

IMPACT OF CLIMATE CHANGE-INDUCED DROUGHT ON
TREE ROOT HYDRAULIC PROPERTIES AND
COMPETITION BELOWGROUND

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Summary

Drought has been projected to increase as global warming progresses, putting forest health in jeopardy. Water availability already is a major factor limiting plant growth, especially in forests and orchards on shallow, sandy soils or in regions with low precipitation. Furthermore, salinisation of agricultural soils is an increasing problem, often caused by the increased water demand for irrigation in drier climates.

Research on drought and salt resistance strategies of plants has classically focussed on the dynamics of stem and leaf water. However, it is in the soil where water uptake occurs and plants compete for water and nutrients. Although an increasing number of studies are addressing belowground traits, a better understanding of the adaptability of tree root systems to water limitation and belowground competition is needed to be able to predict the effects of climate change on mature forest stands and woody crops.

This study on five tree species in temperate mixed forests and Mediterranean fruit tree orchards aims at answering important questions on the influence of reduced soil moisture and competitive interactions on structure and function of tree root systems. In particular, the aims of this study were to test whether (i) root hydraulic conductivity decreases in response to water shortage as does shoot hydraulic conductivity, (ii) fine roots act as ‘hydraulic fuses’ of the soil-plant-atmosphere continuum, (iii) the belowground competitive ability is symmetric and directly linked to root system size, and (iv) belowground competitive ability differs between tree species and is not modified by resource availability.

This study showed that:

i) *Quercus petraea* (MATT.) LIEBL. generally responded to moderate or severe drought with an increase in root axial conductivity, while *Fagus sylvatica* L. mostly did not. The same pattern was found in salt-stressed *Olea europaea* L. roots, the conductivity of which increased in response to increasing salinity. Drought- and/or salt-adapted tree species such as *Quercus petraea* and *Olea europaea* seem to be capable of partly compensating for water shortage-induced root biomass losses by increasing root axial conductivity, a mechanism rarely observed in aboveground organs.

ii) Fine roots can act as ‘hydraulic fuses’ in the soil-plant-atmosphere continuum. In addition to most previous studies, which suggest root shedding as the underlying

mechanism, this study indicates cavitation to be another, potentially reversible, ‘hydraulic fuse’ mechanism. This conclusion is based on the very high vulnerability of small-diameter roots of both *Quercus* and *Fagus* to cavitation and the further increase of this vulnerability in drought-stressed *Quercus* roots.

iii) This study revealed two lines of evidence for the existence of asymmetry in below-ground competition: fine root biomass of *Quercus petraea* was over-proportionally reduced in species-rich allospecific stand patches as compared to monospecific ones, and root growth rates and morphology depended on the competitor present but not on initial root system size differences.

iv) Tree species may be ranked according to their belowground competitive ability. According to data on root biomass and root growth in experimentally altered neighbourhoods, *Fagus sylvatica* seems to be a superior competitor belowground. However, a marked asymmetry in the outcome of root competition only developed when soil moisture in summer was sufficiently high. Resource limitation, i.e. drought, seems to affect the competitive ability of *Fagus sylvatica* and *Quercus petraea* roots in a similar manner with the consequence that species-specific differences in competitive ability are less conspicuous in more stressful environments. Therefore, the overall importance of direct biotic interactions belowground seems to be reduced by limited soil water availability.

Zusammenfassung

Durch die mit dem Klimawandel einhergehende Temperaturerhöhung und den verringerten Niederschlag wird es in Zukunft häufiger zu Trockenperioden kommen. Wasser ist bereits heute ein das Pflanzenwachstum limitierender Faktor, insbesondere in Wäldern und Plantagen auf schwachgründigen, sandigen Böden sowie in Regionen mit geringem Niederschlag. Zudem fördert der erhöhte Bewässerungs-Bedarf unter trockeneren klimatischen Bedingungen die Versalzung von landwirtschaftlichen Böden.

Obwohl die Wasseraufnahme und Konkurrenzprozesse um Wasser und Nährstoffe im Boden stattfinden, lag der Schwerpunkt bei der Erforschung von pflanzlichen Anpassungsstrategien an Trockenheit und Salz-Stress in der Vergangenheit häufig auf den oberirdischen Pflanzenorganen. Um die Effekte des Klimawandels vorhersagen zu können, ist jedoch ein besseres Verständnis für die Anpassungsfähigkeit von Wurzelsystemen an Trockenheit und unterirdische Konkurrenzprozesse nötig.

Diese Studie über fünf Baumarten temperater Mischwälder und mediterraner Obstbaum-Plantagen untersucht den Einfluss reduzierter Bodenwasserverfügbarkeit und unterirdischer Konkurrenzprozesse auf die Struktur und Funktion von Wurzelsystemen.

Insbesondere soll in dieser Studie geklärt werden, ob (i) die axiale hydraulische Leitfähigkeit von Wurzeln, analog zur Anpassung oberirdischer Organe, mit zunehmender Trockenheit abnimmt, (ii) Feinwurzeln im Boden-Pflanze-Atmosphäre-Kontinuum als „hydraulische Sicherungen“ fungieren, und (iii) die unterirdische Konkurrenzkraft symmetrisch zur Größe des Wurzelsystems ist bzw. (iv) zwischen Baumarten und mit der Wasser- und Nährstoffversorgung variiert.

Durch diese Studie konnte nachgewiesen werden, dass

i) Die axiale hydraulische Leitfähigkeit der Fein- und Grobwurzeln von *Quercus petraea* (MATT.) LIEBL., im Gegensatz zu Wurzeln von *Fagus sylvatica* L., bei starker Bodentrockenheit zunimmt. An Wurzeln von *Olea europaea* L. konnte zudem eine Zunahme der hydraulischen Wurzel-Leitfähigkeiten mit zunehmendem Salzgehalt des Bodens beobachtet werden.

An Trockenheit und/oder Salz-Stress angepasste Baumarten wie *Quercus petraea* und *Olea europea* sind vermutlich in der Lage, den durch den Verlust an Wurzelbiomasse erhöhten hydraulischen Widerstand durch eine Verminderung der axialen Wurzel-

Leitungswiderstände zu kompensieren. In Sprossen und Zweigen konnte ein ähnlicher Anpassungsmechanismus bislang nur vereinzelt nachgewiesen werden.

ii) Feinwurzeln als „hydraulische Sicherungen“ im Boden-Pflanze-Atmosphäre-Kontinuum wirken können. Das Xylem von *Quercus petraea* und *Fagus sylvatica* Feinwurzeln emboliiert bereits bei geringfügig verminderten Wasserpotentialen. Darüber hinaus erhöht sich die Embolieanfälligkeit der Feinwurzeln von *Quercus petraea* nach Bodentrockenheit. Neben dem Absterben von lateralen Feinwurzeln scheinen Embolien als weiterer, eventuell reversibler, hydraulischer Sicherungsmechanismus zu wirken.

iii) Verschiedene Anzeichen auf die Asymmetrie der unterirdischen Konkurrenzprozesse hindeuten. Zum Einen ist die Feinwurzelbiomasse von *Quercus petraea* unter interspezifischen Konkurrenzbedingungen im Vergleich zu Reinbeständen überproportional reduziert, zum Anderen hängt die Wachstumsrate und Morphologie von Wurzeln von der Anwesenheit eines Konkurrenten und nicht von der Anfangsbiomasse ab.

iv) Baumarten anhand ihrer unterirdischen Konkurrenzkraft gegliedert werden können. Den Ergebnissen über Wurzelbiomasse und -wachstum unter unterschiedlichen Konkurrenzbedingungen zur Folge, ist *Fagus sylvatica* nicht nur ober-, sondern auch unterirdisch eine der konkurrenzstärksten Baumarten Mitteleuropas. Unter zunehmendem abiotischem Stress verlieren artspezifische Unterschiede in der Konkurrenzkraft jedoch an Bedeutung und die Wichtigkeit biotischer Interaktionen ist vermindert. Eine Einschränkung der Ressourceverfügbarkeit, z.B. durch Trockenheit, scheint die Konkurrenzkraft von *Fagus sylvatica* und *Quercus petraea* in gleicher Weise zu beeinflussen.

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‘Now would I give a thousand furlongs of sea for an acre of barren ground - long heath, brown furze, any thing. The wills above be done, but I would fain die a dry death.’

William Shakespeare, The Tempest

Chapter 1

INTRODUCTION

1.1 IMPACT OF CLIMATE CHANGE ON CENTRAL EUROPEAN AND MEDITERRANEAN FORESTS

Forests cover more than 4.1×10^7 km² of the Earth's land area, contain 80% of the world's aboveground and 40% of belowground terrestrial carbon, and host much of the world's biodiversity (e.g. Dixon *et al.* 1994, Lindenmayer and Franklin 2002). They provide wood and crops as well as important 'services' such as facilitating ground water recharge, stabilizing slopes, providing space for recreation, and acting as carbon sinks (Ziemer 1978, Riestenberg and Sovonickdunford 1993, Goodale *et al.* 2002, Zandersen *et al.* 2007).

There is now convincing evidence that the global climate is changing at an unprecedented rate, putting forest health in jeopardy (IPCC 2007). A large proportion of the observed rise in global temperatures has been attributed to human activities: changes in the albedo of the earth's surface due to land-use changes and the increasing greenhouse gas emissions from intensive agriculture and fossil fuel burning have been identified as the main causes for global climate warming (Houghton 1994, Crowley 2000, IPCC 2007).

The general effects of increasing CO₂ and the associated changes in temperature on aboveground tree function and growth have been reviewed elsewhere (Eamus and Jarvis 1989, Norby *et al.* 1999, Broadmeadow *et al.* 2005), whereas information about belowground responses is still scarce (Brunner and Godbold 2007). In brief, rising concentrations of CO₂ are known to enhance photosynthesis and above- and belowground growth of tree seedlings as long as water and nutrient supply are sufficient (Broadmeadow and Randle 2002). This holds also true for some mature forest stands (Spiecker 1999, Lukac *et al.* 2003, Norby *et al.* 2005). Nevertheless, no enhancement of productivity could be observed in forests subjected to free-air CO₂ enrichment that were possibly limited by water and nutrient supply (Oren *et al.* 2001, Karnosky 2003, Luo *et al.* 2004).

Water availability is a major factor limiting forest growth (Pigott and Pigott 1993, Stephenson 1990, Olson *et al.* 2001). In most parts of Central Europe, moderate drought stress is typically to be expected during short rainless periods that occur at irregular intervals in most summers (Backes and Leuschner 2000, Czajkowski *et al.* 2005) while severe droughts are episodic events (Lloyd-Huges and Saunders 2002). In the Mediter-

anean Basin water is strongly limiting plant growth and survival (Roy *et al.* 1987, Lloret *et al.* 2004), which is especially true for most Mediterranean tree genera, since they are thought to have evolved before the onset of the present summer-dry climate (Petit *et al.* 2005).

Model calculations of the future climate predict an increasing frequency and severity of exceptional summer droughts and heatwaves in various parts of Central Europe (Kunstmann *et al.* 2004, Rowell 2005, Forkel and Knoche 2006, Frei *et al.* 2006), and a disproportionately strong increase of summer temperature and aridity in the Mediterranean Basin (Fig. 1.1; Iglesias *et al.* 2000, IPCC 2007).

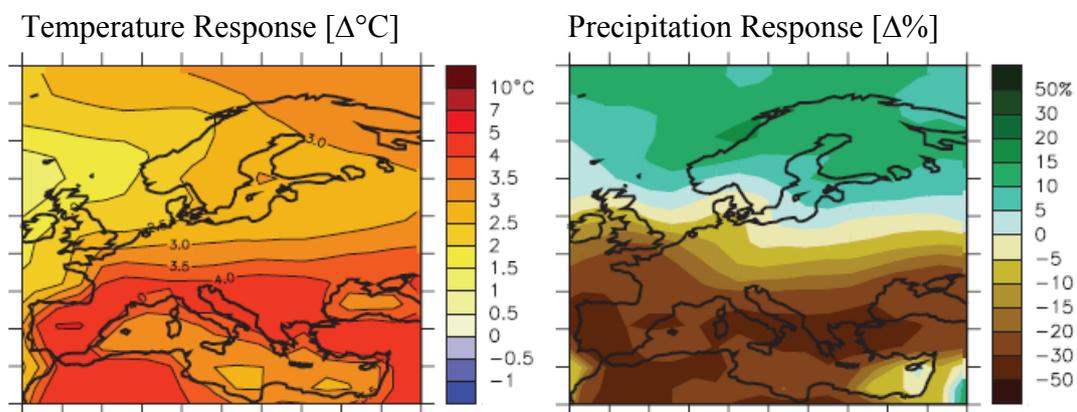


Fig. 1.1 Projected temperature (left) and precipitation (right) changes in Europe and the Mediterranean Basin between 1980-1999 and 2080-2099. Means of summer months (June - August) are given (IPCC 2007, modified).

The most vulnerable regions to climate change in Central Europe and the Mediterranean Basin are those, where soil moisture is already limited by geographical (e.g. warm and dry areas in Eastern Germany and Southern Europe) or pedological aspects (e.g. shallow or sandy soils resulting in low water storage capacity) under present site conditions (Kellomäki *et al.* 2000). The Mediterranean is particularly prone to climate change due to the high natural climate variability (Lionnello *et al.* 2006), the already most severe and precarious water scarcity (ESCWA 2007, Iglesias *et al.* 2007), and the susceptibility to secondary soil salinization by the increased demand for irrigation in drier climates (Centritto 2002).

Consequently, predictions of the effects of climate change on tree species and forests cannot be based on CO₂ concentration only: water availability and temperature will play central roles in determining the future structure and function of forest ecosystems (Kellomäki *et al.* 2000, Pan *et al.* 2001, Christensen *et al.* 2007).

1.2 INFLUENCE OF WATER SHORTAGE ON THE HYDRAULIC SYSTEM OF TREES

The soil-plant-atmosphere continuum refers to the coherence of water columns from the soil into plant roots, through stems and twigs into the leaves and, via transpiration, to the atmosphere (van den Honert 1948). Increasing evaporative demands and drier soils as predicted for the future will subject this ‘hydraulic rope’ to aggregated stress, thus endangering the continuous water supply to the leaves (Tyree and Zimmermann 2003, Santiago *et al.* 2004).

The whole-plant acclimation to water deficits has been reviewed by Bartels and Sunkar (2005), and Maseda and Fernández (2006). In summary, maximizing gas exchange while avoiding hydraulic failure requires the harmonization of at least three parameters: stomatal sensitivity, xylem vulnerability to embolism, and leaf-specific hydraulic conductivity. Studies investigating plant responses to water shortage, induced either by drought or salinity, have highlighted the importance of adjustments in the hydraulic system (Tables 1.1, A 6, A 7; Sperry *et al.* 1998, Holbrook and Zwieniecki 2005), as part of an whole-plant adaptation to drought stress (Shumway *et al.* 1991, Bond and Kavanagh 1999, Meinzer 2002). In the hydraulic system, axial hydraulic conductivity (k_h), which gives the mass flow rate (kg s^{-1}) of water through a shoot or root segment relative to the pressure gradient (MPa m^{-1}), is of particular importance.

Table 1.1 Changes in the hydraulic system due to water shortage that influences axial hydraulic conductivity (k_h ; Maseda and Fernández 2006, modified).

