respect to yields in timber production, positive tree mixture effects (overyielding) have been observed prior to the ecological debate in European silviculture as reviewed by Pretzsch (2005, 2013). More recently, numerous studies from forests and plantations have demonstrated overyielding by species mixture in above-ground biomass (Piotto et al. 2008, Pretzsch and Schütze 2009, Morin et al. 2011, Paquette and Messier 2011, Gamfeldt et al. 2013, Vilà et al. 2013). Even though some contrasting results have been found (Szwagrzyk and Gazda 2007, Jacob et al. 2010), evidence for a positive diversity-productivity relationship is broadly provided (Zhang et al. 2012). However, it is less clear to what extent and under which conditions this relation is mirrored in enhanced resource use and biogeochemical cycling. With regard to tree water consumption, results on the effects of tree species richness for experimental plantations (Forrester et al. 2010, Kunert et al. 2012, Grossiord et al. 2013) as well as for forests are mixed (Schume et al. 2004, Krämer and Hölscher 2010, Gebauer et al. 2012, Grossiord et al. 2014). However, it seems plausible that higher stand transpiration is linked to increased stand productivity (Law et al. 2002, Forrester 2014). With respect to various ecosystem processes, tree diversity seems to generally foster ecosystem functioning and services, although tree identity itself is usually a more effective driver (Nadrowski et al. 2010, Scherer-Lorenzen 2014).

Effects of climate change on the BEF relationship and stability of forest ecosystems

One major challenge forests are facing worldwide are alterations in climatic conditions as a consequence of global change. Due to the anthropogenic increase in atmospheric greenhouse gas concentrations (Le Quéré et al. 2013), the Earth's climate is responding by raising surface temperatures. The most recent calculations predict an increase in global temperature by 3.2-5.4 °C until the end of this century in comparison to the average between the years 1850 – 1900 (IPCC 2013). Changing energy fluxes at the global scale will most likely affect hydrological cycles (Huntington 2006, Gerten et al. 2007) with consequences for precipitation regimes and water budgets in space and time. For Central Europe, summer heat waves are expected to occur more frequently and to be more intense in future times (Rowell and Jones 2006, Fischer and Schär 2009). Shifting temperatures and amounts of precipitation are supposed to deteriorate growing conditions during the vegetation period in many parts of Europe including Germany (Fischer et al. 2012).

In general, trees are susceptible to deficient water supply with respect to hydraulic functioning, growth and plant survival (Allen et al. 2010, Anderegg et al. 2011, Choat et al. 2012, Hartmann et al. 2013). In this context, it is fundamentally important to know whether tree mixtures in diverse forests stands might be better buffered against anticipated droughts than monocultural stands. Indeed, some authors suppose higher stability for more diverse forest ecosystems in response to biotic or abiotic hazards (Jactel et al. 2009), and more specifically with respect to global change or climatic fluctuations (Thompson et al. 2009, Brang et al. 2014, Grossiord et al. 2014c). On the one hand, this can be due to the higher importance of favorable species interactions (complementary resource use or facilitation) when site conditions are harsher and some resources limited (Paquette and Messier 2011, Pretzsch et al. 2013, del Río et al. 2013, Jucker et al. 2014). The stress gradient hypothesis (SGH, Bertness and Callaway 1994, He et al. 2013), which defines the contrasting meaning of facilitation and competition in plant interactions along environmental gradients, was often referred in mixed forest studies to describe such behavior (Forrester 2013, Pretzsch 2013, Grossiord et al. 2014a, 2014b). However, observational studies usually lack to differentiate between facilitative and complementary interactions among trees. Furthermore, the degree and direction of mixture effects on forest BEF is assumed to depend not only on abiotic conditions, but also on the tree functional types present and on stand structural properties (Forrester 2014). On the other hand, some authors refer to the insurance hypothesis (Yachi and Loreau 1999), assuming that ecosystem stability is related to the size of the present species pool. According to that, species asynchrony may realize shifting contributions to the community performance when site conditions alter. This is most likely when varying abundances in species composition account for higher chances of remaining stability in ecosystem functioning (i.e. diversity-community resistance hypothesis). Such compensatory effects in a fluctuating environment are well described for high dynamic aquatic and herbaceous communities (Hector et al. 2010, Steudel et al. 2012). Whether this mechanism contributes to the stability of less dynamic forest ecosystems is less clear yet (Jucker et al. 2014, Morin et al. 2014). In summary, complementary and compensatory effects in mixed forests stand presumably intensify or maintain ecosystem services under changing environmental conditions. However, mixed-induced enhancement in community functioning can also deteriorate community stability when, for instance, more productive diverse stands deplete limited resources more rigorously (Gebauer et al. 2012, Grossiord 2014). The interplay of a higher resource demand causing tenuous overexploitation represents a manifestation of the tragedy of the commons (Hardin 1968).

Tree individual response and phenotypic plasticity

The adaptive capacity of plants to cope with changing environmental conditions can be associated to phenotypic plasticity (acclimation), genotypic evolution (adaptation), changes in spatial distribution (migration) and extinction (Bussotti et al. 2015). Considerable changes in growing conditions at certain sites therefor request for adjustments in metabolic processes to assure for suitable fitness and survival. Due to the relatively slow continuance of evolutionary adaptation in comparison to environmental dynamics (i.e. climate change), real time modifications mainly rely on plant's acclimation capacity, which is determined by genotypic potential and expressed as phenotypic plasticity (Sultan 2000, Valladares et al. 2007, Nicotra et al. 2010).

With respect to the increasing threat by drought events, plants have developed several mechanisms to modify their organs in terms of morphological and physiological acclimation, or by adjusting their growth an allocation behavior (Maseda and Fernández 2006, Aroca 2012). In particular, trees are known to be notably sensitive to enhanced soil water tension and/or vapor pressure deficits, which align with impairment of several biochemical and metabolic processes (Kozlowski and Palladry 2002, Bredá et al. 2006, Renneberg et al. 2006). On the one hand, diverse allometric and morphological adjustments in trees might maintain and balance the plant-environment water relation. Belowground, soil water acquisition can be enhanced by higher carbon allocation to the root system under dry conditions (Dreesen et al. 2012). Aboveground, trees are capable to reduce the transpiring leaf area surface, when drought remains progressional (Bredá et al. 2006, Ogaya and Penuelas 2006). On the other hand, physiological and structural adjustments are known to allow for significant acclimation to deficient water supply. In short-time response, the increase in leaf diffusion resistance by stomatal regulation reduces extensive plant water loss (Köcher et al. 2009) while maintaining higher leaf water potentials and xylem functioning. As an intermediate response to drought, cell water relations in foliar tissue can be modified by osmotic, elastic or apoplastic adjustments (Kozlowski and Palladry 2002). Plasticity in size of the symplast, cell wall elasticity and inner cell concentrations of osmotic solutes is supposed to maintain favorable leaf hydration with respect to preservation of leaf water potentials and cell water content (Bartlett et al. 2012). Considering a long-time acclimation process to severe drought, woody species are further capable of xylem structural modifications causing enhanced hydraulic safety at the costs of hydraulic efficiency and growth performance (Sperry et al. 2008, McDowell 2011, Fonti et al, 2013). This can be due to a decreasing vascular conduit size, which hampers hydraulic conductance, but also reduces the chance for air-seeding induced cavitation under high tension (Hacke and Sperry 2001, Sperry et al. 2006, Hajek et al. 2014). Additionally, an increase in vessel densities resulting in pathway redundancy can reduces the risk of hydraulic failure in the vascular system (Ewers et al. 2007).

According to the Productivity Ecology Equation (Monteith 1977), plant individual growth and functional performance are not only related to resource availability (i.e. magnitude of drought), but also to the proportion by which resources can be captured, and to the efficiency of resource use. Not only, but in particular resource capturing is assumed to be modified by species mixture, when reduced competition (induced by complementary resource use) accounts for improved resource availability for individual plants (Richards et al. 2010). Whether this process can in fact be amplified by diminished disposal of a resource is a key aspect of the actual debate in mixed forest ecology (Forrester 2014). Several studies provide evidence that certain tree species are able to reduce their susceptibility to drought and to increase growth performance or survival rate by the admixture of heterospecific neighbors (Lebourgeois et al. 2013, Pretzsch et al. 2013, Mölder and Leuschner 2014, del Río et al. 2013, Neuner et al. 2015). However, a possible manifestation of favorable species interactions in terms of plant physiological- and structural performances was rather seldom taken into account (e.g. Pollastrini et al. 2014).

Shortcomings in BEF research in forests

By applying complemental but distinct approaches, BEF research in forests varies considerably with regard to spatiotemporal scales and methodological procedures. Inventory surveys are widely used to analyze enormous data on the diversity-productivity relationship at regional to global scales (Víla et al. 2013, Belote at al. 2010, Paquette and Messier 2011); though it remains difficult to account for the effects of co-variation of climatic and edaphic conditions or land use history (“hidden treatments”, e.g. Huston et al. 1997). Observational studies in forests already refer to various ecosystem functions while considering stand structural properties (Jacob et al. 2010, Pretzsch et al. 2010, Krämer and Hölscher 2010, Gebauer et al. 2012, Forrester 2013). However, their results are commonly bound to specific site conditions and lack in global validity. Furthermore, as mature forests usually do not provide certain species combinations in appropriate number for statistical validation (in particular monocultural stands), partitioning between effects of tree species identity and diversity can be hampered. Additionally to modelling studies (Bittner et al. 2010, Morin et al. 2011, Vallet and Perrot 2011), artificial stand approaches can be used to overcome those shortcomings in real forest research (Scherer-Lorenzen et al. 2005). During the last years, an increasing amount of experimental plantations has been established all over the world (Scherer-Lorenzen et al. 2007, Hector et al. 2011, Potvin et al. 2011, Verheyen et al. 2013, Bruelheide et al. 2014) to complement the findings on BEF in real forest systems. Tree diversity experiments with young trees planted in a specific design certainly fail in reproducing the complex process patterns in old-growth forests. Despite this shortcoming, such experiments can provide steep gradients in species richness, functional- or genetic diversity in various species combinations under consideration of low stand structural variability and mostly homogenous or controlled abiotic conditions. In summary, all approaches have their pros and cons and should best be combined in order to generate sound conclusions on the role of tree diversity for forest ecosystem functioning (Leuschner et al. 2009). In addition to aspects of tree diversity, controlled experiments are requested to allow for comprehensive comparisons of species' functional traits with respect to life history strategies and for the ability and realization of phenotypic plasticity in response to a varying environment (Anderegg and Meinzer 2015).

The DFG Research Training Group 1086

This thesis is embedded within the framework of the interdisciplinary Research Training Group, entitled "The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests", funded by DFG (RTG 1086). The reference site and study area of this joint project is the Hainich National Park forest in Central Germany, Thuringa. The Hainich Tree Diversity Matrix (Leuschner et al. 2009) represents various mixed species stands with heterogeneous species compositions and a varying abundance of dominant European beech. Because of its exceptional management history, these old grown forests provide a notably high amount of broad-leaved tree species in close vicinity and thus a naturally steep gradient in tree diversity, while the abiotic conditions are widely comparable.

The Research Training Group was conducted in three phases, each constituted by a cohort of ~13 PhD candidates. All members belonged to the University of Göttingen or the Max-Planck Institute for Biogeochemistry in Jena and represented diverse sub-projects of different disciplines, aiming to consider multiple aspects of forest ecosystem processes and functioning, and focusing on either, (i) biodiversity analysis and biotic interactions, (ii) biogeochemical cycling, or (iii) synthesis. During the first phase (starting in 2005) permanent plots (50 m × 50 m) with diluting beech abundance (and thus increasing tree diversity; 1, ≥3 or ≥5 species) were investigated in comparative studies. The design enabled the determination of tree diversity effects on forest ecosystem functioning, but hardly allowed to distinguish between species complementarity and species identity or selection effects. The second phase (starting in 2008) was featured by a tree cluster design. 100 micro-plots consisting of three trees each were used to consider all possible one-, two-, and three-species combinations with respect to the five target species. The cluster approach provided the possibility to separate for complementarity and selection effects at the plot level with regard to all types of monocultures, but the tree diversity gradient was rather short. The final phase of the project (starting in 2011) was not intended to follow an integrative study design, but compounded several approaches for the extension, complementation and synthesis of the existing results, which comes along with various observational, experimental and theoretical studies.

The topic of this thesis is framed by the theme block "biogeochemical cycling" and mainly considers complementarity effects in tree water use and the characterization of hydraulic traits of five co-occurring broad-leaved tree species in the Hainich forest (sub-project B4). In previous work, Gebauer et al. (2012) investigated stand transpiration at the plot level based on sap flux measurements and revealed enhanced water use for the high diverse stands during a wet summer, but not during a dry summer. Those results were partially confirmed by a complemental soil water balance study (Krämer and Hölscher 2010) and it was interpreted as a species identity effect, based on the high water consumption of *Tilia spec.* in the mixed stands. However, the design did not allow for a clear distinction between effects of diluting contribution of beech trees and tree diversity per se. Meißner et al. (2012, 2013) analyzed complementarity in tree water use at the cluster level based on deuterium signals in the soil- and plant water. They found some indication for soil water partitioning among certain species, but they also referred to the superior importance of stand structural attributes in comparison to tree species richness. The work of Köcher et al. (2009, 2012, 2013) was primarily conducted to characterize species-specific traits in tree water use and their sensitivity to drought, which provides a valuable contribution to the role of species identity in those temperate broad-leaved mixed forests.

Thesis concept and general objectives

In order to complement the findings from observational studies on tree diversity effects on stand productivity and tree water use conducted in the Hainich forest, this thesis summarizes the outcome of a replicated common-garden tree diversity experiment. This trial, representing numerous types of tree sapling assemblages, consisted of a similar species composition and was subdivided into two treatments of soil water supply (moist and dry). In the first study (Chapter 3), effects of tree diversity and tree identity on stand-level water consumption are discussed under consideration of resource availability. The second study (Chapter 4) provides a distinct analysis of stand- and tree level productivity in the tree diversity experiment. The impact of tree diversity, tree identity and soil water supply was determined, but we put also special attention on the role of tree neighbor identity. In the third study (Chapter 5), tree functional performances (physiological and structural modifications) were examined in consideration of soil drought and tree mixture effects.

The main objectives of the present thesis can be summarized as follows:

i) Determining the effect size of tree diversity on stand-level water consumption and productivity for the young tree sapling assemblages in the experiment, and to disentangle the role of species complementarity and species selection.

ii) Determining the role of tree species identity in tree community functioning.

iii) Investigating the role of deficient resource supply and altering stress intensity (soil drought) on the BEF relationship in tree water use and growth.

iv) Investigating tree individual responses along environmental gradients (shifts in tree neighborhood and soil water supply) with respect to morphological, physiological and structural adjustments.

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Chapter 2

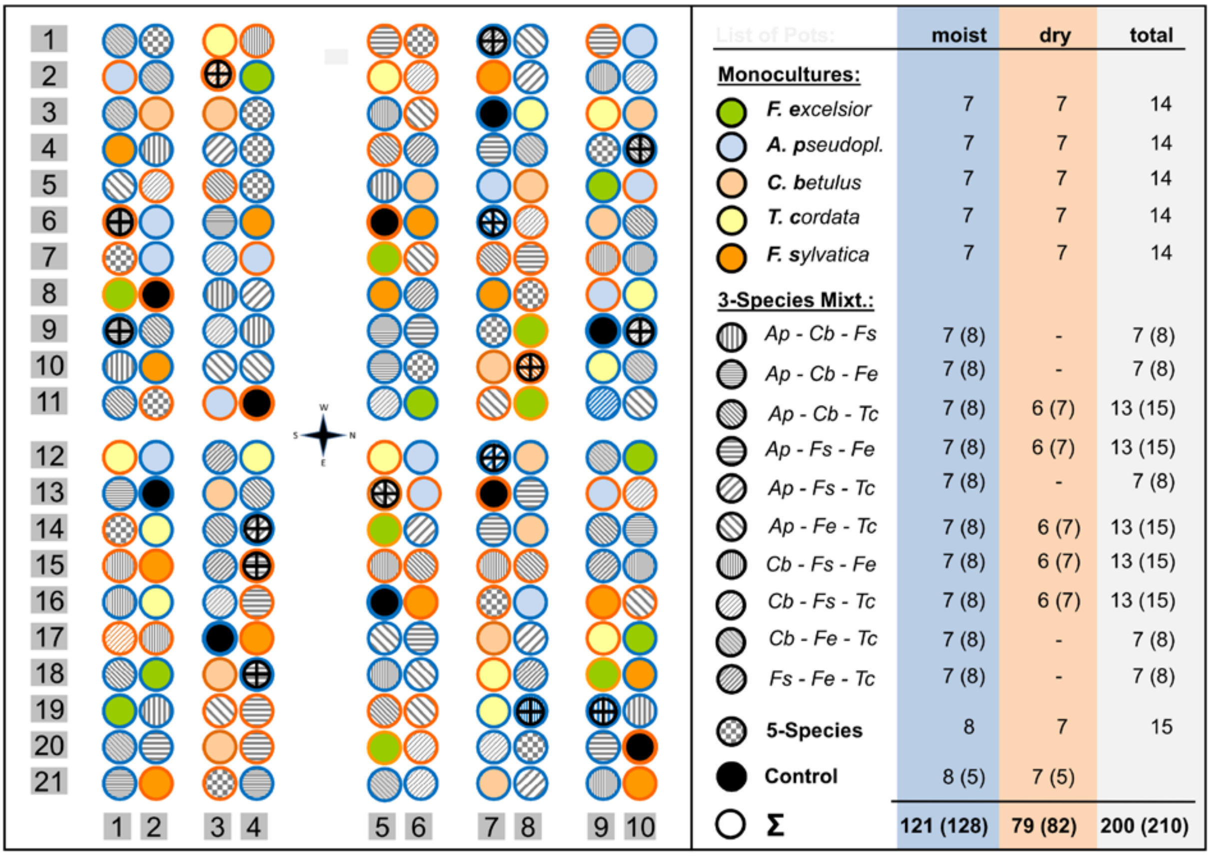
Materials and methods

Design of the tree diversity experiment

A replicated tree diversity experiment containing five temperate deciduous tree species (*Acer pseudoplatanus* L. (sycamore maple), *Carpinus betulus* L. (European hornbeam), *Fagus sylvatica* L. (European beech), *Fraxinus excelsior* L. (European ash) and *Tilia cordata* L. (small-leaved linden)) was established in April 2011 and lasted for two vegetational periods until August 2012 (~16 month). The chosen species are the most abundant in the Hainich tree diversity matrix (Leuschner et al. 2009). Thus, this experimental approach complements numerous observational studies examined in the framework of the DFG research training group 1086 (Jacob et al. 2009, Krämer and Hölscher 2010, Gebauer et al. 2012, Meißner et al. 2012, 2013, Mölder and Leuschner 2014). The species belong to five different families which account for a broad variety of tree functional types, differing in light demand and shade tolerance, canopy architecture, mycorrhizal type, drought tolerance and successional status (Ellenberg and Leuschner 2010, Köcher et al. 2013, Legner et al. 2013).

The experiment was located at the Experimental Botanical Garden of the University of Goettingen (51°33' N, 9°57' E; 177 m a.s.l.). The 1- to 2-yr old tree saplings used were reared in a nursery in the region of Göttingen and originated from the same cohorts with supposedly low genetic variability. The saplings had an initial height of ~40-60 cm with marginal deviations among species (Table A.4.1). In total, 1000 saplings were used to establish 200 tree assemblages, each consisting of five plants (Fig. 2.1.). The trees were grown together in pots of 0.05 m^3 volume (height 0.30 m, diameter 0.58 m) filled with coarse-grained sand (98% sand, 1.8% silt, 0.2% clay). The chosen substrate was slightly basic (pH = 7.5) as the target species prefer neutral to base-rich soils (Ellenberg and Leuschner 2010). A systematic planting scheme was applied to account for mostly equal distances within a sapling group. Four individuals were planted in shape of a square with ~12 cm distance to the pot wall. A fifth tree was set to the center with a minimum distance of ~17 cm to its neighbors around.

By varying the composition of species, 16 different species combinations were installed, while a gradient of tree diversity with 1, 3 and 5 species emerged. Besides five different monocultures (five species; all five plants of the same species), ten possible 3-species mixtures and one 5-species mixture (all plants of different species identity) were established. In the 3-species mixtures, two species each were represented by a pair of plants but a third species by a single plant only. The abundances and spatial positions of species were altered within the replication of species combinations to account for a similar amount of species present and a similar intensity of inter-species interactions. Two plants of the same species were always arranged to opposite corners of the planting square. The single tree was set to the center, which ensured for a minimization of intra-specific competition.



List of Pots:	moist	dry	total
Monocultures:			
F. excelsior	7	7	14
A. pseudopl.	7	7	14
C. betulus	7	7	14
T. cordata	7	7	14
F. sylvatica	7	7	14
3-Species Mixt.:			
Ap - Cb - Fs	7 (8)	-	7 (8)
Ap - Cb - Fe	7 (8)	-	7 (8)
Ap - Cb - Tc	7 (8)	6 (7)	13 (15)
Ap - Fs - Fe	7 (8)	6 (7)	13 (15)
Ap - Fs - Tc	7 (8)	-	7 (8)
Ap - Fe - Tc	7 (8)	6 (7)	13 (15)
Cb - Fs - Fe	7 (8)	6 (7)	13 (15)
Cb - Fs - Tc	7 (8)	6 (7)	13 (15)
Cb - Fe - Tc	7 (8)	-	7 (8)
Fs - Fe - Tc	7 (8)	-	7 (8)
5-Species	8	7	15
● **Control**	8 (5)	7 (5)	
○ **Σ**	**121 (128)**	**79 (82)**	**200 (210)**

Figure 2.1. Scheme and experimental design of the tree diversity experiment in Göttingen (2011-2012). 200 potted tree sapling assemblages differing in tree diversity (1, 3, 5 species), species composition (marked by hatching), and soil water supply (moist: blue circles, dry: orange circles) were arranged in a randomized grid-shaped formation. Crossed circles trace pre-harvested sapling assemblages (all from 3-species mixtures), which have in part been replaced by additional control pots of bare soil (notice the amount of replicates given in parenthesis).

The experiment was complemented with a drought trial by applying two different levels of soil water supply (moist and dry). During July-September 2011 and May-August 2012, the volumetric soil water content (SWC) was set to target values of maximal ~21% in the moist and ~12% in the dry treatment, which is equivalent to 95% and 57% of field capacity, respectively. According to percolation experiments, the 21%-target moisture in the moist treatment did not result in water percolation through the pot bottom. SWC fluctuated moderately between two irrigation events (3-5 days in 2012) below those target values. Accordingly, the mean SWC content varied in a constant range between 12 and 20% in the moist and 7 and 12% in the dry treatment. The minimum SWC corresponded with peak values in soil matrix potentials of -84 kPa in the moist and -869 kPa in the dry treatment, respectively (see Chapter 3 for details). The water balance of the planted pots was quantified by applying a gravimetric approach. The whole experiment was situated under a transparent Plexiglas shelter, which slightly reduced photosynthetically active radiation (PAR, -30%), but mostly excluded any precipitation and thus allowed controlling water turnover.

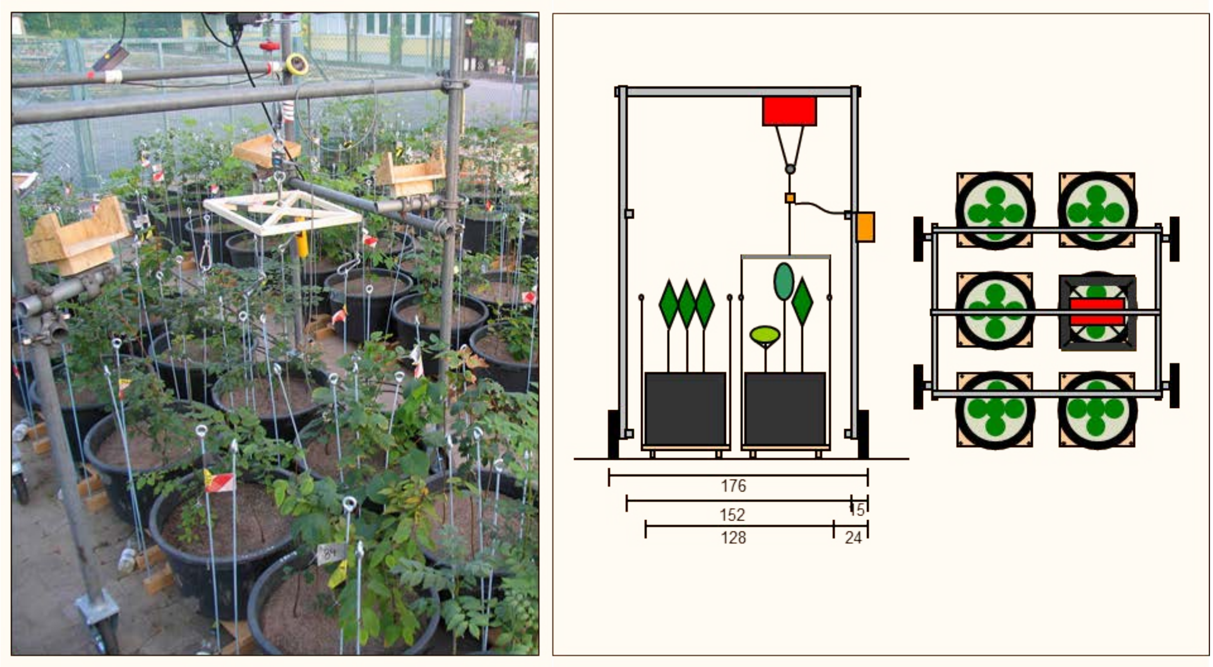


Figure 2.2. Weighing vehicle in use in the experiement (left) and schematic drawing of the construction and functioning (right).

The SWC for each tree assemblage was derived from the total weight of a pot under consideration of the dry weight of the soil and the weight of all components including plants. A digital hanging scale (Vishay Transducers 220; tension cell No. 616; resolution 1g, max. load 150 kg; tot. error 0.02%, i.e. <20 g for pots <100 kg) was used to measure a pot’s weight. The scale was fixed to an electric steel rope winch hanging on top of a self-constructed mobile weighing vehicle made of steel tubes (Fig. 2.2.). The pots were placed on wooden boards equipped with suspension points for hooking and lifting. The transducer measured the traction force on the rope during the lift. The reduction in mass between two irrigation events was used to estimate dynamics in SWC, as the loss in weight was interpreted as evapotranspiration for those short time intervals. Long-term biomass increments were also considered for correcting estimations on SWC by interpolating between plant biomass in spring 2012 and at the end of the experiment. Plant biomass in early May before the start of soil desiccation was estimated from allometric equations established for all five species by harvesting each ten individuals per species (ten 3-species mixtures, moist treatment) of different size and regressing biomass on basal area and shoot height using multiple linear functions. This allowed estimating plant biomass in every pot at any time. During plant establishment (May - June 2011) and the off-season (October 2011 - April 2012), all tree assemblages were treated under moist conditions

The combination of 16 species compositions and two soil moisture levels yielded in 32 potential treatments at the stand level. However, due to limitations in plant material and work force, the dry treatment could not be carried out with the full set of species combinations used in the moist treatment. The ten possible 3-species mixtures were reduced in the dry treatment to five representing each species in three different combinations (Fig. 2.1.). All treatments were initially replicated 7-8 fold (n = 200). With respect to pre-harvest events in July 2011 and May 2012, 6-8 replicates per treatment (n = 185) remained until the end of the experiment.

All planted pots were arranged randomly in a grid pattern under the Plexiglas shelter for minimizing possible effects of environmental gradients. The assemblages were fertilized monthly between May and September 2011 with 4 ml Wuxal$^{©Bayer}$ solution (8.0% N, 8.0% P_2O_5, 6.0% K_2O), and with 6 ml between March and August 2012.

Determination of stand-level water consumption

Measurements of tree water consumption at the stand level were carried out within a core period of five weeks in 2012 (May 29 – July 6), i.e. in the second summer after the experiment's implementation. Data on evapotranspiration from 2011 have been discarded for this aspect because (i) species interactions were presumably low during this early experimental phase, and (ii) soil evaporation could not be sufficiently estimated, as the variability in water loss of control pots (bare soil) was considerably high. For certain measuring intervals in June/July 2012, the soil surface of the pots were tightly covered with plastic sheets. Thus, soil evaporation could be minimized and the measured weight loss was caused nearly exclusively by transpirative water loss. The soil sealing of the control pots suppressed >95% of evaporation, demonstrating the effective applicability of plastic coverage. Plastic sheets were only installed for single measuring periods of 3 to 4 d and subsequently removed (3 to 4 d) to enable unrestricted gas fluxes between soil and atmosphere in order to avoid hypoxia. Net diversity effects on stand water consumption were calculated according to the additive partitioning approach (Loreau and Hector 2001) for ample as well as for limited soil water supply. Additionally, transpiration rates were scaled to the water use-related morphological parameters leaf area (LA) and cumulative sapwood area (LA), which allowed for a separation between tree size and tree identity effects (see Chapter 3 for details).

Determination of growth performances at the stand- and tree-level

Measurements on tree growth and productivity were carried out during a 7-wk harvesting period at the end of the experiment in July/August 2012. Shoot length (L_{Shoot}) and maximum root length (L_{Root}) were determined and the stem diameter at ground level was measured in two directions perpendicular to each other for calculating basal area (BA). Leaf, stem and root mass were oven-dried (70 °C, 72 h) and weighed at a precision of 10 mg. The specific leaf area (SLA) of fully expanded leaves in the upper crown was determined for a subset of trees, which served for calculating the total leaf area (LA) of the trees. Besides metrics related to tree size, biomass and biomass partitioning, root-to-shoot ratio (RS) and the relative increment in BA, shoot length (LI_{Shoot}) and root length (LI_{Root}) for the entire growth period of 450 days by subtracting initial from final size or biomass were calculated. Furthermore, relative growth rates were calculated considering above-ground, below-ground and total biomass (RGR, in g g^{-1} 450 d^{-1}). Those growth related parameters were used to analyze the effects of tree diversity, neighborhood composition, species identity and water supply, both for the stand and for the tree individual level. Special emphasis was taken on the separation between selection- and complementarity effects in diverse tree cultures according to Loreau and Hector (2001) and the importance of tree neighbor identity on the performance of target species. Additionally, transpiration data were used to estimate water use efficiency at the stand level (see Chapter 4 for details).

Determination of tree physiological and structural traits

Tree-physiological properties were measured in order to test for phenotypic plasticity of the species in response to species mixture and soil drought. A subset of tree individuals was sampled, originating from monocultures and 5-species mixtures, and treated with ample and limited soil water supply (each six plants of the five species; n = 120). To avoid pseudo-replication, plants from different pots were investigated as replicates for a species. Non-invasive measurements of leaf stomatal conductance (G_S) were carried out during the core period in June 2012. During harvest in July/August 2012 the same leaves were sampled for carbon isotope analysis ($\delta^{13}C$) with isotope mass ratio spectrometry (see Chapter 3). Additional leaf samples were used for pressure-volume analysis by applying the pressure chamber method according to Tyree and Hammel (1972), aiming to derive leaf hydraulic properties like the tension point of turgor loss (tlp) and the corresponding relative cell water content (RWC_{tlp}), leaf osmotic potentials (π_0, π_{tlp}) and bulk modulus of elasticity (ε; see

Chapter 5). Shoot segments of the target trees were sampled to measure the axial hydraulic conductivity (K_h) and to derive sapwood area-specific hydraulic conductivity (K_s) according to Sperry et al. (1988) (Chapter 3). The samples were further used to measure xylem vulnerability to cavitation by applying the Cavitron-technique (Cochard et al. 2005). Pointer values of the vulnerability curves (P_{50}, P_{88}) characterize the loss of hydraulic conductance (in %) with respect to increasing tension forces. Finally, the wood samples were analyzed for their xylem structural properties like the vessel fraction in cross sectional sapwood area, conduit size given as mean vessel diameter (D) or hydraulic weighted vessel diameter (D_h), vessel density (VD) and theoretical sapwood area-specific hydraulic conductivity (K_p). Wood-anatomical traits were analyzed based on digital image processing of microtome slides (Scholz et al. 2013) (see Chapter 5 for details).

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Chapter 3

Species diversity and identity effects on the water consumption of tree sapling assemblages under ample and limited water supply

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Torben Lübbe · Bernhard Schuldt · Heinz Coners · Christoph Leuschner

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Abstract

Studies examining the influence of biodiversity on ecosystem functioning have rarely considered water turnover, the quantitatively most important biogeochemical flux in ecosystems and a process with high sensitivity to climate warming. With a tree sapling experiment consisting of three diversity levels (1, 3, 5 species), 11 different species combinations and two soil moisture levels (moist and dry), we examined the influence of tree species diversity and species identity on stand transpiration (T) under ample and restricted water supply. We further asked whether growth in mixture leads to adaptive responses in the hydraulic system and water loss regulation in plants with heterospecific neighbors compared to plants in monoculture. In moist soil, T was on average ~11% higher in the mixtures than in the monocultures (significant net diversity effect), which can mostly be attributed to a selection effect. Overyielding in T was highest in mixtures when *Tilia cordata* and/or *Fraxinus excelsior* were present. Both species developed larger leaf areas (LA) and sapwood areas (SA) in monocultures than the other species and furthermore increased LA and SA from the monocultures to the mixtures. Thus, inherent species differences in LA and hydraulics, but also neighbor effects on these traits determined T to a large extend. In dry soil, the diversity effect on T was not larger but slightly smaller, which is not in agreement with other published studies. We conclude that differences between pure and mixed sapling assemblages in stand water consumption and drought response are mainly caused by species identity effects, while species diversity seems to be less influential.

Keywords: *Acer pseudoplatanus*, *Carpinus betulus*, community resistance, complementarity, drought stress, *Fagus sylvatica*, *Fraxinus excelsior*, hydraulics, neighbor effects, transpiration, *Tilia cordata*.

Introduction

Ever rising human impact on ecosystems has raised concern about consequences of biodiversity loss for ecosystem functioning (Tilman 1999, Balvanera et al. 2006). Research into the relationship between biodiversity and ecosystem functioning (B-EF) has recently shifted to forests which are a key resource for humans to meet the wood and fuel demand and that harbor about two thirds of the world's terrestrial biodiversity (e.g. Millennium Ecosystem Assessment 2005). Theory predicts a positive effect of species richness on productivity and other ecosystem functions primarily through three mechanisms, niche complementarity which may reduce competition, facilitation and selection (or sampling) effects (Fridley 2001, Loreau and Hector 2001, Hooper et al. 2005). If valid on larger scales, more diverse forests should produce more timber and sequester more carbon than forests with lower tree species numbers. General evidence for a positive diversity-productivity relationship in tree communities is broadly provided (e.g. Zhang et al. 2012, Scherer-Lorenzen 2014). Another ecosystem function with possible dependence on species richness is plant water consumption, which determines deep seepage and groundwater recharge. Since enhanced productivity is often associated with increased water consumption (Law et al. 2002), more diverse forests could also transpire more water which can have implications for soil water availability and water management.

The effect of tree diversity on water consumption is much less studied than the diversity – productivity relationship. We are aware of only eight studies that compared the plot-level water consumption of monospecific and mixed stands of woody plants; the obtained results on diversity effects were mixed. Two of three experimental studies in tree plantations (boreal, temperate or tropical) showed increases in stand transpiration with higher diversity (Forrester et al. 2010, Kunert et al. 2012), while the third one did not (Grossiord et al. 2013). Higher water consumption of the mixtures was in all cases linked to higher productivity. Observational studies in mixed forests (temperate or Mediterranean) produced inconsistent results as well. Soil water depletion was greater under mixed stands of *F. sylvatica* and *Picea abies* than under the respective pure stands due to the deeper-reaching and more intense root system of beech (Schume et al. 2004). In old-growth 1-, 3- and 5-species stands with diluting beech abundance (*F. sylvatica*) in the Hainich forest (Germany), Gebauer et al. (2012) found in a sap flux study higher transpiration rates for the mixed stands than the pure beech stand in a moist summer, while no stand differences existed in a relatively dry summer. The latter observations are mirrored by patterns of soil water extraction conducted during the same period with a soil water balance modeling approach (Krämer and Hölscher 2010). Also in the

Hainich forest, Meißner et al. (2013) found no systematic differences in water consumption among small-sized tree clusters that differed in species composition and species richness (1-3 species). Different deuterium signatures in the xylem water of coexisting tree species in mixed stands pointed, however, at partitioning of soil water among species during a soil desiccation period and thus may indicate a certain complementarity in water use (Meißner et al. 2012). In drought-exposed Mediterranean mixed oak forests, interactions were driven by competition for water which reduced the transpiration of the inferior species (Grossiord et al. 2014a). In conclusion of the existing results, diversity may enhance plot-level water consumption when productivity increases with diversity, but it is unlikely to be higher in those cases where productivity is not enhanced by diversity.