Structure or process	Level of Organisation	Time scale	Effect on k_h	References (examples)
Decreased aquaporin activity	Subcellular, cell	Minutes, hours	↓	Lovisollo <i>et al.</i> 2007 Secchi <i>et al.</i> 2007
Decreased vessel diameter, density	Tissue	Ontogeny	↓	Arnold and Mauseth 1999 Corcuera <i>et al.</i> 2004 Junghans <i>et al.</i> 2006
Increased vessel diameter, density	Tissue	Ontogeny	↑	Maherali and DeLucia 2000 Cinnirella <i>et al.</i> 2002
Decreased vulnerability to xylem cavitation	Tissue, organ	Ontogeny	↓	Hacke <i>et al.</i> 2000 Willson and Jackson 2006
Increased root:leaf ratio (decreased water potential gradient)	Whole plant	Ontogeny	↑	Brodribb and Hill 2000 Gieger and Thomas 2002

In theory, increased hydraulic conductivities in response to drought stress could be as beneficial as decreased conductivities. Whereas an increase of k_h could facilitate water uptake (Nardini and Pitt 1999, Mencuccini 2003, Maseda and Fernández 2006), a decrease is thought to help avoid cavitation (Hacke *et al.* 2001, Maherali *et al.* 2004) and reduce water loss to the atmosphere (Richards and Passioura 1989, Caldwell *et al.* 1998). Although it is known that vulnerability to drought-induced cavitation is not directly linked to xylem vessel diameters, it is associated with thicker cell walls in relation to lumen area (Hacke *et al.* 2001), resulting in reduced conductive areas. However, empirical studies have nearly always found the second response, i.e. a decrease in conductivity as a consequence of drought stress (see Tables A 6, A 7).

Previous work has shown that xylem properties can differ widely between plant organs in their adaptability to environmental stresses and their vulnerability to cavitation (Mills 1989, Martínez-Vilalta *et al.* 2002, Maherali *et al.* 2006). About half of total plant hydraulic resistance is located in the roots (Passioura 1988, Meinzer 2002). Furthermore, there is evidence that (i) ontogeny can modify the effects of water deficits and the sensitivity to drought (Cavender-Bares and Bazzaz 2000, Winkel *et al.* 2001), and (ii) drought-induced changes can hardly be analysed separately from allometric changes during ontogeny (Maseda and Fernández 2006).

Further research in this area is urgently needed to allow for predictions of responses of both mature forests and juvenile trees to future climate changes.

1.3 BELOWGROUND COMPETITION IN MIXED FOREST STANDS – RECIPROCALITY WITH RESOURCE AVAILABILITY

Forests are not expected to respond to climate change as intact units, because of species-specific responses and interactions among species (Hanson *et al.* 2001). Influences of CO₂ and ozone concentrations on trees are known to be modified by competitive interactions (Ceulemans *et al.* 1999, Liu *et al.* 2004), but predictions on the future composition of forests are still largely hampered by our limited understanding of the reciprocal effects of climate change and competitive interactions.

This is particularly true for belowground competition in mature forest stands. Several studies have provided convincing evidence that root competition is an important structuring force in many, if not most, terrestrial plant communities (Wilson 1988, Kajimoto

et al. 2007). However, due to methodological reasons, belowground interactions between woody plants have mostly been studied in agroforestry systems (Nambiar and Sands 1993) or between adult and juvenile trees (Coomes and Grubb 2000, Barberis and Tanner 2005). Thus, the influence of root competition on tree growth, vitality and species coexistence in mixed forests is poorly understood, which makes it even more problematic to predict tree responses to a changing climate.

The mechanisms of belowground competition are assigned to two categories: exploitation (or resource-mediated) competition, and interference competition (e.g. Grace and Tilman 2003). Exploitation competition is based on the reduction of water and nutrient uptake by neighbouring roots. Traits that may influence this type of belowground competition are (i) root morphology and resource uptake rate (Fig. 1.2; Bauhus and Messier 1999, Leuschner *et al.* 2004, Bolte and Villanueva 2006), (ii) spatial and temporal soil occupation and root proliferation (Parrish and Bazzaz 1976, Robinson *et al.* 1999, Schenk 2006), and (iii) mycorrhization (Bolan 1991).

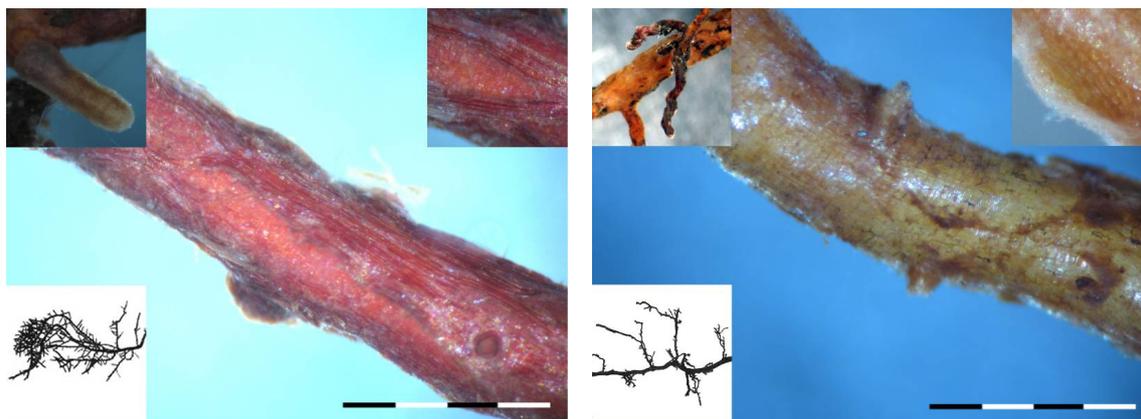


Fig. 1.2 Different morphological characteristics of *Fagus sylvatica* (left) and *Quercus petraea* (right) fine roots from the Unterlüß forest, NW Germany. Scale bars represent 1 mm.

Interference competition includes allelopathy (Mahall and Callaway 1991, Jose *et al.* 2006), yet unknown root-root recognition systems (Callaway 2002, Falik *et al.* 2005), or root interactions with soil fauna or microorganisms (Schenk 2006).

Belowground competition would ideally be measured by quantifying the influence of belowground neighbourhoods on resource uptake, biomass, growth, or fecundity (Goldberg 1990, Schenk 2006) of individuals. However, whole-plant reductions in growth and vitality are difficult to detect in long-lived organisms such as mature trees, and short-term or single-resource-based physiological approaches may be misleading with

regard to their ecological significance (Casper *et al.* 2000). Thus, criteria such as relative root growth rate (Grace 1995), root morphology (Bolte and Villanueva 2006), and the degree of root system overlap are more suitable to investigate belowground competition in mature forest stands, integrating the results of both exploitation and interference competition.

In contrast to aboveground competition, where larger individuals can obviously preempt light, belowground competition has been found to be either symmetric to root system size (Weiner *et al.* 1997, Cahill and Casper 2000) or asymmetric (Fransen *et al.* 2001, Rajaniemi 2003). Whereas the bulk of experimental evidence, mostly obtained in artificial ‘communities’, suggests that soil resource acquisition is size-symmetric, this may not be valid in natural environments with a considerable heterogeneity (Tables A 3-A 5; Jackson and Caldwell 1993, Schwinning and Weiner 1998). Larger and faster growing root systems may be able to exploit resources more completely (Thomas and Weiner 1989, Campbell *et al.* 1991, Van Lear and Kapeluck 1995), and uptake kinetics may differ between competing plant species (Aerts and Chapin 2000).

It is yet unclear whether belowground competition is symmetric or asymmetric, a property which may substantially influence population and community dynamics (Łomnicki 1980, Aikio and Pakkasmaa 2003). Moreover, there is a vital debate on the influence of resource availability on root competition. Two contrasting hypotheses have been formulated with regard to the intensity of belowground competition depending on nutrient and water availabilities: belowground competitive intensity can be either dependent (Grime 1979, Keddy 1989, Wilson and Tilman 1993), or independent (Newman 1973, Welden *et al.* 1988, Peltzer *et al.* 1998) of resource availability.

Modelling approaches predict strong responses of forest species composition to dryer climates (Kräuchi and Kienast 1993, Shao *et al.* 2003). However, these models are known to be largely hampered by the poor integration of biological processes, such as competition (Hallgren and Pitman 2000). A better understanding of competition in forests is therefore imperative.

1.4 STUDY DESIGN

This study, including five tree species from Central Europe and the Mediterranean Basin, uses both descriptive and experimental approaches to assess the impact of water shortage on the morphology, structure and functionality of tree root systems.

The research was conducted at four locations in Central Germany and Southern Israel:

1. Unterlüß forest: Studies on the influence of drought stress on root hydraulic properties and belowground competition were carried out in an unmanaged old-growth mixed forest consisting of 120-year-old *Fagus sylvatica* L. (European beech) and 200-year-old *Quercus petraea* (MATT.) LIEBL. (Sessile oak) trees close to the village of Unterlüß (Lower Saxony, NW Germany; 52°14'50 N, 10°13'00 E; Fig. A 4).
2. Experimental Botanical Garden Göttingen: A study on the influence of drought stress on the root hydraulic properties of 4 to 6-year-old *Fagus sylvatica* and 5 to 7-year-old *Quercus petraea* saplings took place at the Experimental Botanical Garden of the University of Göttingen, Central Germany (51°56'N, 09°96'E; Fig. A 4).
3. Ramat Negev Experimental Station: A study on the influence of root hydraulic properties on the salt resistance of three 9-year-old *Olea europea* L. (olive) varieties was conducted in the orchards of the Ramat Negev Experimental Station, located in the central Israeli Negev Desert (31°05'00 N, 34°41'03 E; Fig. A 5).
4. Ziegelrodaer forest: A study on belowground competition was carried out in a four-species mixed forest consisting of 120 to 130-year-old *Fagus sylvatica* and *Quercus petraea* trees, and of 70 to 90-year-old *Tilia cordata* MILL. (linden) and *Carpinus betulus* L. (hornbeam) trees in the Ziegelrodaer forest in Saxony-Anhalt, Central Germany (51°25'N, 11°31'E; Fig. A 6).

The following parameters were measured to assess the hydraulic properties and the competitive interactions of root systems of saplings and mature trees under different soil moisture availabilities:

1. root area index, specific root area, root bio- and necromass,
2. vertical and horizontal root distribution,
3. relative root growth rates,
4. root- and shoot-specific conductivity,
5. degree of embolism in roots and shoots,
6. root vulnerability to cavitation,
7. root xylem anatomy,
8. leaf area index, leaf biomass, and
9. basal area increment.

1.5 STUDY OBJECTIVES AND HYPOTHESIS

This study focussed on five tree species from temperate mixed forests and Mediterranean fruit tree orchards and aimed at answering important questions on the influence of reduced soil moisture on structure and function of tree root systems. Our knowledge is particularly limited with respect to competitive interactions belowground and hydraulic adaptations of root systems.

Thus, the study placed particular emphasis on (i) the adaptability of the root hydraulic system to drought and salt stress, and (ii) the intensity and direction of belowground competition under conditions of limited water availability.

In particular, the aims of this study were:

1. to compare the root- and shoot-specific conductivities of contrasting tree species, varieties and ontogenetic stages under drought and salt stress,
2. to quantify the degree of root embolism and root vulnerability to cavitation,
3. to assess the contribution of root hydraulic properties to drought- and salt-resistance,
4. to quantify the extent of root system overlap,
5. to compare the influence of reduced soil moisture and/or interspecific competition on root morphology,
6. to attempt a ranking of the tree species with respect to belowground competitive ability,
7. to determine whether belowground competition in mature forests is symmetric or asymmetric, and
8. to analyse whether root competition asymmetry changes with soil moisture availability or not.

I tested the hypotheses that (i) root hydraulic conductivity decreases in response to drought as well as shoot hydraulic conductivity, (ii) fine roots act as ‘hydraulic fuses’ of the soil-plant-atmosphere continuum to prevent runaway cavitation in the whole plant, (iii) the belowground competitive ability is symmetric to root system size, and (iv) belowground competitive ability differs between tree species and is not modified by resource availability.

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Chapter 2

DROUGHT-INDUCED CHANGES IN AXIAL CONDUCTIVITY AND VULNERABILITY TO EMBOLISM IN ROOTS OF TWO BROAD- LEAVED TREE SPECIES WITH CONTRASTING DROUGHT- TOLERANCE

Christoph Leuschner and Boris Rewald

2.1 ABSTRACT

Theory predicts that fine roots may be particularly weak elements in the hydraulic system of the plant due to elevated cavitation risk and high drought-induced mortality, thereby acting as ‘fuses’ in the hydrologic soil-plant-atmosphere continuum which protect the plant from further turgor loss and plant-wide xylem cavitation. We tested this hypothesis by investigating specific conductivity (k_s) of fine and coarse root (i.e. axial conductivity per root cross-sectional area) and the degree of embolism in the root xylem of saplings and mature trees of drought-sensitive European beech (*Fagus sylvatica* L.) and relatively drought-tolerant Sessile oak (*Quercus petraea* (MATT.) LIEBL.) that were exposed to experimental water shortage.

Fine and coarse roots of both species were much more vulnerable to cavitation (water potentials causing 50% conductivity loss, Ψ_{PLC50} : -0.3 to -0.5 MPa) than shoots (-2 to -3 MPa). Mature beech and oak trees had 3 to 15 times higher k_s values of their small-diameter roots than saplings, indicating a large increase in root specific conductivity with age. However, fine roots (< 2 mm in diameter) and coarse roots (> 2 mm) differed not significantly in k_s . In oak, drought led to an increase in root k_s , which contrasts with shoots where conductivity generally decreased. However, a decrease in root conductivity was found in severely drought-stressed beech saplings and adult trees, which supports the view of oak being more drought-tolerant than beech.

We conclude that small-diameter roots of beech and oak with their height cavitation susceptibility are much more drought-sensitive than shoots. However, drought-adapted tree species such as *Quercus petraea* seem to be capable of partly compensating for drought-induced root conductivity losses by increasing root k_s .

2.2 INTRODUCTION

Drought limits tree growth not only in arid environments but also in temperate oceanic regions such as Central Europe. For example, stem diameter growth of *Fagus sylvatica* L., the most important tree species of the natural forest vegetation, is primarily dependent on sufficient rainfall in the lowlands of Central Europe (Ellenberg 1996, Dittmar *et al.* 2003). Regional models of future climate change predict an increasing frequency and severity of exceptional summer droughts and heatwaves in various parts of Central Europe, in particular in sub-continental and continental regions (Wetherald and Manabe 2002, IPCC 2007). Further, summer rainfall has already decreased in certain areas of Germany during the past 100 years, as, for example, in the state of Lower Saxony (DWD 2007). Less rainfall together with higher summer temperatures and elevated evaporative demand will increase soil water deficits and drought exposure. Therefore, the adaptability to water shortage may decide about the growth potential and vitality of trees in a future warmer climate even under a temperate oceanic climate (Hanson and Welzin 2000).

Studies concerning plant adjustment to drought have highlighted the importance of adaptational changes in the plant conducting system to maximize water uptake and to reduce water deficits (Sperry *et al.* 1998, 2002, Ladjal *et al.* 2005). Plastic responses of the xylem with respect to hydraulic conductivity and vulnerability to cavitation under altered water supply may be a key trait of the drought response of trees and other plants. Various studies have emphasized differences in hydraulic properties among tree species (Whitehead and Jarvis 1981, Tyree and Zimmermann 2003). Moreover, previous work has shown that xylem properties of different plant species and plant organs can differ widely in their adaptability to environmental stresses and their susceptibility to cavitation (Martínez-Vilalta *et al.* 2002, Maherali *et al.* 2006). However, surprisingly few comparisons of plants of the same species or ecotypes grown under contrasting moisture regimes exist. Our knowledge is particularly limited with respect to the hydraulic adaptation of root systems in mature forest stands (Cinnirella *et al.* 2002, Leuschner *et al.* 2004a) even though increasing empirical evidence is accumulating showing that root system conductance plays a crucial role for water flux control in the soil-plant-atmosphere continuum (Passioura 1988, Trillo and Fernández 2005).

Experiments on root hydraulic conductivity usually measure total conductivity of root branches, thereby including both radial and axial conductivity (Kolb *et al.* 1996). Root radial conductivity is thought to be orders of magnitude smaller than axial conductivity (Sands *et al.* 1982). However, Hacke *et al.* (2000) demonstrated a good agreement between whole-plant water use and axial conductivity of woody plants during drought stress, suggesting that differences in root radial resistance across sites either become negligible during drought, or parallel the change in axial resistance. The path length of radial water flow is much less than axial length, indicating the importance of axial conductivity especially in large woody plants (Sperry *et al.* 2002, Addington *et al.* 2006). Moreover, meta-xylem differentiation in growing roots can be slow (Staubin *et al.* 1986, Vercambre *et al.* 2002); hindering longitudinal water transport especially in the finest roots (Doussan *et al.* 1998). For a better understanding of root system functioning, measurements of root axial conductance are urgently needed, especially with an emphasis on variations related to environmental stress and tree age under field conditions (Maseda and Fernández 2006).

We studied the axial conductivity, the occurrence of embolism and the vulnerability to embolism in fine root and coarse roots of mature trees and saplings of *Fagus sylvatica* L. and *Quercus petraea* (MATT.) LIEBL. which were exposed to experimental summer drought. Diffuse-porous *Fagus* is the most competitive tree species in large parts of Central Europe under conditions of ample moisture supply (Ellenberg 1996; Leuschner *et al.* 2001). In contrast, *Quercus petraea* has a higher tolerance of summer droughts (Backes and Leuschner 2000, Raftoyannis and Radoglou 2002), but is outcompeted by *Fagus* in most non-water limited environments (Brockmann *et al.* 1987, Aranda *et al.* 2000). Thus, these two tree species exemplify the trade-off between a species' ability to cope with drought stress, and high growth rates under more favourable soil water regimes (Orians and Solbrig 1977, Fotelli *et al.* 2001).

This paper reports on a combined field manipulation and pot study with mature trees and saplings of *Fagus sylvatica* and *Quercus petraea* which investigated the adaptability of the hydraulic system of fine and coarse roots to moderate and severe drought stress. We tested the hypotheses that (i) root specific conductivity decreases upon drought stress, (ii) fine roots are more vulnerable to cavitation than roots with larger diameters, (iii) root systems of mature trees and saplings differ in their adaptability to soil drought, and (iv) the root systems of *Quercus* are better adapted to drought stress

than those of *Fagus*. Axial conductivities of sapling shoots were studied for comparison as well.

2.3 MATERIAL AND METHODS

Study sites and plant material

Saplings and mature trees of *Fagus sylvatica* L. (European beech) and *Quercus petraea* (MATT.) LIEBL. (Sessile oak) were investigated in their response to experimental drought between April 2004 and September 2006.

The study on mature trees was conducted in an unmanaged mixed oak-beech forest located in the diluvial lowlands of Lower Saxony (NW Germany) in the Lüneburger Heide at 115 m a.s.l. close to the village of Unterlüß (52°83'N, 10°26'E; Table 2.1).

Table 2.1 Structural characteristics of the mixed oak-beech forest at Unterlüß (NW Germany).

	Age of dominant trees [yrs]	Stem density* [ha ⁻¹]	Tree height [m]	Stem basal area [m ² ha ⁻¹]	Leaf area index [m ² m ⁻²]
<i>Fagus</i>	120	176	30	15.2	3.3
<i>Quercus</i>	200	44	28	12.3	1.6
Stand total	-	220	-	27.5	4.6

*all trees >10 cm dbh

Fagus and *Quercus* trees show a patchy distribution in the stand with monospecific groups of beech or oak. Except for saplings of the two tree species, no herbaceous layer does exist. The climate is humid sub-oceanic (annual means: 8.1°C, 801 mm precipitation). The cumulative precipitation during the 30-month experimental period was 1675 mm, which is 350 mm below the long-term precipitation mean (H. Meesenburg, Northwest German Forest Research Station, unpublished). The soil is a spodo-dystric cambisols with a thick (mean depth of 7.2 cm) and highly acidic (pH_{KCl}: 2.6-3.0) organic layer (Leuschner 2002). Medium-grained sand is the dominant size fraction of the sediment (40-60% of dry mass) while the clay content is very low (< 5%).

Four plots (8 m x 8 m) were chosen for study, two in *Fagus*- and two in *Quercus*-dominated parts of the forest. The stands on the four plots had a closed canopy with

comparable tree densities and tree height, and showed no signs of soil disturbance by wild boar. The plots were fenced. Each one *Fagus* and one *Quercus* plot was equipped with a below-canopy roof (treatment D_{Sev.}), while the two other plots served as a control with ambient rainfall (Ctrl). The control and the roofed plot of each tree species lay adjacent to each other, while the paired *Fagus* and *Quercus* plots were about 130 m distant to each other. The roofs had a size of 11 m x 11 m, situated about 2 m above the ground. They consisted of a permanent timber-frame construction, covered with removable transparent PVC plates. Eight of the nine supporting pillars were placed outside the plot, the central pillar was carefully dug into the soil inside the plot to a depth of 50 cm. Rainfall was collected with gutters and channelled away.

The roofs were operated in three consecutive summers (2004 to 2006) from mid/end of June until end of September (i.e. 13-14 weeks per year) to simulate severe summer droughts as they occur occasionally in dry years in the region. From end of September to mid of June, the roofs were opened and ambient rainfall reached the D_{Sev.} plots in a similar intensity as the control plots. Volumetric soil water content was recorded once per month in all four plots with a mobile TDR probe (Trime FM2, Imko, Ettlingen, Germany) at six randomly selected locations per plot at a depth of 0-16 cm. Since the three summers differed in rainfall, soil water depletion was high in the summer 2004, but less severe in the summers 2005 and 2006 (Table 2.2).

Table 2.2 Soil moisture content (vol%) during the summer months in the surface layers (0-16 cm) of the control plots (Ctrl) and roofed plots (Severe drought, D_{Sev.}) in the Unterlüß forest (mean of *n* TDR measurements ± SE).

Year	Month	<i>n</i>	<i>Fagus</i>		<i>Quercus</i>	
			Ctrl	D _{Sev.}	Ctrl	D _{Sev.}
2004	June	64	15.3±0.4	8.2±0.2	14.5±0.7	14.7±0.5
	July	6	18.8±1.7	5.8±0.1	20.5±2.3	8.8±0.7
	August	6	11.3±1.0	6.7±0.5	15.1±2.1	8.6±0.3
	September	6	18.9±0.3	5.8±0.4	14.8±0.5	9.1±0.4
2005	June	6	27.9±2.0	27.9±2.0	27.9±1.8	28.1±2.2
	July	6	23.7±1.1	20.7±1.3	24.9±2.0	18.9±2.0
	August	6	21.6±0.9	12.1±2.0	22.2±2.0	13.5±1.2
	September	6	18.7±1.2	10.4±0.7	18.8±2.0	10.1±1.8
2006	June	6	26.8±2.4	27.1±1.4	-	-
	July	6	13.4±0.9	17.3±1.5	14.6±1.1	16.1±1.7
	August	6	25.5±1.4	11.1±1.0	27.1±1.9	13.8±2.1
	September	6	19.2±1.5	9.0±2.0	18.0±1.2	12.2±0.9

In general, soil water content at 0-16 cm depth was lower by 5 to 15 vol% in the two roof plots than in the control plots in the period July to September of the three years. Although the throughfall patterns under the oak-beech forest canopy revealed a certain heterogeneity in space, we detected no significant differences in mean summer soil water content between the two control plots (beech and oak), nor between the beech and oak drought plots (see Table 2.2).

Temperature measurements with iButton sensors (DS1921, Maxim, Sunnyvale, USA) revealed no differences between control and roofed plots with respect to air temperature. The soil temperature at 7 cm depth was marginally reduced by 0.5-1.0 K beneath the roofs during the summer months (June-August, data not shown). In addition, the soil of the *Quercus* plots was by 0.5-1.0 K colder than that in the *Fagus* plots. For minimizing soil compaction, mobile wooden footbridges were used to access the inner plot sections.

The experiment with ninety 4-yr-old *Fagus* saplings and ninety 5-yr-old *Quercus* saplings took place at the Experimental Botanical Garden of the University of Göttingen, Germany (51°56'N, 09°96'E). Beech and oak acorns were collected in close proximity of the Unterlüß stand by the Forest Seed Centre of Lower-Saxony (Munster-Oerrel, Germany) and were planted at a tree nursery (Forestry office Göhrde, Lower Saxony, Germany). At the age of 4 (beech) or 5 (oak) years, saplings of similar size were selected from this culture in early April 2004 and individually planted in 45-l pots, filled with nutrient-poor medium-grained quartz sand. The field capacity of the sandy substrate was about 9-10 vol% of water.

The potted beech and oak saplings (180 pots in total) were grown for three summers from April 2004 to September 2006 outdoor next to a mobile, transparent polycarbonate roof equipped with a rain sensor; the roof automatically covered the plants when rain fell. Thus, the plants grew under the local microclimate (mean annual temperature: 8.7°C) while precipitation and soil moisture could be controlled. We applied three soil water treatments, severe drought ($D_{\text{Sev.}}$, mean volumetric soil water content 3%), moderate drought ($D_{\text{Mod.}}$, 6 vol%) and a well-watered control (Ctrl, 9 vol%). Each treatment consisted of 30 replicates, i.e. pots. From October to May, all pots were watered to field capacity. Soil water content in the pots was controlled by TDR measurements every second day. Water content was used to calculate the required amount of water needed to meet target soil moisture. For simulating realistic radiation regimes as they prevail in the forest understory shade nets (Type 9021, Wunderlich, Osterode, Ger-

many) were mounted over the culture, which reduced radiation to about 55% of incident PPFD. The 180 pots were placed in a randomized block design. Twice per year, in April and September, the plants were fertilized with 500 ml solution made of a commercial NPK-fertilizer (1% Hakaphos blau, Compo, Münster, Germany). A contact insecticide against aphids (0.1% Spruzit, Neudorff, Emmerthal, Germany) was applied once a year.

Measurement of hydraulic conductivity

We measured axial hydraulic conductivity in fine and coarse roots and also in shoots of the saplings in the Botanical Garden, and in fine and coarse roots of the mature trees in the mature stand applying the protocol given by Sperry *et al.* (1988; see Fig. A 1).

In the sapling experiment, roots and shoots were sampled at the end of the 13 to 14-wk drought periods end of September 2005 and 2006. Fifteen to 56 fine and coarse root samples and 12-17 shoot samples were investigated per tree species and soil moisture treatment. The samples were obtained by first cutting off the sapling stems under water. The shoot segments had a minimum length of 20 cm (diameter: 5.0-9.0 mm). The root system was carefully cleaned from soil, and cut under water into several coarse root branches with attached fine roots. These root branches had a length of ≥ 12 cm (fine root diameters: 0.7-2.0 mm, coarse root diameters: 2.0-6.0 mm). In the forest, fine and coarse roots of beech and oak trees were selected by random in the organic layer and identified by species according to the colour and morphology of the root cortex (see Leuschner *et al.* 2001). Branch root systems ≥ 12 cm length were cut, transferred immediately to polyethylene bags filled with cold water and transported to the laboratory, where they were stored at 4°C until measurement. For measuring axial hydraulic conductivity in the root and shoot segments, gravity-induced flow with pressure differences of 6-7 kPa per 5 cm was used. We used deionised, degassed water containing a sodium-silver-chloride complex ($16 \mu\text{g l}^{-1}$ Ag, 8mg l^{-1} NaCl, Micropur, Katadyn, Wallisellen, Switzerland) to prevent long-term decline in conductivity. Prior to measurement, the solution was passed through a $0.2 \mu\text{m}$ membrane filter (Maxi Capsule, Pall, New York, USA). Immediately before measurement, the samples were cut to a length of 5 cm and mounted under water on the tubing system. The exact length and proximal and distal diameters of the segments were measured with a precision-calliper after the conductivity measurements. The maximum length of the investigated root segments was determined by root morphology, i.e. the occurrence of root sections without ramifications. The length of shoot segments was chosen accordingly to allow for comparisons. We

consider the possibility that in a few cases (probably less than 5%) bilaterally truncated vessels may have resulted in a slight overestimation of shoot axial conductivity (see Cochard and Tyree 1990, Hacke and Sauter 1995). In a first measurement of hydraulic conductivity, a flow period of 5 min was allowed to give actual conductivity. The water passing through the segments was collected quantitatively at the distal end of the segment in pre-weighed plastic cups filled with cellulose. Subsequently, the root or shoot segment was flushed for 5 min at a pressure difference of 0.12 MPa in order to remove air bubbles from the vessels. Afterwards, a second measurement was conducted to determine maximum axial conductivity in the unblocked xylem. Flushing and subsequent flow measurements were repeated at least twice to approach maximum conductivity values. Hydraulic conductivity (k_h) was expressed in the unit $\text{kg m MPa}^{-1} \text{s}^{-1}$ which gives the mass flow rate [kg s^{-1}] of the solution through the shoot or root segment relative to the pressure gradient [MPa m^{-1}]. Specific conductivity [$k_s, \text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$] was calculated by dividing k_h by the root cross-sectional area [m^2]. To quantify the degree of vessel cavitation (embolism), the difference between actual conductivity and maximal conductivity was expressed as percentage of maximum conductivity (Sperry *et al.* 1988). Because the saplings investigated in the second or third year (2005 and 2006) showed no differences in hydraulic conductivity k_h (data not shown), the data of the two years were pooled.

Detection of vulnerability to cavitation

We used the air-injection method after Sperry and Saliendra (1994; see Fig. A 2) to conduct an experimental analysis of the vulnerability of the root xylem to cavitation. Sample preparation was similar to the procedure described for the measurement of hydraulic conductivity. However, vulnerability curves were only established for the fine and coarse roots of the sapling experiment at the end of the second drought period (end of September 2005), comparing the control (Ctrl) and severely droughted ($D_{\text{sev.}}$) treatments ($n = 5-11$). For comparison, two roots per species of the moderately drought-stressed treatment ($D_{\text{mod.}}$) were investigated as well. Root segments of 1.0 to 3.2 mm in diameter and 12 cm in length were placed in a self-constructed pressure chamber with two opposite openings where the root endings protruded. Shallow notches (depth: 0.1-0.2 mm) were cut into the opposite side of the root to allow air entering into the root xylem. The proximal end was attached to the tube of the hydraulic conductivity measurement system (see above), equipped with an additional air vent to prevent the

intrusion of air into the tube (Fig. A 2). Prior to the first measurement, the roots were flushed with degassed water for 5 min at a pressure of 0.1 MPa in order to remove air bubbles from the vessels. Hydraulic conductance was then measured at a pressure difference of about 8 kPa, with air pressure inside the chamber held at about 0.1 MPa to prevent leakage of solution from the root into the chamber. The solution pouring out of the distal root end was collected quantitatively in plastic cups filled with cellulose. After the initial measurement, air pressure inside the chamber was increased stepwise to 0.25, 0.50, 0.75, 1.00, 1.25, 1.50, 2.00, ... 4.50 MPa. In each step, pressure was held constant for 10 min. After pressurization, the pressure was released to 0.1 MPa before conductance was remeasured. Hydraulic conductance was calculated as the average of three one-minute readings during steady flow. Exposure of the segment to progressively higher air pressures continued until hydraulic conductance had dropped to less than 95% of the initial value. By this procedure, vulnerability curves were established for control (Ctrl) and severely drought-stressed ($D_{\text{Sev.}}$) saplings of *Fagus* and *Quercus* by plotting the percentage of remaining hydraulic conductivity against the applied air pressure which is thought to be equal to xylem water potential (Jarbeau *et al.* 1995, Alder *et al.* 1996). The water potential resulting in a 50% loss of conductivity (Ψ_{PLC50}) was calculated for saplings of the Ctrl, $D_{\text{Mod.}}$ and $D_{\text{Sev.}}$ treatments, and plotted against root cross-sectional area ($n = 33$).