Certain tree species such as *Abies alba* and *Fagus sylvatica* were found to be less sensitive to summer droughts when growing in mixtures as compared to monocultures (Lebourgeois et al. 2013, Pretzsch et al. 2013, Mölder and Leuschner 2014). Possible underlying mechanisms are hydraulic redistribution, complementary use of soil water and species differences in water consumption that result in reduced competition for water in mixed as compared to pure stands (Pretzsch 2013, Forrester 2014).

The diversity – water consumption relation may be influenced by climate, soil fertility, stand structure, and the functional properties of the tree species (Forrester 2014). The dependence on resource availability is addressed by the stress-gradient hypothesis which predicts that the net outcome of biotic interactions shifts along gradients of limiting physical conditions. Positive diversity effects (facilitation) should be more common in severely resource-limited environments while negative interactions (competition) should dominate in richer and less-stressful environments (Callaway and Walker 1997). Since climate change scenarios predict increasing drought frequencies for various regions of Europe (IPCC 2013), facilitative interactions could become more important in forests that are increasingly affected by drought. This could result in a growing diversity effect on the carbon and water cycles in forests, because facilitation is one of the mechanisms that may drive a diversity effect. In contrast to this assumption, the modeling study by Morin et al. (2011) and some empirical evidence suggest that the benefit from mixtures could be greater in favorable and not in unfavorable and stressful environments (e.g. Dieler and Pretzsch 2013, Forrester et al. 2013). Thus, some uncertainty remains with respect to the importance of diversity effects under ample and limited soil moisture.

Deeper insights into the mechanisms, by which diversity or tree identity are influencing water turnover in forest ecosystems under both unlimited and resource-limited conditions, are urgently needed. This requires measurement of water consumption in monospecific and mixed stands at the stand and tree level and examination of plant traits underlying drought tolerance. The latter can reveal possible adaptive responses of leaf area and the water conducting system of the species to variable neighborhood constellations as are characteristic for mixed stands.

Here, we present the results of a diversity experiment with tree saplings aimed at investigating the diversity - water consumption relationship at the stand and tree levels, and for moist and dry soil. The experiment was conducted with five temperate broad-leaved tree species (*Fraxinus excelsior*, *Acer pseudoplatanus*, *Carpinus betulus*, *Tilia cordata*, *Fagus sylvatica*), which are common in Central European mixed forests and known to differ substantially with respect to their drought response (Köcher et al. 2009; Table A1). *F. excelsior*, *T. cordata and C. betulus* are classified as more or less drought tolerant with respect to growth, while *F. sylvatica* and *A. pseudoplatanus* exhibit drought-sensitive properties (Zimmermann et al. 2015). We conducted a replicated outdoor growth experiment in large pots with 1- to 2-year-old saplings of the five species which consisted of three diversity levels (1-, 3- and 5-species), 11 species combinations and two soil moisture treatments (moist vs. dry). Stand transpiration was measured by gravimetric quantification of the water balance of the pots. Six morphological and physiological plant traits related to tree water consumption (total leaf area, sapwood area in the stem, sapwood area-specific hydraulic conductivity, Huber value, stomatal conductance and leaf carbon isotope ratio) were measured to test the following hypotheses: (i) Stand-level water consumption increases with tree species diversity, (ii) diversity effects on stand-level water consumption are enhanced in dry soil due to the increasing importance of positive interactions, (iii) more diverse stands reduce leaf conductance and stand transpiration upon drought to a lesser degree than the average monoculture due to the expansion of drought-adapted species in the mixtures (diversity-community resistance hypothesis), and (iv) the water flux regulation and hydraulic properties (leaf conductance and xylem hydraulic conductivity) of individual trees in mixed stands are influenced by the water consumption of heterospecific neighbors.

Materials und methods

Plant material and experimental design

In April 2011, a diversity experiment with saplings of *Acer pseudoplatanus* L. (sycamore maple), *Carpinus betulus* L. (European hornbeam), *Fagus sylvatica* L. (European beech), *Fraxinus excelsior* L. (European ash) and *Tilia cordata* L. (small-leaved linden) was established in the Experimental Botanical Garden of Göttingen University (51°33' N, 9°57' E; 177 m a.s.l.). These species belong to five different families representing a broad variety of tree functional types differing in light demand and shade tolerance, canopy architecture, mycorrhizal type, drought tolerance and successional status (Köcher et al. 2013, Table A.3.1.). The 1- to 2-yr-old plants with an initial height of ~40-60 cm were obtained from a nursery close to Göttingen. They were cultivated outdoors under uniform conditions for 16 months to enable comparative measurements of water consumption, productivity, and a number of morphological and physiological parameters related to hydraulic architecture and growth. Five saplings were grown in each pot of 0.05 m^3 volume (height 0.30 m, diameter 0.58 m) filled with coarse-grained sand (98% sand, 1.8% silt, 0.2% clay) in a systematic planting scheme with equal distances between the plants (ca. 17 cm; distance to pot walls: ca. 12 cm). The sand had a pH of 7.5 (Table A.3.2.) for accommodating *F. excelsior*, *C. betulus* and *A. pseudoplatanus* which prefer neutral to base-rich soils (Ellenberg and Leuschner 2010). Four saplings were planted at the corners of a square placed on the pot surface and the fifth was positioned in the center. Experimental plants were selected from a larger number of plants according to similarity in plant height and number of leaf buds. We established three diversity levels (1, 3 and 5 species) and grew all five species either in monoculture (all five plants of the same species; five types of monocultures), in 3-species mixture (five of the ten possible three-species mixtures were established), or in 5-species mixture (all plants of different species identity; Table 3.1.). In the 3-species mixtures, two species were present with each two plants and a third species with a single plant. The saplings were arranged in a pattern that minimized intraspecific competition (either two plants of the same species in opposite corners of the square, or a single plant in the center). The abundance of the species (one or two plants) and their spatial position differed among the replicates, i.e. three species reached on average equal abundances in the seven pots of a treatment and were exposed to comparable interspecific competition intensity.

Table 3.1. Design of the experiment with diversity levels, species combination, the two moisture treatments (moist versus dry), and number of replicates. Each 50-l pot contained five saplings. Mono – monoculture, mix 3 – 3-species mixtures, mix 5 – 5-species mixture. A.p. – *Acer pseudoplatanus*, C.b. – *Carpinus betulus*, F.e. – *Fraxinus excelsior*, F.s. – *Fagus sylvatica*, T.c. – *Tilia cordata*.

		Replicates	
Diversity level	Species combination	Moist	Dry
mono	*F. excelsior*	7	7
	A. pseudoplatanus	7	7
	C. betulus	7	7
	T.cordata	7	7
	F.sylvatica	7	7
mix3	A.p. - C.b. - F.e.	7	6
	A.p. - C.b. - T.c.	7	6
	A.p. - F.s. - F.e.	7	6
	C.b. - F.s. - T.c.	7	6
	F.e. - F.s. - T.c.	7	6
mix5	A.p. - C.b. - F.s. - F.e. - T.c.	8	7

The experiment consisted of a moist and a dry treatment, yielding 22 treatments in total (11 species combinations × 2 water levels), which were replicated 6 to 8-fold (Table 3.1.). Drought was applied in the period July to September 2011 and May to August 2012. The volumetric soil water content (SWC) of each pot was kept in a constant range by adding every 3-5 days that amount of water which had been lost through evapotranspiration since the last adjustment. The target value of maximal SWC in the moist treatment was set to ~21% (95% of field capacity in the sandy soil) and ~12% for the dry treatment (i.e. 57% of field capacity). The difference between a pot's actual total and target weight in the respective treatment determined the amount of water to be added. The individual target weight was obtained from the mass of dry soil in the pot (derived from soil bulk density and soil volume in the pot) and target SWC. Regular rewetting resulted in moderate fluctuation of SWC and soil matric potential (Ψ_{soil}) below the target value (Fig. 3.1.). Estimates of Ψ_{soil} in the pots were obtained from volumetric soil moisture data with an empirically-derived soil moisture-soil water potential curve implemented in the LeachM model (British Soil Service, Hutson and Wagenet 1992) under consideration of grain size distribution, soil bulk density and soil organic carbon concentration. In the last phase of the experiment (summer 2012), the target values for the dry treatment were allowed to vary slightly between pots (11-14% SWC) according to the variable water consumption of the assemblages, in order to generate comparable stress intensities in all pots at the end of the measurement intervals.

The pots were placed outdoors under a rain shelter made of transparent plexiglass, which excluded rainfall and thus allowed controlling water turnover. Although the flux density of photosynthetically active radiation (PAR) was reduced by approx. 30%, a pronounced greenhouse effect could be excluded. The pots were arranged randomly in a grid pattern for minimizing possible effects of environmental gradients. We fertilized all pots monthly between May and September 2011 with 4 ml Wuxal$^{©Bayer}$ solution (8.0% N, 8.0% P_2O_5, 6.0% K_2O), and with 6 ml between March and August 2012.

PAR was measured continuously at a weather station close to the experimental site using a LI190 Quantum Sensor (Li-Cor Inc., Lincoln, NE, USA). In close vicinity of the pots, relative air humidity and air temperature (CS215, Campbell Scientific, Shepshed, UK) were continually recorded and 30-min means stored (CR200, Campbell Scientific, Shepshed, UK).

Transpiration measurement

Pot-specific transpiration was measured by weighing every 3-4 d with a digital hanging scale (Vishay Transducers 220; tension cell No. 616; resolution 1g, max. load 150 kg; tot. error 0.02%, i.e. <20 g for pots <100 kg). The scale was fixed to a self-constructed mobile weighing vehicle made of steel tubes. The pots were placed on wooden boards equipped with suspension points for hooking and lifting the pots with an electric steel rope winch. The transducer measured the traction force on the rope during the lift. For every pot, we calculated pot total weight (dry soil plus pot weight) and pot target weight at 21% (moist treatment) or 12% SWC (dry treatment). Weight loss between two sequential measuring dates (time interval: 3-4 d) was assumed to represent water loss through transpiration and soil evaporation. According to percolation experiments, the 21%-target moisture in the moist treatment did not result in water percolation through the pot bottom. By covering the soil surface of the pots in certain measuring periods tightly with plastic sheets, soil evaporation could be minimized and the measured weight loss was caused nearly exclusively by transpirative water loss. This was confirmed by using control pots containing only bare soil (n = 8 in the moist and 7 in the dry treatment). In June 2012, soil sealing of these synchronously weighed control pots suppressed >95% of evaporation, demonstrating the effective applicability of plastic coverage. Plastic sheets were only installed for the measuring periods of 3 to 4 d and subsequently removed (3 to 4 d) to enable unrestricted gas fluxes between soil and atmosphere in order to avoid hypoxia (Fig. 3.1.). We neglected biomass increment in the short weighing intervals, because it was too small to significantly influence the water balance. Thus, we interpreted the entire weight reduction in the measuring interval as water loss caused by transpiration. Mean daily water loss (in mm d^{-1}) was taken as transpiration rate (T). The net biodiversity effect on the transpiration of mixed pots was calculated from equation (1) according to Loreau and Hector (2001),

$$NE = Y_0 - Y_E = Y_0 - \sum_i RY_{Ei} M_i \tag{1}$$

as the deviation of observed (Y_O) and expected (Y_E) transpiration. RY_{Ei} determines the expected relative transpiration of species i in mixture (derived from the relative abundance of individuals of species i in the mixture at planting). M_i is the transpiration of the respective monoculture.

When calculating the temporal fluctuation of soil moisture in the pots from known soil dry weight and measured actual pot fresh weight, we accounted for long-term biomass increment by interpolating between plant biomass at harvest and biomass at the start of the main measuring period (early May 2012). Plant biomass in early May before the start of soil desiccation was estimated from allometric equations established for all five species by harvesting each ten individuals of different size and regressing biomass on basal area and shoot height using multiple linear functions. This allowed estimating plant biomass in every pot at any time. For comparing water consumption among the species combinations, we focused on a core measuring period in June/July 2012, i.e. in the second summer after the experiment's implementation. In this five-week period (May 29 – July 6) before plant harvest in July/August 2012, the weather conditions were sufficiently stable and saplings had shown height growth and the formation of additional leaves, which indicates that they had successfully adapted to the specific water regimes since July 2011.

Tree physiological measurements

Stomatal conductance (G_s, mmol m^{-2} s^{-1}), foliar carbon isotope signature ($\delta^{13}C$, ‰), and stem sapwood area-specific hydraulic conductivity (K_s, kg m^{-1} MPa^{-1} s^{-1}) was measured in selected plants of the five species in order to detect species differences and neighbor effects on the water loss regulation of target plants. During the core measuring period in June/July 2012, each six plants of the five species were investigated in monoculture and in 5-species mixture in the moist and dry treatment, yielding 120 plants (6 × 5 × 2 × 2). To avoid pseudo-replication, plants from different pots were investigated as replicates for a species. Measurements of G_s were conducted with an AP4 Porometer (Delta-T Devices Ltd, Cambridge, UK) on each two fully developed leaves per plant in the upper canopy. The leaves were tagged and measurements repeated on four occasions in June 2012 at midday during conditions of bright sky with non-fluctuating radiation climate. Two of the four measuring dates refer to the days immediately before an irrigation event; the two others were placed immediately after irrigation.

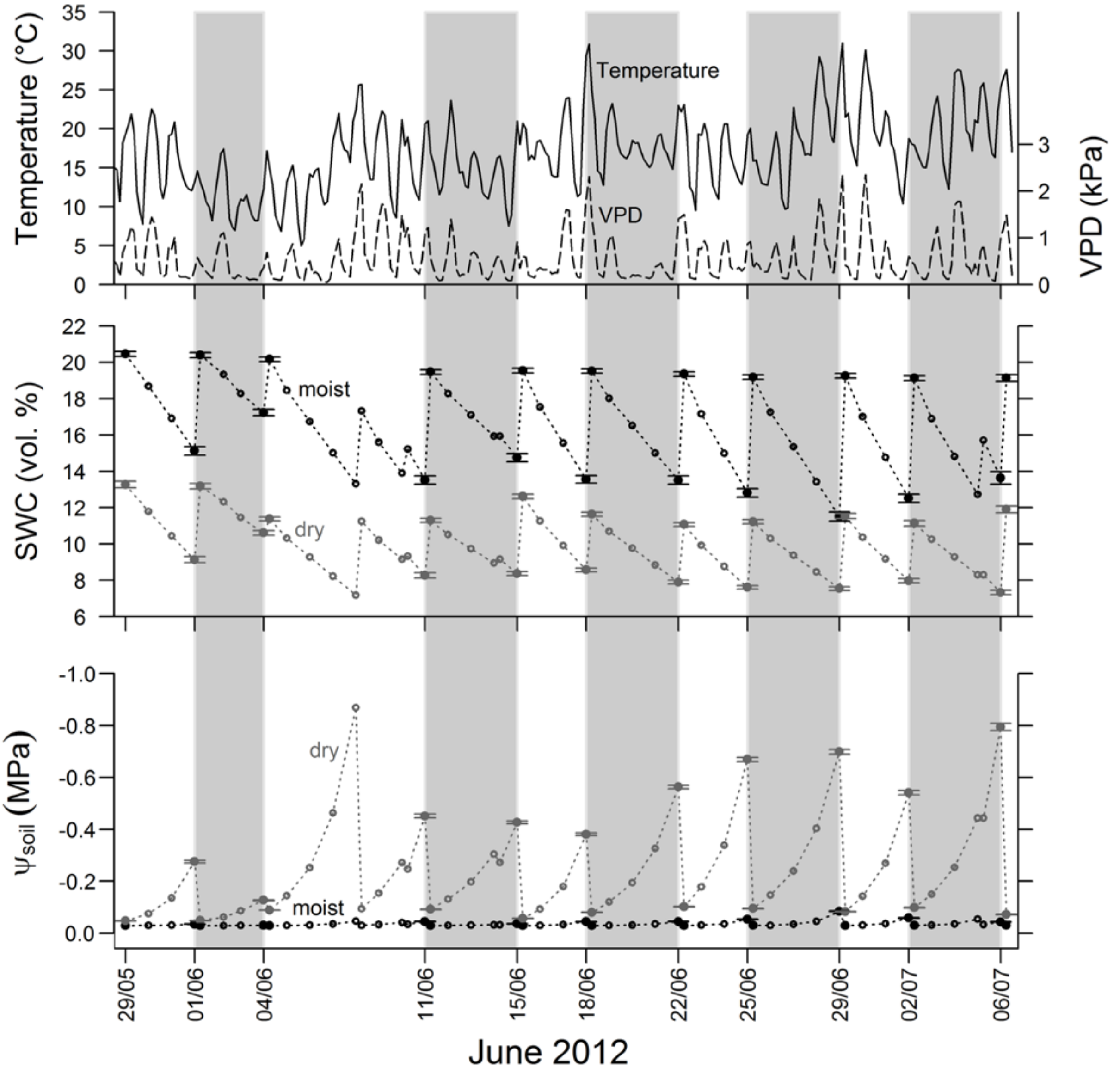

Figure 3.1. Air temperature and vapor pressure deficit (VPD) at the experimental site together with volumetric soil water content (SWC) and soil matrix potential (Ψ_{soil}) in the pots during the core measuring period from 29 May to 6 July 2012. Periods in grey indicate measuring intervals with soil surface sealing that were used to measure transpiration while excluding soil evaporation. Soil matrix potential was derived from soil water content using the soil moisture–matrix potential relationship according to LeachM, British Soil Service, Hutson and Wagenet (1992).

The same leaves were sampled at the date of harvest in July/August 2012 for carbon isotope analysis in the Center for Stable Isotope Research and Analysis, University of Göttingen, using an isotope mass ratio spectrometer (MAT Delta plus, Finnigan, Bremen, Germany). Axial hydraulic conductivity (K_h, kg m MPa^{-1} s^{-1}) was measured with a XYL'EM apparatus and the software XylWin 3.0 (Bronkhorst, Montigny-les-Cormeilles, France) according to Sperry et al. (1988) in the main shoot (segment length ca. 30 cm), which was harvested at the experiment's end in July/August 2012. Appending branches and twigs were cut off and lateral scars sealed with quick-drying glue (Loctite 431 and 7455, Henkel, Düsseldorf, Germany) to prevent water loss. Immediately after cutting, the basal end of the shoot was air-tightly connected to the XYL'EM apparatus and hydraulic conductivity measured at low pressure (6 kPa) with filtered (0.20 µm) and degassed water containing 10 mM KCl and 1 mM $CaCO_3$. Maximum hydraulic conductivity was obtained after embolism removal by iterative flushing at high pressure (120 kPa) for 10 min until constant values were reached. For determining stem cross-sectional area (A_{cross}) and the corresponding xylem cross-sectional area without pith and bark (A_{xylem}) of the basal part of the shoot segment, we digitized transversal cuts using a stereo-microscope (SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany) and analyzed the images with the software ImageJ (v1.44p, http://rsb.info.nih.gov/ij). Empirical sapwood area-specific hydraulic conductivity (K_s, kg m^{-1} MPa^{-1} s^{-1}) was calculated for the mean diameter of the shoot segment by dividing K_h by A_{xylem}, which was derived from the specific ratio $A_{cross} : A_{xylem}$.

Tree morphological analysis

All plants were harvested in a seven-week period in July and August 2012 in a rotating scheme with each one replicate pot of a treatment harvested every week, which guaranteed the same duration of the experimental treatment in all categories. Stem diameter at stem base was measured in two directions to calculate basal area (BA). The corresponding sapwood area (SA) at the stem base was extrapolated with the measured A_{cross}/A_{xylem} ratio from the stem segment that had been inspected microscopically. The specific leaf area (SLA, cm^2 g^{-1}) of fully expanded leaves in the upper crown was determined for all species in six selected treatment categories (3 different diversity levels in the moist and dry treatment) with each six plants from different pots investigated per category. At least ten leaves per tree (depending on species) were sampled by random and leaf area (LA) analyzed on a flatbed scanner using WinFolia 2005b software (Régent Instruments, Québec, Canada). The samples were subsequently oven-dried (70 °C, 72 h) and weighed. The mean SLA of a treatment was used for calculating plant leaf area from leaf dry mass. The water comsumption of the tree assemblages was found to be significantly affected by tree size as well as by water-use related morphological properties LA and SA (Fig. A1). To account for these size effects, daily transpiration rate was expressed per leaf area (T_{LA}) or sapwood area (T_{SA}) in the stem by dividing water loss per pot by the pot's total leaf area or cumulative sapwood area.

Statistical analysis

Statistical analyses were conducted with R software (version 3.0.0; R Foundation for Statistical Computing, Vienna, Austria). A significance level of $p<0.05$ was used in most tests; in a few cases, marginally significant results ($p<0.1$) are also reported. All data sets were tested for normal distribution (Shapiro–Wilk test) and homogeneity of variances (Levene's test). The grand means of a net diversity effect on stand transpiration were tested against zero using a one-sample t-test to examine whether they differed significantly from the weighted average transpiration of the monocultures. To test for treatment effects and possible interactions between soil moisture level and species composition or tree diversity on transpiration rate (parameters T, T_{LA}, or T_{SA}), we applied two-way analysis of variance (ANOVA). When testing for diversity effects, two-way ANOVA was adjusted (Type III sum of squares, *Anova (), car* package) to account for unbalanced data. Tukey contrasts (*glht* procedure, *multcomp* package) were used for multiple comparisons among different species combinations and diversity levels in the moist and dry treatment. Differences between the moist and dry treatments for the given species compositions or diversity levels were investigated with Student's t-test. Multiple comparisons among species or diversity levels of morphological or physiological parameters were conducted with one-way ANOVA followed by the Tukey contrasts procedure. Pairwise comparisons between the moist and dry treatments or the diversity levels (mono vs. mix5 category) were conducted with Student's t-test, Welch's t-test or Mann-Whitney U-test depending on the structure of the data.

Data from this investigation are publically available in the Plant Trait Database (TRY)<www.try-db.org/TryWeb/Data.php#8;>

Results

Weather and soil moisture conditions

In the core measuring period (May 29 to July 6, 2012), daily air temperature means varied between 9.5 and 22.8 °C with an absolute maximum of 31.7 °C at the end of June (Fig. 3.1.: upper panel). Daily maximal vapor pressure deficit ranged between 0.21 kPa and 2.54 kPa and reached peak values > 1.5 kPa during ten days. Volumetric soil water content (SWC) typically fluctuated between 13.0 and 20.5% in the pots of the moist treatment and between 7.2 and 13.3% in the dry treatment with minima recorded before and maxima after irrigation events (Fig. 3.1.: central panel). Soil matrix potential (Ψ_{soil}) minima were calculated as -0.08 MPa in the moist and -0.86 MPa in the dry treatment immediately before irrigation events (Fig. 3.1.: lower panel).

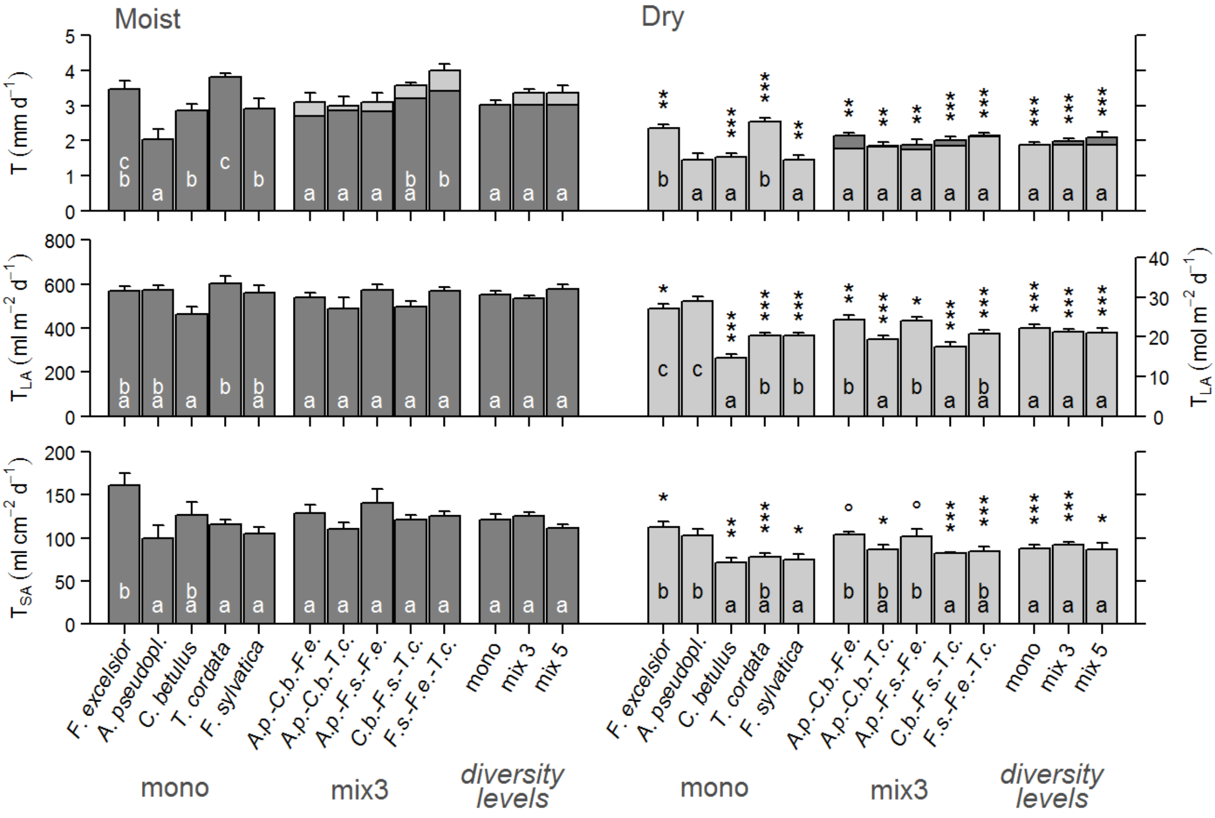

Figure 3.2. Transpiration rate per pot (T, top) and transpiration rate normalized to leaf area (T_{LA}, middle) or to cumulative sapwood area (T_{SA}, bottom) in the five monospecific culture types (first group), the five 3-species mixtures (second group), and the averages of the 1-species, 3-species and the 5-species combinations (third group) in the moist (left part of Fig.) and dry treatment (right part of Fig.). The unit of T (mm d^{-1}) is equivalent to l m^{-2} d^{-1}; the small light or dark tops of the bars display the fraction of stand transpiration assignable to a net biodiversity effects in that mixture. T_{LA} is given in ml m^{-2} s^{-1} (left y axis) or, for convenience, in mol m^{-2} d^{-1} (right y axis) for both the moist and dry treatments. Different small letters indicate significant differences at $p<0.05$ between the species combinations or diversity levels in a group. Asterisks indicate significant differences between soil moisture treatments at the levels:°: $p<0.1$, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$.

Stand-level water consumption: species diversity effects

In the five-week core measuring period, stand-level (pot-level) transpiration means (T; five plants each) ranged between 0.54 and 1.06 L d^{-1} in the moist treatment (expressed per pot surface area: means of 2.04 – 3.99 mm d^{-1}). A significant net diversity effect was found for the moist treatment (grand mean tested against zero: t = 4.98, p<0.01). The transpiration rate increased on average from the monocultures to the 3-species mixtures by 11.0% and to the 5-species mixture by 11.8%. However, the transpiration means of the three diversity levels (3.02, 3.35 and 3.37 mm d^{-1}; Fig. 3.2.) were not significantly different at $p<0.05$ (ANOVA). Transpiration normalized to leaf area (T_{LA}; given as mL m^{-2} d^{-1} which is equivalent to 10^{-3} mm d^{-1}; for convenience, fluxes in mol m^{-2} d^{-1} are also given) was also not significantly different between the three diversity levels (moist treatment: 534 – 576 mL m^{-2} d^{-1}, i.e. 29.6 – 32.0 mol m^{-2} d^{-1}; Fig. 3.2.: center panel).

Table 3.2. Summary of results of two-way ANOVAs testing for effects of the moisture treatment (moist versus dry) and species composition or diversity level and their interaction on three transpiration parameters. The ANOVAs were calculated for different samples (group of comparison: all species combinations, only monocultures, only 3-species mixtures, and data pooled at the diversity level). Transpiration is given per pot surface area (T), per leaf area (TLA) and per sapwood area (TSA). Significance levels: *: p<0.05, **: p<0.01, ***: p<0.001.

		Moisture treatment			Species composition			Interaction		
Group of comparison	Transpiration	*Df*	*F*	Signif.	*Df*	*F*	Signif.	*Df*	*F*	Signif.
Diversity levels (3)	T	1,148	73.51	***	2,147	0.52		2,144	0.45	
	T_{LA}		51.63	***		0.49			0.47	
	T_{SA}		19.20	***		0.65			1.09	
All species compositions (11)	T	1,148	241.23	***	10,139	10.31	***	10,128	1.50	
	T_{LA}		212.55	***		9.21	***		2.74	**
	T_{SA}		71.87	***		4.71	***		1.60	
Monoculture types (5)	T	1,68	92.29	***	4,65	19.18	***	4,60	1.63	
	T_{LA}		94.89	***		16.70	***		5.49	***
	T_{SA}		28.84	***		7.12	***		2.76	*
3-species mixture types (5)	T	1,63	125.13	***	4,60	4.19	**	4,55	1.80	
	T_{LA}		81.77	***		5.17	**		0.91	
	T_{SA}		38.05	***		2.70	*		0.52	

In the dry treatment, average transpiration rate (T) was reduced to 59-62% of the corresponding water loss in the moist treatment (means of 0.39 – 0.67 L d^{-1}, equivalent to 1.46 – 3.54 mm d^{-1} per pot surface area). A significant net diversity effect on T existed (grand mean: t = 2.48, p<0.05) with average increases to the 3-species and the 5-species mixtures by

6.8 and 11.6%, respectively, but the differences between the group means again were not significant. One-, 3- and 5-species pots showed very similar reductions of leaf area-specific transpiration in the dry treatment (to 401, 382 and 379 mL m^{-2} d^{-1} or 21.0 – 22.3 mol m^{-2} d^{-1}, Fig. 3.2.: right part) with no diversity effect in the degree of reduction.

Two-way ANOVA with transpiration rate (three different parameters) as dependent and moisture treatment, species composition, and the interaction of moisture treatment × species composition as independent variables revealed a highly significant effect of moisture treatment (moist vs. dry) and a less influential effect of species composition on water consumption. Species composition effects were detected when different sets of combinations were pooled (all 11 combinations, all monocultures, or all 3-species combinations) but not when the three diversity levels were compared indicating that species identity, but not diversity, influenced water consumption. Significant interaction effects (moisture treatment × species composition) were detected mainly in case of T_{LA} as dependent variable (Table 3.2.).

Stand-level water consumption: species identity effects

The monocultures of *T. cordata* and *F. excelsior* had the highest, those of *F. sylvatica* and *C. betulus* intermediate, and that of *A. pseudoplatanus* the lowest T means in the moist treatment (Fig. 3.2.). The five investigated 3-species combinations differed by up to 25% in T in the moist treatment. A particularly high transpiration rate was recorded for the *Fagus-Fraxinus-Tilia* mixture (3.99 mm d^{-1}) which differed significantly from most of the other mixtures and represented the highest degree of 'overyielding' in terms of water consumption (by 0.58 mm d^{-1}, i.e. +17.0% deviation from the expected T; Fig. 3.2.: upper panel). In contrast, the diversity effect was rather small for the *Acer-Carpinus-Tilia* mixture (+3.7% overyielding).

In the dry treatment, the species ranking was comparable to the moist monocultures with *F. sylvatica, C. betulus* and *A. pseudoplatanus* reaching relatively low T means. The five 3-species mixtures had more similar T means that differed by not more than 15% among the different species combinations (Fig. 3.2.). However, the deviation from the expected water consumption was large in the *Acer-Carpinus-Fraxinus* mixture (+20.9% overyielding) while it was negligible in the *Acer-Carpinus-Tilia* (-1.3%) and *Fagus-Fraxinus-Tilia* mixtures (+0.7%).

Stand-level water consumption scaled to leaf area and sapwood area

Transpiration scaled to leaf area (T_{LA}) differed less between the species in the monospecific pots than transpiration per ground area (T), but a broadly similar species ranking appeared (*T. cordata* > *F. excelsior, A. pseudoplatanus, F. sylvatica* > *C. betulus*; Fig 3.2.: left part). *T. cordata* (higher) and *C. betulus* (lower) differed significantly in their T_{LA} means in the moist treatment. In contrast to stand-level transpiration (T), T_{LA} was not significantly different between the five 3-species combinations in the moist treatment (489 – 574 mL m^{-2} d^{-1}; Fig. 3.2.: left part).

Table 3.3. Species differences in six morphological or physiological traits (sapwood area-specific hydraulic conductivity of the stem, K_s; stomatal conductance of sun leaves, G_s; carbon isotope ratio of sun leaf mass, $\delta^{13}C$; total leaf area, LA; sapwood area in the stem, SA; Huber value (ratio LA : SA)) of the five species (means ± SE over all species combinations) in the moist and dry treatments. Different capital letters indicate significant ($p<0.05$) differences between the species, asterisks significant differences between the species in the moist and dry treatment at:° : $p<0.10$, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$.

	Sample size [n]		K_s [kg m^{-1} MPa^{-1} s^{-1}]		G_s [mmol m^{-2} s^{-1}]		$\delta^{13}C$ [‰]	
Species	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry
F. excelsior	12	12	2.28 ± 0.33 BC	1.97 ± 0.25 B	254.00 ± 14.50 AB	189.90 ± 10.30 C**	-28.09 ± 0.20 AB	-25.99 ± 0.24 A***
A. pseudopl.	12	12	1.04 ± 0.13 A	0.72 ± 0.08 A°	277.70 ± 12.60 B	205.10 ± 18.40 BC*	-27.56 ± 0.16 A	-26.77 ± 0.20 A*
C. betulus	12	12	1.25 ± 0.12 AB	0.87 ± 0.09 A*	201.90 ± 12.90 A	94.90 ± 8.10 A***	-29.25 ± 0.12 C	-28.23 ± 0.21 B**
T.cordata	12	12	1.92 ± 0.20 BC	1.79 ± 0.22 B	240.80 ± 14.60 AB	165.10 ± 22.30 BC**	-29.31 ± 0.25 BC	-28.37 ± 0.21 B*
F.sylvatica	12	12	2.13 ± 0.17 C	1.61 ± 0.14 B*	253.60 ± 15.50 AB	148.40 ± 9.50 B***	-28.69 ± 0.14 BC	-28.17 ± 0.16 B
	Sample size [n]		LA [m^2]		SA [cm^2]		Huber value [m^2 cm^{-2}]	
Species	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry
F. excelsior	35	32	0.39 ± 0.03 B	0.31 ± 0.03 B*	1.77 ± 0.13 C	1.27 ± 0.07 C***	0.22 ± 0.01 AB	0.24 ± 0.01 AB
A. pseudopl.	36	32	0.17 ± 0.02 A	0.16 ± 0.02 A	0.86 ± 0.05 A	0.72 ± 0.05 A*	0.20 ± 0.01 A	0.22 ± 0.01 AB
C. betulus	34	32	0.35 ± 0.02 B	0.33 ± 0.02 BC	1.33 ± 0.07 B	1.19 ± 0.06 C	0.26 ± 0.01 B	0.27 ± 0.01 B
T.cordata	36	31	0.54 ± 0.03 C	0.42 ± 0.03 C**	2.51 ± 0.13 D	1.81 ± 0.09 D***	0.21 ± 0.01 A	0.22 ± 0.01 A
F.sylvatica	35	31	0.21 ± 0.01 A	0.20 ± 0.01 A	1.03 ± 0.05 A	0.90 ± 0.04 B	0.20 ± 0.01 A	0.21 ± 0.01 A

In the dry treatment, the species ranking was partly reversed due to strong transpiration reductions in *T. cordata, C. betulus* and *F. sylvatica* but only weak responses in *A. pseudoplatanus* and *F. excelsior*, leading to a ranking regarding T_{LA} in the sequence *A. pseudoplatanus* > *F. excelsior* > *T. cordata, F. sylvatica* > *C. betulus* (Fig. 3.2.: right part). The significant interaction between the variables 'species composition' and 'moisture treatment' in the two-way ANOVA ($F_{(4,60)}$ = 5.49, $p<0.001$) for the monocultures reflects these species differences in transpiration reduction upon soil desiccation (Table 3.2.). The two 3-species mixtures, in which both *A. pseudoplatanus* and *F. excelsior* were present, had significantly higher leaf area-specific water losses than the other three combinations. These species reduced transpiration only little in the monocultures and also in the mixtures. Lowest

T_{LA} rates in dry soil were measured in the only mixture (*Carpinus-Fagus-Tilia)* where *A. pseudoplatanus* and *F. excelsior* were absent (Fig. 3.2.: right part).