Statistical analysis

All data sets were tested for Gaussian distribution with a Shapiro-Wilk test. We used a non-parametric Kruskal-Wallis H test to detect significant differences in conductivity or embolism among different age classes, species, organs (fine roots, coarse roots), soil moisture treatments or harvest dates. Because conductivity and cavitation data were found to be not significantly different between the two harvests (2005 and 2006) in the sapling experiment, the data were pooled. A Scheffé test was used to test for significant differences among the treatments in specific conductivity, degree of shoot embolism, and root Ψ_{PLC50} values. All calculations were conducted with SAS version 9.1 (SAS Institute, Cary, USA). The criteria of Velleman and Hoaglin (1981) were applied to identify outliers in those data sets that were plotted as box-whisker plots. Linear and non-linear regressions were calculated with the program Xact 8.03 (SciLab, Hamburg, Germany).

2.4 RESULTS

We found a large variability in specific conductivity k_s (axial hydraulic conductivity related to cross-sectional area) of fine roots and coarse roots of the same tree species and soil moisture treatment. In the majority of samples investigated, certain roots had 4 to 10-fold higher k_s values than the mean of the respective samples (see crosses marking outliers in Fig. 2.1).

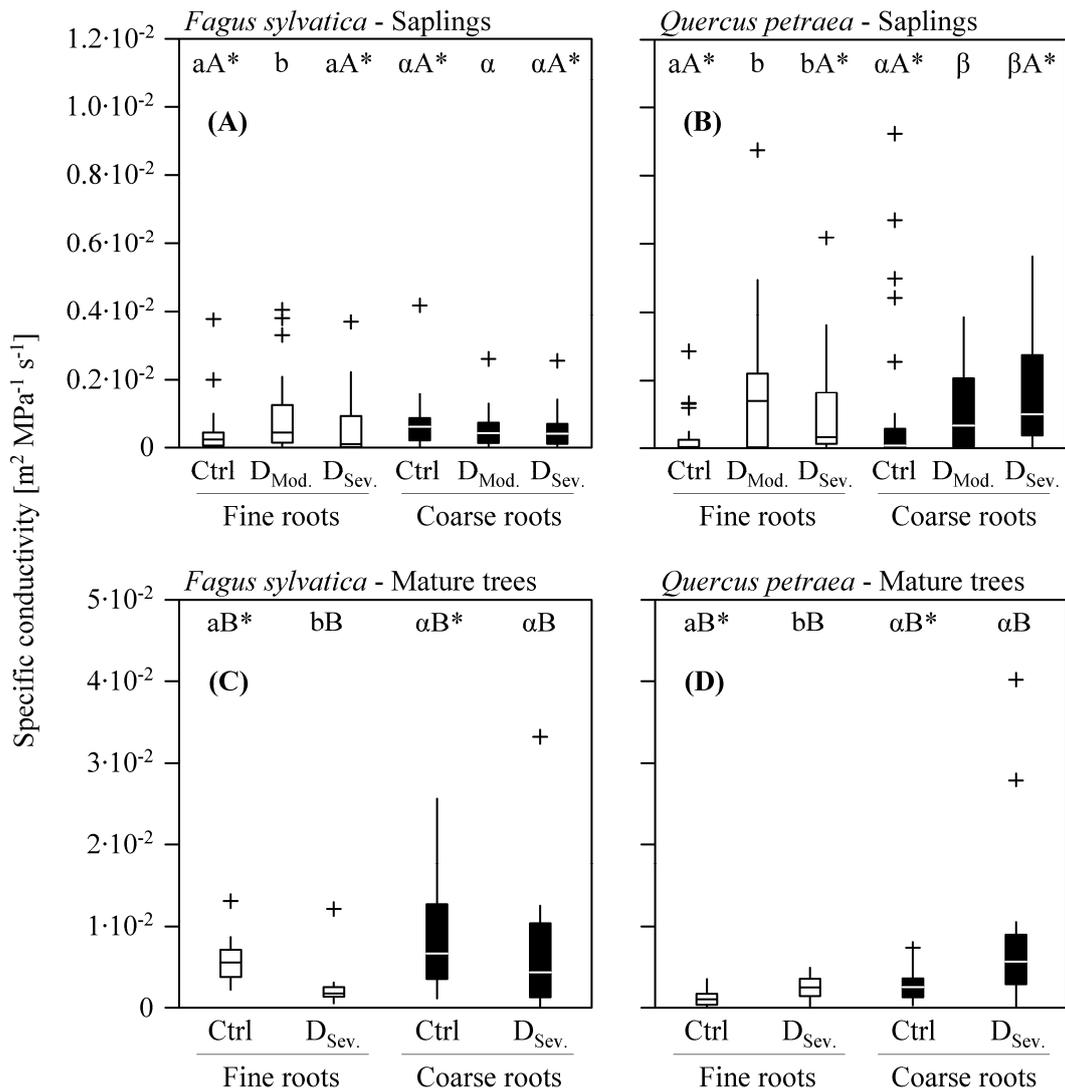


Fig. 2.1 Specific conductivity (k_s) of fine roots (diameter $d \leq 2$ mm) and coarse roots ($d = 2-6$ mm) of saplings (Fig. 2.1a,b) and mature trees (Fig. 2.1c,d) of *Fagus sylvatica* (Fig. 2.1a,c) and *Quercus petraea* (Fig 2.1b,d) in three soil moisture treatments [well-watered Control (Ctrl), moderate drought stress (D_{Mod.}) and severe drought stress (D_{Sev.})]. Box-plots design represents the median (horizontal line), 25 and 75% percentiles (box limits), and 5 and 95% percentiles (bars). Outside values (see Statistical analyses) are plotted as + symbols. Significant differences in root conductivities within a moisture treatment are indicated by different lower case letters, significant differences between age stages by capitals, and significant differences between species are marked by asterisks (Kruskal-Wallis H test, $P < 0.05$, sample sizes are given in Table 2.3).

This large variability was observed in fine roots (investigated diameters: 0.7-2.0 mm) and coarse roots (2.0-6.0 mm) of both the 5 to 7-yr-old saplings and the mature trees. In general, no systematic differences in k_s existed between these two root diameter classes in the same treatment; however, coarse roots tended to have higher average specific conductivities than fine roots in both species in the drought treatment conducted in the forest (Fig. 2.1c,d).

Table 2.3 Mean specific conductivity (k_s) and degree of embolism in fine roots (diameter $d = 0.7\text{--}2\text{ mm}$) and coarse roots ($d = 2\text{--}6\text{ mm}$) of saplings and mature trees of *Fagus sylvatica* and *Quercus petraea* after being exposed to two or three different soil moisture treatments. Treatments were Control (Ctrl), moderate drought stress ($D_{\text{Mod.}}$), and severe drought stress ($D_{\text{Sev.}}$), see text. Significant differences in the degree of embolism between the soil moisture treatments within an age class are indicated by different Latin lower case letters (fine roots) or different lower case Greek letters (coarse roots). Significant differences between fine roots and coarse roots within a given age class are marked by different capital letters, and significant differences between the two species by asterisks (Kruskal-Wallis H test, $P < 0.05$, mean \pm SE, sample size = n). Significant differences between specific conductivities (k_s) are indicated in Fig. 2.1.

Organ	Treatment	n	k_s [$10^{-3}\text{ m}^2\text{ MPa}^{-1}\text{ s}^{-1}$]	Degree of embolism [%]
<i>Fagus</i> - Saplings				
Fine roots	Ctrl	46	0.42 \pm 0.10	36.0 \pm 4.4 aA
	$D_{\text{Mod.}}$	30	0.86 \pm 0.21	40.0 \pm 5.8 aA
	$D_{\text{Sev.}}$	48	0.54 \pm 0.12	45.1 \pm 4.9 aA
Coarse roots	Ctrl	40	0.68 \pm 0.11	37.3 \pm 4.3 α A
	$D_{\text{Mod.}}$	24	0.55 \pm 0.12	38.5 \pm 7.4 α A
	$D_{\text{Sev.}}$	49	0.50 \pm 0.07	33.0 \pm 4.0 α A
<i>Fagus</i> - Mature trees				
Fine roots	Ctrl	9	6.09 \pm 1.14	17.6 \pm 4.1 aA
	$D_{\text{Sev.}}$	11	2.70 \pm 0.97	33.3 \pm 9.3 aA
Coarse roots	Ctrl	15	8.73 \pm 1.73	4.0 \pm 1.3 α B
	$D_{\text{Sev.}}$	10	7.51 \pm 3.13	14.4 \pm 6.7 α A*
<i>Quercus</i> - Saplings				
Fine roots	Ctrl	38	0.29 \pm 0.09	39.1 \pm 5.4 aA
	$D_{\text{Mod.}}$	15	1.81 \pm 0.62	39.4 \pm 10.1 aA
	$D_{\text{Sev.}}$	28	1.09 \pm 0.27	41.1 \pm 6.2 aA
Coarse roots	Ctrl	56	0.76 \pm 0.23	36.4 \pm 4.0 α A
	$D_{\text{Mod.}}$	39	1.07 \pm 0.20	42.3 \pm 5.2 α A
	$D_{\text{Sev.}}$	32	1.55 \pm 0.27	46.2 \pm 6.9 α A
<i>Quercus</i> - Mature trees				
Fine roots	Ctrl	14	1.21 \pm 0.28	20.8 \pm 6.7 aA
	$D_{\text{Sev.}}$	12	2.46 \pm 0.43	36.7 \pm 9.3 aA
Coarse roots	Ctrl	10	2.96 \pm 0.76	10.5 \pm 5.3 α A
	$D_{\text{Sev.}}$	11	9.95 \pm 3.79	46.3 \pm 10.9 β A*

Large and significant differences in k_s existed between roots of the saplings and of the mature trees with the latter showing about 3 to 15 times larger root k_s values than 5 to 7-yr-old saplings. The large increase in root k_s from juvenile to mature trees was not only found in the well-watered control but persisted in the drought treatments.

The specific conductivity of fine roots of *Fagus* and *Quercus* saplings increased significantly when reared for two or three summers under moderate drought stress ($D_{Mod.}$; Fig. 2.1a,b, Table 2.3). For *Quercus*, this was also true when exposed to severe drought ($D_{Sev.}$, Fig. 2.1b), which contrasts with *Fagus* saplings where fine root k_s was on average lower in plants subjected to severe drought than in plants growing under moderate drought (Fig. 2.1a). Unlike *Quercus*, coarse roots of *Fagus* saplings showed changes in k_s neither after moderate nor after severe drought. In *Quercus*, large (and mostly significant) increases in specific conductivity were observed in fine and coarse roots of drought stressed trees as compared to the well-watered control. Such an adaptive response in root axial conductivity was found in both saplings and mature trees of *Quercus* (Fig. 2.1b,d). In contrast, specific conductivity of fine roots of adult *Fagus* trees was significantly lower after drought, whereas coarse roots showed no significant changes.

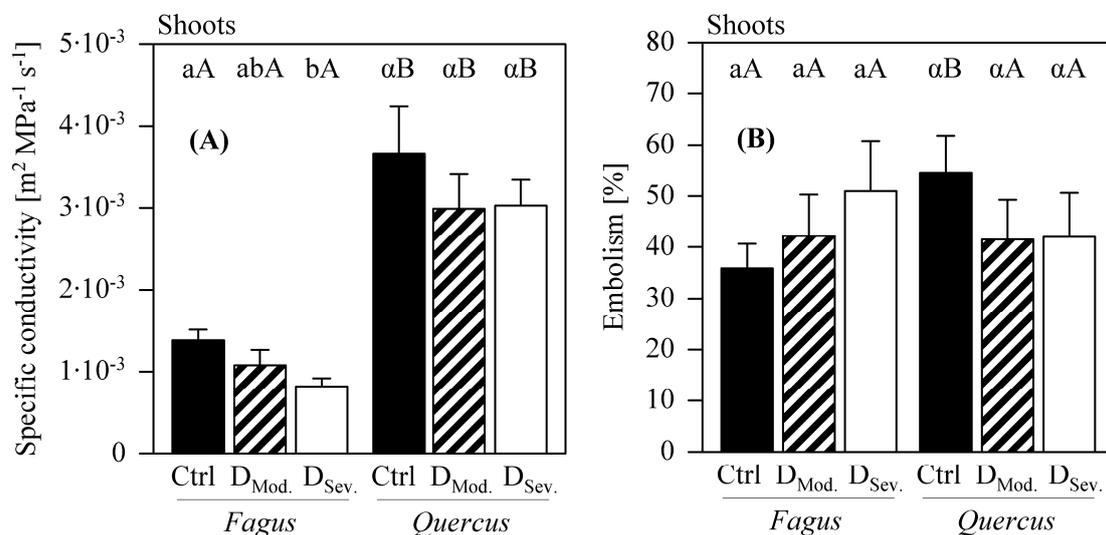


Fig. 2.2 Specific conductivities (k_s , Fig. 2.2a) and degree of embolism (Fig. 2.2b) of shoots of differently droughted *Fagus sylvatica* and *Quercus petraea* saplings. Soil moisture treatments are well-watered Control (Ctrl), moderate drought stress ($D_{Mod.}$), and severe drought stress ($D_{Sev.}$). Significant differences in shoot conductivity and embolism within species are indicated by different lower case letters, and significant differences between species by capitals (Scheffé, $P < 0.05$, mean+SE, $n = 12-17$).

When comparing the k_s values of the two tree species, no consistent picture emerged in the different treatments and life stages. For example, the specific conductivities of fine

and coarse roots of mature oaks were significantly lower than those of beech trees in the control treatment. In contrast, root k_s after severe drought was significantly higher in roots of *Quercus* saplings than in *Fagus* saplings (Fig. 2.1a,b), whereas no significant differences could be found between drought-stressed mature trees (Fig. 2.1c,d, Table 2.3).

Contrary to our expectation, the degree of embolism in fine roots was not significantly higher in drought-stressed saplings or mature trees than in well-watered ones, even though tendencies were visible in certain cases (Table 2.3). In coarse roots of mature trees, however, embolism rate was significantly higher under drought in *Quercus*, and tended to do so in *Fagus*.

The specific conductivity of shoots of *Fagus* saplings was significantly lower in severely droughted than in control plants, whereas k_s of *Quercus* shoots was only marginally reduced under drought application (Fig. 2.2a). In all treatments, the specific conductivities of *Quercus* shoots were significantly higher than those of *Fagus* shoots. With $1\text{--}4 \times 10^{-3} \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$, k_s of shoots was considerably larger than k_s of the corresponding fine roots in both species (Fig. 2.2a, Table 2.3). *Fagus* saplings showed a (non-significant) tendency for higher shoot embolism with increasing drought, whereas in *Quercus* the opposite trend appeared (Fig. 2.2b). With 35 to 55%, the degree of embolism tended to be somewhat higher in shoots than in fine and coarse roots (Fig. 2.2b, Table 2.3).

Table 2.4 Estimates of water potentials inducing 50% loss of hydraulic conductivity (Ψ_{PLC50}) in small-diameter roots of well-watered (Ctrl) and severely drought-stressed ($D_{\text{Sev.}}$) saplings of beech and oak (Scheffé, $p < 0.05$, mean \pm SE, sample size = n).

Species	Treatment	n	Diameter [mm]	Ψ_{PLC50} [MPa]	
<i>Fagus</i>	Ctrl	7	2.83 \pm 0.53	0.40 \pm 0.10	a
	$D_{\text{Sev.}}$	5	2.28 \pm 0.52	0.53 \pm 0.14	ab
<i>Quercus</i>	Ctrl	11	2.14 \pm 0.32	0.53 \pm 0.08	a
	$D_{\text{Sev.}}$	6	2.82 \pm 0.35	0.30 \pm 0.05	b

The vulnerability to cavitation, expressed as Ψ_{PLC50} , was not significantly different in small-diameter roots between the two species under ample water supply (Table 2.4), but *Quercus* roots exhibited a significantly higher relative conductivity at a xylem pressure potential of 0.5 MPa than *Fagus* roots (Fig. 2.3a,b).

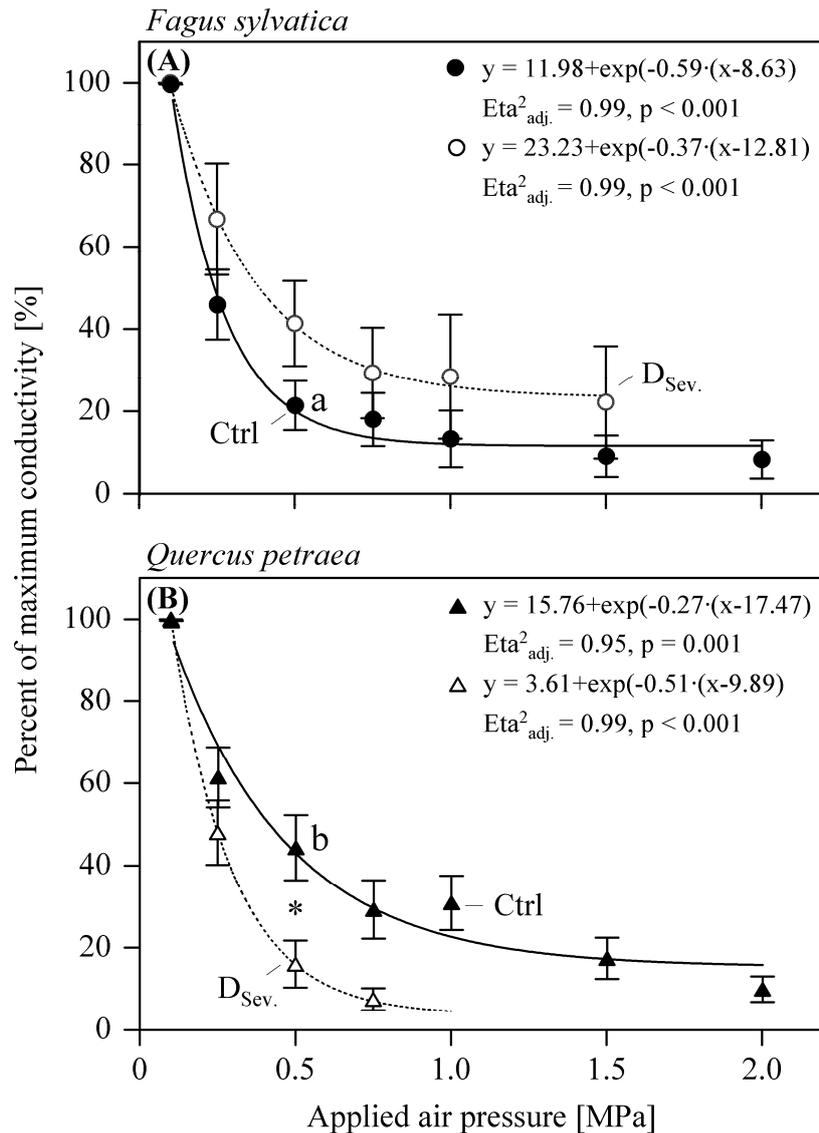


Fig. 2.3 Vulnerability curves of *Fagus sylvatica* (Fig. 2.3a) and *Quercus petraea* (Fig. 2.3b) small-diameter roots showing percentage of maximum conductance (%) in xylem versus the applied air pressure used in air-injection experiments. Samples originate from Control (Ctrl) and severely drought-stressed (D_{Sev.}) saplings after two years (September 2005) of soil moisture treatment. Roots with diameters between 1.0 and 3.2 mm were used. Only conductivities with a mean > 5% of maximum conductivity are plotted. Significant differences between species are indicated by lower case letters, significant differences between soil moisture treatments are marked by asterisks (Kruskal-Wallis H test, $p < 0.05$, mean \pm SE, $n = 5-11$).

Severe drought led to a significant increase in the cavitation vulnerability (Ψ_{PLC50}) in *Quercus* roots, whereas in *Fagus* roots, the vulnerability tended to decrease (Table 2.4). No correlation was found between root cross-sectional area and the xylem pressure potential inducing a 50% loss of axial conductivity in roots (Ψ_{PLC50} , Fig. 2.4).

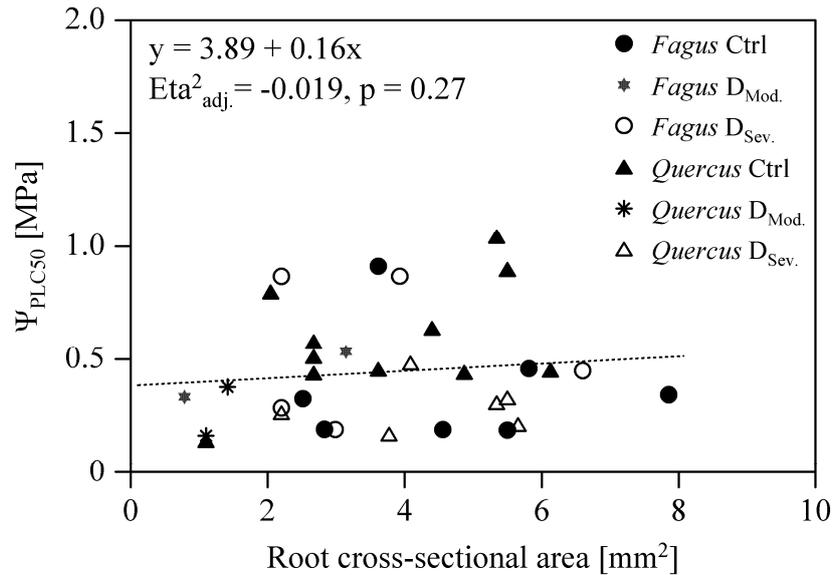


Fig. 2.4 Xylem pressure potential inducing 50% loss of conductivity (Ψ_{PLC50}) in roots of *Fagus sylvatica* and *Quercus petraea* saplings grown under three different moisture regimes as a function of root cross-sectional area (Control = Ctrl, moderately drought-stressed = D_{Mod.}, and severely drought-stressed = D_{Sev.}). Plants were harvested in September 2005 after two 13 to 14-wk-long drought periods. The correlation analysis was conducted for all six data sets that were pooled ($n = 33$).

2.5 DISCUSSION

Drought-induced changes in the hydraulic system of root and shoot

Drought has been found to reduce not only stomatal conductance for water vapour, but also the hydraulic conductivity of roots and shoots (Tognetti *et al.* 1995, Nardini and Salleo 2000, Maherali *et al.* 2002). Such a reduction in conductivity along the plant's water conducting system may result from an increase in embolism rate, thus being temporary, or can be caused by the formation of new roots and shoots with a lower axial conductivity, then representing a lasting acclimation to drought. Whatever the cause of the conductivity reduction, it may help to reduce water loss to the atmosphere and the soil, thereby improving the plant's water balance (North and Nobel 1992, Meinzer *et al.* 1996, Trillo and Fernández 2005). In our sapling study, both species showed reduced specific conductivities of the shoot after moderate or severe drought treatment, which is in agreement with the results of various other studies on the drought adaptation of saplings (Tognetti *et al.* 1995, Searson *et al.* 2004). In contrast, we did not find a general reduction in axial hydraulic conductivity of the coarse or fine roots upon drought exposure. In the majority of cases, k_s remained unchanged after moderate or severe drought, or even increased, as in the fine roots of moderately drought stressed beech and oak

saplings and also in the roots of mature oak trees. Similarly, root specific conductivity increased upon drought in coarse roots of oak saplings and mature trees. A drought-induced increase in root axial conductivity may facilitate water uptake (Nardini and Pitt 1999) by reducing the flow resistance at the water uptake side of the SPAC. Decreases in the conductivity at the loss side, i.e. at the leaf and twig levels, and maintenance or increases at the uptake side, i.e. in the root system, would be structural adaptations of plants for improving the water balance under limited water supply (Nardini and Pitt 1999). Increases in root conductivity would be particularly straightforward adaptations in plants that respond to drought with a reduction in fine root biomass and, thus, in water absorbing surface area, as was observed, for example, in beech saplings (Meier and Leuschner 2008). Our data are among the very few reports showing that drought-induced losses in root biomass may partly be compensated by increases in root hydraulic conductivity, when drought stress is not too severe (see Fig. 2.1a). The underlying mechanisms must remain speculative, possibly including the growth of new fine roots or secondary growth with elevated axial conductivities.

Resistance to water stress-induced cavitation via air seeding depends on the surface tension of the meniscus in pores of the pit membrane that connects adjacent conduits (Jarbeau *et al.* 1995, Pockman and Sperry 2000). Increased resistance to cavitation was therefore thought to be accompanied by decreased pore hydraulic conductivity and, ultimately, axial hydraulic conductivity (Martínez-Vilalta *et al.* 2002, Sperry and Hacke 2004). Our results reveal no correlation between root axial conductivity and degree of root embolism, neither when all roots of a treatment (see Table 2.3), nor single roots are investigated (data not shown). Although Cochard *et al.* (1999) reported a slight decrease of safety with respect to cavitation risk with increased shoot-specific conductivity in *Fagus* branches, our results are indicating no trade-off between root axial conductivity and the occurrence of embolism. The apparently contrasting behaviour of aboveground and belowground organs with respect to the assumed safety-conductivity trade-off could have several reasons including an only weak relationship between pit membrane pore size and axial hydraulic conductivity in roots and perhaps so far unknown diurnal embolism repair mechanisms in roots.

Another adaptation of the root system of woody plants to soil water limitation could be the development of root branches with diverging hydraulic properties, thereby exploring the spatial heterogeneity of water reserves in the soil. Although the knowledge about the hydraulic properties of woody root systems is still scarce (Jackson *et al.* 2000), a grow-

ing body of evidence suggests that root axial conductivity, and consequently water uptake rate, can differ substantially within root systems, e.g. between deep and shallow roots (Pate *et al.* 1995, Leuschner *et al.* 2004b).

In most of the root samples investigated in the sapling experiment and in the mature stand, we found a very large variation in root axial conductivity among the co-occurring roots with certain outliers showing up to ten times higher k_s values than the sample mean (see Fig. 2.1, Table 2.3). Such ‘high-conductivity roots’ were found in the well-watered control treatments and under drought application, but the variability of fine root axial conductivity generally increased in the root samples with two or three years of exposure to moderate or severe drought. Since individual roots or root branches are thought to act as ‘physiologically autonomous units’ (Shani *et al.* 1993), the differentiation of the root population in high-conductivity and low-conductivity roots has been postulated as a favourable adaptation particularly in soils with a high heterogeneity of soil moisture, as is typical for soils exposed to periodic drought (Göttlein and Manderscheid 1998).

Do fine roots act as ‘hydraulic fuses’ in the SPAC?

Peripheral organs such as leaves and fine roots have been proposed as possible weak, replaceable segments of the soil-plant-atmosphere continuum (Sperry and Saliendra 1994, Domec *et al.* 2004). They were thought to act as ‘hydraulic fuses’ of the plant during extreme droughts (Zimmermann 1983), uncoupling stems, larger roots and branches hydraulically from transpiring surfaces and drying soil, thereby allowing tissue water potential to remain lower than in the soil and preventing plant-wide xylem cavitation (Nobel and North 1992, Alder *et al.* 1996, Sperry and Ikeda 1997, Hacke *et al.* 2000). Roots could act as ‘hydraulic fuses’ by shedding of fine roots, as is usually suggested (Jackson *et al.* 2000, Chapin *et al.* 2004, Espeleta *et al.* 2004). In accordance with Alder *et al.* (1996), we propose cavitation to be another, potentially reversible ‘hydraulic fuse’ mechanism in roots. In our study, evidence for such a mechanism is provided by the very high vulnerability to cavitation (Ψ_{PLC50} : 0.3-0.5 MPa) of small-diameter roots in saplings (Fig. 2.3, Table 2.4). Previous studies on larger roots have reported much lower water potentials down to -8.0 MPa to induce 50% loss of conductivity (Alder *et al.* 1996, Martínez-Vilalta *et al.* 2002, Froux *et al.* 2005). The previously reported Ψ_{PLC50} values of shoots of *Fagus sylvatica* (-2 MPa) and *Quercus petraea* (-3 MPa) (Cochard *et al.* 1992, 1999) underline the large difference in cavi-

tation vulnerability of fine roots and shoots in these two tree species. The significant increase in the Ψ_{PLC50} value from -0.53 to -0.30 MPa in drought stressed *Quercus* roots may be interpreted as a hint that small-diameter roots indeed function as a ‘hydraulic fuse’ in tree saplings (Table 2.4).

However, we were not able to detect a correlation between the size of small-diameter roots and Ψ_{PLC50} (Fig. 2.4). This may indicate that, over narrow size differences, other parameters such as the ‘degree of maturation’ or root order may be more precise indicators of vulnerability to embolism than root diameter.

The high standard errors in the embolism data of Table 2.3 indicate that co-occurring fine roots or coarse roots are differently affected by cavitation. Hacke *et al.* (2000) assume that the cavitation resistance of different root branches differs within root systems. Moreover, different roots of the same root system are known to show considerable differences in tissue water potential, thus holding different positions on the vulnerability curve. Embolism has been found to develop more or less gradually rather than appearing at a certain threshold (Fig. 2.3). Well-watered plants may show root cavitation not only under dry, but under moist conditions as well (Alder *et al.* 1996, Domec *et al.* 2004), a fact that is supported by our fine and coarse root data from saplings and mature trees (Table 2.3). Thus, there may be a considerable spatial variability in the degree of embolism in tree root systems even in the absence of water shortage.

Do the root hydraulic properties of saplings differ from those of adult trees?

Although it is known that young trees are often more vulnerable to drought stress than adult trees (e.g. Bolte and Roloff 1993), the knowledge about ontogenetic influences on the hydraulic system is still very limited (Mencuccini 2002). In our study, the root-specific conductivities (k_s) of adult trees of both species were 3 to 15 times higher than those of saplings (Fig. 2.1). Not only shoot-specific conductivity (Domec and Gartner 2003), but also leaf-area-based total root conductivity, which includes radial and axial conductivity, has been reported to be higher in adult than in young trees (Ito *et al.* 1995). One possible explanation is different progress in meta-xylem maturation in roots of young and mature trees (Staubin *et al.* 1986, Vercambre *et al.* 2002, Tyree 2003), a second one the much larger size of the roots of adult trees which implies a greater path length and diverging potential gradients in the roots. Further, the fine root:leaf biomass ratio typically increases with age (Grier *et al.* 1981, Vanninen *et al.* 1996). Moreover, a higher root-specific conductivity may be required to compensate for the increased

hydraulic resistance in the growing path length of maturing root systems, stems and branches (West *et al.* 1999, Magnani *et al.* 2000, Addington *et al.* 2006).

We found a tendency (but generally not a significant trend) for adult trees to be less affected by embolism in fine and coarse roots than saplings. If valid, this apparent difference could be a consequence of the deeper extension and larger size of the root system of mature trees. By reaching deeper soil horizons with additional water sources, water may be redistributed by the plant's hydraulic system towards superficial horizons (Persson *et al.* 1995, Brooks *et al.* 2002) which could help to reduce root embolism. In support of our finding, Domec *et al.* (2004) also observed a higher embolism rate in young than in adult trees. Thus, a higher root embolism in juvenile trees may be one factor causing seedlings and saplings generally to be the most drought-sensitive ontogenetic stage in tree life.

Are the roots of drought-tolerant Quercus better adapted than those of Fagus?