Transpiration scaled to sapwood area (T_{SA}) was for both soil moisture treatments highest in ring-porous *F. excelsior* with significant differences to *A. pseudoplatanus, F. sylvatica* and *T. cordata* (moist treatment) and to *C. betulus* and *F. sylvatica* (dry treatment) (Fig. 3.2.). The drought-induced reduction in T_{SA} differed markedly among the species and was most pronounced in *T. cordata* but lacking in *A. pseudoplatanus*. The contrasting species ranking in the moist and dry treatments with respect to T_{SA} is reflected by the significant interaction term 'species composition' × 'moisture treatment' in the two-way ANOVA ($F_{(4,60)} = 2.76$, $p = 0.03$; Table 3.2.).

Table 3.4. Total leaf area (LA), stem sapwood area (SA) and Huber value (ratio between LA and SA) of plants of the five species grown either in monoculture (mono), 3-species mixture (mix3) or 5-species mixture (mix5) in the moist and dry treatments (means ± SE of n replicate pots). Different small letters indicate significant ($p < 0.05$) differences between the plants in 1-species, 3-species or 5-species combinations of a species.

		Sample size [n]		LA [m^2]		SA [cm^2]		Huber value [m^2 cm^{-2}]	
Species	Diversity level	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry
F. excelsior	mono	7	7	0.34 ± 0.04 ab	0.25 ± 0.01 a	1.37 ± 0.14 a	1.17 ± 0.11 a	0.25 ± 0.02 a	0.23 ± 0.02 a
	mix3	21	18	0.44 ± 0.05 b	0.33 ± 0.04 a	2.00 ± 0.19 b	1.29 ± 0.09 a	0.22 ± 0.02 a	0.25 ± 0.02 a
	mix5	7	7	0.27 ± 0.05 a	0.29 ± 0.04 a	1.49 ± 0.21 ab	1.34 ± 0.22 a	0.18 ± 0.02 a	0.23 ± 0.03 a
A. pseudopl.	mono	7	7	0.19 ± 0.02 a	0.15 ± 0.02 a	0.91 ± 0.10 a	0.69 ± 0.08 a	0.21 ± 0.01 a	0.21 ± 0.01 a
	mix3	21	18	0.18 ± 0.02 a	0.16 ± 0.02 a	0.85 ± 0.07 a	0.71 ± 0.07 a	0.21 ± 0.01 a	0.22 ± 0.01 a
	mix5	8	7	0.14 ± 0.02 a	0.18 ± 0.04 a	0.86 ± 0.09 a	0.79 ± 0.15 a	0.17 ± 0.01 a	0.22 ± 0.01 a
C. betulus	mono	7	7	0.33 ± 0.02 a	0.31 ± 0.01 a	1.28 ± 0.08 a	1.08 ± 0.04 a	0.25 ± 0.01 a	0.28 ± 0.01 a
	mix3	20	18	0.34 ± 0.03 a	0.33 ± 0.04 a	1.25 ± 0.09 a	1.24 ± 0.11 a	0.26 ± 0.01 a	0.26 ± 0.01 a
	mix5	7	7	0.40 ± 0.06 a	0.37 ± 0.03 a	1.59 ± 0.19 a	1.18 ± 0.09 a	0.26 ± 0.03 a	0.32 ± 0.02 a
T.cordata	mono	7	7	0.34 ± 0.02 a	0.37 ± 0.01 a	1.98 ± 0.07 a	1.68 ± 0.07 a	0.17 ± 0.01 a	0.22 ± 0.01 a
	mix3	21	17	0.58 ± 0.04 b	0.45 ± 0.05 a	2.58 ± 0.19 b	1.87 ± 0.15 a	0.22 ± 0.02 ab	0.24 ± 0.01 a
	mix5	8	7	0.61 ± 0.04 b	0.41 ± 0.05 a	2.77 ± 0.24 b	1.81 ± 0.15 a	0.23 ± 0.01 b	0.23 ± 0.02 a
F.sylvatica	mono	7	7	0.28 ± 0.03 b	0.21 ± 0.02 a	1.25 ± 0.10 b	1.00 ± 0.04 b	0.22 ± 0.02 a	0.21 ± 0.02 a
	mix3	20	17	0.19 ± 0.01 a	0.20 ± 0.01 a	0.92 ± 0.05 a	0.82 ± 0.04 a	0.20 ± 0.01 a	0.24 ± 0.01 a
	mix5	8	7	0.21 ± 0.03 ab	0.19 ± 0.02 a	1.12 ± 0.14 ab	0.99 ± 0.10 ab	0.19 ± 0.02 a	0.20 ± 0.02 a

Stand-level transpiration as influenced by leaf and sapwood area

Due to different inherent growth rates, the five species developed different leaf areas during the 16-month period between planting and harvest. In general, *T. cordata* had a larger total leaf area per plant than *C. betulus* and *F. excelsior. A. pseudoplatanus* and *F. sylvatica* developed the smallest leaf areas with less than half of that of *T. cordata* (Table 3.2.). Corresponding to the leaf area differences, the five species showed considerable differences in sapwood area in the stem xylem (SA, cm^2) with highest SA values in *T. cordata*, intermediate ones in *F. excelsior* and *C. betulus,* and lowest values in *F. sylvatica* and *A. pseudoplatanus*

(Table 3.2.). This species sequence existed also in the dry treatment but SA was by 10-20% smaller (Table 3.3.). The Huber value (plant leaf area per stem sapwood area; unit: m^2 cm^{-2}) was similar among the species (most values between 0.20 and 0.27 m^2 cm^{-2}) except for a higher mean in *C. betulus* (Table 3.3.). Upon soil desiccation, the ratio was not significantly altered.

Stand-level transpiration as influenced by leaf conductance and stem hydraulic conductivity

In the moist treatment, measurements of stomatal conductance (G_s) showed highest species means for *A. pseudoplatanus* and lowest for *C. betulus* (difference significant; Table 3.3.). In the dry treatment, G_s was particularly high in *A. pseudoplatanus* and *F. excelsior* and low in *C. betulus* (difference significant). This pattern matches the species ranking with respect to the drought-induced reduction in leaf conductance (largest reduction in *C. betulus*: -53%, smallest reduction in *A. pseudoplatanus*: -26%). All species showed less negative $\delta^{13}C$ values of sun leaf mass in the dry than in the moist treatment (significant in all species except for *F. sylvatica*) reflecting the significant reduction in leaf conductance (Table 3.3.). Empirically determined hydraulic conductivity in the stem xylem (K_s) was in general lower in the dry than in the moist treatment (difference significant in three species).

Performance of target species in pure and mixed stands: neighbor effects on leaf area, hydraulics and water consumption

In the moist treatment, leaf area (LA), sapwood area (SA) and Huber value were significantly higher in *T. cordata* plants grown in mixture than in monoculture. *F. excelsior* exhibited greater LA in the 3-species mixtures than in the 5-species mixture and larger SA in the 3-species mixtures than in the monoculture. In contrast, the *F. sylvatica* plants achieved higher LA and SA in monoculture than in the 3-species mixtures (Table 3.4.).

Stomatal conductance (G_s) tended to be higher for all species in the 5-species mixtures than in the monocultures in the moist treatment, but differences were not significant. In the dry treatment, G_s of *F. excelsior* was significantly higher in mixture than in monoculture (Table 5), which was also observed when pooled across both water levels ($p<0.05$). This trend was also reflected in the $\delta^{13}C$ signatures with a significantly lower mean in *F. excelsior* (moist and dry treatment) and *F. sylvatica* (dry treatment) grown in 5-species mixture as compared to monoculture (Table 3.5.). A similar tendency existed also for *C. betulus* in the dry treatment.

For *C. betulus*, we also measured significantly higher K_S in 5-species mixture than in monoculture in the dry treatment, but the opposite relation in the moist treatment (Table 3.5.). A similar pattern was observed for *F. excelsior* in the moist treatment were K_S increased marginally significantly in mixture; this tendency was significant when both moisture treatments were pooled ($p<0.05$).

Table 3.5. Three traits related to hydraulics and water consumption (sapwood area-specific hydraulic conductivity of the stem, K_S; stomatal conductance of sun leaves, G_S; carbon isotope ratio of sun leaf mass, $\delta^{13}C$) of plants of the five species either growing in monoculture (mono) or in 5-species mixture (mix5) in the moist and dry treatments (means ± SE of n replicate pots). Different small letters indicate significant ($p<0.05$) differences between the plants in monoculture or mixture of a species.

		Sample size [n]		K_s [kg m^{-1} MPa^{-1} s^{-1}]		G_s [mmol m^{-2} s^{-1}]		$\delta^{13}C$ [‰]	
Species	Diversity level	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry
F. excelsior	mono	6	6	1.70 ± 0.47 a	1.73 ± 0.12 a	221.60 ± 20.10 a	167.30 ± 13.70 a	-27.49 ± 0.18 a	-25.61 ± 0.32 a
	mix5	6	6	2.86 ± 0.36 a	2.18 ± 0.44 a	286.30 ± 28.10 a	212.50 ± 8.40 b	-28.67 ± 0.59 b	-26.37 ± 0.30 b
A. pseudopl.	mono	6	6	0.99 ± 0.18 a	0.77 ± 0.11 a	270.60 ± 22.10 a	238.50 ± 30.00 a	-27.59 ± 0.38 a	-26.74 ± 0.31 a
	mix5	6	6	1.11 ± 0.22 a	0.67 ± 0.12 a	284.80 ± 34.70 a	171.60 ± 12.20 a	-27.53 ± 0.28 a	-26.79 ± 0.26 a
C. betulus	mono	6	6	1.51 ± 0.17 b	0.69 ± 0.09 a	197.50 ± 12.60 a	84.60 ± 11.30 a	-29.19 ± 0.16 a	-27.91 ± 0.18 a
	mix5	6	6	0.99 ± 0.11 a	1.06 ± 0.11 b	206.30 ± 27.80 a	105.20 ± 10.90 a	-29.31 ± 0.25 a	-28.54 ± 0.24 a
T.cordata	mono	6	6	2.03 ± 0.26 a	2.28 ± 0.37 a	241.30 ± 18.60 a	179.80 ± 37.20 a	-29.25 ± 0.54 a	-28.60 ± 0.35 a
	mix5	6	6	1.79 ± 0.33 a	1.38 ± 0.15 a	252.30 ± 30.20 a	150.40 ± 26.90 a	-29.36 ± 0.50 a	-28.14 ± 0.24 a
F.sylvatica	mono	6	6	2.27 ± 0.25 a	1.67 ± 0.18 a	228.80 ± 29.20 a	140.80 ± 15.30 a	-28.49 ± 0.41 a	-27.82 ± 0.17 a
	mix5	6	6	1.95 ± 0.22 a	1.54 ± 0.24 a	278.40 ± 18.60 a	156.00 ± 11.90 a	-28.89 ± 0.29 a	-28.52 ± 0.15 b

Discussion

Diversity effects on stand-level water consumption

We observed a significant net biodiversity effect on water consumption across all mixtures for the moist treatment in support of our first hypothesis, but the effect size was small. Transpiration per pot surface area (T) was on average ~11% higher in the 3- and 5-species mixtures than in the monocultures. The transpiration increase most likely bases on a selection effect, because (i) the species' transpiration rates differed considerably in the monocultures, and (ii) the presence of intensively transpiring species (*T. cordata* and *F. excelsior)* was directly linked to large positive deviations in T from the expected value ('overyielding') in the mixtures. The 3-species mixture containing *T. cordata* and *F. excelsior* transpired even more than the 5-species mixtures, in which both species were diluted by others. In monoculture, the saplings of *T. cordata* and *F. excelsior* developed together with *C. betulus* the largest leaf areas (and sapwood areas) of all species within 16 months after planting. *T. cordata* also showed the highest leaf area-specific transpiration rate. Further, the presence of heterospecific neighbors tended to increase the leaf and sapwood areas of these species. Thus, the relevance of selection effects for the water consumption of the mixtures is striking. Complementary water use in the mixtures may also have taken place, but our design did not allow for a quantitative separation between selection and complementarity effects in the sense of Loreau and Hector (2001). In our experiment, complementarity in water uptake is less likely due to the defined volume of the pots, while some stratification of the crowns, and thus complementarity in space occupation, of different species was observed in the mixtures, which may have resulted in enhanced transpiration.

Our findings partly agree with results obtained in other diversity experiments or observational studies, in which mixed stands showed enhanced stand transpiration (Forrester et al. 2010, Kunert et al. 2012). It appears that enhanced stand transpiration was mostly driven by a selection effect when soil water was not limiting (as in the studies of Gebauer et al. 2012 and in this study), while complementarity effects on stand transpiration were visible in the studies of Forrester et al. (2010) and Kunert et al. (2012) with influence of summer drought. Apart from the significant though minor diversity effect on water consumption, species identity was the main factor responsible for the considerable variation in T among the different species combinations. Matching results were obtained with sap flux measurements in a mature stand of the same species in the Hainich forest (Gebauer et al. 2012) and in a boreal tree plantation (Grossiord et al. 2013). Such species effects on stand transpiration are not surprising given the well-known species differences in transpiration rate among temperate tree species (e.g. Lyr et al. 1992).

Does drought enhance positive diversity effects?

The net diversity effect on stand-level water consumption was slightly smaller in the dry than in the moist treatment (T increased on average by ~8% from the monocultures to the mixtures compared to an 11%-increase in the moist treatment). Even though the mixtures depleted the soil moisture reserves on average more rigorously than the monocultures, we did not find the expected stronger ‘overyielding’ in the dry as compared to the moist treatment. While *C. betulus, F. excelsior* and *T. cordata* indeed tended to slightly increase their leaf and/or sapwood areas in the mixtures compared to the monocultures, overyielding in T was the exception under dry conditions and occurred markedly only in the *Acer-Carpinus-Fraxinus* mixture and the 5-species mixture. Our results do not support hypothesis (ii) because the assumed positive effect of diversity on water consumption was generally not higher under dry conditions. A possible explanation could be that in agreement with Forrester et al. (2013) canopy interactions including complementarity for space and light use were less important under dry conditions. This is indicated by generally smaller leaf areas in comparison to the moist treatment. On the other hand, we found some indication that a net diversity effect may be larger under dry than under moist conditions in certain species constellations (e.g. in the *Acer-Carpinus-Fraxinus* mixture). This observation together with the findings of Forrester et al. (2010) and Kunert et al. (2012) suggest that positive effects of diversity on water consumption occur under water-limited conditions but that species identity and thus functional traits and their differentiation between species are the important drivers of such an effect.

The dominant influence of species identity on T is indeed not only effective under moist but also under dry conditions. The species effects were closely related to the presence of *F. excelsior* and *T. cordata* in the mixtures; both species maintained relatively large leaf areas and/or high leaf conductance under dry conditions in the experiment. This matches the sap flux data of Gebauer et al. (2012) in the mature forest, where *T. cordata* had a particularly high water consumption early in a dry period leading to drier soil and reduced transpiration in the mixed stand later in summer. The coupling between higher productivity and greater resource depletion, which ultimately feeds back on stand vitality, can be viewed as manifestation of the ‘tragedy of the commons’ hypothesis with respect to water consumption. Similar negative effects of diversity have also been observed in other hydrological studies (e.g. Forrester et al. 2010, Kunert et al. 2012). In our experiment, we avoided soil water over-exploitation in pots with higher water consumption by carefully adding water to achieve similar soil moisture conditions across all species combinations. Such a design favors water spending assemblages to a certain degree, but it is inevitable when a homogenous drought regime shall be established across all species combinations in the dry treatment.

By considering the reduction in stand-level transpiration from the moist to the dry treatment, we tested the third hypothesis that more diverse stands reduce leaf area-specific transpiration (T_{LA}) on average to a smaller extent than monospecific stands, because less sensitive species may achieve larger leaf areas in mixtures. Our results do not support this hypothesis by showing that the 5-species mixture reduced T_{LA} more rigorously in both relative (-34%) and absolute terms (-197 mL m^{-2} d^{-1}) than the monocultures (mean of five species: -27%, -152 mL m^{-2} d^{-1}) and 3-species mixtures (mean of five combinations: -28%, -152 mL m^{-2} d^{-1}). The five different 3-species mixtures differed substantially in their relative transpiration reduction (-19 to -37%) with largest reduction found in the mixtures that contained *T. cordata* and *F. sylvatica*, the two species with largest transpiration reduction in monoculture (besides *C. betulus*). Thus, species identity largely determined the extent of transpiration reduction in the tree assemblages. *T. cordata* with high water consumption in moist soil and apparent drought-sensitive stomatal regulation was most likely the main cause of the relatively rigid down-regulation of water loss in mixtures containing this species, while 3-species mixtures with *A. pseudoplatanus* (which reduced T_{LA} only minimally) represented species combinations with relatively small transpiration reduction. Corresponding to the T_{LA} reduction, leaf conductance showed a higher average reduction upon drought in the 5-species mixture (-38%) than in the monocultures (-30%).

Our results on species differences in transpiration reduction do principally match observations on the drought sensitivity of the five species obtained from ecophysiological measurements in adult trees (Köcher et al. 2009). When applied to short time horizons (weeks to months), the diversity – community resistance hypothesis (Yachi & Loreau 1999) is not supported by our data. Over longer time spans (decades to centuries), species-richer forests might well be more resistant to drought, if the species sample includes trees with better drought adaptation that may replace more drought-sensitive species. On the other hand, higher diversity could also lead to the opposite effect, higher susceptibility of the community to drought, if water consumption is enhanced by species diversity (Grossiord et al. 2014b).

Does species mixing influence the water consumption and hydraulics of target trees?

We found some evidence in support of hypothesis (iv) that heterospecific neighbors with higher or lower water consumption than a target species seem to influence the water flux regulation of trees of that species through alterations in plant leaf area, leaf conductance and the stem hydraulic system. We observed the most consistent species-specific response to heterospecific neighbors in the mixtures for *T. cordata* that significantly increased its plant leaf area (from 0.34 to 0.61 m^2), sapwood area (from 1.98 to 2.77 cm^2) and Huber value (from 0.17 to 0.23 $m^2\ cm^{-2}$) from plants grown in monoculture to those grown in the 5-species mixture (moist treatment); sapwood area-specific conductivity (K_s) and leaf conductance (G_s) were not altered in this species. A different response to heterospecific neighbors was observed in *F. excelsior*, which increased G_s (mirrored in significantly reduced $\delta^{13}C$ values) and tended to increase K_s in the 5-species mixture compared to monoculture; this species did not modify its leaf and sapwood area in a consistent manner. Due to their relatively high transpiration rates, *T. cordata* and also *F. excelsior* must have profited from the presence of neighbors with lower water consumption such as *C. betulus* and *A. pseudoplatanus*. Most likely, *T. cordata* responded to an improved plant water status with extension of its leaf area which required a larger sapwood area. *F. excelsior* may also have profited from neighbors with more conservative water use because it increased leaf and xylem conductance and consumed more water, which probably was associated with higher carbon gain. In contrast to *T. cordata*, leaf area showed no consistent increase in *F. excelsior*. A species that may have suffered from heterospecific neighbors compared to monoculture growth in terms of leaf area and hydraulic properties enhancing water consumption was *F. sylvatica*. In the moist treatment, beech plants in 5-species mixture had a smaller leaf area and sapwood area than plants in monoculture which fits to the increase in leaf area and/or leaf conductance in *T. cordata* and *F. excelsior* in the same mixture, pointing to asymmetric competition in favor of the latter species.

Our findings about neighborhood effects on the physiology of target species in mixtures match dendrochronological results obtained in the Hainich mixed forest where a target species (*F. sylvatica*) profited in its mean growth rate and susceptibility to drought events from the presence of certain heterospecific neighbors in comparison to growth with conspecific neighbors (Mölder et al. 2011, Mölder and Leuschner 2014).

Conclusions

A main result of our experiment is that diversity effects on stand transpiration are relatively weak in these assemblages and transgressive overyielding in terms of water consumption occurs only as an exception. Several results suggest that species identity effects, i.e. inherent differences in the species' water consumption and drought tolerance, are more important drivers than complementary water use and facilitation. Moreover, the diversity effect on water consumption was not principally different between conditions of ample and limited water supply. Rather, diversity effects tended to be more influential under favorable than unfavorable moisture conditions, which contrasts with several earlier findings (e.g. Vilà et al. 2007, Río et al. 2013, Pretzsch et al. 2013). The observed significant modification in morphology, physiology and water consumption in response to specific neighborhood conditions is a clear sign that neighbor effects are an important structuring force in mixed stands and deserve more attention.

No doubt, pot experiments with saplings lack the realism of observational studies in old-growth forests along diversity gradients and do not allow conclusions on the performance of larger trees as they may be possible from diversity experiments with planted trees. However, a main strength of our study is the relatively precise measurement of transpiration and the good control of soil moisture, which is often not possible in drought experiments in the field. In addition, plant morphology and physiology could be recorded in a more comprehensive way than is possible in large-scale tree diversity experiments. Our experiment has the additional advantage that the findings can be compared to results obtained from comparative hydrological measurements in an old-growth forest varying in tree diversity. The three main findings (only small diversity effect on water consumption; greater importance of species identity effects; importance and direction of neighbor effects on water consumption) agree with the field results, which is support for our main conclusions.

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Appendix

Table A. 3.1. Some functional traits of the five investigated tree species after Ellenberg and Leuschner (2010)[1], Köcher et al. (2009)[2] and others. Shade intensity – reduction of light transmissivity by adult trees.

Species	*F. excelsior*	*A. pseudoplatanus*	*C. betulus*	*T.cordata*	*F.sylvatica*
Family	Oleaceae	Aceraceae	Betulaceae	Tiliaceae	Fagaceae
Successional status [1]	Early/mid	Mid/Late	Mid/late	Mid/late	Late
Drought tolerance [2]	High	Mid/low	Mid	Mid	Low
Shade intensity	moderate	high	high	high	very high
Xylem anatomy	Ring	Diffuse	Diffuse	Diffuse	Diffuse
Type of mycorriza	Arbuscular	Arbuscular	Ekto	Ekto	Ekto

Table A. 3.2. Chemical properties of the soil used in the pots. CEC – cation exchange capacity. Presin – resin-exchangeable phosphorus

Variable	Mean ± SE
pH(H_2O)	7.527 ± 0.052
pH(KCl)	6.710 ± 0.054
C_{tot} (g kg^{-1} dw)	0.991 ± 0.080
N_{tot} (g kg^{-1} dw)	0.021 ± 0.006
C/N_{org} (g g^{-1})	2.931 ± 0.204
P_{resin} (g kg^{-1} dw)	0.022 ± 0.004
CEC (mmol kg^{-1} dw)	44.645 ± 1.142
Base saturation (%)	99.936 ± 0.036

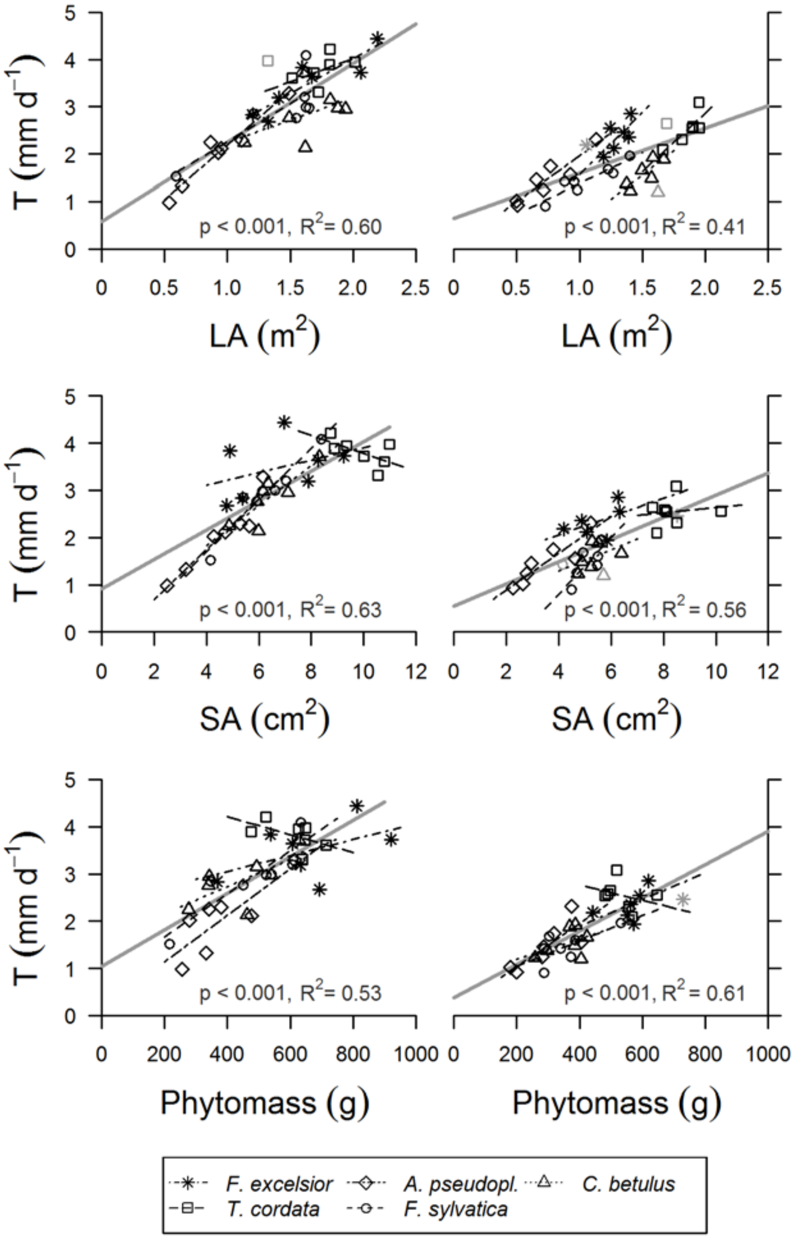

Figure A. 3.1. Relationships between gravimetrically-determined transpiration rate of the pots (all five plants) and (a) cumulative leaf area LA (upper panels), (b) cumulative sapwood area SA (central panels) and (c) total phytomass (lower panels) of the monospecific pots of the five species for the moist (left) and dry treatment (right). Note the reduced transpiration of the dry treatments. Given are the p- and R^2 values for the pooled data (all species). The p-values (first number) and R^2 values (second number) for the five species are as follows: LA – F.e: 0.007, 0.79, A.p.: <0.001, 0.94, C.b.: 0.28, 0.23; T.c.: 0.28, 0.28, F.s.: 0.02, 0.69; SA – F.e.: 0.39, 0.15, A.p.: 0.001, 0.90, C.b.: 0.02, 0.71, T.c.: 0.16, 0.36, F.s.: 0.001, 0.92; Phytomass: F.e.: 0.26, 0.24, A.p.: 0.02, 0.68, C.b.: 0.10, 0.45, T.c.: 0.22, 0.28, F.s.: 0.007, 0.80 (moist treatment).

Chapter 4

Species identity and neighbor size surpass the impact of tree species diversity on productivity in experimental broad-leaved tree sapling assemblages under dry and moist conditions

Torben Lübbe · Bernhard Schuldt · Christoph Leuschner

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Abstract

Species diversity may increase the productivity of tree communities through complementarity (CE) and/or selection effects (SE), but it is not well known how this relationship changes under water limitation. We tested the stress-gradient hypothesis, which predicts that resource use complementarity and facilitation are more important under water-limited conditions. We conducted a growth experiment with saplings of five temperate broad-leaved tree species that were grown in assemblages of variable diversity (1, 3 or 5 species) and species composition under ample and limited water supply to examine effects of species richness and species identity on stand- and tree-level productivity. Special attention was paid to effects of neighbor identity on the growth of target trees in mixture as compared to growth in monoculture. Stand productivity was strongly influenced by species identity while a net biodiversity effect was significant in the moist treatment (mostly assignable to CE) but of minor importance. The growth performance of some of the species in the mixtures was affected by tree neighborhood characteristics with neighbor size likely being more important than neighbor species identity. Diversity and neighbor identity effects visible in the moist treatment mostly disappeared in the dry treatment, disproving the stress-gradient hypothesis. The mixtures were similarly sensitive to drought-induced growth reduction as the monocultures, which may relate to the decreased complementarity effect on growth upon drought in the mixtures.

Keywords: *aboveground productivity, belowground productivity, complementarity effect, drought sensitivity, interspecific competition, neighbor effect, selection effect*

Introduction

Recent findings from several biodiversity experiments with planted young trees and observational studies in forests suggest that forest productivity is often enhanced by higher tree diversity (e.g. Zhang et al., 2012; Scherer-Lorenzen, 2014). Contradicting evidence does also exist, however, showing no or even a negative relationship of diversity to forest productivity in diversity experiments (Lang et al., 2012; Grossiord et al., 2013; Li et al., 2014) or in forests (Firn et al., 2007; Szwagrzyk and Gazda, 2007; Jacob et al., 2010; von Oheimb et al., 2011). Theory predicts that three mechanisms may lead to a positive diversity effect on stand productivity, a selection effect (the probability of including productive species in the sample increases with increasing species richness), greater complementarity in resource consumption at the stand level, and facilitative interactions that enhance growth (Vandermeer 1992; Loreau and Hector, 2001). A key process in the diversity–function relationship in forests is competition, which is underlying the selection process in mixed forests, but which is also important for the complementarity effect as complementary resource use should reduce competition intensity. Increasing diversity should lead to increasingly asymmetric competitive interactions in a stand. Species identity influences stand productivity not only through the traits of the occurring species, but also via neighbor effects on the growth of target trees; the latter effects may be species-specific.

Only few experiments with planted young trees are able to separate between true diversity effects on productivity as caused by resource use complementarity and/or facilitation, and selection effects, which are driven by the presence of certain species with specific properties (Potvin and Gotelli, 2008; Lang et al., 2012; Grossiord et al., 2013). This is also true for effects of tree neighbor composition on growth. In dependence of their competitive strength, neighbors may decrease or increase the growth of target trees in relation to growth in monoculture. Consequently, these effects should differ between pure stands and mixtures and vary with neighbor species identity (Stoll and Newberry, 2005; Pretzsch and Schütze, 2009; Mölder et al., 2011; Lang et al., 2012). The size and density of neighbors are known as key factors influencing the competitive ability and performance of target plants (e.g. Weiner, 1990). However, their effect has been found difficult to separate from tree identity effects, i.e. neighbor properties other than plant size and density acting on target plants. Several studies showed that neighbor identity effects can be modified or even masked by crowding or tree size effects (Uriarte et al., 2004; Potvin and Dutilleul, 2009; von Oheimb et al., 2011; Lang et al., 2012).

The interplay between species identity and diversity effects on forest productivity and the relative importance of neighbor effects on tree growth are not well understood. Even less is known about the environmental dependence of these processes on forest ecosystem functioning. The stress-gradient hypothesis applied to forests predicts that resource use complementarity and facilitation are of greater significance in stressful environments (Callaway and Walker, 1997), i.e. in forests exposed to dry, cold, or nutrient-poor conditions, which seems to be supported by empirical studies (e.g. Vilà et al., 2007; Paquette and Messier, 2011; Pretzsch et al., 2010). If positive diversity effects on productivity were indeed larger under stressful conditions, tree species richness could serve to enhance community resistance against environmental hazards. However, it is not well known whether more diverse forests capture resources more rigorously under limiting conditions compared to monocultures (Forrester, 2014). Functional biodiversity research in forests would also benefit from deeper insights into the role of species identity and associated selection effects on productivity and other ecosystem functions.

Recent comprehensive observational studies along a natural diversity gradient in an old-growth temperate deciduous forest with decreasing abundance of European beech (*Fagus sylvatica L.*) in Hainich National Park (Thuringia, Germany) showed that tree species identity exerted a large influence on various ecosystem functions, while diversity itself seemed to be only of secondary importance (Gebauer et al., 2012; Jacob et al., 2013). Three- and 5-species stands were not more productive above-ground than monospecific beech stands (Jacob et al. 2010) but had a higher fine root productivity in ingrowth cores (Meinen et al. 2009). In addition, the stem wood production of beech was higher and its sensitivity to environmental fluctuation lower in more diverse neighborhoods on clay-rich soils, highlighting the role of tree neighborhood effects (Mölder et al., 2011; Mölder and Leuschner, 2014).

Here, we present the results of a tree diversity experiment with potted sapling assemblages, designed to complement the findings obtained from the observational studies in the Hainich mixed forest. The five temperate broad-leaved tree species used in the study (*Fraxinus excelsior L.*, *Acer pseudoplatanus L.*, *Carpinus betulus L.*, *Tilia cordata L.*, *Fagus sylvatica L.*) are also the most abundant species in the Hainich forest; they differ in important morphological and functional traits (Köcher et al., 2009, 2012; Legner et al., 2013). We established three diversity levels (1-, 3- and 5-species) with all possible monocultures (5) and 3-species combinations (10) and cultivated the plants for 16 months at both ample and water-limited conditions. Study goal was to disentangle the effects of tree diversity and tree species identity on the productivity at the stand level (5 trees each) and the tree level under both favorable and resource-limited conditions. Special emphasis was put on neighborhood effects on tree growth and their alteration with increasing diversity.

We tested the hypotheses that (i) stand productivity increases with diversity, but species identity is a more influential factor, (ii) the growth performance of target trees is significantly influenced by the species composition of the neighborhood, (iii) the neighborhood effect is mainly a tree size effect rather than a species identity effect, and (iv) diverse stands reduce their productivity under drought less than monocultures because they reach a higher resource use complementarity.

Materials und methods

Experimental design

A replicated diversity experiment with 1- to 2-yr-old saplings of the five common Central European broad-leaved tree species (F. excelsior (European ash), A. pseudoplatanus (sycamore maple), C. betulus (European hornbeam), T. cordata (small-leaved lime) and F. sylvatica (European beech)) was established in April 2011 in the Experimental Botanical Garden of the University of Göttingen (coordinates: 51°33’ N, 9°57’ E, 177 m a.s.l.) and conducted for two vegetation periods until harvest in August 2012 (duration: 15 months, ~450 days). Five saplings were planted together each in a pot of 0.05 m3 volume (height: 0.30 m, diameter: 0.58 m) filled with coarse-grained sand (98% sand, 1.8% silt, 0.2% clay). The plants were arranged systematically at equal distances to each other to expose them to similar competition intensities. We established three diversity levels (1, 3 or 5 species per pot) and grew all five species in monoculture (all five plants of the same species; five types of monocultures), in 3-species mixture (ten possible combinations with three out of five species) and in 5-species mixture (all plants of different species identity). Thus, 16 different species combinations were investigated. The experiment was further conducted with two different soil moisture treatments (moist, dry), which allowed us to test for diversity and species identity effects on growth under optimal and resource-limited conditions. Due to limitations in plant material and work force, the dry treatment could not be carried out with the full set of species combinations used in the moist treatment. The ten possible 3-species mixtures were reduced in the dry treatment to five representing each species in three different combinations (Table 4.1). We defined target values of maximal volumetric soil water content (SWC) for the moist (~21%) and the dry treatment (~12%), equivalent to 95% and 57% of field capacity, respectively. In total, 185 pots with 925 tree individuals were monitored. For details see Lübbe et al. (2016).

Table 4.1. Design of the experiment with five tree species, three diversity levels (mono, monocultures; mix 3, 3-species mixtures; mix 5, 5-species mixtures) and moist and dry treatments with the number of replicates. In the dry 3-species mixtures, only five of the ten possible combinations were realized. A.p., *Acer pseudoplatanus*; C.b., *Carpinus betulus*; F.e., *Fraxinus excelsior*; F.s., *Fagus sylvatica*; T.c.,*Tilia cordata*.