Different genotypes or species of woody plants may differ substantially with respect to root axial conductivity (Huber 1956, Korn 2004), and vulnerability to cavitation (Domec and Gartner 2003, Alsina *et al.* 2007). In contrast to our hypothesis, the fine and coarse roots of ring-porous oak and diffuse-porous beech showed no systematic difference in their mean k_s values. This is different in shoots and stems with *Quercus* showing a higher specific conductivity than *Fagus* (see Fig. 2.2, and Steppe and Lemeur 2007). It appears that the seasonality of vessel formation in early- and late-wood in the stem, which guarantees maximum water transport to the new leaves, is of minor relevance for the development of the hydraulic system in roots. Presumably, other factors such as soil moisture, soil density and temperature, and water potential gradients in the root system are more decisive in the control of root hydraulic conductivity.

The Central European *Quercus* species (*Q. petraea* and *Q. robur*) possess a number of adaptations that make them more drought-tolerant than *Fagus sylvatica*. Shoots of *Quercus petraea* generally have been found to be more resistant to cavitation than those of *Fagus sylvatica* (Cochard *et al.* 1992, 1999, Cruziat *et al.* 2002), despite a higher hydraulic conductivity. Further, *Quercus* trees showed a higher capability of drought-induced osmotic adjustment in the leaves and a lower sensitivity of its photosynthetic apparatus to drought than *Fagus* (Backes and Leuschner 2000, Dreyer *et al.* 2001). More important, oak stem diameter growth was found to be much less drought-sensitive than in beech (e.g. Bonn 1998). With respect to the root system, several lines of evi-

dence support the notion that *Quercus petraea* is more drought-tolerant than *Fagus sylvatica*. In a mixed oak-beech stand, Hertel (1999) and Leuschner *et al.* (2001) found a pronounced increase in fine root mortality during a severe drought period in *Fagus* but much less on *Quercus*. In accordance with this observation, *Quercus* fine roots grew more superficially in the topsoil than those of *Fagus* (Leuschner *et al.* 2001). Our data suggest that *Quercus* fine and coarse roots are also capable of responding more flexibly to drought in terms of root physiology: fine and coarse roots of *Quercus* generally responded with an increase in k_s to moderate or severe drought, while those of *Fagus* mostly did not. Indeed, Meier and Leuschner (2008) concluded from a hydrologic gradient study in different beech forests that water shortage leads to a reduction in stand fine root biomass, with fine roots being much more sensitive than leaves. *Fagus* seems not capable of a sufficient adjustment of its fine and coarse root system to drought, neither in terms of biomass maintenance, nor with respect to the provision of root hydraulic capacity for water uptake.

2.6 CONCLUSION

We conclude that our study provided multiple evidences of small-diameter roots functioning as fuses in the SPAC of temperate trees in a certain sense, thereby supporting our second hypothesis. However, our data do not support our first hypothesis (k_s decrease upon drought), since we found no evidence of a different adaptability of the root systems of mature trees and saplings to drought, even though k_s was much higher in mature trees. The superior drought tolerance of *Quercus petraea* compared to *Fagus sylvatica* is to a large extent related to the greater plasticity and lower drought-sensitivity of the root system, with *Quercus* saplings revealing a better drought adaptation of the root system than *Fagus* especially in this highly sensitive ontogenetic stage. Further research on ontogenetic differences in the drought response of root growth and root functioning of trees is urgently needed.

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Chapter 3

DOES ROOT XYLEM PLASTICITY AFFECT SALT TOLERANCE?

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3.1 ABSTRACT

Cultivation of olive (*Olea europaea* L.) is highly encouraged in Mediterranean countries because of its low water requirement and considerable salt tolerance, which however, varies strongly between varieties. Salt exclusion capacities of roots are known to play a significant role in salinity tolerance.

Three varieties of olive, Barnea, Arbequina and Proline, expressing different levels of salinity tolerance, were examined. Three levels of saline water were used for irrigation of mature trees. Axial conductivities and embolism rates of roots and branches were estimated by low pressure conductivity measurement. Cross-sections were analyzed with respect to xylem anatomy.

The more salt-resistant varieties Barnea and Arbequina possess lower root specific conductivities than salt-sensitive Proline. However, fine and coarse roots of the three olive varieties showed an overall increase in specific conductivity as level of salinity increased. Barnea covers twice as much of root axial conductivity with small-sized (< 10 μm) conduits than both other varieties.

We suggest that under severe salt stress an amplified functional differentiation in high conductivity roots and a relative high proportion of small conduits may guarantee sufficient hydraulic safety while it allows rapid water uptake from soil patches with ample water supply. The high plasticity of the root hydraulic system in the highly salt tolerant olive variety Barnea is seen as a favourable trait for water uptake in soils with heterogeneous salinity by reducing the threat of embolism in shoots.

3.2 INTRODUCTION

Salinisation of agricultural soils is a world-wide problem of increasing severity, often caused by irrigation (Kozłowski 1997). In many arid and semi-arid regions, agriculture is forced to utilise saline groundwater which intensifies salinisation (Beltran 1999). Therefore, salinisation has significant economic, social, and environmental impacts world-wide (Pannell 2001). In Mediterranean countries, the cultivation of the olive (*Olea europaea* L.) for fruit and oil production is highly encouraged (Chartzoulakis *et al.* 1992, Gucci *et al.* 1997), not least because of its considerable salt tolerance. Olive plants typically tolerate soil water salinities as high as 3–6 dS m⁻¹ (FAO 1985). However, large variation in salt sensitivity exists among olive genotypes (Gucci *et al.* 1997). Despite a detailed understanding of salt tolerance and avoidance mechanisms on molecular and physiological levels (Flowers and Flowers 2005, Dajic 2006), and numerous experimental studies on the salt tolerance of herbaceous crops and tree seedlings, our understanding of salt tolerance mechanisms of adult trees or woody crops is still very limited (Tabatabaei 2006). Salt tolerance mechanisms on the physiological level include salt exclusion, excretion and compartmentation (Waisel 1972, Verslues *et al.* 2006), and are often associated with active osmotic adjustment (Tattini *et al.* 2006), and conservative water use (Shannon, 1997). Although roots are the first organs to be affected by salt stress (Waisel and Breckle 1987, Córdoba *et al.* 2004), most research on salt tolerance focussed on aboveground organs but neglected morphological and physiological responses of the roots, especially in woody plants (Demiral 2005, Junghans *et al.* 2006). This is astonishing because important processes of plant salt tolerance are thought to be located in the roots (Bernstein and Hayward 1958, Lacan and Durand 1995). Plasticity of the hydraulic system (Azaizeh and Steudle 1991) is still far less understood than altered growth pattern, salt-exclusion, or osmoregulation mechanisms (Carter *et al.* 2006). Photosynthesis and growth of plants in general, and olive trees in particular, are to a considerable degree determined by the plant's hydraulic conductance (Tyree 2003, Nardini *et al.* 2006) as well as by the vulnerability of xylem to cavitation (Salleo *et al.* 2000). Understanding the forces and resistances that control the movement of water through the soil–plant system, with special consideration of the root system, is essential in order to understand the influence of salinity on plant survival.

In the following, we present the results of a comprehensive study on root hydraulic and root anatomical properties of three differently salt-sensitive varieties of mature olive trees. The aims of this study were to test whether salinity has a major influence on the axial conductivity and on the degree of embolism, and to relate the hydraulic properties to xylem morphology. We analysed changes in specific conductivity, degree of embolism, and morphology of fine roots, coarse roots, and branches of trees irrigated with water of different salinities.

3.3 MATERIAL AND METHODS

Study site

The study was conducted during December 2006 in the Ramat Negev Experimental Station located in the central Israeli Negev Desert (31°05'00"N, 34°41'03"E, altitude 305 m a.s.l.). The soil type of this region is Typic Torrifluent derived from loess, with a clay content of 6–8% (pH_{KCl}: 7.9–8.2). Maximal daily temperature is about 35°C during July and August, and minimal temperature is close to 5.5°C during January. The average annual precipitation in this area is approximately 90 mm, falling between November and April. Three olive (*Olea europea* L.) varieties, Barnea, Arbequina, and Proline, were planted in 1997 in plots irrigated either by saline or fresh water. Barnea and, to a minor degree, Arbequina olive trees are known to be more tolerant to salinity (Aragüés *et al.* 2005, Wiesman *et al.* 2004) than Proline trees (Wiesman, unpublished). This conclusion is based on seven years of observation of above-ground biomass increment and fruit yield in an orchard in the Israeli Negev.

The experimental site was divided into two plots. The first plot contained the three olive varieties, arranged in rows at random order. The distance between tree individuals in a row was 3 m, with a distance of 6 m between rows. Rows were either irrigated with fresh water [Control, electrical conductivity of the soil (EC) = 1.2 dS m⁻¹], or moderately saline water (EC 4.2 dS m⁻¹, moderate salinity). In a second plot (approx. 150 m apart), Barnea trees were irrigated with water of a higher content of NaCl (EC 7.5 dS m⁻¹, high salinity), which was previously found to be harmful to both other varieties (Wiesman, unpublished). The second plot had the same soil characteristics and trees were planted in the same density (3 m × 6 m).

The saline water originated from local wells and was adjusted by mixing with fresh water or by adding NaCl. The olive trees were drip-irrigated, according to estimated water losses as calculated from local pan evaporation data (class A pan evaporation: approx. 2294 mm a⁻¹). The average quantity of water supplied annually to the olive plots was 656 mm. During the first three years after planting, irrigation water was supplied immediately after each rainfall event to avoid salinisation of the rhizosphere. Volumetric soil moisture at the time of harvest was 25.2±1.6 vol% (mean±SE) in the Control, 24.7±1.4 vol% in the moderate salinity treatment, and 28.9±3.8 in the high salinity treatment, respectively. These soil moisture levels equal the moisture content at field capacity (Oron *et al.* 1999). Usually twice a year, in March and November, supplements of 100 mm water were added in order to leach salt excesses from the rhizosphere (Wiesman *et al.* 2004). During the experimental period in December 2006, neither soil leaching nor precipitation events occurred at the experimental site. NPKB-fertilization was based on results of annual leaf nutrient analyses (Wiesman *et al.* 2004).

Root and twig sampling

Three randomly selected trees per variety and salinity treatment were sampled in December 2006 for roots and branches. Fine roots (diameter $d = 0.9\text{--}2$ mm) and coarse roots ($d = 2\text{--}10$ mm) were excavated at a distance of 0.1–0.2 m to the bole and 0.1–0.3 m to the next irrigation-dripper. All root segments longer than 10 cm were collected within the excavation (approx. 25 cm wide and 15 cm deep). Thus, 8–30 fine or coarse root segments per variety and salinity treatment were gathered in total. Twelve branches ($d = 4\text{--}6$ mm, 30–40 cm length) per variety and treatment were collected from the same three tree individuals. The sampling took place three times at weekly intervals during mid-morning (9–11 am EET). The segments were placed in sludge-filled polyethylene bags or boxes, transported immediately to the laboratory and stored for up to 6 days at 4°C until measurements were carried out.

Measurement of hydraulic conductivity

Axial hydraulic conductivity in fine roots, coarse roots and branches was measured according to the protocol given by Sperry *et al.* (1988). In brief, a gravity-induced flow with pressure differences of 7–8 kPa was applied to the root and branch segments. Filtered tap water (0.25 µm) with a sodium-silver chloride complex (16 µg l⁻¹ Ag,

8 mg l⁻¹ NaCl, Micropur MC 1T, Katadyn, Switzerland) was used as perfusing solution to prevent long-term decline in conductivity. Before entering the root and branch segments, the solution was forced through a 0.20 µm membrane filter (Maxi Capsule, Pall, USA). In the laboratory, all samples were cut under water to 5 cm long segments and mounted on adapters. The segment length was chosen according to data of mean vessel length (275 µm) in Mediterranean tree and shrub species (Fahn *et al.* 1986). Two conductivity measurements were carried out: Firstly, a 5-min flow measurement was conducted with the untreated root or branch segments in order to determine ‘initial hydraulic conductivity’ under field conditions. The traversed solutions were collected in pre-weighed vials filled with cellulose strips. Following the initial conductivity measurement, the segments were flushed with solution for 5 min at a pressure gradient of 0.12 MPa in order to remove air bubbles from the vessels. Secondly, maximum conductivity was determined by repeating the measurement and flushing procedure at least twice. Subsequently, length and diameter of the segments were determined and the samples stored in 70% ethanol. The data were expressed as hydraulic conductivity (k_h , m⁴ s⁻¹ MPa⁻¹), i.e. solution mass flow rate (kg s⁻¹) through the segment per pressure gradient (MPa m⁻¹). Specific conductivity (k_s , m² s⁻¹ MPa⁻¹) was calculated by relating k_h to the cross-sectional area of the segment. A few roots had exceptionally high conductivities which met the criteria of outliers in the statistical analysis; these roots were termed ‘high conductivity’ roots. The difference between initial and maximum conductivity, expressed in percent of maximum conductivity, was used as a measure of the degree of embolism (Sperry *et al.* 1988).

Anatomical analysis

Eight fine root and eight coarse root samples per variety and salt treatment (Barnea 7.5 dS m⁻¹: 12 fine roots) were dehydrated with PEG/ethanol-series (Polyethylene glycol 2000, Carl Roth, Karlsruhe, Germany) consisting of PEG-concentrations of 25% (temperature: 55°C, exposure period: 1 h), 50% (58°C, 1 h), 75% (60°C, 1 h), and 100% PEG 2000 (60°C, 2×1 h). Finally, the samples were embedded in 100% PEG 2000. Seven to 10 µm thick cross-sections were cut with a rotation microtome (2040, Reichert-Jung, Heidelberg, Germany). The cross-sections were mounted on slides and photographed at a magnification of 80× using a light microscope (Photomikroskop III, Carl Zeiss, Germany) and a digital camera (PowerShot A620, Canon, Japan). Due to irregular vessel distribution within the stele, whole cross-sections, or at least fractions as

large as possible ($> 80\%$), were analysed. An object micrometer (scale resolution: $10\ \mu\text{m}$) was photographed as scale reference. Pictures (covering $\geq 80\%$ total stele area) were analysed with ImageJ (v1.38h, <http://rsb.info.nih.gov/ij>) via particle analysis-function. All conduits with lumen areas (A) smaller than $20\ \mu\text{m}^2$ and non-vessel cells (particularly from medullary rays) with lumen areas $A \geq 20\ \mu\text{m}^2$ were excluded. Conduits ($A \geq 20\ \mu\text{m}^2$), which includes vessels and tracheids, were analyzed with respect to number and individual area (Core *et al.* 1979). Idealized radii (r) were calculated by means of lumen area ($A = r^2\pi$). Mean conduit diameter, xylem total lumen area, total root cross-sectional area (TCSA), and proportion of the stele in the total root cross-section area (stele TCSA ratio) were determined. Hydraulically weighted average conduit diameter (HWCD), was calculated [$2 \times (\sum r^5 / (\sum r^4)^{-1})$; Lewis and Boose 1995] to reflect that vessel conductivity is proportional to the 4th power of the vessel radius. The theoretical hydraulic conductivity (k_h^{theo} , $\text{m}^4\ \text{s}^{-1}\ \text{MPa}^{-1}$) of segments was calculated with the Hagen-Poiseuille equation (Huber 1956). For these calculations we set the viscosity constant $\eta_{\text{H}_2\text{O}/20^\circ\text{C}}$ to $1.002 \cdot 10^{-3}\ \text{Pa}\ \text{s}$ (Zwieniecki *et al.* 2001). The cumulative theoretical k_h curves were calculated by summarizing the relative contributions of conduit diameter classes to k_h^{theo} .