Tree diversity	Species combination	Replication (n)	
		moist	dry
mono	*A. pseudoplatanus*	7	7
	C. betulus	7	7
	F.sylvatica	7	7
	F. excelsior	7	7
	T.cordata	7	7
mix3	A.p. - C.b. - F.s.	7	
	A.p. - C.b. - F.e.	7	6
	A.p. - C.b. - T.c.	7	6
	A.p. - F.s. - F.e.	7	6
	A.p. - F.s. - T.c.	7	
	A.p. - F.e. - T.c.	7	
	C.b. - F.s. - F.e.	7	
	C.b. - F.s. - T.c.	7	6
	C.b. - F.e. - T.c.	7	
	F.s. - F.e. - T.c.	7	6
mix5	A.p. - C.b. - F.s. - F.e. - T.c.	8	7

The pots were installed under a light-transmitting roof, which excluded all precipitation. The pots were set up at random position in a grid pattern for minimizing the impact of possible environmental gradients.

During July-September 2011 and May-August 2012, mean SWC content varied between 12 and 20% in the moist and 7 and 12% in the dry treatment. Accordingly, lowest soil matrix potentials reached -84 kPa in the moist and -869 kPa in the dry treatment, respectively (Lübbe et al., 2016). Soil moisture content and the amount of required irrigation water were determined gravimetrically. For details on plant care and soil moisture control see Lübbe et al. (2016). Details on climatic conditions are provided in Figure A.4.1.

Measurement of productivity, allocation patterns and plant morphology

The final harvest of all plants took place within a 7-wk period in July/August 2012, i.e. 15 months after the onset of the experiment. By applying a rotating harvesting scheme, one replicate pot per treatment and species combination was collected every week, thereby avoiding different experimental durations of the treatments. The roots were washed out from the substrate under flowing water. Shoot length (L_{Shoot}) and maximum root length (L_{Root}) were determined and the stem diameter at ground level was measured in two directions perpendicular to each other for calculating basal area (BA). Leaf, stem and root mass were oven-dried (70 °C, 72 h) and weighed at a precision of 10 mg. The specific leaf area (SLA) of fully expanded leaves in the upper crown was determined for a subset of trees using WinFolia software (Régent, Quebec, Canada); it served for calculating the total leaf area (LA) of the trees. Besides metrics related to tree size, biomass and biomass partitioning, we calculated the root-to-shoot ratio (RS) and the relative increment in BA (BAI), shoot length (LI_{Shoot}) and root length (LI_{Root}) for the entire growth period of 450 days by subtracting initial from final size or biomass (initial plant metrics are given in Table A.4.1). Furthermore, relative growth rates were calculated considering aboveground, below-ground and total biomass (RGR, in g g^{-1} 450 d^{-1}). Growth was measured with the aim (i) to compare the productivity of a tree assemblage in a pot among different species combinations, diversity levels and soil moisture levels, and (ii) to analyze the productivity of the five species on the tree individual level in its dependence on diversity, neighborhood and soil moisture level. Net biodiversity effects (NE), selection effects (SE), and complementarity effects (CE) on stand productivity were calculated after Loreau and Hector (2001) using equation (1):

$$NE = CE + SE = N\,\overline{\Delta RY}\,\overline{Y_M} + N\,cov(\Delta RY, Y_M) \qquad (1)$$

where N is the number of species in mixture and ΔRY is the difference between observed and expected relative yield (the latter being derived from the species' relative abundance in the mixture upon planting). Y_M is the yield of a species in monoculture. Horizontal bars above terms symbolize average values across the species in mixture. COV is the covariance of the two variables in parentheses. Neighborhood effects on the growth performance of a target species were investigated in the 3-species mixtures, where for every species all six possible neighborhood constellations with the four other species were realized in the moist treatment. In the dry treatment, only three of the six possible combinations were available (Table 4.1). We calculated the competitive ability index (CA) after Grace (1995), which compares the growth performance of a target species in mixture with that in monoculture (equ. 2).

$$CA = \frac{(RGR_{mix} - RGR_{mono})}{RGR_{mono}} \qquad (2)$$

We did this for all six neighborhood constellations of a species in the 3-species mixtures (moist treatment; only 3 in the dry treatment). To disentangle the effect of the each two neighbors in the 3-species mixtures, we also calculated the CA of a target species for all species combinations where one of the four possible neighbors was present.

Statistical analysis

To avoid pseudo-replication, we used the pots as replicate units in samples consisting of the different individuals of a species. We thus averaged over all individuals of a species in a pot. Statistical analyses were done with R software, version 3.0.0 (R Core Team, 2012). We conducted two-way ANOVAs to test for effects of the factors species composition (Type II SS considering incomplete data) or tree diversity (Type III SS for unbalanced designs) in assumed interaction with soil moisture treatment on parameters characterizing productivity and biomass partitioning at the pot level (*car* package). For the additive partitioning procedure of biodiversity effects, grand means of the net biodiversity effect, selection effect and complementarity effect were tested against zero by one-sample t-tests. We further tested the effect size of species richness (3 or 5 species; t-test) or species composition (ANOVA) on the variance of the three diversity effects. At the tree-individual level, three-way ANOVAs were conducted for analyzing effects of species identity, diversity level and moisture treatment on various growth-related parameters. The effect of the neighbor constellation in 3-species mixtures on the relative growth rate (RGR) and competitive ability (CA) of the five species was tested individually by one-way ANOVAs in the moist and dry treatment. To test for the influence of certain neighbor species on the $\mathrm{RGR}_{\mathrm{total}}$ and CA of a target species in 3-species mixtures, we applied generalized linear models (glm), where the presence of heterospecific neighbors was introduced through dummy variables (yes/no). For separating between effects of neighbor identity and crowding on the growth of target species in the mixed pots, we further conducted ANCOVA analyses with the species composition of the neighborhood as predictor variable and several parameters characterizing the size of the neighbors (biomass, leaf area, shoot length, root length) introduced separately as co-variables. The residuals of all models were tested for violation of the normality (Shapiro-Wilk test) and homoscedasticity assumptions (Levene’s test). Multiple comparisons among the means of different species, species combinations or diversity levels were performed with Tukey contrasts (glht( ), *multcomp* package). Pairwise comparisons among the two moisture treatments were done with Student’s t-test, Welch’s t-test or the Mann-Whitney U-test, depending on data structure.

Results

Stand productivity and biomass partitioning

While average phytomass production and RGR of the sapling assemblages tended to increase slightly from the monospecific to the 3-species and the 5-species mixtures for most studied parameters (phytomass, LA, BA, RGR_{above}, RGR_{below}, RGR_{total}), the increase was significant only for LA (in the moist treatment) and LI_{Root} (Table 4.2). In contrast, L_{Shoot} and root:shoot ratio (RS) were not affected. These results are consistent with those from two-way ANOVA, which showed a significant diversity effect only for LA ($F_{(2,183)} = 3.78$, $p<0.05$) but not for the other productivity parameters including RGR_{total} ($F_{(2,183)} = 1.10$, $p>0.10$).

Table 4.2. Various parameters characterizing productivity and plant-internal biomass partitioning (pot-level data: 5 plants each) averaged over the three diversity levels in the moist and dry treatments. For phytomass, leaf *area* (LA) and basal area (BA), cumulative values for the five plants are given, for root:shoot ratio (RS), shoot length (L_{Shoot}), root length (L_{Root}), shoot and root length increment (LI_{Shoot}, LI_{Root}, in percent of initial value), basal area increment (BAI, in percent) and RGR, averages over the five plants are presented. Relative growth rates (RGR) are given in g g^{-1} 450 d^{-1}. Different small letters indicate significant differences between diversity levels ($p<0.05$); asterisks in the dry treatment indicate significant differences between moisture treatments in a diversity level (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$). Note different no. of replicates in the diversity levels.

Moisture treatment	Diversity level	No. of replicates [n]	Phytomass [g]	RS [g g^{-1}]	LA [m^2]	BA [cm^2]
moist	mono	35	511.90 ± 27.88 a	1.08 ± 0.06 a	1.46 ± 0.07 a	10.32 ± 0.81 a
	mix3	70	547.70 ± 15.37 a	1.12 ± 0.03 a	1.65 ± 0.04 b	10.99 ± 0.31 a
	mix5	8	554.88 ± 42.04 a	1.11 ± 0.06 a	1.55 ± 0.08 ab	11.81 ± 0.68 a
dry	mono	35	425.70 ± 22.70 a *	1.11 ± 0.06 a	1.29 ± 0.07 a ◦	8.60 ± 0.70 a *
	mix3	30	434.59 ± 13.69 a ***	1.10 ± 0.04 a	1.41 ± 0.05 a ***	8.75 ± 0.38 a ***
	mix5	7	445.49 ± 23.88 a	1.02 ± 0.02 a	1.45 ± 0.05 a	9.36 ± 0.29 a **
Moisture treatment	Diversity level	No. of replicates [n]	L_{Shoot} [cm]	L_{Root} [cm]	LI_{Shoot} [%]	LI_{Root} [%]
moist	mono	35	100.37 ± 4.06 a	70.94 ± 3.27 a	121.51 ± 12.18 a	184.89 ± 8.37 a
	mix3	70	97.87 ± 1.36 a	76.67 ± 1.67 a	108.46 ± 4.13 a	205.78 ± 5.43 b
	mix5	8	98.45 ± 3.45 a	82.75 ± 3.43 a	107.36 ± 7.28 a	230.15 ± 13.70 b
dry	mono	35	86.62 ± 2.62 a **	64.66 ± 2.48 a	90.34 ± 8.79 a *	162.98 ± 9.39 a *
	mix3	30	85.44 ± 1.72 a ***	65.75 ± 1.48 a ***	82.78 ± 5.98 a ***	164.64 ± 6.45 a ***
	mix5	7	87.98 ± 1.18 a *	69.52 ± 3.87 a *	85.33 ± 2.49 a *	177.36 ± 15.43 a *
Moisture treatment	Diversity level	No. of replicates [n]	BAI [%]	RGR_{above}	RGR_{below}	RGR_{total}
moist	mono	35	337.15 ± 22.90 a	6.10 ± 0.43 a	3.77 ± 0.24 a	4.68 ± 0.28 a
	mix3	70	329.00 ± 11.76 a	6.38 ± 0.19 a	4.23 ± 0.18 a	5.11 ± 0.17 a
	mix5	8	341.58 ± 25.37 a	6.44 ± 0.52 a	4.33 ± 0.47 a	5.19 ± 0.47 a
dry	mono	35	258.73 ± 16.61 a **	4.70 ± 0.30 a **	3.06 ± 0.20 a *	3.70 ± 0.21 a **
	mix3	30	240.75 ± 11.02 a ***	4.96 ± 0.22 a ***	3.14 ± 0.13 a ***	3.85 ± 0.15 a ***
	mix5	7	250.03 ± 11.03 a **	5.22 ± 0.33 a ◦	3.11 ± 0.22 a *	3.97 ± 0.27 a *

Additive partitioning of biodiversity effects after Loreau and Hector (2001) showed, for the moist treatment only, a significant net biodiversity effect on biomass ($t = 3.87$, $p<0.01$), which was mainly due to a positive complementarity effect ($t = 3.67$, $p<0.01$; Figure 4.1). Across all 11 mixtures, a significant SE on biomass production was not detected. CE, SE and NE were not influenced by species richness (3-species vs. 5-species mixtures), and the species composition of the mixtures influenced only the size of the selection effect significantly (F = 3.34, $p<0.01$). Similar patterns for the NE and CE were detected for various other growth-related parameters with strongest effects for LA and L_{Root} (Table A.4.3). Significant selection effects co-occurred in case of below-ground biomass, LA and BA.

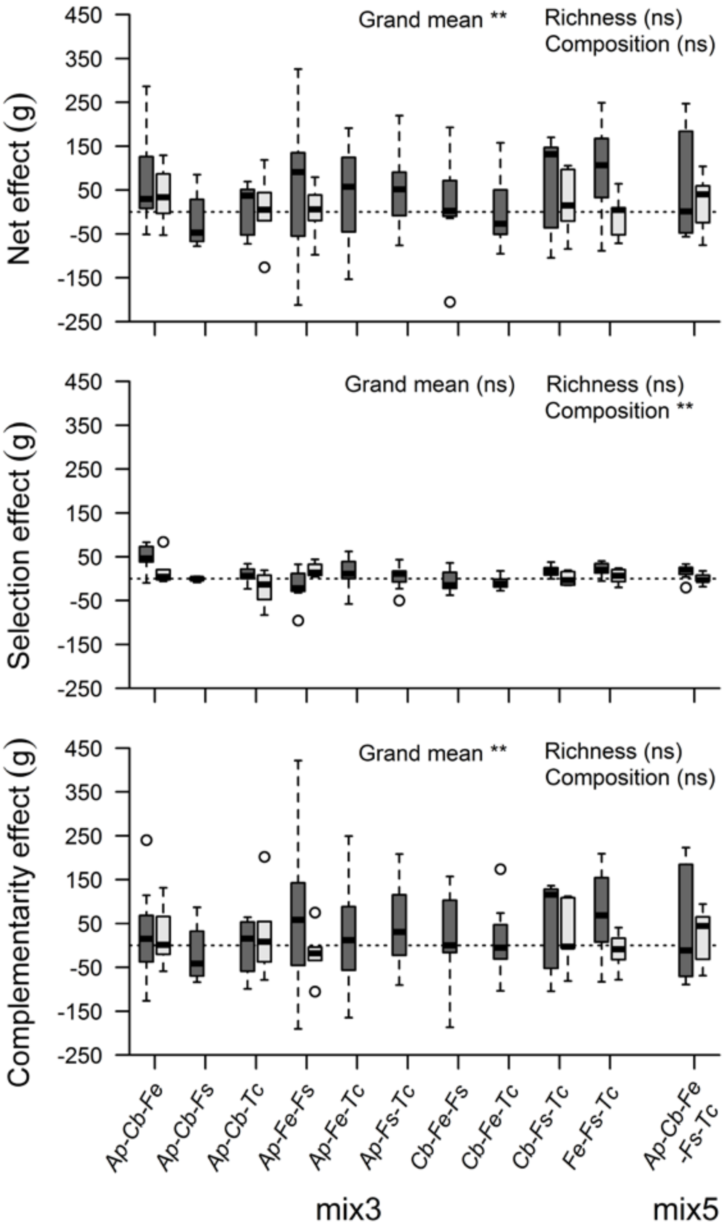

Figure 4.1. Additive partitioning of biodiversity effects on accumulated biomass of mixed tree assemblages: Net diversity effect, selection effect and complementarity effect in their dependence on species richness (3 vs. 5 species) and species composition. Asterisks indicate significant effects for the moist treatment (dark boxes; **: $p<0.01$; ns: non-significant). In the dry treatment, no significant effects were detected (bright boxes).

All twelve productivity-related parameters except RS were significantly affected by the moisture treatment (Table 4.2). In contrast to the moist treatment, significant NE and CE occurred in the dry treatment only by exception (above-ground biomass and LA, Table

A.4.3). The reduction in RGR from the moist to the dry treatment tended to increase with diversity and it was more conspicuous in root growth than in shoot growth (RGR_{below}: 19, 26 and 28% reduction in the monospecific, mix 3 and mix 5 category, respectively).

Species identity effects on stand productivity and biomass partitioning

Comparing the pot-level productivity of the 16 (moist treatment) or 11 species combinations (dry treatment) with two-way ANOVA revealed highly significant effects of the species combination ($F_{(15,169)} = 3.75$, $p<0.001$) and of the moisture treatment ($F_{(1,183)} = 38.28$, $p<0.001$) on RGR_{total}. The largest productivity differences existed among the five monocultures (3.7 - 6.0 g g^{-1} 450 d^{-1} in the moist treatment, 2.6 - 5.3 g g^{-1} 450 d^{-1} in the dry treatment) with highest RGR_{total} in *F. excelsior* and lowest in *A. pseudoplatanus* (difference significant in both treatments; Figure 4.2). Except for one 3-species mixture (*Fagus-Fraxinus-Tilia*: 6.3 g g^{-1} 450 d^{-1} in the moist treatment), the RGR of all 3- and 5-species mixtures remained in the productivity range set by the five monocultures, and transgressive over-yielding was restricted to this single mixture.

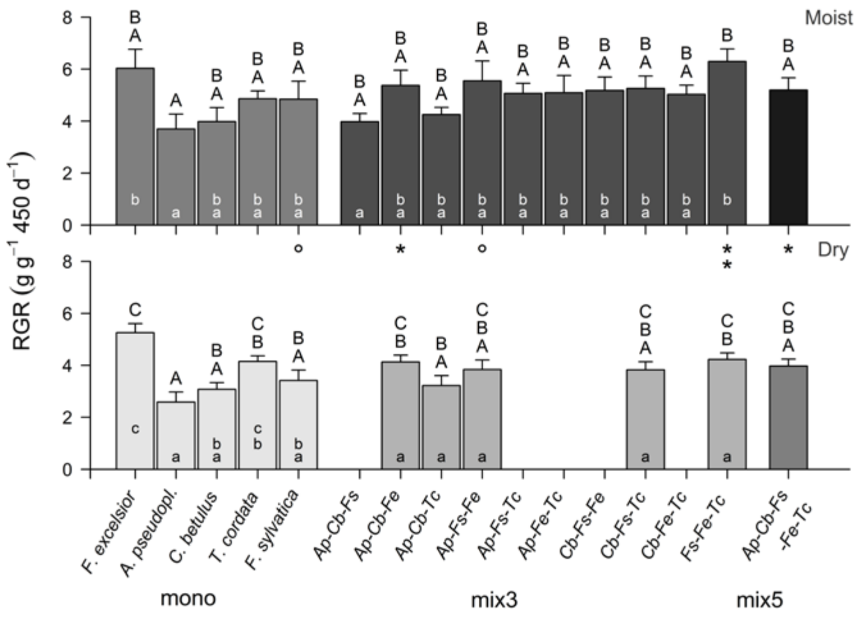

Figure 4.2. Average relative growth rates (RGR; above- and belowground) of tree assemblages differing in species composition and diversity in the moist (upper panel) and dry (lower panel) treatment (mean ± SE of 6-8 replicate pots). Different capital letters indicate significant differences ($p<0.05$) between the species combinations in the full sample (moist: 16, dry: 11 combinations), different small letters indicate significant differences between the species combinations in a diversity level. Asterisks indicate significant differences between the moisture treatments for a species combination (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$). For species abbreviations see Table 4.1.).

Variation in pot-level RGR_{total} among the different mixtures was smaller in the dry than in the moist treatment, and significantly different productivities of the various 3-species combinations appeared only in the moist treatment.

Growth of the five species as dependent on neighborhood diversity and composition

The individual-based RGR_{total} analysis allows comparing the growth performance of the species in defined neighborhood constellations. Three-way ANOVA indicated for all growth-related parameters highly significant effects of species identity (RGR_{total}: $F_{(4,420)} = 20.30$, $p<0.001$) and also of the moisture treatment (RGR_{total}: $F_{(1,423)} = 21.57$, $p<0.001$), except for RS. Diversity effects were significant only for L_{Root} ($F_{(2,422)} = 8.17$, $p<0.001$) and LI_{Root} ($F_{(2,422)} = 8.53$, $p<0.001$).

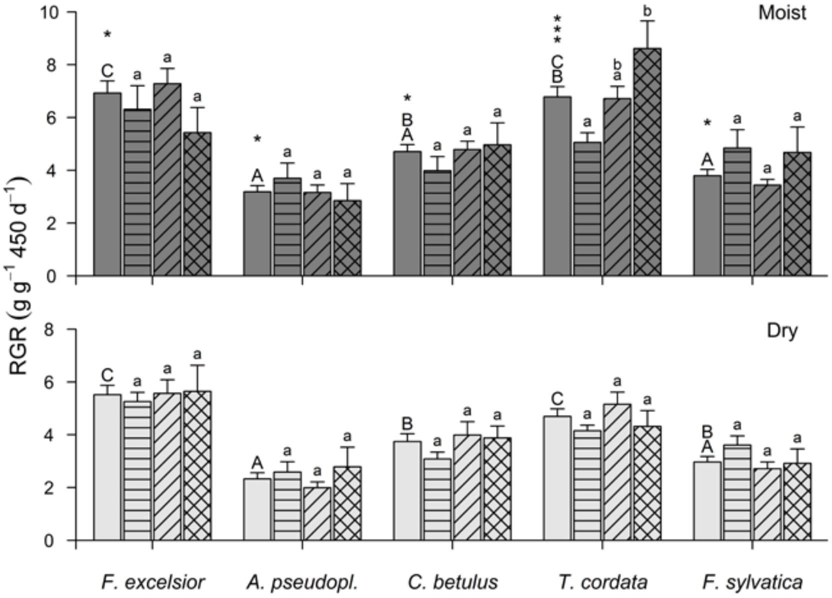

Figure 4.3. Relative growth rate (above- and belowground) of the five species in the moist (upper panel) and dry treatment (lower panel) in monoculture (second bar of a group), 3-species mixture (3rd bar), 5-species mixture (4th bar) and as average of all constellations (first bar, no hatching) (means ± SE). Different capital letters indicate significantly different species averages ($p<0.05$), different small letters significant differences between the three diversity levels within a species. The number of asterisks gives the level of significance for the growth reduction from the moist to the dry treatment of a species (*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

When all individuals of a species from all species combinations were pooled in the analysis, productivity (RGR_{total}) decreased in the sequence *Fraxinus* > *Tilia* > *Carpinus* > *Fagus* > *Acer* in the moist and the dry treatment (Figure 4.3: first bars of the species blocs).

For the other productivity parameters, the species ranking differed in some cases (Table A.4.2).

When comparing a species' RGR_{total} in monoculture, 3-species mixture and 5-species mixture (Figure 4.3), RGR_{total} of *T. cordata* was significantly higher in 5-species mixture than in monoculture (5.05, 6.71 and 8.61 g g^{-1} 450 d^{-1} in 1-, 3- and 5-species assemblages), which was reflected in the significant increase in LA of *Tilia* plants from 1- to 3-species assemblages (Table A.4.7). A non-significant tendency for higher growth rates with increasing diversity was also observed in *C. betulus* (Table A.4.6), while *F. sylvatica*, *A. pseudoplatanus* and *F. excelsior* showed no productivity trend across the three diversity levels. However, *A. pseudoplatanus* increased both L_{Root} and LI_{Root} in 5-species mixture compared to the monoculture (moist treatment), but decreased RS in 5-species mixture in the dry treatment (Table A.4.5). In contrast, *F. sylvatica* saplings tended to grow better in monoculture than in 3-species mixtures, which was also visible in higher LA, BA, RGR_{above} and a smaller RS (Table A.4.8).

In *T. cordata*, the drought-induced reduction in RGR_{total} increased with diversity (monoculture: -18%, 3-species mixtures: -23%, 5-species mixtures: -50%). For *F. excelsior* (-17, -24, -4%), *A. pseudoplatanus* (-30, -37, -2%), *C. betulus* (-23, -17, -22%) and *F. sylvatica* (-26, -21, -38%), no consistent trends with increasing diversity were visible. In the 5-species mixture, *A. pseudoplatanus* and *F. excelsior* reduced growth only marginally compared to the moist treatment, while *F. sylvatica* and *T. cordata* suffered larger reductions.

Importance of neighbor species identity

Analysis of variance indicated significant neighborhood effects on the growth response of target species. The superior growth of *F. excelsior* and *T. cordata* in certain 3-species constellations of the moist treatment is reflected in significantly higher competitive ability indices (CA) of the target species in the respective mixtures (Figure 4; ANOVA: $F_{(5,35)} = 3.72$, $p<0.01$ for *F. excelsior*; $F_{(5,34)} = 2.24$, $p<0.1$ for *T. cordata*). RGR_{total} of *F. excelsior* was remarkably high in coexistence with *Acer* and *Carpinus* (Figure A2: upper panel) in the moist treatment and the corresponding CA indices were significantly higher than for mixtures with *Acer - Fagus*, *Carpinus - Fagus* and also *Carpinus - Tilia* (Figure 4.4). However, the outstanding performance of *F. excelsior* in combination with *Acer - Carpinus* was not observed under dry conditions (Figure 4.4: lower panel). All CA scores for *T. cordata* were positive indicating better growth in mixture than monoculture with highest values for the coexistence with *Fagus* - *Fraxinus*. In contrast, *F. sylvatica* reached highest growth rates in monoculture resulting in negative CA scores across all heterospecific constellations. Species-specific neighbor effects were less important in the dry treatment. The RGR of *C. betulus* was higher in monoculture than in mixture with *Fagus* – *Tilia* (Figure A2: lower panel), but the CA scores of the different 3-species constellations did not differ (Figure 4.4).

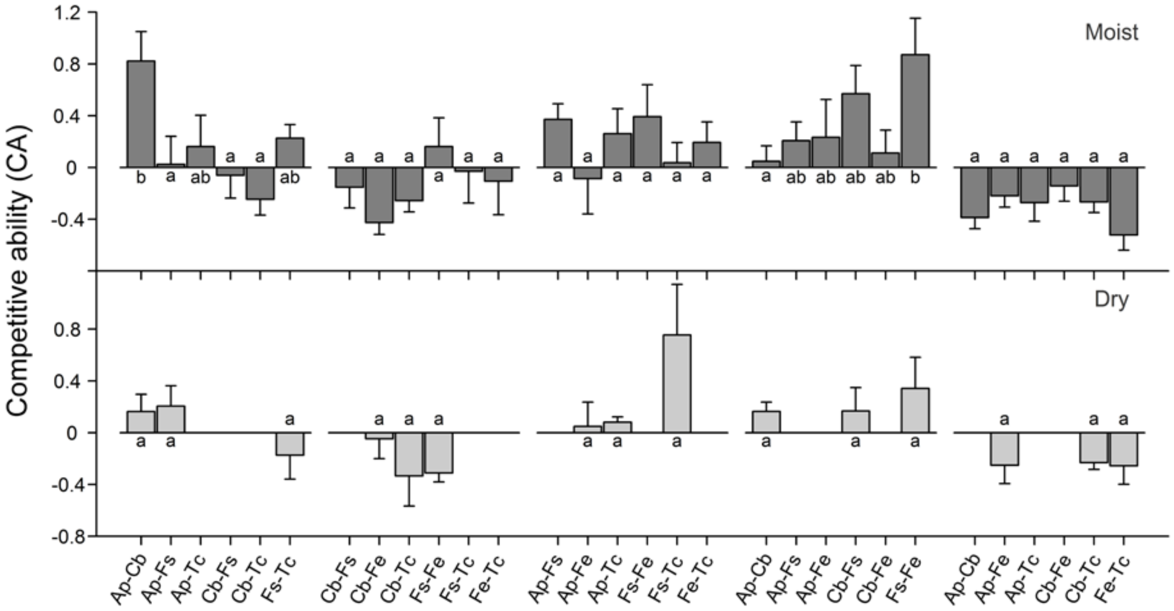

Figure 4.4. Competitive ability (expressed as CA index) of the five species when grown in six (moist treatment) or three (dry treatment) different 3-species neighborhood constellations (means ± SE of 6-7 replicate pots). For species abbreviations see Table 1. Different small letters indicate significant ($p<0.05$) differences in CA of the target species between different neighborhood constellations. A positive CA indicates better growth in mixture than in monoculture.

The explicit analysis of pairwise neighbor interactions on the growth performance of target species in the moist treatment showed *A. pseudoplatanus* and *F. sylvatica* to grow fastest in conspecific neighborhood (negative CA scores; Figure 4.5; GLM, *glht*), while *F. excelsior, C. betulus* and *T. cordata* performed better in mixture. Three of the five species did not show significantly different competitive abilities in response to different neighbor species. Only *T. cordata* achieved a significantly higher CA score in neighborhood to *Fagus* than in vicinity to *Acer* ($p<0.05$). *F. excelsior* showed highest CA scores in coexistence with *Acer*, which tended to be higher than the scores for *Tilia* or *Fagus* as neighbors ($p<0.10$).

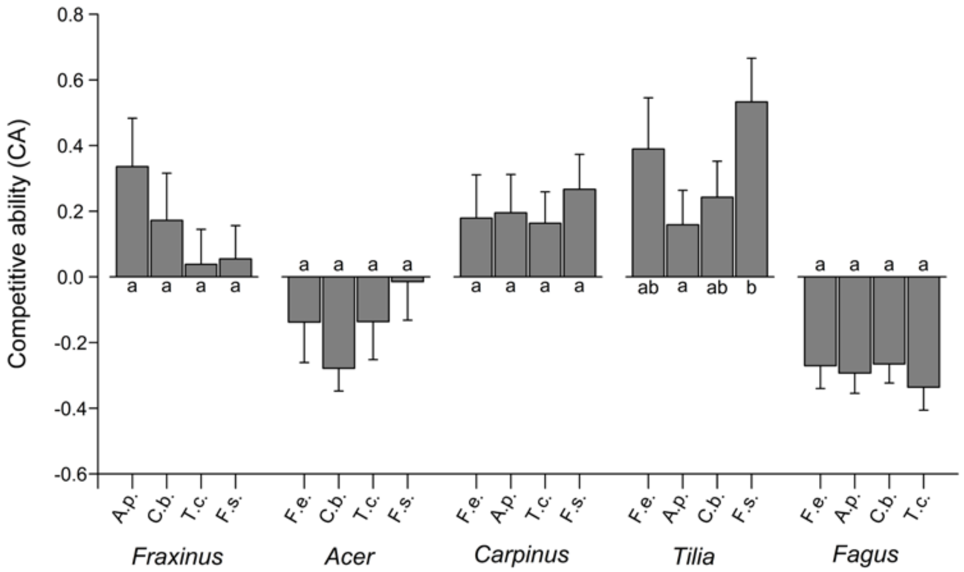

Figure 4.5. Competitive ability of the five species in the moist treatment when grown in neighborhood of the respective four other species (means ± SE of 21 neighborhood replicates). CA was calculated by pooling the each three 3-species neighborhood constellations in which that neighbor species occurred. Different small letters indicate significant differences (p<0.05) in CA between neighbor constellations of a target species. A.p. – *Acer pseudoplatanus*, C.b. – *Carpinus betulus*, F.e. – *Fraxinus excelsior*, F.s. – *Fagus sylvatica*, T.c. – *Tilia cordata*.

The importance of neighbor size for competitive interactions

Table 4.3. ANCOVA results for the five species on the dependence of competitive ability index (CA) on the predictor variable species composition of the neighborhood (6 or 3 constellations in the moist or dry treatments, respectively) and the most influential parameter characterizing neighbor plant size (leaf area LA, basal area BA or biomass) as covariate.

	Moist treatment					Dry treatment				
Species	Predictor	*df*	*SS*	*F*	*p*	Predictor	*df*	*SS*	*F*	*p*
F. excelsior	LA	1	3.18	**17.76**	**< 0.001**	LA	1	0.45	2.84	0.116
	SpecComp	5	0.39	**2.18**	**0.081**	SpecComp	2	0.1	0.30	0.743
	Error	32	0.18			Error	13	2.08		
A. pseudopl.	LA	1	0.65	2.70	0.111	LA	1	0.3	**3.57**	**0.085**
	SpecComp	5	0.66	0.55	0.736	SpecComp	2	0.3	1.78	0.214
	Error	32	7.68			Error	11	0.92		
C. betulus	LA	1	1.86	**8.14**	**0.007**	LA	1	0.22	0.56	0.469
	SpecComp	5	0.62	0.54	0.744	SpecComp	2	1.43	1.87	0.201
	Error	34	7.76			Error	11	4.2		
T. cordata	Biomass	1	0.19	0.84	0.366	LA	1	0.92	**6.02**	**0.032**
	SpecComp	5	3.7	**3.34**	**0.018**	SpecComp	2	0	0.00	0.999
	Bm × SpecComp	5	3.11	**2.81**	**0.036**	Error	11	1.69		
	Error	27	5.97							
F. sylvatica	BA	1	0.17	2.16	0.151	LA	1	0.08	1.09	0.315
	SpecComp	5	0.39	0.97	0.448	SpecComp	2	0.32	2.04	0.17
	Error	33	2.63			Error	13	1.01		

Effects of neighbor size on the CA score of the target species were tested by introducing either neighbor biomass, leaf area or plant size as co-variable in ANCOVA runs (Table 4.3).

For *F. excelsior* and *C. betulus* in the moist treatment, the models explaining CA were significantly improved when the neighbor's leaf area was included as co-variable while the interaction term of biomass × neighborhood species composition was the most important covariate for *T. cordata*. The species identity of the neighbors (factor SpecComp) was, however, only influential for the competitive ability of *F. excelsior* (secondary to leaf area) and *T. cordata*, where it was the dominant factor. In the two species with negative CA scores in interspecific interaction (*F. sylvatica* and *A. pseudoplatanus*), variation neither in neighbor size nor neighbor species identity influenced CA. In the dry treatment, neighbor size effects on productivity were much smaller (significant effect of LA in *T. cordata*, marginally significant effect in *A. pseudoplatanus*) (Table 4.3).

Discussion

Tree diversity and identity effects on productivity

We found a significant net biodiversity effect on total (above- and belowground) biomass production and growth-determining parameters such as leaf area in the moist treatment in support of our first hypothesis. Additive partitioning of biodiversity effects after Loreau and Hector (2001) showed that the diversity effect was mainly caused by a complementarity effect and not by a selection effect; the latter refers to a replacement process in which more productive species achieve dominance in the assemblage. This result meets the assumptions for an experiment with tree saplings because a positive selection effect could only result from canopy expansion of the more productive species, but not from competition-induced alteration of species abundances in the assemblages, as may take place in communities of more short-lived plants.

The resulting net diversity effect increased RGR_{total} in the mixtures by ~10% compared to the average of the monocultures and thus was relatively small. Moreover, a productivity increase occurred only from the monospecific to the 3-species mixtures but not from the 3- to the 5-species mixture. Thus, a diversity increase from one to three species seems to enhance resource use complementarity, but not a further diversity increase from three to five species. This matches the stand transpiration data from this experiment, which show a comparable net diversity effect on water consumption but no difference in transpiration rate between 3-species and 5-species mixtures (Lübbe et al., 2016). Due to the large contribution of water spending species (*F. excelsior* and *T. cordata*) to stand transpiration in the mixed tree assemblages in the moist treatment, the net diversity effect was interpreted mainly as a selection effect. The observed leaf area increase with diversity, which is a main determinant of plant water loss, was assigned to both complementarity and selection effects (Table A.4.3). In contrast to earlier studies (e.g. Forrester et al. 2010), water use efficiency of productivity was not different between the diversity levels (Table A.4.9), i.e. the productivity increase was not greater than the transpiration increase with growing species diversity.

The small diversity effect in our experiment might in part be a consequence of the young age of the saplings and the short duration of the experiment. Complementarity in resource use could increase with the development of structurally more complex canopies and root systems, and the manifestation of a substantial selection effect in tree assemblages might take years or decades. A meta-analysis of plant diversity experiments indeed found that complementarity effects on productivity increase over time (Cardinale et al., 2007). However, diversity effects on forest productivity do not seem to be a universal phenomenon (Forrester 2014). Diversity experiments with planted trees produced mixed results with either positive (e.g. Erskine et al., 2006; Healy et al., 2008) or lacking diversity effects on productivity or biomass (e.g. Nguyen et al., 2012; Grossiord et al., 2013). Further, a sapling experiment with tropical tree species also did not show diversity effects on tree growth (Lang et al., 2012; Li et al., 2014), even though positive interactions were observed.

Various explanations for only small or lacking diversity effects on stand productivity have been proposed including a low potential for growth stimulation under non-limiting conditions, young tree age and not fully developed tree interactions, low species numbers, and more or less symmetric competition due to missing functional differentiation among the tree species (von Oheimb et al., 2011; Lang et al., 2012; Grossiord et al., 2013; Li et al., 2014). Niche differentiation certainly requires the presence of species with sufficient functional dissimilarity as given for instance in case of *Fagus sylvatica* and *Picea abies* (Pretzsch and Schütze, 2009) or *Eucalyptus globulus* and *Acacia mearnsii* (Forrester, 2004), for which complementary resource use and overyielding were observed. Our five broad-leaved species differ in important morphological and physiological traits, but they are functionally more similar than these species pairs, in particular at young age.