Statistical analyses

All data sets were tested for Gaussian distribution with a Shapiro-Wilk test. We used a parametric Scheffé's multiple comparison procedure to test for significant differences in stele TCSA ratio, total xylem lumen area, and mean, hydraulically weighted and maximum conduit diameters. Comparisons of normally distributed parameters were made with three-way general linear models (GLM), testing for salinity, olive variety, and root diameter class (fine root, coarse root) and cross effects. Only at least marginally significant results ($p < 0.1$) are given. A non-parametric Mann-Whitney U test was used to determine if varieties, treatments, and/or organs differed with respect to measured specific conductivity and degree of embolism. Calculations were conducted with SAS version 8.02 (SAS Institute, Cary, USA). Outliers in box plots were calculated according to Velleman and Hoaglin (1981; k_s value $> 1.5 \times$ the interquartile range). Non-linear regressions were calculated with the program Xact 8.03 (SciLab, Hamburg, Germany).

3.4 RESULTS

Proportion of the stele and conduit lumen area

Although only marginally significant (data not shown), the proportion of the stele (stele TCOSA ratio) of Barnea and Arbequina fine roots tended to decrease in response to saline irrigation, while the stele TCOSA ratio of Proline increased (Table 3.1; GLM result, salinity effect: $F = 2.46$, $p = 0.0937$). Thus, the fine root stele TCOSA ratio of salt resistant Barnea was significantly lower than that of salt sensitive Proline under moderate salt stress (4.2 dS m^{-1}). No significant differences were found between stele TCOSA ratios of coarse roots, whereas the root diameter class (fine root, coarse root) was significantly correlated with the stele TCOSA ratio (GLM result, diameter class effect: $F = 12.35$, $p = 0.0006$, Table 3.1).

Table 3.1 Anatomical properties [proportion of stele in total cross-sectional area- (stele TCOSA ratio), mean conduit diameter, and total xylem lumen area] of fine roots and coarse roots of three *Olea europaea* varieties under different salinities (1.2 , 4.2 , and 7.5 dS m^{-1}). Barnea fine roots are separated into ‘normal’ and high-conductivity (‘HC’) roots by outlier analysis (see Statistical analyses). Significant differences are indicated by different lower case letters (Scheffé, $p < 0.05$, mean \pm SE, n = sample size).

Olive variety	Salinity [dS m^{-1}]	n	Stele TCOSA ratio [%]	Mean conduit diameter [μm]	Total xylem lumen area [%]
<i>Fine roots</i>					
Barnea	1.2	8	41.2 \pm 1.5 ab	8.8 \pm 0.4 a	9.9 \pm 1.7 a
Barnea	4.2	8	40.4 \pm 2.2 a	9.5 \pm 0.5 a	11.9 \pm 1.0 a
Barnea ‘normal’	7.5	6	31.2 \pm 2.9 ab	8.6 \pm 1.6 a	11.2 \pm 5.1 a
Barnea ‘HC’	7.5	4	41.0 \pm 4.2 ab	21.9 \pm 5.1 b	33.2 \pm 6.5 b
Arbequina	1.2	8	46.8 \pm 3.2 ab	10.5 \pm 0.4 a	13.8 \pm 3.8 a
Arbequina	4.2	8	39.4 \pm 3.9 ab	9.5 \pm 0.6 a	12.6 \pm 2.5 a
Proline	1.2	8	36.2 \pm 3.3 ab	8.9 \pm 0.5 a	8.7 \pm 1.9 a
Proline	4.2	8	49.1 \pm 4.7 b	9.6 \pm 0.4 a	8.8 \pm 2.1 a
<i>Coarse roots</i>					
Barnea	1.2	8	46.5 \pm 1.8 ab	10.7 \pm 0.8 a	11.1 \pm 1.4 a
Barnea	4.2	11	46.4 \pm 1.1 b	11.2 \pm 0.3 a	10.8 \pm 1.4 a
Barnea	7.5	8	43.7 \pm 3.3 ab	11.7 \pm 0.9 a	15.8 \pm 3.2 ab
Arbequina	1.2	8	46.5 \pm 5.4 ab	11.0 \pm 0.6 a	13.1 \pm 1.6 a
Arbequina	4.2	8	46.7 \pm 2.0 ab	10.0 \pm 0.5 a	15.5 \pm 2.4 ab
Proline	1.2	8	49.1 \pm 1.8 ab	11.9 \pm 0.8 a	12.4 \pm 1.3 a
Proline	4.2	8	45.7 \pm 1.3 ab	11.2 \pm 0.5 a	13.4 \pm 1.3 a

GLM results, stele TCOSA ratio: salinity effect, $F = 2.46$, $p = 0.0937$, diameter class effect, $F = 12.35$, $p = 0.0006$. GLM results of mean conduit diameter: salinity effect, $F = 6.21$, $p = 0.0028$. GLM results, total xylem lumen area: salinity effect, $F = 8.68$, $p = 0.0003$, variety*salinity effect, $F = 3.53$, $p = 0.0032$.

With total xylem lumen areas of 8.7% (control) and 8.8% (4.2 dS m^{-1}), the steles of Proline fine roots were found to contain the lowest conducting areas while the high conductivity roots of Barnea showed significantly higher xylem lumen areas under severe salt stress (Fig. 3.1, Table 3.1). Significantly increased total xylem lumen areas were found with increasing level of salinity and by including cross effects of variety and salinity (GLM results, salinity effect: $F = 8.68$, $p = 0.0003$; variety*salinity effect: $F = 3.53$, $p = 0.0032$).

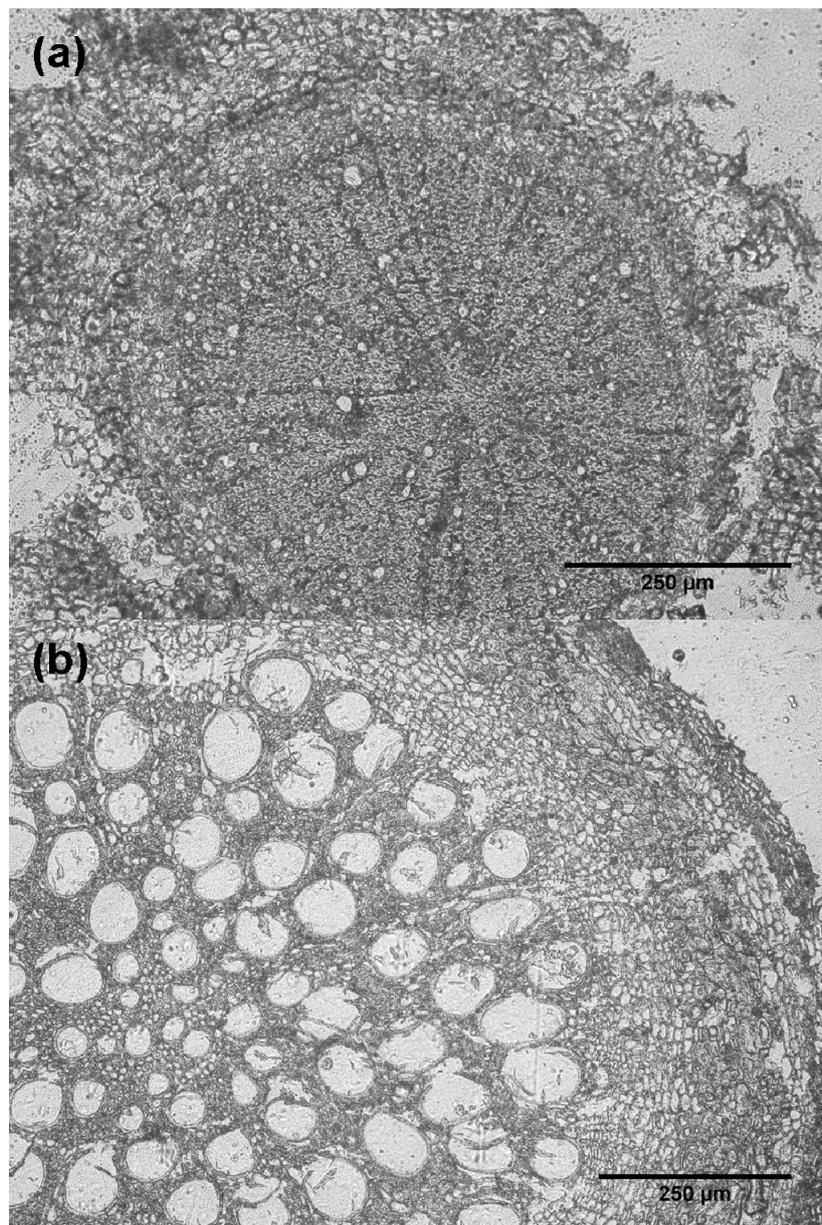


Fig. 3.1 LM-micrographs of a normal (Fig. 3.1a) and a high conductivity (Fig. 3.1b) fine root of *Olea europaea* var. Barnea under severe salt stress (7.5 dS m^{-1}). Scale bars represent 250 µm.

Xylem conduit diameter and distribution pattern

The hydraulically weighted conduit diameter (HWCD) of Barnea fine roots under fresh water and moderately saline irrigation tended to be lower than that of Arbequina and Proline under the same conditions (Fig. 3.2). The HWCD of Barnea was significantly increased ($p < 0.05$) in high conductivity roots under severe salinity (7.5 dS m⁻¹, Figs. 3.1, 3.2a, Table 3.1).

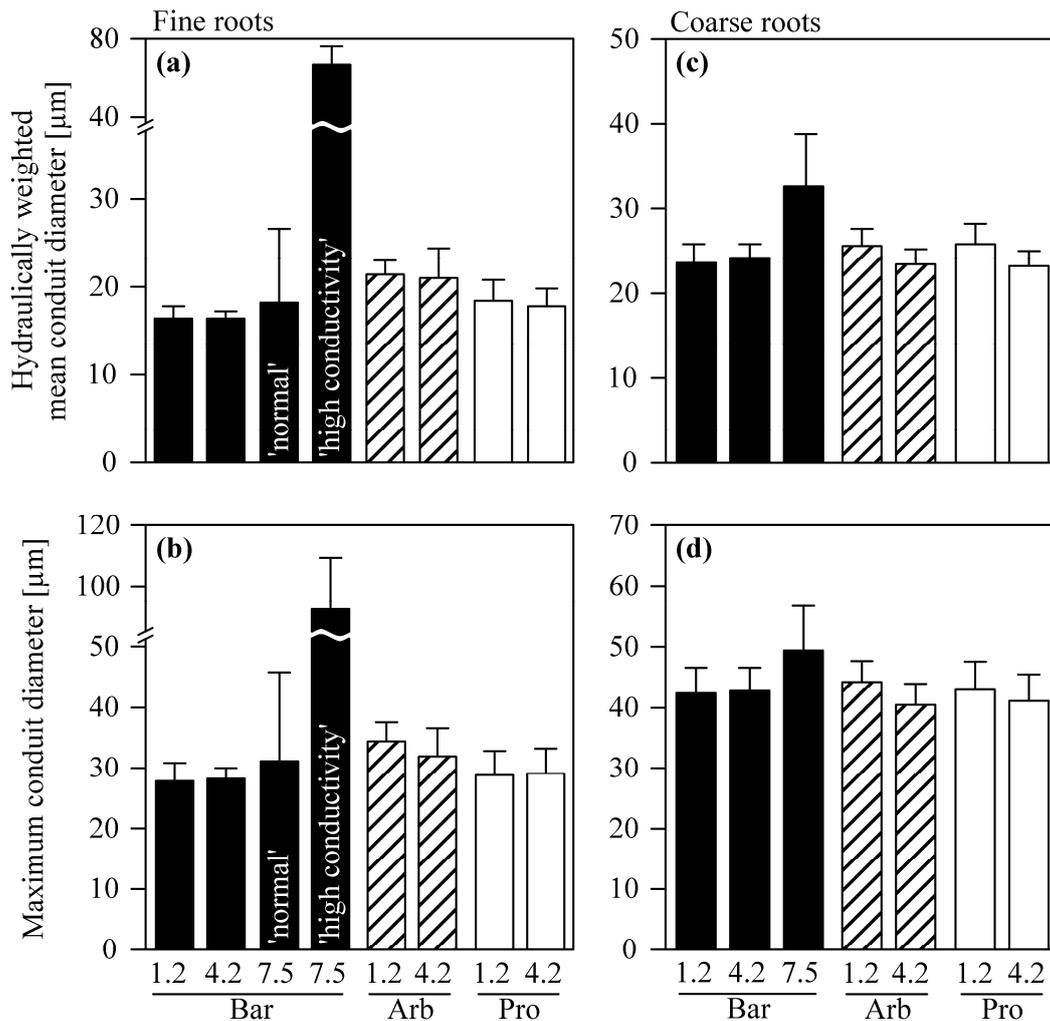


Fig. 3.2 Xylem conduit diameters in fine roots ($d \leq 2$ mm, Fig. 3.2a,b) and coarse roots ($d = 2-10$ mm, Fig. 3.2c,d) of three *Olea europaea* varieties [Barnea (Bar), Arbequina (Arb), and Proline (Pro)]. Conduits are tracheids and vessels. Hydraulically weighted mean conduit diameter (HWCD) is shown in Fig. 3.2a,c and maximum conduit diameter (MAXCD) in Fig. 3.2b,d. Data are presented as mean+SE ($n = 4-8$). HWCD weights the importance of the radii in proportion to the estimated hydraulic conductance of the conduits. GLM result of HWCD: salinity effect, $F = 12.86$, $p < 0.0001$. GLM results of MAXCD: salinity effect, $F = 7.78$, $p = 0.0007$; diameter class effect, $F = 6.89$, $p = 0.01$.

The mean conduit diameter, the HWCD and the MAXCD were found to be significantly influenced by salinity, thereby increasing slightly in Barnea but decreasing in both other varieties with increasing salinity (Fig. 3.2a,c; GLM result of mean conduit diameter,

salinity effect: $F = 6.21$, $p < 0.0028$; GLM result of HWCD, salinity effect: $F = 8.68$, $p < 0.0001$; GLM result of MAXCD, salinity effects: $F = 7.78$, $p < 0.0007$).

Mean diameter and hydraulically weighted conduit diameters tended to be larger in coarse roots than in fine roots (Fig. 3.2a,c, Table 3.2). This difference was statistically significant for the maximum conduit diameter (MAXCD, Fig. 3.2b,d; GLM result, diameter class effect: $F = 6.89$ $p = 0.01$). However, the MAXCD in high-conductive Barnea fine roots (7.5 dS m^{-1}) was found to be even larger than in coarse roots ($P < 0.05$).

Table 3.2 Relative conduit diameter distributions of fine and coarse roots of the *Olea europaea* varieties Barnea, Arbequina, and Proline at different salinity treatments (1.2, 4.2, and 7.5 dS m^{-1}). For Barnea fine roots under severe salt stress (7.5 dS m^{-1}), ‘normal’ and high conductivity (‘HC’) roots were distinguished by means of outlying data (see Statistical analyses, mean \pm SE, n = sample size).