The most and the least productive monocultures (*F. excelsior* and *A. pseudoplatanus*) differed nearly by a factor of two in their biomass production in the moist treatment. Similarly large interspecific differences were found for the water consumption of the trees, as the most productive species also transpired most (Lübbe et al. 2016). The majority of other tree diversity experiments also reported a prominent tree identity effect on productivity (e.g. Lang et al., 2012; Grossiord et al., 2013). Our experimental results match observations in the

Hainich mixed forest in that species identity was much more influential than diversity. However, the diversity effect on above-ground productivity in the sapling experiment, even though weak, was not detected in the mature stands with 1, 3 or 5 species (Jacob et al. 2010).

Is the neighbor identity effect mainly a size effect?

Loreau and Hector (2001) quantified the selection effect by the covariance between the monoculture yield of the species and the change in relative yield of the species in the mixtures. Species that profit from the mixture will expand their canopies and root systems at the expense of inferior species and will eventually dominate the mixture by numbers. Our detailed analysis of neighborhood effects on the species’ growth in mixture and monoculture allows insights into the mechanisms underlying selection and species identity effects on productivity. Accordingly, the large observed variation in productivity among the different mixture types is only in part caused by the species constellations and species-specific differences in yield; specific neighbor effects (positive or negative) on the productivity of a target species in mixture add to the variation in yield, thus supporting our second hypothesis. This result is in accordance with other studies demonstrating effects of neighborhood composition on tree growth (Massey et al., 2006; Mölder et al., 2011; von Oheimb et al., 2011; Lang et al., 2012). Most neighborhood interactions in our study were markedly asymmetric as has been found for other tree mixtures as well (Canham et al., 2004, 2006; Potvin and Dutilleul, 2009; Mölder and Leuschner, 2014).

We found considerable differences in the competitive ability (CA) of the five species; the species’ CA scores depended largely on neighbor identity. While the fast-growing species generally were better competitors in mixture, slower-growing species (*A. pseudoplatanus* and *F. sylvatica*) were inferior competitors. Fast-growing species (in particular *F. excelsior* and *T. cordata*) were more sensitive to the specificity of the neighborhood constellation than the less productive trees.

A neighbor’s tree height and biomass are properties likely influencing the growth of a target species, as these attributes typically correlate with the consumption of light, water and nutrients. Our ANCOVA results indicate that neighbor size is a dominant factor, supporting our third hypothesis. In four of the five species (moist or dry treatment), determinants of light interception and canopy space occupation (leaf area or biomass) were detected as influential variables affecting the neighbor’s competitive ability. Due to fixed plant numbers and distances in the pots, differences in plant size are the main determinant of variation in neighbor crowding. The dominant effect of neighbor size on the growth of target trees is in agreement with results obtained in other tree mixing studies (Uriarte et al., 2004; Potvin and Dutilleuil 2009), which found a larger effect of crowding than neighbor species identity. Our results meet the expectation that neighbor effects on the target tree's growth rate are mainly resource depletion effects controlled by the size of the neighbors, while traits unrelated to size (leaf and root physiological properties, direct chemical and mechanical interactions, indirect biotic interactions, etc.) must be of secondary importance.

No support for the resource gradient hypothesis

From the resource gradient hypothesis, we had expected stronger resource complementarity effects in the dry than the moist treatment and a less pronounced growth decline in the mixtures than the monocultures (He et al., 2013; Forrester 2014). However, we obtained no clear indication that more diverse stands were more resistant against drought-induced productivity reduction, disproving our fourth hypothesis. This finding is in agreement with the results of a quantification of stand water consumption in our experiment revealing a smaller net diversity effect with respect to transpiration in the dry than in the moist treatment (Lübbe et al., 2016). It also concurs with findings on radial growth in mixed coniferous mountain forests, in which species composition, but not species richness, determined community resistance against drought (DeClerck et al., 2006). In fact, species richness may increase drought exposure in mixed forests when more diverse stands exploit soil water reserves more completely than monospecific stands do (e.g. Grossiord et al., 2014). Beneficial effects of mixed stands with respect to drought resistance have been demonstrated in the form of reduced drought sensitivity of growth in certain tree species (Lebourgeois et al., 2013; Pretzsch et al., 2013; Mölder and Leuschner, 2014). In our study, none of the species showed clear improvement in growth performance in mixture than in monoculture in the dry treatment. The lacking complementarity effect with respect to transpiration (Lübbe et al., 2015) and growth in the mixtures of the dry treatment might also be related to the restrictions set by a pot trial, when limited soil volume does not allow distinct root space partitioning. In the moist treatment of our experiment, in contrast, canopy space partitioning between different species likely has taken place which may have reduced competition for light. This would fit to the prediction of reduced competition for light driving mixture effects in stands with high resource supply (Forrester, 2014), matching findings from other tree diversity experiments (Potvin and Dutilleul, 2009, Lang et al., 2012).

Conclusion

This sapling study was conducted in conjunction with an observational study in an old-growth mixed forest containing the same species composition. The setting allows some careful extrapolation of the experimental results to real world systems. A complementarity effect on productivity existed but it was relatively small and less influential than species identity. Moreover neighbor effects were found to strongly determine the individual growth performance of tree saplings.

Under drought, the complementarity effect was smaller and not greater. Contradicting the insurance hypothesis of biodiversity, diverse tree assemblages showed no higher resistance to drought than monocultures. Future biodiversity experiments with trees should search for both positive and negative diversity effects in other water-limited mixed stands and assess the evidence for the proposed insurance function of tree diversity in forests under drought.

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Appendices

Table A. 4.1. Initial size and biomass of the tree saplings of the five species used in the experiment (mean ± SE, n=12): Phytomass, root-shoot ratio (RS), basal area (BA), shoot length and root length. Different small letters indicate significant differences among species ($p<0.05$).

Species	Phytomass [g]	RS [g g^{-1}]	BA [cm^2]	L_{Shoot} [cm]	L_{Root} [cm]
A. pseudoplatanus	16.92 ± 0.89 a	1.21 ± 0.05 a	0.30 ± 0.00 a	61.76 ± 2.92 c	20.05 ± 1.13 a
C. betulus	20.41 ± 1.54 ab	1.35 ± 0.07 ab	0.38 ± 0.01 a	54.16 ± 2.42 bc	20.32 ± 0.94 a
F.sylvatica	16.20 ± 0.43 a	1.59 ± 0.06 cd	0.27 ± 0.00 a	36.90 ± 1.70 a	27.27 ± 1.62 b
F. excelsior	20.27 ± 1.10 ab	1.48 ± 0.03 bc	0.50 ± 0.01 a	44.46 ± 1.12 ab	22.52 ± 1.18 ab
T.cordata	21.43 ± 1.29 b	1.75 ± 0.07 d	1.24 ± 0.01 b	40.09 ± 1.77 a	35.18 ± 1.67 c

Table A. 4.2. Parameters characterizing productivity and plant-internal biomass partitioning at the level of the plant individual for the five species in the moist and dry treatment (means ± SE). Data are averages over all species combinations to show species differences (n = 57 and 32 pots in the moist and dry treatment, respectively). Relative growth rates (RGR) are given in g $g^{-1}450$ d^{-1}. Different capital letters indicate significant differences among species ($p<0.05$) in the moist or dry treatment. Asterisks indicate significant differences among the treatments (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Species	Treatment	Phytomass [g]	RS [g g^{-1}]	LA [m^2]	BA [cm^2]
F. excelsior	moist	147.20 ± 8.60 C	1.09 ± 0.04 B	0.36 ± 0.02 B	2.47 ± 0.14 C
A. pseudoplatanus	moist	68.22 ± 3.85 A	1.45 ± 0.06 C	0.17 ± 0.01 A	1.21 ± 0.05 A
C. betulus	moist	99.87 ± 4.79 B	0.73 ± 0.02 A	0.38 ± 0.02 B	1.81 ± 0.07 B
T. cordata	moist	161.49 ± 8.10 C	1.08 ± 0.04 B	0.53 ± 0.02 C	4.51 ± 0.19 D
F. sylvatica	moist	77.70 ± 3.83 AB	1.09 ± 0.03 B	0.21 ± 0.01 A	1.30 ± 0.05 A
F. excelsior	dry	121.05 ± 6.66 C *	1.14 ± 0.03 B	0.29 ± 0.02 B	1.87 ± 0.09 C **
A. pseudoplatanus	dry	54.28 ± 3.75 A *	1.41 ± 0.06 C	0.15 ± 0.01 A	0.97 ± 0.06 A **
C. betulus	dry	82.57 ± 5.24 B *	0.73 ± 0.02 A	0.34 ± 0.02 B	1.55 ± 0.08 BC *
T. cordata	dry	115.53 ± 6.14 C ***	1.02 ± 0.04 B	0.43 ± 0.03 C *	3.44 ± 0.16 D ***
F. sylvatica	dry	64.20 ± 3.34 AB *	1.04 ± 0.04 B	0.20 ± 0.01 A	1.20 ± 0.06 AB

Species	Treatment	L_{Shoot} [cm]	L_{Root} [cm]	LI_{Shoot} [%]	LI_{Root} [%]
F. excelsior	moist	127.66 ± 4.34 D	68.75 ± 1.81 B	187.12 ± 9.77 D	205.28 ± 8.04 B
A. pseudoplatanus	moist	73.53 ± 2.60 A	81.23 ± 2.54 C	34.90 ± 3.83 A	305.10 ± 12.67 C
C. betulus	moist	109.43 ± 2.50 C	58.06 ± 1.30 A	103.13 ± 4.37 B	185.72 ± 6.40 B
T. cordata	moist	102.33 ± 2.43 C	108.40 ± 2.38 D	156.26 ± 5.92 C	208.14 ± 6.77 B
F. sylvatica	moist	88.43 ± 2.50 B	68.48 ± 1.86 B	139.64 ± 6.78 C	151.12 ± 6.81 A
F. excelsior	dry	101.82 ± 3.10 B ***	64.13 ± 1.77 B °	129.02 ± 6.96 C ***	184.76 ± 7.84 C °
A. pseudoplatanus	dry	68.19 ± 2.83 A	74.16 ± 2.50 C °	23.99 ± 4.00 A	269.83 ± 12.47 D °
C. betulus	dry	97.04 ± 2.50 B **	48.95 ± 1.24 A ***	79.19 ± 4.61 B ***	140.90 ± 6.12 B ***
T. cordata	dry	94.28 ± 3.89 B *	86.02 ± 2.38 D ***	135.17 ± 9.70 C *	144.51 ± 6.76 B ***
F. sylvatica	dry	72.42 ± 2.26 A ***	56.87 ± 1.81 B ***	96.25 ± 6.14 B ***	108.53 ± 6.65 A ***

Species	Treatment	BAI [%]	RGR_{above}	RGR_{below}	RGR_{total}
F. excelsior	moist	399.30 ± 29.23 C	8.60 ± 0.63 D	5.77 ± 0.40 B	6.92 ± 0.46 B
A. pseudoplatanus	moist	307.86 ± 17.66 AB	2.92 ± 0.25 A	3.42 ± 0.25 A	3.18 ± 0.24 A
C. betulus	moist	378.52 ± 18.70 BC	6.67 ± 0.40 C	3.22 ± 0.19 A	4.71 ± 0.26 A
T. cordata	moist	264.90 ± 15.22 A	9.47 ± 0.55 D	5.35 ± 0.32 B	6.78 ± 0.39 B
F. sylvatica	moist	383.85 ± 18.03 BC	5.01 ± 0.32 B	3.02 ± 0.19 A	3.80 ± 0.24 A
F. excelsior	dry	277.65 ± 18.68 BC **	6.56 ± 0.44 C °	4.81 ± 0.33 C °	5.52 ± 0.36 C *
A. pseudoplatanus	dry	228.11 ± 21.33 AB **	2.16 ± 0.29 A °	2.48 ± 0.21 A *	2.33 ± 0.23 A *
C. betulus	dry	311.40 ± 21.63 C *	5.22 ± 0.40 B *	2.47 ± 0.22 A **	3.67 ± 0.30 B *
T. cordata	dry	182.74 ± 12.39 A ***	6.95 ± 0.50 C **	3.41 ± 0.19 B ***	4.64 ± 0.29 C ***
F. sylvatica	dry	347.52 ± 20.89 C	4.07 ± 0.30 B °	2.29 ± 0.16 A *	2.99 ± 0.21 AB *

Table A. 4.3. Additive partitioning of biodiversity effects on productivity as measured by various growth-related parameters: above- and belowground biomass (Bm), leaf area (LA), basal area (BA), shoot and root length (L). Asterisks indicate the significance levels of the effect size (grand mean, t-test) and the significance of species richness (3 vs. 5 species; Wilcoxon-test) or species composition influences on the three effects (ANOVA; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

		Moist treatment			Dry treatment		
Parameter		Net effect	Selection	Complementarity	Net effect	Selection	Complementarity
Bm_{Above}	Grand mean	**		**	*		*
	Richness						
	Composition		***			*	
Bm_{Below}	Grand mean	**	*	**			
	Richness						
	Composition		**				
LA	Grand mean	***	*	***	**		***
	Richness						
	Composition		***				
BA	Grand mean	**	**	**			
	Richness						
	Composition						
L_{Shoot}	Grand mean						
	Richness						
	Composition		**				
L_{Root}	Grand mean	***		**			
	Richness						
	Composition		*				

Table A. 4.4. Growth performance of *Fraxinus excelsior* in the moist and dry treatments and the three diversity levels as measured by 12 productivity and biomass partitioning parameters (means ± SE). Relative growth rates (RGR) are given in g $g^{-1}450\ d^{-1}$. Different small letters indicate significant differences between the diversity levels ($p<0.05$) in the moist or dry treatment. Asterisks indicate significant differences among the treatments (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Moisture treatment	Diversity level	No. of replicates [n]	Phytomass [g]	RS [g g^{-1}]	LA [m^2]	BA [cm^2]
moist	mono	7	135.93 ± 16.48 a	0.97 ± 0.08 a	0.34 ± 0.04 a	2.08 ± 0.21 a
	mix3	41	153.87 ± 10.68 a	1.12 ± 0.05 a	0.38 ± 0.03 a	2.58 ± 0.18 a
	mix5	7	119.38 ± 17.70 a	1.07 ± 0.09 a	0.27 ± 0.05 a	2.25 ± 0.33 a
dry	mono	7	116.25 ± 6.46 a	1.18 ± 0.05 a **	0.25 ± 0.01 a *	1.78 ± 0.16 a
	mix3	17	122.05 ± 9.60 a *	1.14 ± 0.05 a	0.30 ± 0.03 a *	1.84 ± 0.09 a **
	mix5	7	123.43 ± 18.38 a	1.10 ± 0.09 a	0.29 ± 0.04 a	2.03 ± 0.33 a
Moisture treatment	Diversity level	No. of replicates [n]	L_{Shoot} [cm]	L_{Root} [cm]	LI_{Shoot} [%]	LI_{Root} [%]
moist	mono	7	131.26 ± 6.93 a	60.37 ± 4.01 a	195.25 ± 15.59 a	168.20 ± 17.84 a
	mix3	41	126.35 ± 5.39 a	69.10 ± 2.11 a	184.15 ± 12.13 a	206.80 ± 9.38 a
	mix5	7	132.45 ± 12.86 a	75.09 ± 4.76 a	197.92 ± 28.93 a	233.47 ± 21.13 a
dry	mono	7	104.21 ± 2.07 a **	60.41 ± 2.27 a	134.39 ± 4.65 a *	168.37 ± 10.10 a
	mix3	17	98.48 ± 4.46 a ***	64.44 ± 2.41 a	121.50 ± 10.02 a ***	186.12 ± 10.71 a
	mix5	7	107.54 ± 8.27 a	67.07 ± 4.74 a	141.90 ± 18.61 a	197.88 ± 21.07 a
Moisture treatment	Diversity level	No. of replicates [n]	BAI [%]	RGR_{above}	RGR_{below}	RGR_{total}
moist	mono	7	320.34 ± 41.95 a	8.38 ± 0.70 a	4.91 ± 0.78 a	6.32 ± 0.89 a
	mix3	41	420.38 ± 36.68 a	8.95 ± 0.79 a	6.15 ± 0.50 a	7.28 ± 0.57 a
	mix5	7	354.78 ± 65.71 a	6.83 ± 1.30 a	4.47 ± 0.79 a	5.43 ± 0.95 a
dry	mono	7	259.07 ± 32.47 a	6.08 ± 0.36 a *	4.69 ± 0.37 a	5.26 ± 0.35 a
	mix3	17	271.64 ± 17.22 a **	6.56 ± 0.61 a *	4.89 ± 0.49 a ◦	5.57 ± 0.52 a *
	mix5	7	310.81 ± 67.05 a	7.01 ± 1.32 a	4.71 ± 0.80 a	5.64 ± 0.99 a

Table A. 4.5. Growth performance of *Acer pseudoplatanus* in the moist and dry treatments and the three diversity levels as measured by 12 productivity and biomass partitioning parameters (means ± SE). Relative growth rates (RGR) are given in g g^{-1}450 d^{-1}. Different small letters indicate significant differences between the diversity levels ($p<0.05$) in the moist or dry treatment. Asterisks indicate significant differences among the treatments (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Moisture treatment	Diversity level	No. of replicates [n]	Phytomass [g]	RS [g g^{-1}]	LA [m^2]	BA [cm^2]
moist	mono	7	76.58 ± 9.40 a	1.57 ± 0.19 a	0.19 ± 0.02 a	1.28 ± 0.14 a
	mix3	40	67.84 ± 4.62 a	1.44 ± 0.06 a	0.17 ± 0.01 a	1.19 ± 0.06 a
	mix5	8	62.76 ± 10.55 a	1.43 ± 0.18 a	0.14 ± 0.02 a	1.21 ± 0.12 a
dry	mono	7	58.51 ± 6.31 a	1.63 ± 0.13 b	0.15 ± 0.02 a	0.98 ± 0.12 a
	mix3	15	48.82 ± 3.59 a *	1.45 ± 0.05 b	0.13 ± 0.01 a *	0.89 ± 0.05 a *
	mix5	7	61.76 ± 12.05 a	1.10 ± 0.11 a	0.18 ± 0.04 a	1.11 ± 0.21 a
Moisture treatment	Diversity level	No. of replicates [n]	L_{Shoot} [cm]	L_{Root} [cm]	LI_{Shoot} [%]	LI_{Root} [%]
moist	mono	7	72.55 ± 6.17 a	68.59 ± 2.01 a	24.50 ± 8.77 a	242.05 ± 10.00 a
	mix3	40	73.33 ± 2.70 a	81.20 ± 2.97 ab	34.40 ± 3.95 a	304.92 ± 14.82 ab
	mix5	8	75.39 ± 11.20 a	92.46 ± 7.45 b	57.10 ± 18.87 a	361.16 ± 37.16 b
dry	mono	7	67.88 ± 4.03 a	70.04 ± 3.69 a	23.15 ± 4.40 a	249.38 ± 18.43 a
	mix3	15	63.48 ± 2.34 a **	73.29 ± 2.76 a	13.89 ± 2.06 a **	265.45 ± 13.78 a
	mix5	7	78.59 ± 9.24 a	80.13 ± 7.75 a	43.17 ± 13.18 a	299.64 ± 38.65 a
Moisture treatment	Diversity level	No. of replicates [n]	BAI [%]	RGR_{above}	RGR_{below}	RGR_{total}
moist	mono	7	333.02 ± 47.50 a	3.25 ± 0.70 a	4.07 ± 0.52 a	3.70 ± 0.58 a
	mix3	40	303.38 ± 21.66 a	2.93 ± 0.29 a	3.39 ± 0.31 a	3.16 ± 0.28 a
	mix5	8	308.26 ± 41.04 a	2.63 ± 0.79 a	3.03 ± 0.60 a	2.85 ± 0.65 a
dry	mono	7	231.18 ± 39.96 a	2.16 ± 0.41 a	2.98 ± 0.41 a	2.59 ± 0.39 a
	mix3	15	201.66 ± 17.53 a *	1.69 ± 0.20 a *	2.25 ± 0.25 a ◦	1.99 ± 0.22 a *
	mix5	7	277.32 ± 71.68 a	3.16 ± 1.00 a	2.47 ± 0.54 a	2.79 ± 0.74 a

Table A. 4.6. Growth performance of *Carpinus betulus* in the moist and dry treatments and the three diversity levels as measured by 12 productivity and biomass partitioning parameters (means ± SE). Relative growth rates (RGR) are given in g g^{-1}450 d^{-1}. Different small letters indicate significant differences between the diversity levels ($p<0.05$) in the moist or dry treatment. Asterisks indicate significant differences among the treatments (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Moisture treatment	Diversity level	No. of replicates [n]	Phytomass [g]	RS [g g^{-1}]	LA [m^2]	BA [cm^2]
moist	mono	7	88.06 ± 9.48 a	0.81 ± 0.03 a	0.33 ± 0.02 a	1.64 ± 0.10 a
	mix3	41	100.94 ± 5.74 a	0.71 ± 0.02 a	0.39 ± 0.02 a	1.80 ± 0.08 a
	mix5	7	105.41 ± 14.66 a	0.78 ± 0.05 a	0.40 ± 0.06 a	2.04 ± 0.24 a
dry	mono	7	72.11 ± 4.55 a	0.71 ± 0.03 a *	0.31 ± 0.01 a	1.38 ± 0.05 a ◦
	mix3	16	85.56 ± 8.99 a ◦	0.72 ± 0.03 a	0.35 ± 0.03 a	1.65 ± 0.14 a ◦
	mix5	7	86.19 ± 7.96 a	0.76 ± 0.04 a	0.37 ± 0.03 a	1.51 ± 0.12 a
Moisture treatment	Diversity level	No. of replicates [n]	L_{Shoot} [cm]	L_{Root} [cm]	LI_{Shoot} [%]	LI_{Root} [%]
moist	mono	7	108.49 ± 4.59 a	58.27 ± 3.81 a	100.31 ± 8.47 a	186.83 ± 18.76 a
	mix3	41	110.41 ± 3.12 a	57.43 ± 1.50 a	105.32 ± 5.39 a	182.60 ± 7.41 a
	mix5	7	104.63 ± 6.03 a	61.54 ± 3.76 a	93.19 ± 11.12 a	202.92 ± 18.53 a
dry	mono	7	92.39 ± 4.05 a *	48.67 ± 1.69 a *	70.59 ± 7.48 a *	139.51 ± 8.33 a *
	mix3	16	99.54 ± 3.21 a *	48.58 ± 1.59 a ***	83.80 ± 5.94 a *	139.01 ± 7.81 a ***
	mix5	7	95.99 ± 6.88 a	50.10 ± 3.81 a *	77.23 ± 12.71 a	146.60 ± 18.73 a *
Moisture treatment	Diversity level	No. of replicates [n]	BAI [%]	RGR_{above}	RGR_{below}	RGR_{total}
moist	mono	7	333.98 ± 27.66 a	5.29 ± 0.59 a	3.09 ± 0.46 a	3.98 ± 0.54 a
	mix3	41	375.46 ± 22.07 a	6.91 ± 0.50 a	3.16 ± 0.20 a	4.79 ± 0.31 a
	mix5	7	440.98 ± 62.87 a	6.61 ± 0.99 a	3.69 ± 0.74 a	4.97 ± 0.83 a
dry	mono	7	266.17 ± 14.30 a ◦	4.47 ± 0.28 a	2.04 ± 0.22 a ◦	3.08 ± 0.26 a
	mix3	16	336.11 ± 37.22 a	5.49 ± 0.69 a ◦	2.56 ± 0.38 a *	3.99 ± 0.52 a
	mix5	7	300.15 ± 31.24 a ◦	5.37 ± 0.64 a	2.72 ± 0.32 a	3.88 ± 0.45 a

Table A. 4.7. Growth performance of *Tilia cordata* in the moist and dry treatments and the three diversity levels as measured by 12 productivity and biomass partitioning parameters (means ± SE). Relative growth rates (RGR) are given in g g^{-1}450 d^{-1}. Different small letters indicate significant differences between the diversity levels ($p<0.05$) in the moist or dry treatment. Asterisks indicate significant differences among the treatments (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Moisture treatment	Diversity level	No. of replicates [n]	Phytomass [g]	RS [g g^{-1}]	LA [m^2]	BA [cm^2]
moist	mono	7	122.01 ± 6.20 a	1.12 ± 0.09 a	0.34 ± 0.02 a	3.73 ± 0.13 a
	mix3	40	160.66 ± 9.60 ab	1.09 ± 0.05 a	0.55 ± 0.03 b	4.51 ± 0.23 a
	mix5	8	200.17 ± 21.80 b	1.03 ± 0.09 a	0.61 ± 0.04 b	5.23 ± 0.45 a
dry	mono	7	107.26 ± 4.40 a ◦	1.01 ± 0.04 a	0.37 ± 0.01 a	3.16 ± 0.12 a **
	mix3	15	121.67 ± 10.25 a *	0.99 ± 0.06 a	0.48 ± 0.05 a	3.59 ± 0.27 a *
	mix5	7	110.67 ± 12.43 a **	1.07 ± 0.08 a	0.41 ± 0.05 a **	3.42 ± 0.28 a **

Moisture treatment	Diversity level	No. of replicates [n]	L_{Shoot} [cm]	L_{Root} [cm]	LI_{Shoot} [%]	LI_{Root} [%]
moist	mono	7	92.60 ± 3.70 a	104.03 ± 5.11 a	138.85 ± 3.62 a	195.79 ± 14.52 a
	mix3	40	102.29 ± 3.01 a	108.20 ± 2.80 a	155.13 ± 7.50 a	207.57 ± 7.98 a
	mix5	8	111.09 ± 5.40 a	113.20 ± 7.52 a	177.08 ± 13.46 a	221.82 ± 21.37 a
dry	mono	7	93.74 ± 1.49 a	86.19 ± 3.60 a *	133.82 ± 3.71 a	144.97 ± 10.21 a *
	mix3	15	98.12 ± 6.52 a	83.30 ± 2.61 a ***	144.75 ± 16.27 a	136.77 ± 7.43 a ***
	mix5	7	86.60 ± 7.88 a *	91.69 ± 7.37 a ◦	116.00 ± 19.66 a *	160.66 ± 20.96 a ◦

Moisture treatment	Diversity level	No. of replicates [n]	BAI [%]	RGR_{above}	RGR_{below}	RGR_{total}
moist	mono	7	209.49 ± 11.26 a	7.02 ± 0.40 a	4.07 ± 0.38 a	5.05 ± 0.37 a
	mix3	40	264.42 ± 18.88 a	9.39 ± 0.67 ab	5.29 ± 0.37 a	6.72 ± 0.46 ab
	mix5	8	322.42 ± 36.12 a	11.97 ± 1.21 b	6.70 ± 1.04 a	8.61 ± 1.05 b
dry	mono	7	155.66 ± 10.05 a **	6.14 ± 0.27 a	3.02 ± 0.21 a ◦	4.15 ± 0.21 a ◦
	mix3	15	190.01 ± 22.14 a *	7.66 ± 0.82 a	3.68 ± 0.30 a **	5.15 ± 0.47 a *
	mix5	7	176.51 ± 22.99 a **	6.23 ± 0.99 a **	3.22 ± 0.40 a *	4.32 ± 0.60 a **

Table A. 4.8. Growth performance of *Fagus sylvatica* in the moist and dry treatments and the three diversity levels as measured by 12 productivity and biomass partitioning parameters (means ± SE). Relative growth rates (RGR) are given in g g^{-1}450 d^{-1}. Different small letters indicate significant differences between the diversity levels ($p<0.05$) in the moist or dry treatment. Asterisks indicate significant differences among the treatments (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Moisture treatment	Diversity level	No. of replicates [n]	Phytomass [g]	RS [g g^{-1}]	LA [m^2]	BA [cm^2]
moist	mono	7	94.67 ± 11.24 a	0.90 ± 0.06 a	0.28 ± 0.03 b	1.62 ± 0.13 b
	mix3	40	71.87 ± 3.55 a	1.09 ± 0.03 b	0.20 ± 0.01 a	1.21 ± 0.05 a
	mix5	8	91.99 ± 15.57 a	1.21 ± 0.07 b	0.21 ± 0.03 ab	1.46 ± 0.18 ab
dry	mono	7	71.58 ± 6.49 a	1.03 ± 0.07 a	0.21 ± 0.02 a ◦	1.29 ± 0.06 a *
	mix3	17	61.47 ± 4.20 a ◦	1.05 ± 0.04 a	0.20 ± 0.01 a	1.13 ± 0.08 a
	mix5	7	63.44 ± 8.85 a	1.05 ± 0.12 a	0.19 ± 0.02 a	1.28 ± 0.13 a

Moisture treatment	Diversity level	No. of replicates [n]	L_{Shoot} [cm]	L_{Root} [cm]	LI_{Shoot} [%]	LI_{Root} [%]
moist	mono	7	98.61 ± 7.48 a	64.81 ± 2.67 a	167.22 ± 20.27 a	137.74 ± 9.79 a
	mix3	40	87.26 ± 2.86 a	67.23 ± 2.21 a	136.48 ± 7.75 a	146.50 ± 8.09 a
	mix5	8	85.35 ± 6.86 a	77.80 ± 5.19 a	131.30 ± 18.58 a	185.33 ± 19.03 a
dry	mono	7	74.90 ± 2.80 a *	57.97 ± 2.18 a ◦	102.99 ± 7.60 a *	112.64 ± 7.99 a ◦
	mix3	17	71.90 ± 3.24 a ***	55.69 ± 2.63 a **	94.84 ± 8.77 a ***	104.18 ± 9.64 a **
	mix5	7	71.19 ± 6.03 a	58.61 ± 4.70 a *	92.91 ± 16.35 a	114.97 ± 17.22 a *

Moisture treatment	Diversity level	No. of replicates [n]	BAI [%]	RGR_{above}	RGR_{below}	RGR_{total}
moist	mono	7	502.51 ± 48.29 b	7.09 ± 0.99 b	3.40 ± 0.55 a	4.84 ± 0.69 a
	mix3	40	351.51 ± 17.16 a	4.50 ± 0.29 a	2.75 ± 0.18 a	3.44 ± 0.22 a
	mix5	8	441.71 ± 65.65 ab	5.75 ± 1.30 ab	3.99 ± 0.76 a	4.68 ± 0.96 a
dry	mono	7	381.52 ± 21.02 a *	4.67 ± 0.58 a ◦	2.78 ± 0.28 a	3.61 ± 0.35 a
	mix3	17	321.76 ± 30.82 a	3.80 ± 0.36 a	2.15 ± 0.21 a *	2.71 ± 0.26 a *
	mix5	7	376.09 ± 49.76 a	4.10 ± 0.86 a	2.15 ± 0.39 a *	2.92 ± 0.55 a

Table A. 4.9. Pot-level water use efficiency (WUE) of tree assemblages differing in species composition and diversity in the moist and dry treatments (means ± SE, for no. of replicates see Table 1). WUE is given as total biomass per plant produced in the 450 d-experiment divided by the mean daily transpiration in June 2012 at peak transpiration (data after Lübbe et al., 2016). Different small letters indicate significant differences in WUE of the species or species combinations in the monospecific or mix 3 groups, or between the diversity levels. Asterisks in the dry treatment column mark significantly higher WUE in the dry than the moist treatment (*: p<0.05; **: p<0.01; ***: p<0.001).

Diversity level /	WUE [(g 450d^{-1})/(ml d^{-1})]	
Species combination	Moist	Dry
mono		
F. excelsior	0.58 ± 0.30 a	0.77 ± 0.13 b *
A. pseudoplatanus	0.52 ± 0.47 a	0.51 ± 0.13 a
C. betulus	0.44 ± 0.30 a	0.65 ± 0.16 ab *
T. cordata	0.49 ± 0.31 a	0.64 ± 0.13 ab *
F. sylvatica	0.47 ± 0.34 a	0.69 ± 0.15 ab **
mix 3		
A.p. - C.b. - F.e.	0.54 ± 0.18 a	0.61 ± 0.07 a
A.p. - C.b. - T.c.	0.48 ± 0.35 a	0.59 ± 0.14 a
A.p. - F.s. - F.e.	0.54 ± 0.43 a	0.64 ± 0.07 a
C.b. - F.s. - T.c.	0.49 ± 0.27 a	0.64 ± 0.11 a *
F.s. - F.e. - T.c.	0.53 ± 0.20 a	0.67 ± 0.09 a *
Diversity level		
mono	0.50 ± 0.13 a	0.65 ± 0.15 a ***
mix 3	0.52 ± 0.10 a	0.63 ± 0.10 a ***
mix 5	0.51 ± 0.13 a	0.63 ± 0.11 a *

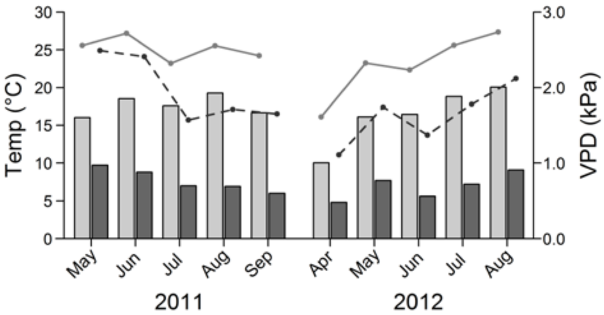

Figure A. 4.1. Temperature (bright bars, solid line) and vapor pressure deficit (dark bars, dashed line) at the experimental site in the summers of 2011 and 2012 (means per month). Lines give monthly means of daily maxima.

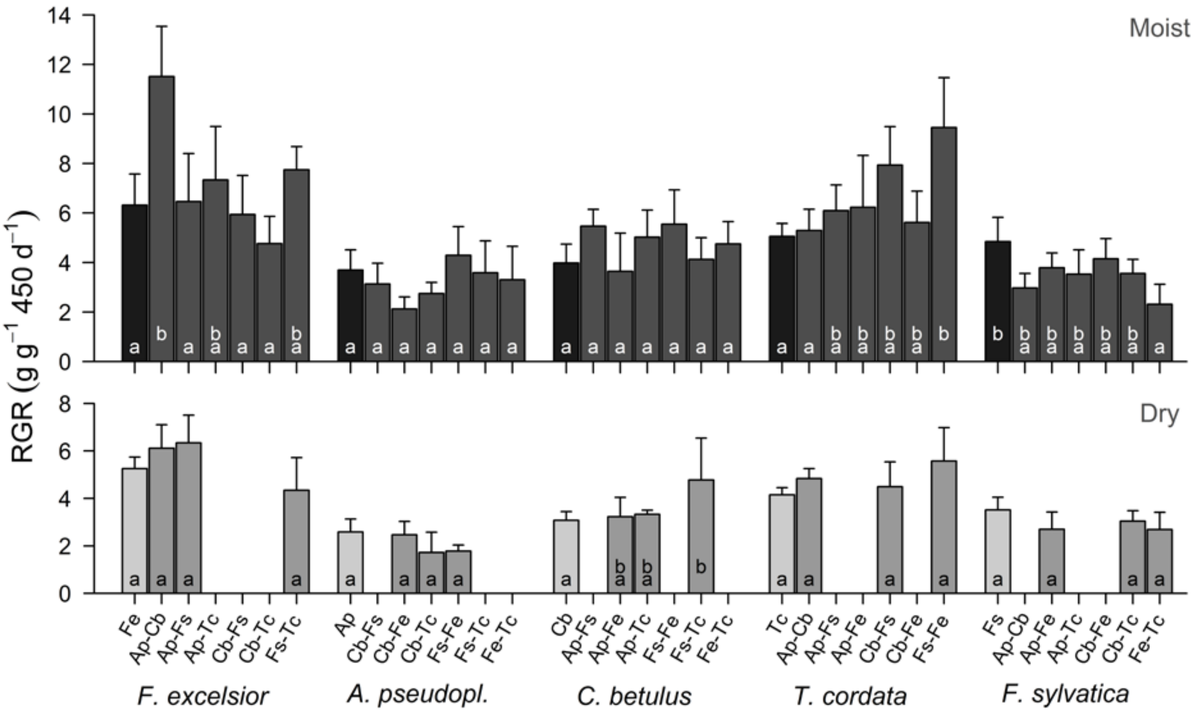

Figure A. 4.2. Relative growth rates of the five species either in monoculture (first bar in a bloc) or in the six different 3-species combinations in the moist (upper panel) and dry treatment (lower panel) (means ± SE of 7 or 6 replicate pots). In the dry treatment, only three 3-species combinations were realized. For species abbreviations see Table 1. Different letters indicate significant differences within a species ($p<0.05$).

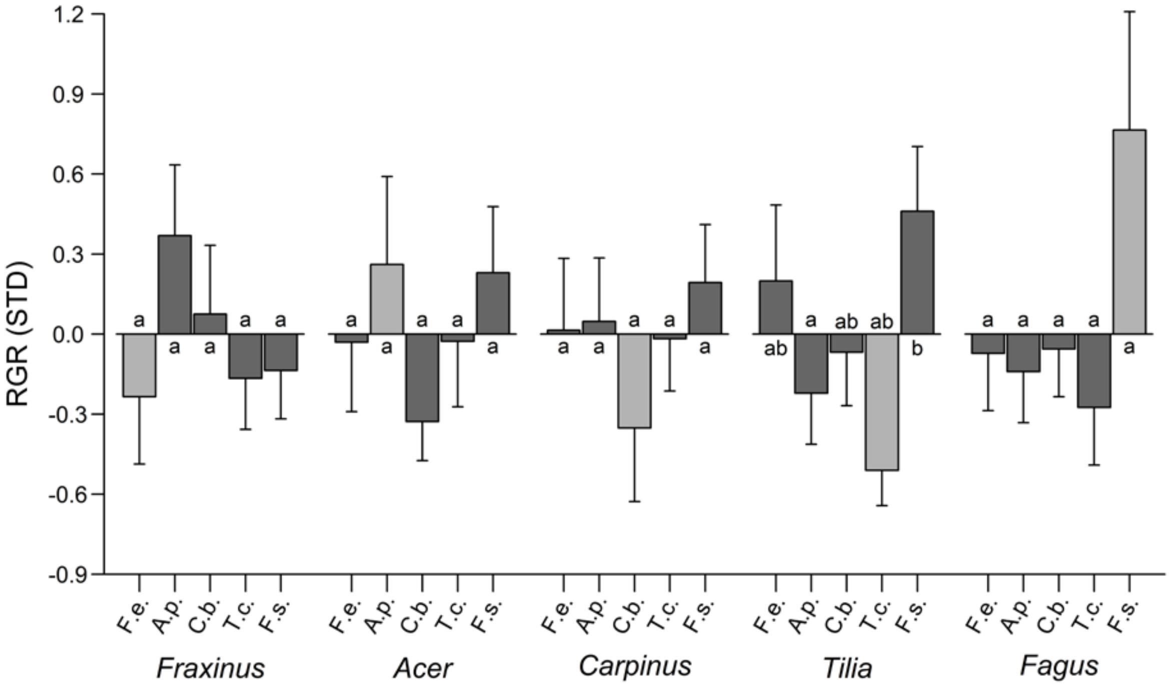

Figure A. 4.3. Relative growth rates of the five species in monoculture (grey bars) or mixture with the other four species (black bars) standardized to the mean performance of the species in all combinations (means ± SE). Different small letters indicate significantly different standardized RGR between the neighbor constellations for a species ($p<0.05$).

Chapter 5

Acclimation of leaf water status and stem hydraulics to drought and tree neighborhood: alternative strategies among saplings of five temperate deciduous tree species

Torben Lübbe · Bernhard Schuldt · Christoph Leuschner

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Abstract

Adjustment in leaf water status parameters and modification in xylem structure and functioning can be important elements of a tree's response to continued water limitation. In a growth trial with saplings of five co-occurring temperate broad-leaved trees species (genera *Fraxinus, Acer, Carpinus, Tilia* and *Fagus*) conducted in moist or dry soil, we compared the drought acclimation in several leaf water status and stem hydraulic parameters. Considering the extremes in the species sample, *F. excelsior* improved its leaf tissue hydration in the dry treatment through osmotic, elastic and apoplastic adjustment, while *F. sylvatica* solely modified its xylem anatomy, which resulted in increased embolism resistance at the cost of hydraulic efficiency. Our results demonstrate the contrasting response strategies of coexisting tree species and how variable trait plasticity among species can be. The comparison of plants grown either in monoculture or in 5-species mixture showed that the neighbourhood of a tree can significantly influence its hydraulic architecture and leaf water status regulation. Droughted *C. betulus* (and to a lesser extent: *A. pseudoplatanus*) plants developed a more efficient stem hydraulic system in heterospecific neighbourhood, while that of *F. sylvatica* was generally more efficient in conspecific than heterospecific neighbourhood.

We conclude that co-occurring tree species may develop a high diversity of drought response strategies, and exploring the full diversity of trait syndromes requires synchronous study of acclimation at the leaf and stem (and possibly also the root) levels and to consider physiological as well as morphological and anatomical modifications.

Keywords: *Drought tolerance, mixed tree assemblages, phenotypic plasticity, pressure-volume curve, tree hydraulics, turgor loss point, vulnerability to cavitation, wood anatomy.*

Introduction

Climate change scenarios predict that most ecosystems of the world will be exposed to more extreme environmental conditions in future (IPCC 2013). Forests are particularly vulnerable to a rise in the frequency and intensity of drought events which may reduce tree vitality, productivity and survival (Bréda et al. 2006, Allen et al. 2010, Zimmermann et al. 2015). The mechanisms underlying the tree drought response at the molecular, organ and tree level are not yet fully understood. Maintenance of hydraulic functioning in the root-to-leaf water flow path under water scarcity is certainly a key element of a successful drought tolerance strategy (Anderegg et al. 2011, Bartlett et al. 2012, Choat et al. 2012).

Whether forests can adapt to climatic change depends largely on which tree functional types are present, their specific trait syndromes, and the species' phenotypic plasticity (Valladares et al. 2007, Nicotra et al. 2010, Bussotti et al. 2015). Even in the same environment, different tree species have developed contrasting drought acclimation strategies which involve modification of leaf, stem and root traits (Kozlowski and Pallardy 2002, Maseda and Fernandez 2006). At the whole-plant level, trees may enhance water acquisition through a variety of adjustments of plant morphology and C allocation patterns, including a rise in the root:shoot ratio, increase in fine-root surface area, and deeper rooting (e.g. Brunner et al. 2015). Alternatively, the critical water demand can be lowered by reducing the transpiring leaf area (Le Dantec et al. 2000, Vilagrosa et al. 2003, Ogaya and Penuelas 2006).

Trees may also modify their water transport system in response to prolonged drought through physiological and structural adjustments in the root, stem and leaf xylem. At the leaf level, modification of cell water status through osmotic, elastic or apoplastic adjustments in response to water scarcity may help to maintain stomatal conductance, when Ψ_{leaf} is falling (Kozlowski and Pallardy 2002, Lenz et al. 2006, Bartlett et al. 2012). These adjustments directly influence the osmotic potential at turgor loss point (π_{tlp}) and the corresponding relative leaf water content ($\mathrm{RWC}_{\mathrm{tlp}}$), and help to reduce the risk of hydraulic failure in the leaf tissue.

Adjustment in xylem anatomical properties can also help to tolerate Ψ_{leaf} reductions while maintaining hydraulic functioning (Sperry et al. 2008, Schuldt et al. 2016). Several studies have demonstrated considerable intraspecific plasticity in vascular traits across water availability gradients (Fonti et al. 2013, Schreiber et al. 2015, Schuldt et al. 2016), which might increase hydraulic safety at the cost of hydraulic efficiency (McDowell 2011). Although vessel size has frequently been found to relate to hydraulic safety, both within and across species (Cai and Tyree 2010, Domec et al. 2010), the negative relation between these parameters is presumably a consequence of the close association between pit membrane properties and embolism resistance (Lens et al. 2013, Li et al. 2016). Yet, many studies have shown that a vessel diameter decrease reduces not only hydraulic conductivity, but also lowers the risk of embolism caused by air-seeding (Hacke and Sperry 2001, Sperry et al. 2006, Hajek et al. 2014). Another modification leading to higher safety in the vascular system is the increase of vessel density, which results in higher redundancy in the hydraulic pathway (Ewers et al. 2007, Schuldt et al. 2016). Plasticity in sapwood anatomical traits may thus enable plants to balance hydraulic safety with efficiency under conditions of water limitation (Vilagrosa et al. 2012, Fonti et al. 2013).

Although various studies have addressed species differences in the acclimation potential of either leaf hydration status (relating to cell wall properties and osmotic regulation), or stem and branch hydraulic traits in response to water deficits, studies considering both aspects and possible mutual interactions are scarce. While some recent results seem to indicate that the sensitivity of stomates to Ψ_{leaf} is related to xylem characteristics (Klein 2014), it remains unclear whether stem and leaf level responses are coordinated or not.

Soil water availability as a determinant of tree water status is certainly influenced by abiotic site characteristics and stand structural properties like tree size, plant density and species identity. However, the water budget of forests can be also altered by the tree community composition, the number and functional types of coexisting species and their degree of complementary resource use (Bravo-Oviedo et al. 2014, Forrester et al. 2014, 2015). Spatial and temporal differences in the water consumption of neighbouring trees of different species identity may lead to reduced interspecific competition for water, but they can also result in higher water consumption of mixed than monospecific assemblages and thus greater soil desiccation (e.g. Grossiord et al. 2014a). Tree individuals growing in proximity of water spenders may suffer from the higher consumption of these neighbours, while trees close to individuals with low transpiration may profit. Thus, the specific neighbourhood constellation in mixed stands may affect the water status of target trees and this effect could feed back on the hydraulic architecture and leaf water status regulation of these individuals. In fact, several recent studies provided evidence that trees of certain species are less susceptible to drought and may even be more productive, when growing in mixture as compared to monoculture (Lebourgeois et al. 2013, Pretzsch et al. 2013, Mölder and Leuschner 2014, del Río et al. 2014, Metz et al. 2015, Neuner et al. 2015). This should be the case when intraspecific competition for water is more intense than interspecific competition. A recent meta-analysis on the carbon isotope signature of latewood from different European forest types showed that higher tree species diversity can enhance drought resistance through positive neighbourhood effects, but this effect was only evident in drought-prone environments and not under conditions of ample water supply (Grossiord et al. 2014b). The roles of conspecific or heterospecific neighbours have mostly been investigated with respect to productivity, while functional traits related to carbon gain or water turnover have only rarely been investigated (Forrester et al. 2010, Kunert et al. 2012, Pollastrini et al. 2014). Furthermore, our understanding of neighbour effects on plant drought responses at the leaf and stem levels is limited.

Here, we present the results of a tree sapling experiment on the drought acclimation of five temperate broad-leaved tree species that were exposed to either conspecific or heterospecific competition. By examining drought-induced modification in leaf water status and stem xylem traits in the five co-occurring species with different pre-adaptation to drought, we aimed to clarify, whether temperate tree species confine trait modification either to the foliage level or to the woody conducting tissue. As we found in earlier studies relevant neighbourhood effects on the productivity and stem hydraulics of these tree species (Lübbe et al. 2015, 2016), we here investigate the relevance of tree neighbourhood effects on leaf water status regulation and stem hydraulics by comparing the drought acclimation of plants grown in monoculture with that in mixture. We measured important pressure-volume traits in the leaf tissue and analysed the anatomy of the stem vascular system and its embolism resistance. These data are complementary to measurements on stem hydraulic conductivity, leaf conductance and above- and belowground productivity conducted in the same plants and presented by Lübbe et al. (2015, 2016). We tested the hypotheses that (i) species identity is a more important source of variation in morphological and physiological traits than the effect of a severe drought, (ii) different tree species that co-occur in a common habitat develop plasticity in response to soil desiccation either mostly at the foliage level (leaf water status regulation) or at the stem level (xylem anatomy and hydraulic properties), but normally do not modify both, and (iii) morphological and physiological adjustments to drought depend in mixture, at least in certain species, on neighbour identity..

Material and methods

Experimental design

We conducted a replicated tree diversity experiment of 16 months duration (~450 days) from April 2011 to August 2012 in the Experimental Botanical Garden of the University of

Göttingen (51°33’ N, 9°57’ E, 177 m altitude). Five temperate broad-leaved tree species (*Acer pseudoplatanus* L. (sycamore maple), *Carpinus betulus* L. (European hornbeam), *Fagus sylvatica* L. (European beech), *Fraxinus excelsior* L. (European ash) and *Tilia cordata* Mill. (small-leaved lime)) were investigated, which represent a broad variety of tree functional types differing in light demand and shade tolerance, canopy architecture, mycorrhiza type, drought tolerance and successional status (Köcher et al. 2013, Legner et al. 2013). The 2-yr-old saplings had been reared from seed in a nursery close to Göttingen. The seed was collected from a few trees per species; this reduced the genetic variability of the experimental plants. The target plants were taken from a larger number of available plants and were selected on the basis of similarity in plant height and number of leaf buds. Nevertheless, the species differed slightly in initial height due to species differences in growth rate (height range: 40-60 cm, Lübbe et al. 2015). Each five saplings were planted in large pots (0.05 m^3 volume, height 0.35 m, diameter 0.58 m) filled with coarse-grained sand (98% sand, 1.8% silt, 0.2% clay). To arrange the plants at equal distance (~17 cm), four saplings were planted at the corners of a square placed on the pot surface (distance to pot walls: ~12 cm) and the fifth was positioned in the center.

For the purposes of this study, we selected monoculture pots (all five saplings of the same species) and 5-species-mixture pots (all five sampling from different species) from a more comprehensive set of available species combinations as described in Lübbe et al. (2016). Each combination was replicated at least 6-fold. In the 5-species mixture, the position of the saplings of different species identity was varied in the replicate pots in order to average over six different neighbourhood constellations.

The experiment consisted of a drought trial with two soil moisture levels (moist: ~21 vol. %, dry: ~12 %) with target values of volumetric soil water content (SWC) equaling ~95 % and ~57 % maximum field capacity, respectively. These targets were maintained by adding every 3-5 days the amount of water that had been lost through evapotranspiration. Thus, soil moisture fluctuated moderately between two subsequent irrigation events below the target moisture values. Accordingly, lowest soil matrix potentials reached -84 kPa in the moist and -869 kPa in the dry treatment, respectively. Soil moisture content and thus the amount of required irrigation water were determined by regular pot weighing with a mobile digital hanging scale. For achieving similar drought stress intensities at the end of each irrigation interval, the target values of SWC varied slightly between the replicates of a moisture treatment in order to avoid soil water over-exploitation and critical soil desiccation in pots with large trees and thus more water-consuming tree assemblages. For details of soil moisture determination and moisture control see Lübbe et al. (2016).

The pots were installed under a light-transmitting roof, which excluded all precipitation but altered the microclimate much less than a glasshouse. Photosynthetically active radiation (PAR) was reduced by ~ 30% compared to incident radiation. The pots were set up at random positions in a grid pattern for minimizing the impact of possible environmental gradients. Each pot was fertilized monthly with 4 ml Wuxal© solution (8.0% N, 8.0% P_2O_5, 6.0% K_2O) between May and September 2011 and with 6 ml from March to August 2012. All pots were randomized and set up in rows to minimize the possible impact of microclimatic heterogeneity. Details on soil water dynamics, nutrient supply and climate conditions are given in Lübbe et al. (2015, 2016).

Tree sampling design

Each six saplings per treatment (5 species × 2 soil moisture levels × 2 diversity levels × 6 replicates; 120 sampled plants in total) were investigated for leaf water status and hydraulic parameters by randomly selecting each one individual per species and pot. If possible, all physiological measurements were executed on the same tree individual. In case of invalid results, the measurements were usually repeated on another individual. The final harvest of the plants was carried out during 7 weeks in July and August 2012 by applying a rotating sampling scheme. In general, one replicate plant was sampled per treatment and week. Leaf samples for pressure-volume curve analysis were taken 1-2 d before the date of harvest. Shoot samples for the measurement of xylem vulnerability to cavitation and wood anatomical structure were taken at the time of harvest. A list of all traits measured, the corresponding acronyms and units is given in Table 5.1.

Pressure-volume curve analysis

Pressure-volume (P-V) curves were established by applying the pressure-chamber method according to Tyree and Hammel (1972). Fully developed single leaves or small terminal shoots were sampled early in the morning from the upper crown and the cut petioles or shoots were immediately placed in tap water, covered by plastic bags and allowed to rehydrate for 24h to 48h at 5 °C. Subsequently, basal twig segments or petiole tips were re-cut with a razor blade, sample weight at full saturation determined at a precision of 0.1 mg (FM_{sat}) and samples inserted in a pressure chamber (M1000, PMS Instrument Co., Albany, OR, USA).

After determining the initial leaf water potential (Ψ_{init}), only fully hydrated leaf samples (Ψ_{init} > -0.3 MPa) were processed. To reach higher pressure levels, samples were pressurized for 10 min and the petioles or twig segments were covered with Eppendorf cups containing cellulose strips to absorb and subsequently weigh the leaking fluid (L_t). Subsequently, samples were relaxed for 10 min by reducing the applied pressure by ca. 0.25 MPa before the actual leaf water potential was determined. Measurements started at 0.3 MPa and were stepwise increased by 0.3 MPa up to 2.7 MPa, followed by 0.2 MPa steps, until the target pressure of 3.5 MPa was reached. Finally, the weight of the dehydrated samples was determined (FM_{wilt}) and the samples were dried to constant mass (DM) at 70 °C for 72h in order to calculate total leaf water content (FM_{sat} – DM). Water lost by transpiration during the measurement (FM_{sat} - FM_{wilt} - ΣL_t) was equally assigned to the pressure steps to correct the measured values. The water potential at turgor loss point (π_{tlp}) and the corresponding relative water content (RWC_{tlp}) were received with the procedure described by von Willert (1995). The osmotic potential at full turgor (π_0) was received by extrapolating the linear segment of the curve by regression analysis to the y axis where RWC is 100%. The symplastic water fraction at saturation (S_f) was estimated as the x-intercept of the linear curve section with $\frac{1}{\Psi} = 0$, allowing to separate the dynamic water fraction S_f and the assumedly constant apoplastic water fraction (A_f). To calculate the ε value near full hydration ($\varepsilon_{\max}$), ΔP/ΔRWC' was obtained from the first 4 points of the P versus RWC-relationship based on the symplastic water fraction. Following Bartlett et al. (2012), we primarily analyzed the P-V curve parameters π_0, π_{tlp}, A_f, RWC_{tlp} and $\varepsilon_{\max}$.

Xylem resistance to cavitation

The Cavitron technique (Cochard et al. 2005) was applied to measure vulnerability to xylem cavitation in all species except for *F. excelsior*, which could not be processed with this technique due to the open-vessel artefact (Jansen et al. 2015). Immediately after harvest, samples of the terminal shoot were stored at 4 °C in a MICROPUR® solution (Katadyn, Wallisellen, Switzerland) and processed within 7 days. Samples were first flushed with the Xyl'em apparatus at 120 kPa (Bronkhorst, Montigny-les-Cormeilles, France) in order to remove all potential emboli and for determination of maximum hydraulic conductivity according to Sperry et al. (1988). Subsequently, the flushed samples were mounted in a custom-built rotor chamber of the Cavitron, which uses a commercially available centrifuge as basis (Sorvall RC-5C, Thermo Fisher Scientific, Waltham, MA, USA). Spinning velocities were defined and recorded using the CaviSoft software (version 2.1, University of Bordeaux, Bordeaux, France). Measurements started at a pressure level of -0.37 MPa and were iteratively increased until the percentage loss of conductivity (PLC) reached at least 90%. Sigmoid functions (Pammenter and Willingen 1998) were fitted for each branch segment to describe the relationship between PLC and xylem pressure (vulnerability curve, VC) using the expression $\mathrm{PLC} = 100/(1 + \exp(s/25 \times (P_\mathrm{i} - P_{50})))$, where P_i is the initial pressure level, P_{50} (MPa) the xylem pressure causing 50% loss of conductivity and s (% MPa^{-1}) the slope of the curve at the inflexion point. The xylem pressures causing 88% loss of conductivity (P_{88}) was additionally calculated according to Domec and Gartner (2001).

Wood anatomical analysis

Transverse sections of the basipetal end of the shoot samples were stained with safranin (1% in 50% ethanol, Merck, Darmstadt, Germany) and cut with a sliding microtome (G.S.L.1, Schenkung Dapples, Zürich, Switzerland). The total transverse sections of the samples were digitalized at ×100 magnification using a stereomicroscope equipped with an automatic stage (SteREOV20, Carl Zeiss MicroImaging GmbH, Jena, Germany; Software: AxioVision v4.8.2, Carl Zeiss MicroImaging GmbH) and image processing was performed using Adobe Photoshop CS2 (Version 9.0, Adobe Systems Inc., San Jose, CA, USA) and the particle analysis function of ImageJ (v1.44p, http://rsb.info.nih.gov/ij). For all subsequent calculations, the complete xylem cross-section without pith and bark was analyzed, yielding on average 3,578 (*Fraxinus*, moist) to 15,201 (*Tilia*, dry) measured vessels per branch sample. Measured parameters included relative vessel lumen area (A_lumen, %), i.e. the ratio of cumulative lumen area to sapwood area, vessel density (VD, n mm^{-2}), the idealized vessel diameter (D, µm) obtained from major (a) and minor (b) vessel radii according to Lewis & Boose (1995) as $D = (32 \times (a \times b)^3/(a^2 + b^2))^{1/4}$, and hydraulically-weighted vessel diameter (D_h, µm) according to Sperry et al. (1994) as $D_\mathrm{h} = \Sigma D^5/\Sigma D^4$. Subsequently, the potential conductivity (K_p, kg m^{-1} MPa^{-1} s^{-1}) was calculated according to the Hagen–Poiseuille equation as $K_\mathrm{p} = (((\pi \times \Sigma r4)/8\eta) \times \rho)/A_\mathrm{xylem}$, where η is the viscosity (1.002×10^{-9} MPa s) and ρ the density of water (998.2 kg m^{-3}), both at 20 °C, and A_xylem (m^2) the corresponding xylem area without pith and bark.

Table 5.1. List of main variables with definition and units employed.

Parameter	Unit	Description
Leaf hydration (Pressure-Volume curve traits)		
π_0	MPa	Leaf osmotic potential at full tugor
π_{tlp}	MPa	Leaf water potential at turgor loss point
RWC_{tlp}	%	Relative water content at turgor loss point
A_f	%	Apoplastic water fraction
ε_{max}	MPa	Maximum modulus of elasticity, calculated from symplastic water content
Leaf conductance		
Gs	$mmol\ m^{-2}\ s^{-1}$	Stomatal conductance
$\delta^{13}C$	‰	Foliar carbon isotope signature
Xylem structural traits (Wood anatomical traits)		
A_{Lumen}	%	Lumen fraction of cross-sectional sapwood area
VD	n/mm^2	Vessel density
D	µm	Mean vessel diameter
D_h	µm	Hydraulically weighted vessel diameter
Xylem hydraulic properties		
K_s	$kg\ m^{-1}\ MPa^{-1}\ s^{-1}$	Empirical hydraulic conductivity of xylem
K_p	$kg\ m^{-1}\ MPa^{-1}\ s^{-1}$	Potential hydraulic conductivity of xylem
P_{50}	MPa	Water Potential inducing 50% loss of hydraulic conductance
P_{88}	MPa	Water Potential inducing 88% loss of hydraulic conductance

Statistical analysis

Statistical analyses were executed in R version 3.0.0 (R Core Team, 2012). We applied three-way analysis of variance (ANOVA) to test for effects of species identity in possible interaction with soil moisture and neighbour constellation on physiological response variables. Tukey contrasts (*glht* procedure, *multcomp* package) were used for multiple comparisons to detect species differences in traits within each soil water treatment. Moreover, we used 2-way ANOVA models to investigate the effects of drought and mixture on trait performance for each species individually. Model residuals were tested for normality (Shapiro–Wilk test) and equality of variances (Levene's test). In case of eminent violation of assumed homoscedasticity (as in the wood anatomy parameters), the ANOVAs were adjusted by applying a heteroscedasticity-corrected coefficient covariance matrix (*Anova*, *car* package). Pairwise comparisons among soil moisture treatments and diversity levels were carried out with Student's t-test, Welch's t-test or a Mann-Whitney U-test depending on the data structure.

For comparing the plasticity between different sapwood- and leaf-related traits in response to soil drought, we calculated the response index (RI, or plasticity index) as the difference between the maximum and minimum mean value of a variable (i.e. the difference between moist and dry treatment), divided by the maximum mean value (Valladares et al. 2006, Quero et al. 2006). Six leaf-related and eight stem-related traits (leaf hydration traits, wood anatomical traits and xylem functional traits, respectively) were applied for this calculation. The relative values of RWC_{tlp} and A_f were replaced by absolute values in equivalent units, i.e. the amount of foliar water at turgor loss and the apoplastic water content per gram foliar dry mass, respectively. For assessing the plasticity in drought-response traits of a plant's foliar and woody tissue, we compared the plasticity indices of both tissue types.

Results

Tree species differences in leaf water status and xylem hydraulics

Table 5.2. Physiological and structural plant traits of the five tree species for the two soil moisture treatments (moist and dry). Given values are means ± SE, capital letters indicate differences among species at a significance level of $p<0.05$. Significant differences among moisture treatments are shown in Table 5.3.

	π_0		π_{tlp}		RWC_{tlp}	
	Dry	Moist	Dry	Moist	Dry	Moist
F. excelsior	-2.12 ± 0.05 C	-1.79 ± 0.07 B	-2.52 ± 0.07 C	-2.21 ± 0.08 AB	0.86 ± 0.01 BC	0.82 ± 0.01 B
A. pseudopl.	-1.69 ± 0.03 A	-1.68 ± 0.05 AB	-2.01 ± 0.05 A	-2.01 ± 0.07 A	0.87 ± 0.01 C	0.86 ± 0.01 B
C. betulus	-2.06 ± 0.03 C	-2.02 ± 0.05 C	-2.59 ± 0.05 C	-2.59 ± 0.05 C	0.85 ± 0.01 BC	0.82 ± 0.02 B
T. cordata	-1.56 ± 0.04 A	-1.52 ± 0.03 A	-2.27 ± 0.07 B	-2.26 ± 0.07 AB	0.78 ± 0.01 A	0.75 ± 0.01 A
F. sylvatica	-1.90 ± 0.06 B	-1.79 ± 0.08 B	-2.49 ± 0.07 C	-2.35 ± 0.10 BC	0.82 ± 0.01 AB	0.83 ± 0.01 B
	A_f		ε_{max}		A_{Lumen}	
	Dry	Moist	Dry	Moist	Dry	Moist
F. excelsior	0.13 ± 0.03 A	0.07 ± 0.02 A	18.81 ± 1.86 C	13.34 ± 1.08 B	3.67 ± 0.26 A	3.53 ± 0.29 A
A. pseudopl.	0.15 ± 0.02 A	0.14 ± 0.02 AB	14.77 ± 1.59 BC	16.74 ± 1.59 BC	5.49 ± 0.33 AB	6.00 ± 0.39 AB
C. betulus	0.28 ± 0.03 B	0.22 ± 0.05 AB	15.56 ± 0.90 BC	18.19 ± 2.00 C	7.50 ± 0.49 B	6.63 ± 0.27 B
T. cordata	0.30 ± 0.02 B	0.25 ± 0.04 B	6.55 ± 0.41 A	6.13 ± 0.49 A	13.70 ± 1.15 C	13.84 ± 1.52 C
F. sylvatica	0.24 ± 0.04 B	0.27 ± 0.06 B	12.44 ± 1.25 B	12.29 ± 1.41 B	12.97 ± 0.48 C	13.59 ± 0.82 C
	VD		D		D_h	
	Dry	Moist	Dry	Moist	Dry	Moist
F. excelsior	56.19 ± 6.97 A	44.13 ± 3.92 A	24.91 ± 0.82 AB	25.82 ± 1.20 AB	80.41 ± 1.57 C	70.66 ± 2.13 C
A. pseudopl.	91.13 ± 5.41 B	90.83 ± 6.36 B	26.58 ± 0.36 BC	27.46 ± 0.61 B	36.46 ± 1.08 B	35.90 ± 0.93 AB
C. betulus	146.97 ± 9.35 C	119.21 ± 6.03 B	22.96 ± 0.56 A	23.66 ± 0.52 A	36.83 ± 1.74 B	39.65 ± 0.81 B
T. cordata	200.97 ± 13.86 D	207.87 ± 22.20 C	27.41 ± 0.26 C	27.78 ± 0.29 B	32.12 ± 0.58 A	32.71 ± 0.69 A
F. sylvatica	206.11 ± 7.26 D	185.54 ± 6.75 C	26.66 ± 0.46 BC	28.23 ± 0.59 B	36.21 ± 0.60 B	38.85 ± 0.82 B
	K_p		P_{50}		P_{88}	
	Dry	Moist	Dry	Moist	Dry	Moist
F. excelsior	4.03 ± 0.35 B	3.65 ± 0.50 B	NA ± NA -	NA ± NA -	NA ± NA -	NA ± NA -
A. pseudopl.	1.81 ± 0.15 A	1.96 ± 0.17 A	-3.76 ± 0.13 A	-3.70 ± 0.10 B	-4.81 ± 0.22 B	-4.49 ± 0.10 A
C. betulus	2.14 ± 0.28 A	2.15 ± 0.11 A	-5.13 ± 0.09 B	-4.90 ± 0.15 C	-6.07 ± 0.15 C	-5.86 ± 0.18 B
T. cordata	3.73 ± 0.39 B	3.91 ± 0.48 BC	-3.56 ± 0.11 A	-3.22 ± 0.12 A	-4.17 ± 0.11 A	-3.94 ± 0.16 A
F. sylvatica	4.22 ± 0.24 B	5.25 ± 0.55 C	-3.83 ± 0.11 A	-3.13 ± 0.14 A	-5.06 ± 0.20 B	-4.22 ± 0.19 A

In all investigated leaf water status and stem hydraulic parameters, species identity was the most influential factor according to 3-way ANOVA (Table A.5.1 in the Appendix). The majority of species differences were significant and certain differences were large (Table 5.2). The modulus of leaf cell wall elasticity near maximum turgor (ε_{max}), for instance, was remarkably low in *T. cordata* (~6.3 MPa) and at least twice as high in the other four species. *C. betulus* had the lowest mean leaf osmotic potential at full turgor (π_0; <-2 MPa) and also the by far lowest xylem pressures causing 50% (P_{50}; <-4.9 MPa) or 88% loss of stem hydraulic conductivity (P_{88}; <-5.8 MPa). The wood of ring-porous *F. excelsior* was characterized by very large hydraulically-weighted vessel diameters (D_h; >70 µm, Table 2) despite a particularly small lumen-to-sapwood area ratio (A_{lumen}; <4 %) and low vessel density (VD; <50 n mm^{-2}). *F. sylvatica* showed the highest potential hydraulic conductivity (K_p, >4 kg m^{-1} MPa^{-1} s^{-1}), which was about twice as high than that of *A. pseudoplatanus* and *C. betulus* (~2 kg m^{-1} MPa^{-1} s^{-1}).

Table 5.3. Means ± SE of selected traits in the monoculture (solid bars) and mixture (hatched bars) and the moist (dark bars) and dry treatment (light bars) for the five species. Different capital letters indicate differences between plants of a species grown in monoculture or in tree mixture across both levels of soil water availability significant at p<0.1. Asterisks mark significant tree mixture effects for a species within the same soil moisture treatment. Significance levels: °: p<0.10, *: p<0.05, **: p<0.01. Differences between the moist and dry treatment that were significant only in the monocultures or the mixtures are given in Table A2.

	Drought					Mixture					Interaction				
Species/ Parameter	*F. excelsior*	*A. pseudopl.*	*C. betulus*	*T. cordata*	*F. sylvatica*	*F. excelsior*	*A. pseudopl.*	*C. betulus*	*T. cordata*	*F. sylvatica*	*F. excelsior*	*A. pseudopl.*	*C. betulus*	*T. cordata*	*F. sylvatica*
π_0	↓***														
π_{tlp}	↓**							↓*							
RWC_{tlp}	↑**			↗											
A_f	↗								↑*						
ε_{max}	↑*											*			
G_s	↓**	↓*	↓***	↓*	↓***	↑**									
$\delta^{13}C$	↑***	↑*	↑***	↑*	↗	↓*				↘					
A_{Lumen}												*			
VD			↑*		↗							*			
D					↓*	↗							***		
D_h	↑**		↓*		↓*			↑**				*	***		°
K_p					↘							**	**		
K_s		↘	↓**		↓*	↑*			↘				***		
P_{50}				↓*	↓**									**	
P_{88}					↓**			↑*							

Drought adjustments at the stem and leaf level

Two-way ANOVA on pressure-volume traits showed for *F. excelsior* significant osmotic and elastic adjustment under drought exposure (Table 5.3, Table A.5.3); π_0 and leaf water potential at turgor loss point (π_{tlp}) decreased significantly from the moist to the dry treatment by 0.33 and 0.31 MPa, respectively ($P<0.001$ and $P<0.01$), while ε_{max} was by 41% larger in the droughted plants (13.3 vs. 18.8 MPa, $P<0.05$). None of the other four species showed significant osmotic or elastic adjustment at the leaf level. In *F. excelsior*, RWC_{tlp} was significantly higher in the dry treatment; this was not the case in the other species.

F. sylvatica was the species with most consistent modification of xylem-related properties in response to soil desiccation (Table 5.3, Table A.5.3). In this species, *D* (28.2 vs. 26.7 µm; -5%) as well as D_h (38.9 vs. 36.2 µm; -7%) decreased significantly ($P<0.05$) in conjunction with an increase in embolism resistance (P_{50} and P_{88}) by 18% (P_{50}, reduction by 0.70 MPa) or 17% (P_{88}, reduction by 0.85 MPa), respectively. Similar to *F. sylvatica*, *C. betulus* showed a higher VD (by 20%) under dry than under moist conditions (147 vs. 119 n mm^{-2}), and D_h decreased by 7% from 39.7 to 36.8 µm ($P<0.05$). However, this was not mirrored in a significant decline neither in *D*, K_p nor in P_{50} (Table 5.3, A.5.2, A.5.3). In *T. cordata*, in

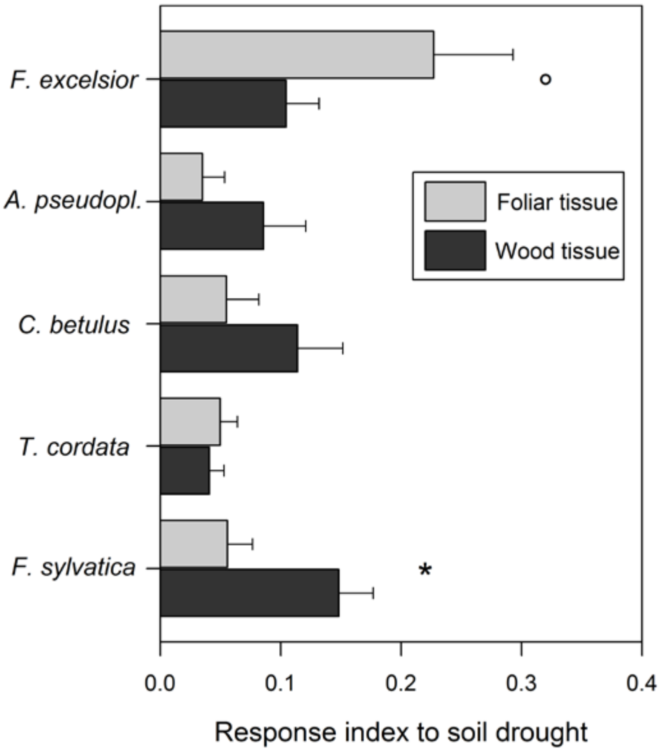

Figure 5.1. Mean values ± SE of response indices (RI) to the drought treatment for six leaf-related (leaf hydration incl. $\delta^{13}C$) and eight stem-related traits (wood anatomy and xylem functioning) of the five tree species. Asterisks mark significant differences between RI at the leaf- and the wood-level (°: p<0.1, *: p<0.05). Please note that for *F. excelsior* no data on cavitation vulnerability were available.

contrast, xylem anatomical traits were not different between the two moisture treatments; only P_{50} was by 10% more negative under dry conditions (reduction by 0.30 MPa, $P<0.05$). In *A. pseudoplatanus*, significant effects of drought on xylem anatomical or vulnerability traits were lacking when considering the pooled sample. In contrast to all other species, *F. excelsior* increased D_h by 14% (70.7 vs. 80.4 µm, $P<0.01$) under dry conditions.

The susceptibility to drought as expressed by the response index to soil drought (RI) was generally higher for leaf hydraulic traits than for xylem properties in *F. excelsior* and *T. cordata*, while this ratio was reversed (higher susceptibility of xylem properties) in *A. pseudoplatanus, C. betulus* and *F. sylvatica* (Figure 5.1). The difference between the RI means of leaf and sapwood traits was significant in *F. sylvatica* ($P<0.05$) and marginally significant in *F. excelsior* ($P<0.10$).

Neighbor effects on leaf water status and their interaction with soil moisture

The neighbourhood of a plant (i.e. conspecific vs. heterospecific) had a significant influence on certain leaf water status parameters in three of the five species (Table 5.3). In *C. betulus*, π_{tlp} was by 6% lower in plants grown with heterospecific neighbours as compared to conspecific neighbours (-2.51 vs. -2.66 MPa, $P<0.05$, Figure 5.2). The apoplastic water fraction (A_f) in *T. cordata* leaves was significantly higher (by 38 %) in plants grown in mixed assemblages than in monocultures (22.7% vs. 31.4%, $P<0.05$). In *A. pseudoplatanus*, none of the tested P-V traits was influenced by the type of neighbourhood, but the significant interaction term 'Drought × Mixture' in ε_{max} (Table 5.3, $P<0.05$) indicates that potential neighbourhood effects on P-V traits seem to act in opposite direction in the moist and dry treatments. In fact, ε_{max} was significantly higher (by 51 %) in this species when grown with heterospecific neighbours (19.7 vs. 13.0 MPa, $P<0.05$) in the moist treatment (Figure 5.2, Table 5.4, Table A.5.3).

In xylem-related traits, direct mixture effects were observed in *C. betulus* and *F. excelsior* (Table 5.3); the latter species tended to increase D by 11% when grown with heterospecific neighbours (from 24.0 to 26.8 µm, $P<0.10$). In *C. betulus*, not D but D_h was significantly increased in mixture (from 36.5 to 40.3 µm, $P<0.01$), while the increase in P_{88} (from -6.2 to -5.7 MPa, $P<0.05$) indicates higher vulnerability to drought (Figure 5.2). The frequent occurrence of significant interactions between soil moisture and neighbourhood, especially in *A. pseudoplatanus* and *C. betulus*, indicates opposite effects of tree neighbourhood on xylem anatomy and hydraulics in the two moisture treatments (Table 5.3). D (21.4 vs. 24.3 µm,

Table 5.4. Significances of mixture effects on the physiological plasticity of the five tree species in the two soil moisture treatments according to pairwise comparisons with Student's t-test or Mann-Whitney U-test. Arrows show direction of shift in mean values (upward: significant increase, downward: significant decrease, diagonal: increase/decrease at p<0.10), significance level: *: p<0.05, **: p<0.01, ***: p<0.001. For *F. excelsior*, no data on cavitation resistance are available.

	Moist					Dry				
Species/ Parameter	*F. excelsior*	*A. pseudopl.*	*C. betulus*	*T. cordata*	*F. sylvatica*	*F. excelsior*	*A. pseudopl.*	*C. betulus*	*T. cordata*	*F. sylvatica*
π_0										
π_{tlp}										
RWC_{tlp}										
A_f										
ε_{max}	↗	↑ *								
Gs						↑ *	↘			
δ13C	↓ *					↓ *		↘		↓ *
A_{Lumen}		↘								
VD		↘								
D			↘				↑ *	↑ **		
D_h					↘		↑ *	↑ ***		
K_p							↑ **	↑ **		
K_s	↗		↓ *					↑ *		
P_{50}				↑ **				↑ **		
P_{88}					↓ *			↑ *		

$P<0.01$), D_h (32.9 vs. 41.8 µm, $P<0.001$) and K_p (1.4 vs. 2.8 kg m^{-1} MPa^{-1} s^{-1}, $P<0.01$) all increased in mixture for *C. betulus* under dry conditions (Table 5.4, Figure 5.2). In parallel, the two measures of embolism resistance P_{50} (-5.4 vs. -4.9 MPa, $P<0.01$) and P_{88} (-6.4 vs. -5.7 MPa, $P<0.05$) increased in this species in response to heterospecific neighbourhood in the dry treatment. Similar to *C. betulus*, saplings of *A. pseudoplatanus* growing in mixture in the dry treatment showed larger D (25.8 vs. 27.2 µm, $P<0.05$), D_h (33.6 vs. 38.4 µm, $P<0.05$) and K_p values (1.4 vs. 2.1 kg m^{-1} MPa^{-1} s^{-1}, $P<0.01$) than in monoculture. In the moist treatment, only tendencies were visible. In addition, tree mixture effects were detected in *F. sylvatica* and *T. cordata* in the moist treatment (Table 5.4). In *F. sylvatica*, P_{88} significantly decreased (from -3.8 to -4.6 MPa, $P<0.05$), while the striking decline in K_p by 29% (from 6.2 to 4.4 kg m^{-1} MPa^{-1} s^{-1}, Table 5.4, Figure 5.2) was not significant. *T. cordata* had by 17% less negative P_{50} value in mixture than in monoculture (-3.5 to -2.9 MPa, $P<0.01$) in the moist treatment.

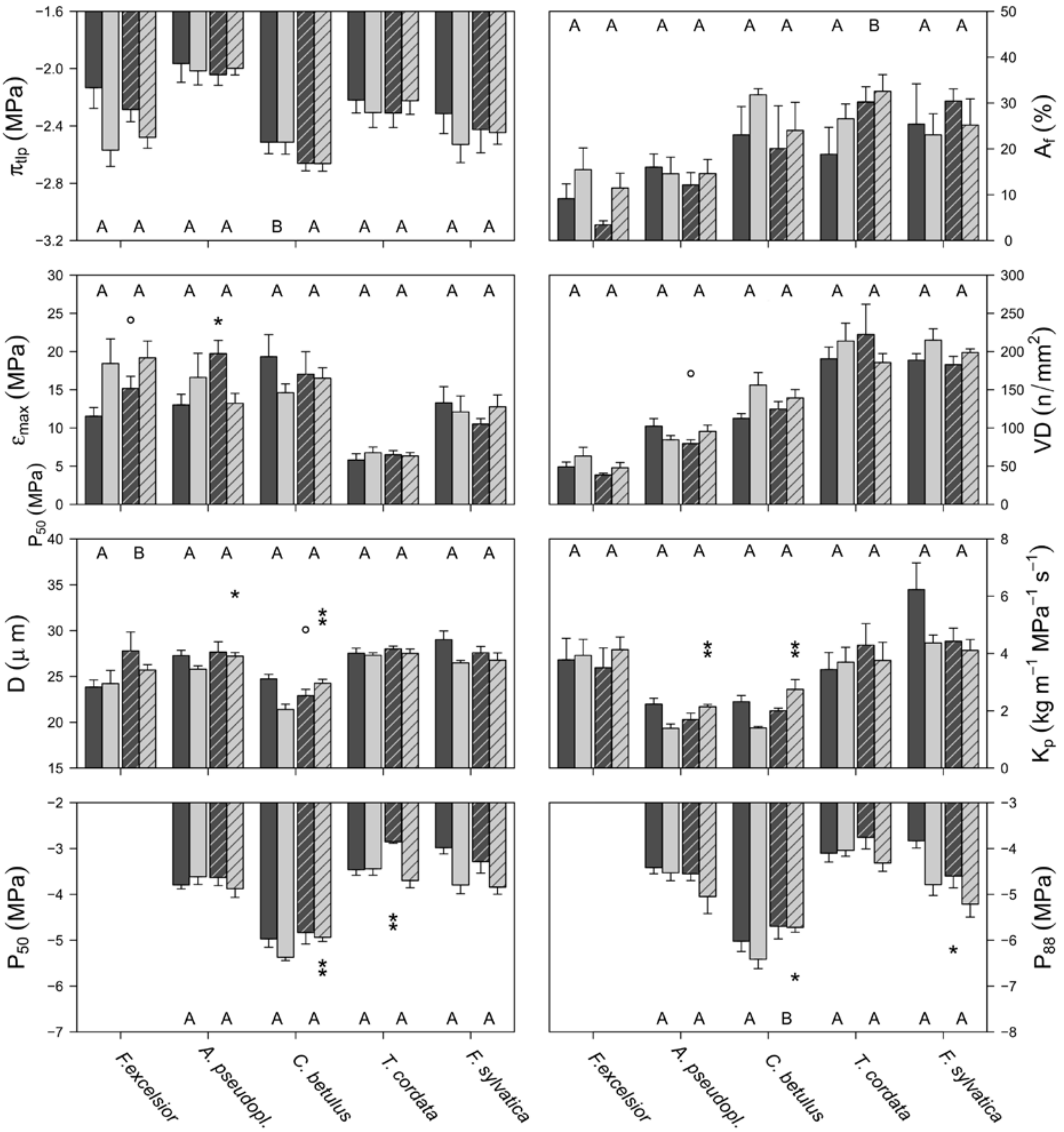

Figure 5.2. Means ± SE of selected traits in the monoculture (solid bars) and mixture (hatched bars) and the moist (dark bars) and dry treatment (light bars) for the five species. Different capital letters indicate differences between plants of a species grown in monoculture or in tree mixture across both levels of soil water availability significant at p<0.1. Asterisks mark significant tree mixture effects for a species within the same soil moisture treatment. Significance levels: °: p<0.10, *: p<**0**.05, **: p<0.01. Differences between the moist and dry treatment that were significant only in the monocultures or the mixtures are given in Table A.5.2.

Discussion

Species-specific differences in plant physiological traits

In accordance with our first hypothesis, species identity was by far the most influential factor explaining the variance of leaf water status and stem hydraulic traits. Although the five species are co-occurring in mixed forests in Central Europe (Leuschner et al. 2009), they represent a fairly broad spectrum of functional types with respect to growth strategy (early-/mid-successional vs. late-successional), hydraulic system (diffuse-porous vs. ring-porous) and drought tolerance (sensitive to relatively insensitive; Köcher et al. 2009, Ellenberg & Leuschner 2010). The high cell sap concentration of osmotic substances in *C. betulus* as visible in a leaf osmotic potential at full turgor (π_0) value <-2.0 MPa and the relatively low turgor loss point (π_{tlp} <-2.5 MPa) in combination with high resistance to xylem cavitation (P_{50} <-4.8 MPa) indicate that this species was the most drought-resistant in our sample. In fact, all other species had higher (more positive) values of π_0, π_{tlp}, P_{50} and P_{88}. In contrast, the ability to accumulate osmolytes in leaf tissue was much lower and the cavitation resistance in the stem sapwood weaker in the saplings of *A. pseudoplatanus* and *T. cordata* (the latter species also showed the steepest growth decline in response to water scarcity, Lübbe et al. 2015) and are thus considered as the most drought-vulnerable species of our sample. In the majority of investigated physiological and anatomical traits, the drought treatment was (besides species identity) the second-most important factor causing trait variation. An exception was hydraulically-weighted vessel diameter (D_{h}) and the derived potential conductivity (K_{p}), which were influenced more by the type of neighbourhood (or an interaction with this factor) than by the drought treatment itself.

Drought responses at the leaf and stem levels

Our data on tree water consumption and plant growth rate evidence a marked drought effect on all species, which demonstrates the effectiveness of soil desiccation in our drought trial (Lübbe et al. 2015, 2016). To cope with the drought stress, trees may produce new organs with better drought acclimation by forming smaller leaves with thicker cuticle or by producing new sapwood with smaller conduit diameters, or postpone tissue dehydration by elastic or osmotic adjustment in the existing leaves or roots (e.g. Bartlett et al. 2012, Fonti et al. 2013). Plasticity in morphological and physiological traits represents an insurance of the plant to maintain its fitness and ensure survival under unfavourable climatic conditions. Plants with restricted plasticity in physiological traits may rely on the modification of morphological properties or shifts in carbon allocation patterns, or alternatively may face severe growth decline and fitness loss. It is likely that some drought-induced modifications of the tree's anatomy, morphology and physiology occur synchronously at leaf, stem and root levels, but it is not well known how these processes are interacting in trees under drought stress, and whether there is a trade-off between leaf and stem response, or if certain species mostly restrict a plastic response to one of these organs. In our sample, only *F. excelsior* revealed a plastic response to water scarcity at the leaf level, while *F. sylvatica* and *C. betulus* modified their stem wood tissue upon drought exposure but not the foliar P-V parameters. Despite the long controversy about the roles of osmotic, elastic and apoplastic adjustment and their importance for leaf water status regulation (Kozlowski and Pallardy 2002, Lenz et al. 2006), it appears that both leaf water potential (π_{tlp},) as well as the relative water content at turgor loss (RWC_{tlp}) are traits controlling the drought tolerance of plants (Bartlett et al. 2012). While π_{tlp} is closely related to π_0 (Bartlett et al. 2012), elastic adjustment (in combination with apoplastic adjustment) was shown to be the main factor, which allows maintaining a high relative water content at turgor loss point, thus preventing cell dehydration below a dangerous threshold.

In *F. excelsior*, all important leaf water status parameters were markedly altered by water limitation, revealing pronounced osmotic, elastic and also apoplastic adjustment. Increased solute concentration in the symplast as well as enhanced cell wall stiffness under dry conditions is well documented for this species and seems to represent a key element of its drought tolerance strategy (Guicherd et al. 1997, Peltier and Marigo 1999, Marigo et al. 2000). Increased ε_{max} values of drought-treated *F. excelsior* saplings in conjunction with an increase in RWC_{tlp} relative to the moist treatment can thus be interpreted as confirmation of the cell water conservation hypothesis (Cheung et al. 1975), which agrees with the interpretation of Peltier and Marigo (1999).

In contrast, *F. sylvatica* showed the highest plasticity in xylem anatomical and hydraulic properties in response to drought. This species reduced its vessel diameter (*D*) in the dry treatment, while vessel density (VD) was increased causing a decline in specific conductivity (K_{s}) and thus in hydraulic efficiency (Lübbe et al. 2016). This confirms earlier results on the marked influence of water availability on conduit size in *F. sylvatica* (Sass and Eckstein 1995, Caquet et al. 2009). Both anatomical adjustments are supposed to enhance the resistance to drought-induced xylem cavitation through increased capillary forces in narrower vessels; these adjustments act in combination with increased vessel density and hence pathway redundancy (Fonti et al. 2013, Schuldt et al. 2016). Correspondingly, drought-exposed *F. sylvatica* saplings in fact developed a more drought-resistant hydraulic system in the stem wood. A similar hydraulic acclimation was found in mature beech trees along a precipitation gradient (Schuldt et al. 2016), in accordance with the high phenotypic plasticity in cavitation resistance observed in *F. sylvatica* in earlier studies (Herbette et al. 2010, Wortemann et al. 2011). The reduction in growth performance and hydraulic efficiency of *F. sylvatica* saplings in dry soil (Lübbe et al. 2015) confirms the hypothesised trade-off in hydraulic functioning, by which higher safety is achieved at the cost of efficiency when water is scarce (McDowell 2011). Although we could confirm this trade-off for our sample, it is not necessarily valid at the global scale (Gleason et al. 2016).

A similar, but less pronounced, drought adjustment was found for the xylem properties of *C. betulus* with a VD increase and a concomitant reduction in D_h. The latter was partially reflected in the large K_p decrease (by 40%) in the monoculture. However, this anatomical modification did not lead to increased cavitation resistance in *C. betulus* under dry conditions. In comparison with the other species, *A. pseudoplatanus* showed only minor or no physiological adjustments in the dry treatment. Cavitation resistance tended to increase and K_p decreased by 40% in response to drought in the monoculture, which is consistent with the observed reduction in K_s (Lübbe et al. 2016).

In conclusion, the five investigated tree species differed markedly in their capability of physiological drought acclimation. In agreement with our second hypothesis, three species (*F. excelsior*, *F. sylvatica*, *C. betulus*) showed a plastic response either at the stem or the leaf level, while the two other species (*A. pseudoplatanus*, *T. cordata*) revealed no clear pattern. Like the other species, *A. pseudoplatanus* and *T. cordata* showed reductions in stomatal conductance as well as growth rate under dry conditions (Lübbe et al. 2015, 2016). *A. pseudoplatanus* was furthermore characterized by the lowest above- to below-ground biomass ratio, and *T. cordata* by the steepest decline in total leaf area under drought (Lübbe et al. 2015). The results demonstrate that observed trait plasticity in response to drought at the leaf level is not principally excluding plasticity at another level, e.g. in the stem xylem, as was shown for same species. Rather, it appears that at least some of the species develop high plasticity in those organs where trait adjustment provides the largest benefit in terms of plant fitness. A coordination of drought acclimation across different organs is also likely which makes it advisable to investigate plasticity within a set of multiple traits (Kleyer and Minden, 2015). A main finding of our study is that the drought-induced plasticity of relevant traits varies largely across the co-occurring tree species within a habitat, and so it does within a given tree functional type. Thus, it is unlikely that drought exposure produces in the different tree species of a habitat a response with similar trait plasticity, even if the species are similar with respect to many other functions.

Effects of species mixing on leaf water status and hydraulic traits

In *C. betulus*, the presence of heterospecific neighbours obviously increased hydraulic efficiency at the cost of a higher susceptibility to embolism. The significant interaction between drought and mixture effects for wood anatomical and hydraulic traits in *C. betulus* is consistent with the opposing effect of heterospecific neighbourhood in the moist and the dry treatment. Under dry conditions, *C. betulus* seems to benefit from the presence of heterospecific neighbours, pointing to less intense interspecific than intraspecific competition in these assemblages when water is scarce. The pronounced drought tolerance and competitive ability of *C. betulus* manifests in a superior performance of this species in water-stressed mixed assemblages and is mirrored by the largest relative growth rate increase from the monoculture to the mixture among the five species (Figure A1, Lübbe et al. 2015).

Similar to *C. betulus*, hydraulic efficiency was higher in *A. pseudoplatanus* saplings growing in mixture than in monoculture under dry conditions, while in the moist treatment, saplings seemed to profit from the monoculture. The increase in $\varepsilon_{\mathrm{max}}$ in presence of heterospecific neighbours in the moist treatment could instead be a sign of reduced fitness, as Khalil and Grace (1992) found cell wall stiffness of *A. pseudoplatanus* leaves to increase as a consequence of drought. In fact, the saplings of *A. pseudoplatanus* were exposed to more intense crowding in the mixtures than in the monocultures, because the other species reached higher biomasses at the end of the experiment (Lübbe et al. 2015). Accordingly, the productivity of *A. pseudoplatanus* was lower in mixture than in monoculture under moist conditions, but not in dry soil (Figure A1).

The physiological adjustments observed in *C. betulus* and *A. pseudoplatanus* in response to the presence of either heterospecific or conspecific neighbours under water limitation confirm our third hypothesis. The observed modifications were exclusively related to xylem structural properties and functionality, but provided distinct benefits to the hydraulic system and growth performance, when saplings were grown in a heterospecific and diverse neighbourhood and exposed to dry soil. In contrast, *F. sylvatica* saplings apparently always profited from the monoculture with respect to hydraulic efficiency; this was visible in the moist as well as in the dry treatment. The wood anatomical and hydraulic traits consistently point to highest fitness of beech saplings when grown in moist monocultures. The performance of *F. sylvatica* saplings was not only reduced by soil desiccation but also by the presence of the other four species. The inferior competitive ability of beech in this experiment refers not only to hydraulic efficiency but similarly to biomass production, especially in the dry treatment (Figure A1). The relatively slow growth of young beech trees is well known (Lei et al. 2012, Beyer et al. 2013, Lübbe et al. 2015), which contrasts with the relatively high productivity and competitive ability in the adult stage (Ellenberg & Leuschner 2010).

F. excelsior slightly increased D in mixture as visible in significant increases in K_s but not in D_h or K_p. In this species, a higher specific hydraulic conductivity in mixture corresponds to a higher leaf conductance (Lübbe et al. 2016). In contrast, no consistent neighbourhood effect on leaf water status and stem hydraulics was observed in *T. cordata*. Nevertheless, *T. cordata* clearly profited from heterospecific neighbours in the moist treatment by showing elevated growth rates as compared to the monocultures (Lübbe et al. 2015). Thus, it was the most competitive species in our sample and achieved dominance irrespective of the water consumption of the neighbouring species.

Conclusions

Our drought trial with five common Central European broad-leaved tree species suggests that drought acclimation at the leaf and the stem level may often represent alternatives rather than interacting components of a drought response strategy. Across different species, a given drought regime is unlikely to trigger a similarly plastic drought response in all species that coexist in a habitat. In our species sample, no species showed significant adjustment at both the leaf and stem levels. However, high trait plasticity in the face of drought in one plant organ does not exclude plasticity in other organs, which suggests that understanding drought response strategies of trees requires studying more than one organ (e.g. leaves, stem and roots).

As in all experiments with juvenile trees, sapling data can hardly be extrapolated to adult trees due to ontogenetic change in many relevant traits. Furthermore, other factors than leaf water status regulation and modification of xylem hydraulic properties should be considered which can also determine a tree's drought sensitivity, among them stem water storage and root system acclimation to drought.

The finding that certain species modify their stem hydraulic system in mixture in response to heterospecific neighbours as compared to monoculture produces evidence that the specific neighbourhood of a tree can have a significant impact on functional traits beyond productivity. The results also show that mixtures can have positive, as well as negative, effects on the performance of trees in comparison to monocultures, which should be taken into account in the recent debate about assumed positive effects of diversity on forest ecosystem functioning.

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Appendices

Table A. 5.1. Summary of results of 3-way ANOVAs on the effects of species identity, moisture treatment, neighbourhood (monoculture vs. mixture) and their interactions on various structural and physiological parameters across the 5-species sample.

	π_0				π_{tlp}				RWC$_{tlp}$				A_f				ε_{max}			
	Df	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*
Species	4	0.95	**26.66**	**<0.001**	4	0.49	**7.85**	**<0.001**	4	0.11	**16.72**	**<0.001**	4	0.49	**7.85**	**<0.001**	4		**52.47**	**<0.001**
Drought	1	0.34	**9.37**	**0.003**	1	0.03	1.62	0.21	1	0.01	**5.57**	**0.02**	1	0.03	1.62	0.21	1		0.09	0.76
Mixture	1	0.01	0.18	0.68	1	0.00	0.01	0.92	1	0.00	0.55	0.46	1	0.00	0.01	0.92	1		0.97	0.33
Species × Drought	4	0.10	**2.85**	**0.03**	4	0.04	0.69	0.60	4	0.01	1.74	0.15	4	0.04	0.69	0.60	4		**2.53**	**0.05**
Species × Mixture	4	0.01	0.36	0.84	4	0.08	1.32	0.27	4	0.01	1.13	0.35	4	0.08	1.32	0.27	4		1.25	0.30
Drought × Mixture	1	0.02	0.62	0.43	1	0.00	0.16	0.70	1	0.00	0.51	0.48	1	0.00	0.16	0.70	1		0.77	0.38
Species × Drought × Mixture	4	0.01	0.38	0.82	4	0.01	0.14	0.97	4	0.00	0.20	0.94	4	0.01	0.14	0.97	4		1.67	0.16
Residuals	98	0.04			93	1.46			97	0.16			93	1.46			97			

	A_{Lumen}				VD				D				D_h				K_p			
	Df	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*
Species	4		**118.28**	**<0.001**	4		**197.81**	**<0.001**	4	302	**17.50**	**<0.001**	4		**236.95**	**<0.001**	4		**52.19**	**<0.001**
Drought	1		0.17	0.68	1		**6.90**	**0.01**	1	22.6	**5.24**	**0.02**	1		0.50	0.48	1		**4.41**	**0.04**
Mixture	1		0.00	0.97	1		2.54	0.11	1	16.7	**3.87**	**0.05**	1		**4.86**	**0.03**	1		**4.94**	**0.03**
Species × Drought	4		0.70	0.59	4		0.82	0.51	4	4.9	**0.29**	0.89	4		**4.23**	**0.003**	4		0.77	0.55
Species × Mixture	4		1.20	0.32	4		0.46	0.76	4	34.1	1.98	0.10	4		**3.99**	**0.005**	4		1.82	0.13
Drought × Mixture	1		2.25	0.14	1		0.04	0.85	1	5.4	1.25	0.27	1		**12.44**	**<0.001**	1		**22.85**	**<0.001**
Species × Drought × Mixture	4		1.44	0.23	4		1.75	0.15	4	41.1	**2.39**	**0.06**	4		**3.28**	**0.01**	4		0.82	0.51
Residuals	95				92				95	409			92				95			

	K_p				P_{50}				P_{88}			
	Df	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*	*Df*	*SS*	*F*	*p*
Species	4		**52.19**	**<0.001**	3	31852	**49.88**	**<0.001**	3	45.1	**49.71**	**<0.001**
Drought	1		**4.41**	**0.04**	1	2794	**13.13**	**<0.001**	1	3.33	**11.02**	**0.001**
Mixture	1		**4.94**	**0.03**	1	2	0.01	0.93	1	0.19	0.64	0.42
Species × Drought	4		0.77	0.55	3	2179	**3.41**	**0.02**	3	1.4	1.54	0.21
Species × Mixture	4		1.82	0.13	3	635	0.99	0.40	3	3.92	**4.33**	**0.007**
Drought × Mixture	1		**22.85**	**<0.001**	1	372	1.75	0.19	1	0.02	0.08	0.78
Species × Drought × Mixture	4		0.82	0.51	3	1922	**3.01**	**0.04**	3	1.04	1.14	0.34
Residuals	95				71	15112			73	22.1		

Table A. 5.2. Significance of drought effects on the physiological plasticity of the five tree species in monoculture or mixture according to pairwise comparisons with Student’s t-test, Welch’s t-test or Mann-Whitney U-test. The G_s, δ^{13}C and K_s data were taken from Lübbe et al. (2016). Arrows show direction of shift in mean values (upward: significant increase, downward: significant decrease, diagonal: increase/decrease at p<0.10), significance level: *: p<0.05, **: p<0.01, ***: p<0.001.

	Monoculture					Mixture				
Species/ Parameter	*F. excelsior*	*A. pseudopl.*	*C. betulus*	*T. cordata*	*F. sylvatica*	*F. excelsior*	*A. pseudopl.*	*C. betulus*	*T. cordata*	*F. sylvatica*
π_0	↓ **					↘				
π_{tlp}	↓ *									
RWC_{tlp}	↑ *					↗				
A_f						↗				
ε_{max}	↗		↘				↓ *			
Gs	↓ *		↓***		↓ *	↓ *	↓ **	↓ *	↓ *	↓***
δ13C	↑***		↑***			↑ **	↗	↗	↗	
A_{Lumen}		↘								
VD			↑ *							
D		↘	↓ **		↓ *					
D_h	↑ *		↓ **		↓ **	↑ *	↗	↑ *		
K_p		↓ *	↓ **		↘			↗		
K_s			↓***		↘		↘			
P_{50}		↘			↓ **				↓ **	↘
P_{88}					↓ *					

Table A. 5.3. Mean ± SE of 12 physiological and xylem anatomical plant traits of the five tree species in the moist or dry treatment and monoculture or mixture. Significant differences between the treatments and monoculture/mixture are indicated in Table 5.4.

		F.excelsior		*A. pseudopl.*		*C. betulus*		*T. cordata*		*F. sylvatica*	
Trait	Mixture	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist
π_0	mono	-2.14 ± 0.09	-1.73 ± 0.10	-1.71 ± 0.06	-1.63 ± 0.07	-2.00 ± 0.06	-2.00 ± 0.07	-1.59 ± 0.07	-1.51 ± 0.06	-1.91 ± 0.07	-1.81 ± 0.12
	mix5	-2.09 ± 0.06	-1.85 ± 0.09	-1.67 ± 0.04	-1.71 ± 0.07	-2.11 ± 0.03	-2.05 ± 0.06	-1.54 ± 0.05	-1.53 ± 0.05	-1.88 ± 0.10	-1.76 ± 0.08
π_{tlp}	mono	-2.57 ± 0.11	-2.13 ± 0.14	-2.02 ± 0.10	-1.96 ± 0.13	-2.51 ± 0.08	-2.51 ± 0.08	-2.31 ± 0.10	-2.22 ± 0.09	-2.53 ± 0.13	-2.31 ± 0.14
	mix5	-2.48 ± 0.08	-2.29 ± 0.09	-2.00 ± 0.05	-2.04 ± 0.07	-2.66 ± 0.05	-2.66 ± 0.05	-2.22 ± 0.10	-2.31 ± 0.10	-2.45 ± 0.08	-2.43 ± 0.16
RWC_{tlp}	mono	0.86 ± 0.01	0.82 ± 0.01	0.87 ± 0.02	0.86 ± 0.02	0.86 ± 0.01	0.84 ± 0.02	0.77 ± 0.01	0.74 ± 0.02	0.82 ± 0.01	0.84 ± 0.01
	mix5	0.86 ± 0.01	0.81 ± 0.02	0.86 ± 0.01	0.86 ± 0.01	0.84 ± 0.01	0.81 ± 0.03	0.80 ± 0.01	0.77 ± 0.02	0.82 ± 0.03	0.82 ± 0.02
A_f	mono	0.15 ± 0.05	0.09 ± 0.03	0.15 ± 0.04	0.16 ± 0.03	0.32 ± 0.01	0.23 ± 0.06	0.27 ± 0.03	0.19 ± 0.06	0.23 ± 0.05	0.25 ± 0.09
	mix5	0.11 ± 0.03	0.03 ± 0.01	0.15 ± 0.03	0.12 ± 0.03	0.24 ± 0.06	0.20 ± 0.09	0.33 ± 0.04	0.30 ± 0.03	0.25 ± 0.06	0.30 ± 0.03
ε_{max}	mono	18.43 ± 3.22	11.53 ± 1.13	16.62 ± 3.15	13.02 ± 1.38	14.61 ± 1.15	19.33 ± 2.89	6.76 ± 0.73	5.82 ± 0.80	12.11 ± 2.09	13.28 ± 2.13
	mix5	19.18 ± 2.19	15.15 ± 1.61	13.23 ± 1.29	19.72 ± 1.73	16.51 ± 1.38	17.05 ± 2.95	6.35 ± 0.43	6.49 ± 0.54	12.77 ± 1.56	10.52 ± 0.71
A_{Lumen}	mono	3.76 ± 0.36	3.34 ± 0.32	4.96 ± 0.39	6.71 ± 0.60	6.70 ± 0.42	6.61 ± 0.37	13.91 ± 1.70	12.47 ± 1.38	13.66 ± 0.80	14.88 ± 1.44
	mix5	3.58 ± 0.39	3.71 ± 0.50	5.83 ± 0.46	5.29 ± 0.31	8.16 ± 0.75	6.65 ± 0.43	13.49 ± 1.70	14.98 ± 2.57	12.48 ± 0.58	12.52 ± 0.77
VD	mono	63.28 ± 11.4	48.90 ± 6.50	84.56 ± 5.54	102.2 ± 10.0	156.1 ± 16.2	112.5 ± 6.30	213.8 ± 23.24	190.5 ± 15.28	214.9 ± 14.83	188.7 ± 8.48
	mix5	47.92 ± 6.80	38.41 ± 2.43	95.51 ± 8.12	79.44 ± 5.12	139.3 ± 10.9	124.8 ± 9.65	185.6 ± 11.71	222.3 ± 39.50	198.8 ± 4.77	182.9 ± 10.8
D	mono	24.22 ± 1.43	23.84 ± 0.78	25.79 ± 0.38	27.27 ± 0.58	21.40 ± 0.56	24.74 ± 0.49	27.31 ± 0.27	27.53 ± 0.55	26.49 ± 0.26	29.02 ± 0.95
	mix5	25.70 ± 0.59	27.80 ± 2.05	27.21 ± 0.39	27.65 ± 1.14	24.26 ± 0.43	22.89 ± 0.70	27.51 ± 0.48	27.99 ± 0.31	26.78 ± 0.78	27.58 ± 0.68
D_h	mono	80.44 ± 2.76	71.53 ± 2.88	33.60 ± 0.98	36.75 ± 1.27	32.85 ± 1.36	40.18 ± 1.47	31.93 ± 0.47	31.92 ± 1.17	36.09 ± 0.34	40.53 ± 1.14
	mix5	80.38 ± 1.80	69.64 ± 3.42	38.37 ± 1.14	35.06 ± 1.39	41.80 ± 0.43	39.11 ± 0.79	32.32 ± 1.11	33.36 ± 0.80	36.29 ± 1.03	37.45 ± 0.87
K_p	mono	3.94 ± 0.56	3.78 ± 0.75	1.39 ± 0.15	2.23 ± 0.20	1.41 ± 0.05	2.32 ± 0.21	3.70 ± 0.52	3.44 ± 0.59	4.37 ± 0.27	6.23 ± 0.94
	mix5	4.14 ± 0.44	3.50 ± 0.69	2.14 ± 0.08	1.69 ± 0.23	2.75 ± 0.34	2.00 ± 0.09	3.76 ± 0.63	4.29 ± 0.75	4.11 ± 0.38	4.43 ± 0.46
P_{50}	mono	NA	NA	-3.62 ± 0.17	-3.79 ± 0.09	-5.37 ± 0.07	-4.97 ± 0.18	-3.44 ± 0.14	-3.46 ± 0.12	-3.79 ± 0.19	-2.98 ± 0.13
	mix5	NA	NA	-3.88 ± 0.19	-3.63 ± 0.18	-4.94 ± 0.09	-4.83 ± 0.25	-3.70 ± 0.16	-2.85 ± 0.03	-3.84 ± 0.15	-3.28 ± 0.25
P_{88}	mono	NA	NA	-4.53 ± 0.17	-4.42 ± 0.14	-6.42 ± 0.20	-6.02 ± 0.23	-4.04 ± 0.13	-4.10 ± 0.19	-4.79 ± 0.24	-3.83 ± 0.16
	mix5	NA	NA	-5.05 ± 0.37	-4.55 ± 0.15	-5.72 ± 0.10	-5.70 ± 0.27	-4.31 ± 0.18	-3.76 ± 0.25	-5.21 ± 0.28	-4.60 ± 0.26

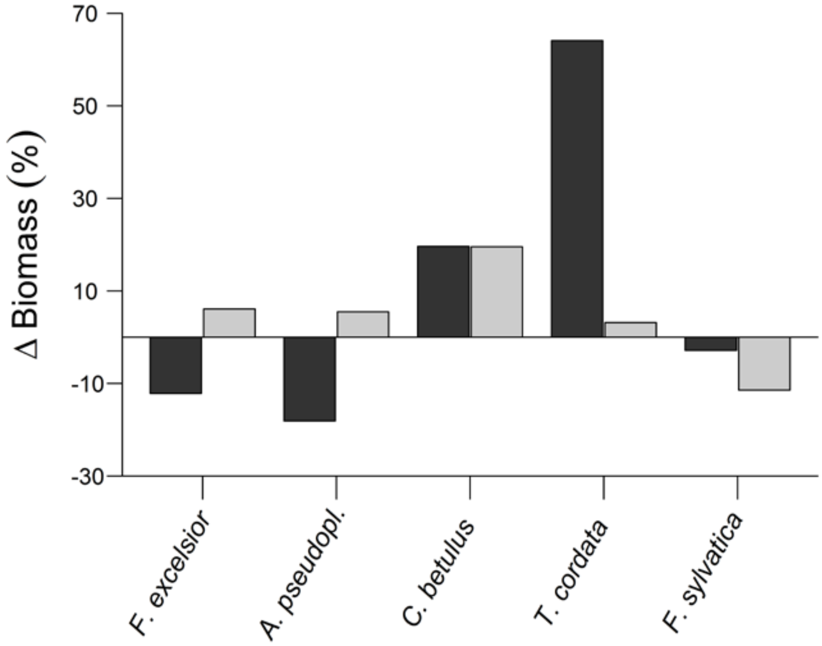

Figure A. 5.1. Relative overyielding in growth rates of the plants in mixture over that in monoculture for the five species according to Lübbe et al. (2015). Dark bars are for the moist, light bars for the dry treatment.

Chapter 6

Synthesis

Under consideration of the general objectives of this thesis ((i) general validity of the BEF relationship in productivity and water consumption, (ii) a higher relevance of tree identity on community functioning, (iii) an amplification of tree diversity effects under limited resources, and (iv) a manifestation of stand-level processes in tree-individual performances), the following chapter aims to summarize, discuss and relate the results from the conducted studies in the tree sapling experiment as presented before.

Effects of tree diversity and tree identity on community functioning

The analysis of both tree water use (Chapter 3) and productivity (Chapter 4) revealed a moderate but comparably strong effect of tree diversity on transpiration rate T as well as on biomass allocation (Bm) and relative growth rates (RGR) under ample water supply. For T and RGR, yield increased on average by ~10% from monocultures to the 3-species mixtures (Fig. 6.1.), although, overyielding was not be linearly enhanced by species richness. Similarities in the yield of 3- and 5-species assemblages indicate the importance of species mixture per se, while the actual species number in such tree communities seems to be of minor importance. Whether the amount of species might be more effective along a broader tree diversity gradient with higher species numbers or a higher range of diversity levels with accordingly more species combinations cannot be answered by this data. Our findings agree with the idea that functional performances might reach saturation at intermediate levels of species richness, when functional diversity is redundant at higher levels (Cardinale et al. 2006, 2011, Potvin and Gotelli 2008). However, other studies on tree diversity experiments also provide some proof for steady increase in the BEF relationship (e.g. Kunert et al. 2012).

While the increase in stand transpiration in Chapter 3 was mainly interpreted as a selection effect, the additive partitioning approach (AP) after Loreau and Hector (2001) clearly indicated a higher importance of species complementarity in case of tree growth and stand productivity (see Chapter 4). Due to the strong connectivity of growth and transpiration (Law et al. 2002) and the comparably high net diversity effects observed, the involvement of different mechanisms is rather unlikely. Thus, it seems crucial to reappraise the possibility for separating selection and complementarity effects and the applicability of AP for tree diversity studies with such a specific experimental design.

The arithmetic mode of AP quantifies the impact of species selection in overyielding by the covariance of species' yields in monoculture (M) and their deviations from expected relative yields in mixtures (RE). To consider parallelism between tree water use and growth, it seems plausible to compare species' rankings of performances in both services. *T. cordata* realized the highest RE values (overyielding) in growth-related traits, but most likely also in transpiration, as indicated by water-use related leaf area (LA) and sapwood area (SA). Albeit *T. cordata* reached highest transpiration rates of all monocultures, the M-values in growth rates and biomass allocation were exceeded by those of *F. excelsior* due to higher water-use efficiency. The lower position of *T. cordata* in the M-ranking for productivity parameters accounts for a lower rating of the selection effect than it could be expected for water consumption. Nevertheless, for our tree sapling experiment the use of AP remains questionable as an overestimation of complementarity effect seems likely. Albeit AP is commonly applied in tree diversity studies (Kunert et al. 2012, Grossiord et al. 2013, 2014), it was originally developed for herbaceous communities, which are highly flexible in terms of replacement and competition-induced alteration of species abundances (Loreau and Hector 2001). In comparison to those short-lived plants, our less dynamic tree sapling assemblages, with fixed numbers of individuals and relatively few species can hardly achieve such clear dominance of a superior species within such a short experimental time frame. Canopy extension of the more productive tree species clearly allows for suppression of inferior species (without replacement or outcompeting only), but the AP procedure might be insensitive to those asymmetries in tree species contribution, which are anyhow prominent for competitive dynamics and yield in young plantations. Therefore, the process of species selection might be underrated and a quantitative separation between both components of the diversity effect is insufficient for a short-running experiment with tree saplings. For instance, overyielding in the 3-species mixture *Acer-Carpinus-Fraxinus* was realized by the asymmetric performance between the superior *F. excelsior* and its inferior neighbors. *F. excelsior* increased RGR by nearly 100% in comparison to the monocultures (reductions in *A. pseudoplatanus* and *C. betulus* by ~40% and ~10%, respectively), which clearly points to the selection effect being the relevant driver in this 3-species mixture (see Fig. 4.4.). Despite of that, the numerical benefit for one out of three species (~33%) reveals a relevant complementarity effect in AP, with comparable impact like species selection on the observed net diversity effect (Fig. 4.1.).

Summarizing the results, evidence for the co-occurrence of species selection and species complementarity in this experiment is obvious. The high contribution of strong-performer species (*T. cordata, F.excelsior*) to overyielding in water consumption and biomass allocation gives proof for the selection effect. Moreover, the occurrence of complementary behavior is likely, because of (i) transgressive overyielding in some species combinations (higher yield in comparison to the most productive monoculture), and (ii) the synchronous benefit of neighboring species in some other mixed species combinations. Tree diversity effects were found to be on average rather low, but the variability among species combinations points to the importance of specific neighbor compositions and tree neighbor identity for favorable interactions. Furthermore, it was shown that species identity was the most important driver beside of soil water availability in tree community functioning. In fact, both tree water consumption and growth performance varied among species by the factor of two, which clearly controlled the stand level performance of the mixtures. These findings on the importance of tree diversity, tree neighbor identity and tree species identity are in agreement with meta-analysis and literature reviews on tree diversity studies (Nadrowski et al. 2010, Scherer-Lorenzen 2014), assuming a relevant but inferior role of the biodiversity-ecosystem functioning (BEF) relationship in forest ecosystems, with dependence on actual species compositions.

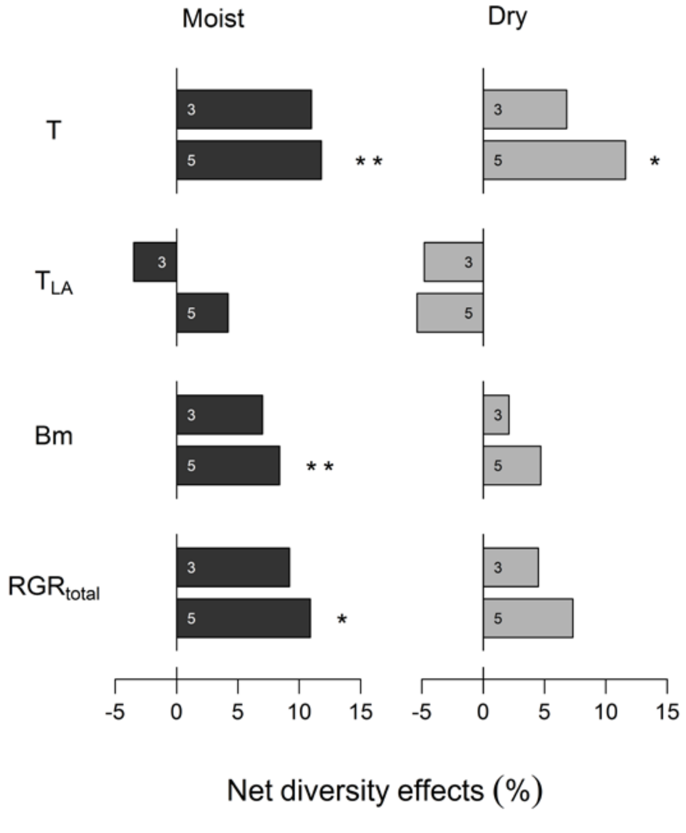

Figure 6.1. Range of relative net diversity effects in stand level performance for water consumption (transpiration rate (T, mm d-1), transpiration rate per leaf area (T_{LA}, ml m^{-2} d^{-1})) and productivity (biomass (Bm, g) and relative growth rate (RGR_{total}, g g^{-1} 450 d^{-1})) for assemblages with three (3) or five (5) species, and under moist (left) or dry (right) conditions. Asterisks indicate significance net effects according to the Grand mean over all mixtures (*: $p<0.05$; **: $p<0.01$).

It needs to be mentioned that the appearance of diversity effects is not self-evident for such young sapling assemblages. First, tree diversity effects in the BIOTREE experiment (fine root growth) were reported for the sixth year after establishment (Lei et al. 2012a). For the subtropical BEF-China, tree diversity was a bad predictor for sapling growth in two year old plots (Lang et al. 2012, Li et al. 2014); even though positive interactions were already observed. This is in accordance with findings that diversity effects on productivity of plant communities become more prominent over time as the magnitude of complementarity increases when experiments are elongated (Cardinale et al. 2007, Reich et al. 2012). In the pot experiment, eminent interactions among tree saplings occurred already during the second year after establishment. This is due to the specific planting scheme and the confined space for the assembled saplings. Narrow distances (15-20cm) and limited soil volume in the pots (~0.05m^3) forced coexisting plants to interact immediately after establishment, or at least during the second year of growth. Such a design is certainly inconvenient with respect to the long-run requirements of tree saplings; but it fits the demand for this short time experiment (2 years), and accounts for the differences in aims and results to other tree diversity experiments (Sardinilla (Potvin et al. 2011), BIOTREE (Scherer-Lorenzen et al. 2007), Forbio (Verheyen et al. 2013, etc.).

Tree diversity- and tree identity effects under deficient water supply

The implication of a drought trial to the tree sapling experiment enabled a distinct analysis of tree diversity- and tree identity effects under limited soil water, and its relevance with respect to community stability. In comparison to the moist treatment, a significant net diversity effect on plot level water consumption was also obtained when soil water was scarce, although the magnitude was smaller (Fig 6.1.). In case of tree productivity net diversity effects were not significant for most of the tested parameters; albeit the statistical power was reduced for the dry treatment because of a smaller sample of tested species combinations. These results are in disagreement with the majority of recent studies on tree mixture effects considering temporal or spatial variation in environmental conditions, which stress that complementary behavior and/or facilitation become more relevant with harsher conditions or limited resources (Binkley 2003, Paquette and Messier 2011, del Río et al. 2013, Pretzsch et al. 2013). Indeed, the contradicting observations obtained from this tree sapling experiment are somehow surprising, because it seems plausible to expect a higher importance of root space partitioning for soil water exploitation when water supply is deficient; which should furthermore stimulate overyielding in plant growth. This process might be hampered by the constraints of a pot experiment, due notable limitations in soil volume and potential rooting depth. In fact, the maximum length of saplings' tap roots exceeded the soil depth in average for all species and thus clearly restrained the development of vertical root segregation. However, even though the occurrence of root space partitioning is unlikely, it cannot totally be excluded.

In agreement with our data, some studies refer to increasing significance of complementarity effects with increasing site quality (Morin et al. 2011, Dieler and Pretzsch 2013, Forrester et al. 2013, Jucker et al. 2014b). Forrester (2014) concluded that competition for light and thus beneficial interactions in canopy space become more prominent when growing conditions are more favorable. Based on that, a conceptual model refers to the contrasting meaning of species complementarity under ample (reduced competition for light) and limited resource supply (enhanced soil resource capturing). Improved light-absorption in mixed sapling assemblages with ample water supply could certainly explain the amplified diversity effects in tree water use and growth in comparison to the dry treatment. This is also in accordance with findings from other tree diversity experiments, when light harvesting efficiency increased in mixed species plots due to plasticity in branch development and crown formation (Potvin and Dutilleul 2009, Lang et al. 2012). The analysis of crown morphological plasticity was out of the scope for this thesis, but the increase in stand level leaf area provides some evidence for more effective light absorption of the mixed tree assemblages; even though the benefit of reduced competition for light might have been selective in favor of the high performing species.

Despite that occurring complementarity effects were in general low in the dry treatment, variability among species combinations was high and some mixtures performed remarkable overyielding in water consumption (*Acer-Carpinus-Fraxinus*, mix5). Simultaneously, analyses of productivity of those mixed assemblages did not reveal conspicuous asymmetric benefits for certain species, which underpins the importance of the specific tree neighbor constellation for the potential of complementary behavior. According to that, species complementarity seems not to be lacking per se when soil water was limited in the experiment, but is obviously depending on the combination of tree functional types present.

The findings on water consumption reveal some discrepancy to the diversity-community resistance hypothesis, as leaf area-specific transpiration (T_{LA}) in the mixed tree assemblages was not reduced less than in the monocultures (Fig 6.1.). This is because less-drought sensitive species did not markedly increase their contribution to stand-level transpiration by canopy extension. Indeed, none of the species enhanced its fraction on stand-level leaf area in the drought-treated mixtures; not even the fast growing and presumably drought-tolerant *F. excelsior* (Köcher et al. 2009) with lower sensitivity in leaf conductance and transpiration. However, it needs to be noticed that the drought trial was just fulfilled after spring foliation, which might have biased the findings on shifting abundances. The missing benefit of any species by tree mixture under dry conditions is further mirrored in patterns of productivity (RGR, Fig. 4.3.). Analogously, biomass allocations and RGR at the stand level were reduced equally strong by deficient water supply for the monocultures and for the mixed pots. According to that, the lack of enhanced community resistance with tree diversity (insurance hypothesis) is aligned to a missing selection effect under dry conditions, when none of the (better-adapted) species took pronounced profit in the mixed tree assemblages. In contrast to that finding, grassland communities are known to be more flexible in terms of shifting species abundances regarding climatic variability, which diminishes inter-annual fluctuations in primary productivity in diverse herbaceous communities (e.g. Hautier et al. 2014). Such a mechanism can truly be considered to stabilize plant communities with higher diversity (Loreau and Mazancourt 2013). Although the role of asynchrony of tree species for the stability in ecosystem services is not clear yet (Morin et al. 2014, Jucker et al. 2014), tree communities rather fail to fulfill compensatory dynamics during periods of desiccation, as it requires a more rapid response in community composition. The latter can be only achieved with respect to long-term climate change in the sense of adaptive succession.

Further, the diversity-stability relationship in plant communities is supposed to be controlled by a negative back-coupling of overyielding in mixtures and an enhanced capturing of resources under limited conditions. Overexploitation of soil water during periods of desiccation was shown to destabilize diverse plant communities in grassland experiments as well as in forests (de Boeck et al. 2006, Verheyen et al. 2008, Gebauer et al. 2012, Grossiord et al. 2014). In this pot experiment a critical depletion of restricted soil water was prevented, as assemblages with bigger trees and higher water demand were treated with slightly rising sums in irrigation. The controlled adjustment in water supply certainly somehow favored water spending cultures, but also allowed for a more homogenous drought regime and stress intensities across the species combinations in the dry treatment.

In summary, the absence or decline of net diversity effects in tree growth and water consumption under limited soil water disagrees with the assumption of higher relevance of species complementarity at low resource availability. On the other hand, the accordance of these results with few other findings points to the complexity of interacting processes in BEF of tree communities, which does not only dependent on abiotic conditions, but also on the plant functional types present and stand structural properties (Forrester 2014).

Tree individual performance in response to water supply and tree neighborhood

The occurrence of tree diversity effects at the stand level under ample and deficient water supply was assumed to be reflected in tree individual performance, with respect to growth, water consumption, and physiological and morphological adjustments. Whether and how different species realized alterations in yield and modification in functional performance in response to certain environmental conditions will be discussed as follows.

The observed growth performance of the target plants in the pot experiment is mainly in agreement with other findings on potential height growth and biomass allocation of seedlings and saplings of these species (Cornelissen et al. 1996, Hölscher et al. 2002, Don et al. 2007). With regard to their successional status (Ellenberg and Leuschner 2010, Köcher et al. 2013) the light-demanding "pioneer species" *F. excelsior* obtained the highest growth rates, while the shade-tolerant "climax species" *F. sylvatica* was minor productive at this young ontogenetic stage. Solely *A. pseudoplatanus* tended to underrate the expectations in growth performance, which is mainly expressed by small achievements in above-ground biomass and height growth. Whether this was caused by genetic variability or by the specific conditions in the experiment remains unclear.

In agreement with current knowledge on the importance of drought for tree performances (e.g. Aroca 2012), soil water availability was identified as a major determinant influencing transpiration and tree growth, but it also accounts for multiple morphological and physiological modifications. Transpiration rates T and T_{LA} of the monocultures were most strongly reduced by soil drought for *C. betulus, T. cordata* and *F. sylvatica*, while *F. excelsior* and *A. pseudoplatanus* were shown to be less sensitive. Accordingly, the sensitivity in water use of *C. betulus* and *F. sylvatica* was reflected in enhanced stomatal resistance (g_s, $\delta^{13}C$) and modifications in xylem formation causing reduced sapwood hydraulic conductivity (k_s), while growth performances were only moderately reduced. *T. cordata*, on the other hand, showed only minor physiological adjustments in response to water scarcity, but morphological plasticity and growth reductions accounted for the diminished effort in transpiration, especially in the mixtures. Significant declines in transpiration rates were missing for *A.pseudoplatanus*, but water-use related traits (g_s, $\delta^{13}C$, k_s) indicated some responsiveness to drought. Similarly, saplings of *F. excelsior* realized only moderate reductions in growth performance in desiccated soils. However, this species displayed a considerable sensitivity in stomatal control (g_s, $\delta^{13}C$), an improved leaf hydraulic status with respect to osmotic, elastic and apoplastic adjustments, and some water-use related morphological plasticity by developing smaller leaf- and sapwood areas. Our findings on species-specific water-use regulation in response to drought are in general confirmed by a ranking among this species in accordance to drought sensitivity (Köcher et al. 2009). The assumed contrast between supposedly drought-tolerant *F. excelsior* and more sensitive *F. sylvatica* fits to the observed differences in regulation of transpiration observed; albeit the low response of *A. pseudoplatanus* appears to be atypical again.

Besides the impact of soil drought, some species realized alterations in resource use, productivity and/or physiological functioning, when competition intensity varied with tree neighbor composition (growth in monocultures vs. mixtures). The superior position of *T. cordata* with respect to water use and productivity in mixtures with ample water supply was already mentioned before, but physiological adjustments were little prominent only. *F. excelsior* could not increase its growth rates in mixtures, but enhanced leaf- and sapwood areas in the moist treatment. Moreover, the improvement in hydraulic traits (g_s, $\delta^{13}C$, k_s, independent of soil water supply) illustrates the benefit for ash saplings growing in mixtures. *A. pseudoplatanus* and *C. betulus* showed only little responsiveness to coexistence with heterospecific neighbors in terms of water consumption and growth. However, both species performed some remarkable plasticity in xylem structure with respect to tree species mixture. While xylem hydraulic efficiency tended to be reduced by mixtures in the moist treatment, there was strong improvement in xylem functioning at low water availability. That points to enhanced water supply for those species in mixtures, which might be caused by complementary behavior and reduced competition intensity in dry soil. *F. sylvatica* is the only species without reference of any benefit by tree species mixture. Even though smaller $\delta^{13}C$ values indicate a tendency of less conservative stomata regulation (mostly in the dry treatment), growth and hydraulic efficiency tend to be declined by the admixture of heterospecific neighbors (mostly in the moist treatment). The overall reduced performance of *F. sylvatica* in mixtures is in accordance with the minor competitive ability of young beech trees reported elsewhere (Lei et al. 2012, Beyer et al. 2013).

In synthesis of the conducted studies, the derivation of a broad section of physiological, morphological and growth-related parameters allows for analyzing covariations among plant functional traits along the environmental gradients (biotic and abiotic) provided within the pot experiment. For a preliminary approach correlations were assessed among varying traits originating from different functional groups of parameters (growth-related traits, xylem-functional traits, xylem structural traits, leaf-functional traits, and pressure volume traits). With respect to intraspecific variability, species revealed some differences in co-evolutionary relationships of phenotypic plasticity, which have been determined for separate plant segments and concurrent process levels (Table 6.1.).

Table 6.1. Selective list of intra-specific covariation of plant functional traits (Pearson product-moment correlations) for five temperate tree species examined in the sapling experiment along gradients of soil water supply and tree diversity. Asterisks indicate significance of Pearson correlations (°: $p<0.10$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Trait1	**Trait2**	***F. excelior***	***A. pseudopl.***	***C. betulus***	***T. cordata***	***F. sylvatica***
RGR_{total}	D_h	0.04	**0.63 ****	**0.40 °**	**0.55 *****	**0.60 ****
LI_{Shoot}	D_h	**-0.49 ***	**0.45 ***	**0.48 ***	**0.49 ***	**0.72 *****
LA	D_h	0.10	**0.67 *****	0.21	**0.41 °**	**0.79 *****
LA	A_{Lumen}	**0.40 ***	**0.45 ***	0.20	0.31	**0.39 °**
RGR_{total}	K_p	**0.38 °**	**0.47 ***	0.28	**0.41 °**	**0.47 ***
BAI	P_{50}	NA	-0.31	0.27	**0.69 *****	**0.47 ***
LI_{Shoot}	g_s	0.18	-0.29	**0.40 °**	**0.56 *****	0.27
LI_{Root}	VD	0.19	**-0.50 ***	**-0.60 *****	-0.05	0.11
K_s	D	0.24	**0.62 ****	**0.60 ****	0.30	**0.68 *****
K_s	$\delta^{13}C$	-0.10	**-0.63 *****	-0.35	-0.11	0.17
π_0	K_s	**0.66 *****	0.02	-0.18	**-0.43 °**	0.06
A_f	K_s	0.17	0.08	0.00	**-0.62 *****	-0.31
ε_{avg}	G_s	-0.25	-0.38	**-0.65 *****	0.04	-0.25
ε_{max}	$\delta^{13}C$	0.19	-0.03	-0.12	**0.54 ***	**0.56 *****
ε_{max}	RS	**0.74 *****	-0.28	0.35	-0.31	0.02
A_f	C/N	-0.45	**-0.46 °**	-0.29	**-0.62 ****	0.01
A_f	$\delta^{13}C$	**0.57 *****	-0.07	0.13	-0.20	**-0.54 ***
P_{88}	K_s	NA	**0.56 ****	-0.12	0.26	**0.75 *****

The most common signal across all species refers to the dependency of growth performance on xylem hydraulic functioning as described by multiple correlations. Hydraulically-weighted vessel diameter (D_h) is obviously an important determinant for all species with exception of *F. excelsior*. In this ring-porous species, only D_h but not the lumen fraction on cross-sectional sapwood area (A_{Lumen}) or potential conductivity (K_p) was found to be enhanced by drought (see Chapter 5). Specifically, stem height increment was sensitive to variations in D_h. Tree saplings obviously render, if possible, strong investments for vertical growth, which might point to the high relevance of light absorption as mentioned before. Interestingly, root length increment (LI_{Root}) of *A. pseudoplatanus* and *C. betulus* was negatively correlated to vessel density (VD). However, hydraulic pathway redundancy in sapwood of those species was stimulated by soil drought, but root elongation was not. In general, growth of *F. excelsior* and *C. betulus* seem to be less sensitive to hydraulic functioning than in case of the other species. Several species showed some relativeness of foliar cell wall elasticity (ε_{max}, ε_{avg}) and stomatal resistance (G_s, $\delta^{13}C$), indicating the importance of leaf hydration for plant hydraulic functioning. As a final example, decreasing carbon-nitrogen ratios (C/N) in foliar tissue of *A.pseudoplatanus* and *T. cordata* were correlated to higher fractions of apoplastic leaf water. In reverse, higher nitrogen use efficiency came along with a bigger symplast, both supposedly being aligned to sufficient water supply. In general, covariation of traits was quite heterogeneous among species, although multiple relationships were detected, which point to divergent adaptive strategies in response to alterations in resource supply and competitive interactions. However, a clear distinction between species, regarding their stomatal control strategies (isohydric vs. anisohydric species) as assumed in Chapter 5, could so far not be manifested by these complementing data.

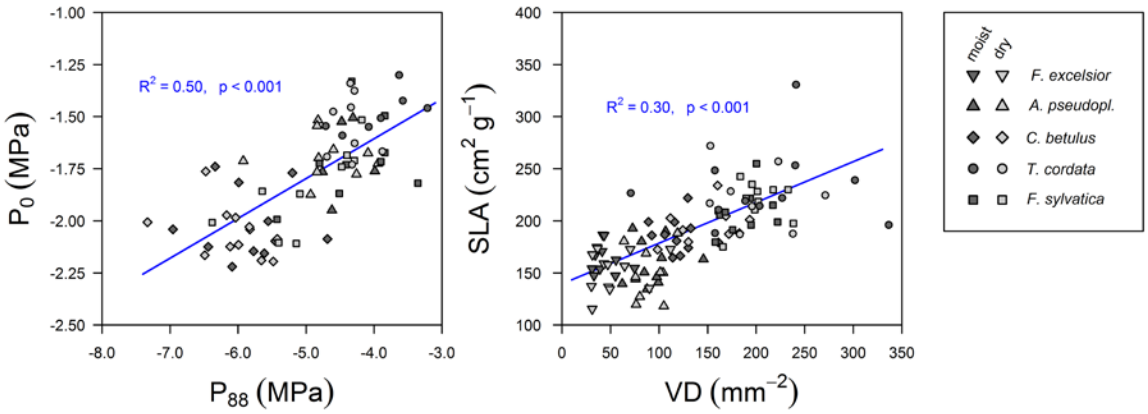

Figure 6.2. Significant relationships between leaf osmotic potential (π_0) and the P_{88} value of xylem vulnerability to cavitation (left), and between specific leaf area (SLA) and xylem vessel density (VD, right) across five temperate deciduous tree species

Furthermore, interspecific variations allow for some insights into the global meaning of covariation in plant functional traits (Fig. 6.2.) across saplings of temperate broad-leaved species in the experiment. For example, leaf osmotic potential (π_0) was shown to correlate strongly with P_{88} representing vulnerability to xylem cavitation. Similar interspecific relationships have been described between leaf water potential at turgor loss (π_{tlp}) and P_{50} across tropical woody species (Choat et al. 2007), and between π_0 and P_{50leaf} at the foliar level only for temperate woody angiosperms (Blackman et al. 2010). As both, reduced values in π_0 and P_{88}, indicate smaller susceptibility to drought, *C. betulus* seems to hold high physiological capacity of drought resistance in comparison to others (*T. cordata*). Another strong correlation was observed between specific leaf area (SLA) and VD (Fig. 6.2.), which is assisted by cross-correlations with carbon isotope discrimination ($\delta^{13}C$) and D_h or A_{Lumen} (data not shown). Variation in SLA is supposed to account for interspecific differences in plant growth as reported for positive relationships of relative growth rates (Cornelissen et al. 1997, 1999), or by carboxylation rates in photosynthesis (Legner et al. 2013) with SLA. On the other hand, plant growth performance is known to depend on xylem hydraulic efficiency (e.g. Hajek et al. 2013). Thus, a positive relationship between SLA and xylem structure across species is plausible and can be confirmed by other findings (Mitchell et al. 2008, Méndez-Alonso et al. 2012).

In conclusion, the analysis of intra- and interspecific covariations in plant functional traits certainly provides potential for further insights to coordinated responses in plant functioning along this environmental gradient.

Concluding remarks and implications for real forest ecosystems

The results of the tree sapling experiment presented in this thesis are mainly in alignment with recent assumptions on the role of diversity (species richness), neighbor interactions and plant functional traits in functional ecology research, but also reveal some new insights on biotic interactions in tree community functioning and services. Certainly, these findings cannot be easily extrapolated to mature trees in silviculture or close-to-nature forests. First, with respect to ontogenesis, juvenile and full-grown trees may differ in many aspects of functioning including hydraulic architecture and growth ability (Ryan et al. 2006, McDowell et al. 2013). Second, the soil volume in the pots was probably too small to allow for significant root-system segregation among different tree species; this may have reduced the potential for complementary resource use. Nevertheless, the pots were large enough to accommodate five tree saplings in the first 16 months after planting without momentous root space limitation, as is indicated by earlier growth experiments. Finally, the duration of the experiment (16 months) may have been too short to allow for a more intense adaptive response of a target tree to the presence of specific neighbors.

However, the observed significant variations in water consumption and productivity, and physiological and morphological modifications clearly reveal the distinct effects of tree diversity and neighbor composition, tree species identity and water supply. Our findings are in alignment with the common state of knowledge of BEF research in forest ecosystems, assuming the general occurrence of tree diversity effects on growth performance and geochemical cycling. Even though the putative effect size of species mixture is rather small, the identity of species occurs to be substantially more important (Nadrowski et al. 2010, Scherer-Lorenzen 2014). Because functional differences among coexisting species account for any relationship between diversity and ecosystem functioning, the actual species composition and tree neighbor constellation is specifically relevant and deserves more attention in future forest ecological research.

Nowadays, the establishment of tree diversity experiments has become a popular and valuable option to complement findings from real forest ecosystems and they can be hold to offset shortcomings of inventorial or observational studies. Though experimental studies with planted young trees lack in realism, they provide clear distinctions of tree identity with respect to possible selection effects and allow for minimizing the chance of hidden treatments (Huston et al. 1997). The tree sapling experiment in this thesis was conducted to complement findings from observational studies in an old-grown temperate deciduous mixed forest with similar species composition (Hainich tree diversity matrix, Leuschner et al. 2009), achieving a main focus on tree water use and tree hydraulic properties. The specific conditions of the experiment allowed for a precise quantification of the water balance under moist and dry conditions and thus for high accuracy in determining soil water conditions and transpiration rates. Additionally, plant growth and physiological and morphological parameters could be explored most comprehensively. Assemblages of planted saplings furthermore provide homogeneity in age structure, plant size and density. Forests, in contrast, are usually characterized by stand structural diversity, which is known to superpose effects of tree species mixture on stand level processes (Meissner 2013, Forrester 2014). Hence, such an artificial approach can be favorable to prove pure effects of species mixture. In spite of all severity and vagueness in comparison of observational and experimental studies in forest ecology the synchronous implementation of both approaches seems plausible to comply for the other deficits each. However, the key findings of this study (high importance of tree species identity but a less relevant meaning of tree diversity effects) could have been derived from both procedures.

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Chapter 7

Summary

Summary

Biodiversity is by now widely known to strengthen functioning and services, like primary production and element cycling, for a broad range of ecosystem types. However, it is less clear yet if and how this relationship also applies for forest ecosystems. Moreover, trees are supposed to be highly susceptible to deficient water supply. In this context, it seems to be most interesting whether mixed species forests might be better buffered against the climate change-induced threat of increasing drought events than monocultural stands.

Under consideration of these questions a tree diversity experiment with potted sapling assemblages of five temperate broad-leaved species was conducted which consisted of various species combinations (n=16) differing in species richness (1, 3 and 5 species). Furthermore, a drought trial was implemented to investigate tree water consumption (stand-level), productivity (stand- and tree level) and physiological properties (tree-level) under ample and limited soil water supply.

In case of stand-level transpiration, a significant net diversity effect was observed for the moist (increase by in average ~11%) as well as for the dry treatment (~8%). In moist soil, the increase was most reasonably realized by a selection effect (enhanced water use of the high performer species *T. cordata* and *F. excelsior* in mixed tree assemblages). Similarly, stand-level productivity was significantly enhanced by tree species diversity in the moist (increase in mean relative growth rates: ~9%), but not in the dry treatment (~5%). In contrast to tree water use, higher plant growth in species mixtures was indicated to be mainly caused by complementarity effects, even though considerable competitive asymmetries in favor of fast growing species were observed. The reduced or lacking diversity effects in the dry treatment contrast with the idea of more intense favorable interactions and increasing resistance to abiotic stress for more diverse communities. In fact, the limited soil volume of the potted tree assemblages might have restricted the potential for complementary use of deficient soil water.

The findings about tree mixture effects on tree community functioning were also mostly apparent at tree-individual level. While *T. cordata* clearly enhanced its growth ability in more diverse tree assemblages, *F. excelsior* showed also increased performance in some water-use related physiological traits (stomatal- and sapwood hydraulic conductance). In dry soil, all species realized some plastic modifications in either the status of leaf hydration (*F. excelsior*) or in stem hydraulic architecture (*C. betulus, F. sylvatica*). Furthermore, *C. betulus* but also *A. pseudoplatanus* achieved some improvement in xylem hydraulic properties when exposed to a heterospecific tree neighborhood. Thus, we found some evidence for the beneficial impact of species mixture on tree functional performance under unfavorable site conditions.

In summary, the thesis results widely coincide with most recent findings from forest diversity research, assuming the general occurrence but inferior importance of tree diversity effects on ecosystem functioning, while tree species identity is obviously a more relevant driver. Soil desiccation clearly hampered tree individual performances, but the question if and how tree species diversity fosters community stability in a drier climate remains unsolved and still deserves more attention.

Zusammenfassung

Positive Effekte von Biodiversität auf Ökosystem-Funktionen und Dienstleistungen (wie Primärproduktion und Stoffumsatze) sind mittlerweile für eine Vielzahl von Ökosystemtypen anerkannt. Allerdings ist bisher unklar, inwieweit diese Zusammenhang auch für Forst-Ökosysteme gültig ist. Bäume sind zudem langlebige Organsimen und in vielerlei Hinsicht anfällig gegenüber Trockenheit. Unter Berücksichtigung von Klimaveränderungen erscheint es besonders interessant zu wissen, ob artenreiche Mischwaldbestände weniger anfällig gegenüber zunehmender Trockenheitsperioden sind als Monokulturen.

Mit Bezugnahme auf diese Fragestellungen wurde ein Diversitätsexperiment mit Jungbäumen von fünf temperaten Laubbaumarten durchgeführt. Hierfür wurden verschiedene Artkombinationen (n=16) über 3 Klassen von Artenvielfalt (1,3 oder 5 Arten) in Töpfen kultiviert. Außerdem wurde das Experiment durch einen Trockenheitsansatz erweitert, um Wasserverbrauch (Bestandesebene), Wachstum (Bestandes- und Baumebene), sowie physiologische Eigenschaften und deren Ausprägungen (Baumebene) bei hoher und niedriger Wasserverfügbarkeit untersuchen zu können.

Auf der Bestandesebene wurden für die Transpiration signifikante Netto-Diversitätseffekte beobachtet (durchschnittliche Zunahmen um ~11% (feucht) und ~8% (trocken)). In feuchtem Boden ist diese Zunahme wahrscheinlich auf einen „Selection Effect“ zurückzuführen (die am stärksten transpirierenden Arten, *T. cordata* und *F. excelsior* konnten ihren Verbrauch in den Baumartmischungen nochmals verstärken). Analog dazu wurde das Wachstum der Jungbaumkulturen durch eine höhere Artenzahl verstärkt; allerdings nur unter feuchten Bedingungen (Zunahme durchschnittl. relativer Wachstumsraten: ~9% (feucht) und ~5% (trocken, nicht signifikant)). Eine Analyse der Diversitätseffekte im Wachstum weist, im Gegensatz zum Wasserverbrauch, auf eine höhere Bedeutung von Artkomplementarität hin („Complementarity Effect“ versus „Selection Effect“), obwohl auch hier erhebliche Asymmetrien in den Konkurrenzbeziehungen, zu Gunsten der produktiveren Arten in den Mischungen, beschrieben werden konnten. Die verminderten Diversitätseffekte unter trockenen Bedingungen stehen im Widerspruch zu der Annahme, dass Artenvielfalt die Stabilität von Gesellschaften bei zunehmendem Stress durch positive Interaktionen verstärkt. Möglicherweise spielt hier eine potenzielle Limitierung des Wurzelraumes in den Töpfen eine Rolle, was die Ausprägung von komplementärer Wassernutzung beschränkt haben könnte.

Die Effekte der Baumartendiversität auf die Funktionalität waren auch auf der Einzelbaumebene sichtbar. Während *T. cordata* das Wachstum in den Mischungen deutlich steigern konnte, zeigte *F. excelsior* Steigerungen in der physiologischen Leistungsfähigkeit

(stomatäre- und hydraulische Leitfähigkeit). In Reaktion auf Trockenheit haben alle Arten zumindest einzelne physiologische Anpassungen realisiert (Blattwasserregulierung bei *F. excelsior,* Architektur des Xylems bei *C. betulus* und *F. sylvatica*). Darüber hinaus konnten *C. betulus* und *A. pseudoplatanus* die hydraulischen Eigenschaften ihres Xylems verbessern, wenn sie in Nachbarschaft mit andern Arten kultiviert wurden. Dieses ist letztlich ein Hinweis für die Begünstigung der funktionellen Ausprägung von Einzelbäumen in Mischkulturen unter unvorteilhaften Umweltbedingungen.

Letztendlich zeigen die Ergebnisse dieses Experimentes eine große Übereinstimmung mit der Mehrheit anderer Resultate aus der Walddiversitätsforschung. Diversitätseffekte in Waldökosystemen sind ein häufiges Phänomen, wobei deren Bedeutung im Vergleich zum Einfluss von Arteigenschaften auf Ökosystemfunktionen eher als gering einzustufen ist. Bodentrockenheit hat sichtbar dazu beigetragen die Fitness und Leistungsfähigkeit der Jungbäume zu verringern. Allerdings bleibt weitestgehend unklar, ob und inwiefern Baumartendiversität zur Stabilität von Beständen bei trockenerem Klima beitragen kann. Diese Frage erfordert weiterhin erhöhte Aufmerksamkeit in der zukünftigen Diversitätsforschung.

Chapter 8

Appendix

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Declaration of originality and certificate of ownership

I, Torben Lübbe, hereby declare that I am the sole author of this dissertation entitled 'EFFECTS OF TREE SPECIES DIVERSITY AND SOIL DROUGHT ON PRODUCTIVITY, WATER CONSUMPTION AND HYDRAULIC FUNCTIONING OF FIVE TEMPERATE BROAD-LEAVED TREE SPECIES'. 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.

Göttingen, July 1, 2016 ____________________

(Torben Lübbe)