Olive variety	Salinity [dS m^{-1}]	n	Fraction of conduit diameter classes [%]				
			5–10 μm	10–15 μm	15–20 μm	20–25 μm	>25 μm
<i>Fine roots</i>							
Barnea	1.2	8	69.3 \pm 4.8	22.8 \pm 3.8	6.4 \pm 1.4	1.0 \pm 0.4	0.4 \pm 0.2
Barnea	4.2	8	70.1 \pm 6.2	19.4 \pm 3.0	7.6 \pm 2.3	2.4 \pm 1.1	0.4 \pm 0.3
Barnea ‘normal’	7.5	6	78.2 \pm 4.9	14.4 \pm 2.1	3.9 \pm 1.0	1.9 \pm 1.0	1.6 \pm 0.9
Barnea ‘HC’	7.5	4	53.4 \pm 4.4	11.8 \pm 0.6	3.5 \pm 0.6	2.5 \pm 0.3	28.8 \pm 3.2
Arbequina	1.2	8	57.8 \pm 4.1	21.8 \pm 2.1	11.8 \pm 1.5	5.5 \pm 0.7	2.3 \pm 1.1
Arbequina	4.2	8	69.3 \pm 4.8	17.3 \pm 2.4	7.9 \pm 2.9	3.0 \pm 1.1	2.0 \pm 1.0
Proline	1.2	8	73.4 \pm 5.0	18.0 \pm 3.3	5.3 \pm 1.7	2.2 \pm 1.0	1.0 \pm 0.4
Proline	4.2	8	62.9 \pm 2.4	23.7 \pm 1.5	9.6 \pm 1.6	3.4 \pm 0.9	1.3 \pm 0.6
<i>Coarse roots</i>							
Barnea	1.2	8	61.3 \pm 5.0	20.0 \pm 2.5	9.1 \pm 1.7	5.3 \pm 1.7	3.1 \pm 1.2
Barnea	4.2	8	57.3 \pm 3.2	18.0 \pm 1.2	12.7 \pm 1.4	6.9 \pm 1.0	3.6 \pm 1.3
Barnea	7.5	8	64.8 \pm 4.0	15.5 \pm 2.1	7.3 \pm 1.0	4.7 \pm 1.0	7.5 \pm 2.1
Arbequina	1.2	8	65.0 \pm 3.3	15.9 \pm 2.4	8.6 \pm 1.2	4.9 \pm 0.6	5.6 \pm 1.1
Arbequina	4.2	8	68.5 \pm 3.1	14.9 \pm 1.9	8.3 \pm 1.1	4.9 \pm 0.8	3.5 \pm 1.4
Proline	1.2	8	58.9 \pm 4.1	22.8 \pm 1.1	10.9 \pm 0.8	5.4 \pm 1.0	6.3 \pm 2.2
Proline	4.2	8	55.8 \pm 2.4	20.8 \pm 1.8	13.3 \pm 0.8	6.6 \pm 1.2	3.4 \pm 1.5

GLM results, conduit diameter class 5–10 μm : salinity*variety effect, $F = 2.46$, $p = 0.0904$; diameter class effect, $F = 4.81$, $p = 0.0306$. GLM results, conduit diameter class 10–15 μm : salinity effect, $F = 4.71$, $p = 0.0112$; variety effect, $F = 3.19$, $p = 0.0455$. GLM results, conduit diameter class >25 μm ; salinity effect, $F = 13.06$, $p < 0.0001$.

Anatomical comparisons of the moderately salt-stressed treatment (4.2 dS m^{-1}) revealed about 10% less conduits of the smallest diameter class (5–10 μm) in fine root of salt sensitive Proline trees than in those of Barnea and Arbequina (Table 3.2; GLM result, salinity*variety effect: $F = 2.52$, $p = 0.0857$). Furthermore, in Barnea variety the propor-

tion of 5-10 μm conduits increased to 78% under high salinity (7.5 dS m^{-1}). The opposite effect was found in the 10-15 μm size class: the fraction of this size class decreased in Barnea and Arbequina but increased in Proline under moderate salinity (GLM results, salinity effect: $F = 4.83$, $p = 0.0101$; variety effect: $F = 3.27$, $p = 0.0423$).

Table 3.3 Proportion of conduit diameter classes on theoretical hydraulic conductivity (k_h^{theo}) of fine roots of the *Olea europaea* varieties Barnea, Arbequina, and Proline at different salinity treatments (1.2, 4.2, and 7.5 dS m^{-1}). For Barnea fine roots under severe salt stress (7.5 dS m^{-1}), ‘normal’ and high conductivity (‘HC’) roots were distinguished by means of outlying data (see Statistical analyses, mean \pm SE, n = sample size).

Olive variety	Salinity [dS m^{-1}]	n	Fraction conduit diameter class on theoretical hydraulic conductivity [%]				
			5–10 μm	10–15 μm	15–20 μm	20–25 μm	>25 μm
Barnea	1.2	8	15.3 \pm 3.9	32.3 \pm 5.8	28.5 \pm 4.1	10.3 \pm 3.8	13.7 \pm 5.9
Barnea	4.2	8	17.5 \pm 5.0	27.5 \pm 5.6	28.3 \pm 3.0	18.3 \pm 4.3	8.5 \pm 3.8
Barnea ‘normal’	7.5	6	22.5 \pm 7.0	26.2 \pm 5.8	17.5 \pm 3.8	10.0 \pm 2.9	23.9 \pm 11.1
Barnea ‘HC’	7.5	4	0.05 \pm 0.01	0.09 \pm 0.02	0.12 \pm 0.03	0.25 \pm 0.08	99.5 \pm 0.15
Arbequina	1.2	8	4.2 \pm 1.0	13.4 \pm 1.8	25.9 \pm 3.1	32.5 \pm 3.2	24.0 \pm 1.8
Arbequina	4.2	8	9.8 \pm 2.4	20.5 \pm 6.5	24.9 \pm 6.2	20.0 \pm 4.3	28.8 \pm 11.6
Proline	1.2	8	15.8 \pm 4.8	28.4 \pm 7.6	19.3 \pm 3.3	15.0 \pm 4.7	21.4 \pm 9.3
Proline	4.2	8	9.1 \pm 2.7	25.8 \pm 7.3	27.6 \pm 4.5	20.5 \pm 3.5	16.9 \pm 7.4

In consequence of these anatomical differences, theoretical conductivity (k_h^{theo}) was assigned to different conduit size classes in the three varieties and salt treatments (Table 3.3). Considering the contribution of the smallest conduit size class ($d = 5\text{-}10 \mu\text{m}$) to k_h^{theo} , moderately salt-stressed fine-roots of Barnea cover 18% of total conductivity by means of those small conduits, while the smallest conduits contribute only about the half (9-10%) to k_h^{theo} in Arbequina and Proline. The differences between moderately salt-stressed varieties become even more apparent, if conduits with diameters $< 15 \mu\text{m}$ are considered: fine roots of Barnea cover nearly half (45%) of conductivity with these small diameter conduits, whereas Arbequina and Proline cover 30 and 35%, respectively. Accordingly, conduits over 20 μm in diameter contribute less to conductivity in fine roots of fresh water irrigated and moderately salt stressed Barnea (24-26%) than those of both other olive varieties under the same treatments (36-56%, Table 3.3). Conductivity of highly conductive Barnea roots (7.5 dS m^{-1}) was mainly (99%) based on conduits with diameters $> 25 \mu\text{m}$ (Table 3.3).

While the proportion of large vessels ($> 25 \mu\text{m}$) was significantly higher in coarse roots than in fine roots (GLM result, salinity*diameter class effect: $F = 3.50$, $p = 0.0342$), the same trends in conduit diameter adjustment to salinity as in fine roots were observed (Table 3.2).

Specific conductivity and degree of embolism

We found a larger variability in specific conductivity k_s (axial hydraulic conductivity related to cross-sectional area) in roots than in branches (Fig. 3.3a-c). This large variability was observed in both fine roots (investigated diameters: 0.9-2.0 mm) and coarse roots (2.0-10.0 mm) of all three varieties. However, the variability was increased in salt-stressed roots of Barnea and Arbequina. Whereas roots and shoots of some varieties and salt treatments sporadically had up to 10-fold higher k_s values than the mean of the respective samples, Barnea possesses some ‘high conductivity’ fine roots with 100-fold higher k_s under severe salt stress (see Fig. 3.1, and crosses marking outliers in Fig. 3.3a-c). Specific conductivities of coarse roots and branches were found to be significantly higher than those of fine roots (Table 3.4).

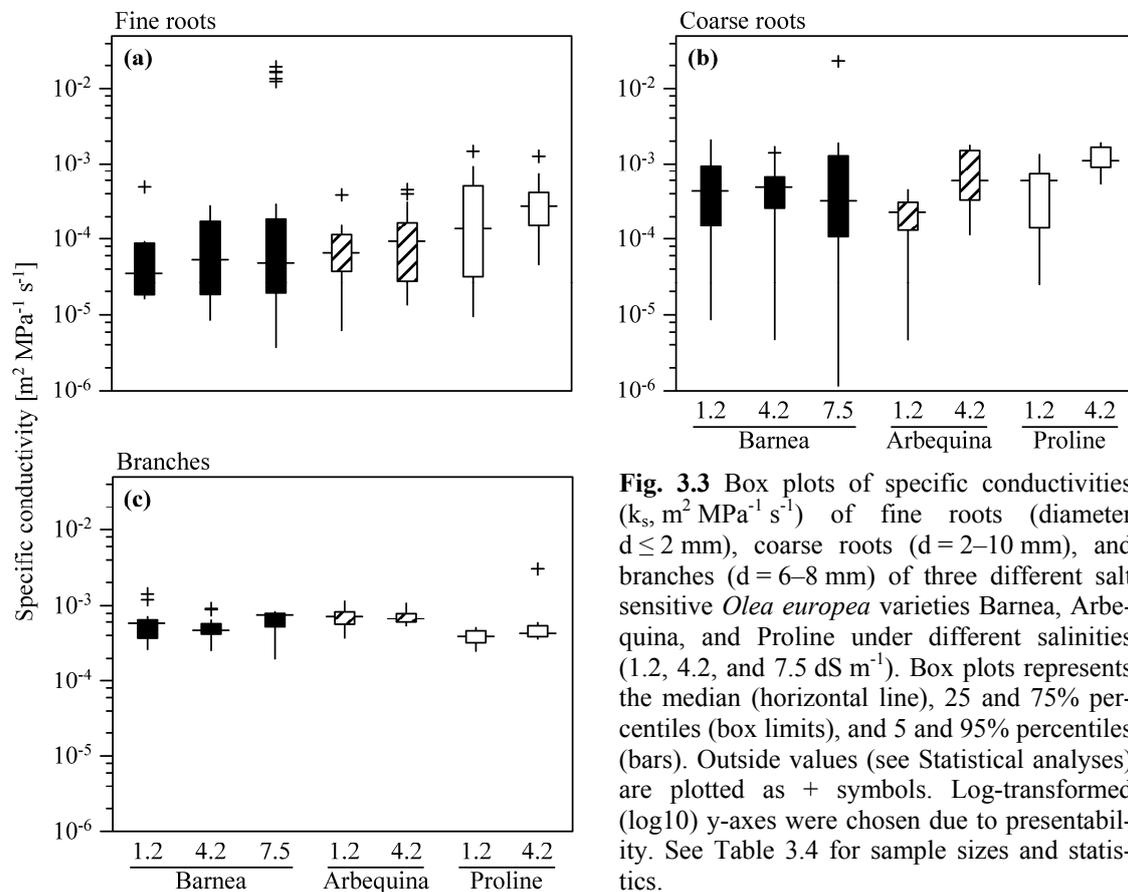


Fig. 3.3 Box plots of specific conductivities (k_s , $\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$) of fine roots (diameter $d \leq 2 \text{ mm}$), coarse roots ($d = 2\text{--}10 \text{ mm}$), and branches ($d = 6\text{--}8 \text{ mm}$) of three different salt sensitive *Olea europea* varieties Barnea, Arbequina, and Proline under different salinities (1.2, 4.2, and 7.5 dS m^{-1}). Box plots represent the median (horizontal line), 25 and 75% percentiles (box limits), and 5 and 95% percentiles (bars). Outside values (see Statistical analyses) are plotted as + symbols. Log-transformed (\log_{10}) y-axes were chosen due to presentability. See Table 3.4 for sample sizes and statistics.

Mean specific conductivities of fine and coarse roots tended to increase with increasing salt stress (Table 3.4). However, due to the high variability in root conductivity, increases of k_s due to salinity were only significant in coarse roots of Arbequina and Proline trees. Large and mostly significant differences in k_s existed between fresh water irrigated fine roots of Barnea and Arbequina on the one hand, and Proline on the other, with the latter showing about 3-times higher fine root k_s values. This difference in fine root k_s between the more salt resistant varieties and Proline was not only found in the fresh water irrigated control but also persisted under moderately saline irrigation. No significant differences were found between branches of the fresh water irrigated and salt-stressed treatments (Fig. 3.3c, Table 3.4).

Table 3.4 Mean specific conductivity (k_s , $\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$) and degree of embolism (%) in fine roots, coarse roots, and branches of the *Olea europaea* varieties Barnea, Arbequina, and Proline under different salinities (1.2, 4.2, and 7.5 dS m^{-1}). Significant differences between salinity treatments within fine roots, coarse roots, and branches are indicated by different lower case letters, and significant differences between fine roots, coarse roots, and branches of the same variety and salinity treatment by different capital letters (Mann-Whitney U test, $p < 0.05$, $\text{mean} \pm \text{SE}$, $n = \text{sample size}$).

Olive variety	Salinity [dS m^{-1}]	n	k_s [$10^{-4} \text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$]		Embolism [%]	
<i>Fine roots</i>						
Barnea	1.2	14	0.9 \pm 0.4	aA	24.8 \pm 8.1	abcA
Barnea	4.2	11	1.0 \pm 0.3	abA	21.2 \pm 11.2	aA
Barnea	7.5	26	30.6 \pm 12.5	abA	22.8 \pm 5.2	abA
Arbequina	1.2	18	1.0 \pm 0.3	abA	18.2 \pm 4.7	abA
Arbequina	4.2	16	1.3 \pm 0.3	abA	33.0 \pm 7.6	bdA
Proline	1.2	20	3.0 \pm 0.9	bcA	36.3 \pm 6.2	cdA
Proline	4.2	22	3.7 \pm 0.7	cA	22.3 \pm 4.8	abcA
<i>Coarse roots</i>						
Barnea	1.2	30	6.2 \pm 1.1	abB	39.5 \pm 4.6	aB
Barnea	4.2	33	4.9 \pm 0.6	aB	26.6 \pm 3.1	bB
Barnea	7.5	23	15.4 \pm 9.9	abB	35.2 \pm 6.8	abA
Arbequina	1.2	11	2.2 \pm 0.4	bB	12.3 \pm 4.1	cdeA
Arbequina	4.2	8	8.4 \pm 2.3	acB	23.0 \pm 11.5	bdA
Proline	1.2	22	5.2 \pm 0.8	aB	33.1 \pm 5.4	abA
Proline	4.2	14	12.2 \pm 1.1	cB	25.9 \pm 6.8	beAB
<i>Branches</i>						
Barnea	1.2	11	6.2 \pm 1.1	abcB	10.5 \pm 2.1	abA
Barnea	4.2	11	5.2 \pm 0.5	acB	11.2 \pm 2.2	aA
Barnea	7.5	11	6.4 \pm 0.7	adB	18.7 \pm 3.7	bdA
Arbequina	1.2	11	7.1 \pm 0.7	bdC	32.8 \pm 3.7	cB
Arbequina	4.2	11	7.1 \pm 0.5	bdB	26.3 \pm 3.8	cdA
Proline	1.2	11	3.8 \pm 0.3	ceAB	29.5 \pm 4.9	cA
Proline	4.2	11	6.8 \pm 2.3	aeC	35.5 \pm 6.8	cB

The degree of embolism in fine roots, coarse roots and branches was not significantly higher in roots and branches of salt-stressed trees of the three olive varieties than in fresh water-irrigated ones (Table 3.4). Changes of coarse root embolism rates of all three olive varieties were in accordance with changes in degree of fine root embolism, and no significant differences were found between organs. However, the degree of embolism in branches of Arbequina and Proline was significantly higher than in branches of Barnea (Table 3.4).

3.5 DISCUSSION

Adjustment of root xylem anatomy to salt stress

Trees are known to respond to drought and salt stress with modifications in their wood anatomy such as changes in xylem density and conduit diameters (Kozłowski 1997). In previous studies, the xylem in salt stressed stems and roots has been found to contain vessels with smaller diameters (Valenti *et al.* 1991, Reinhardt and Rost 1995, Junghans *et al.* 2006) and higher vessel densities (Millner 1934, Solomon *et al.* 1986, Sobrado 2007). Both high vessel density and decreasing vessel dimensions are associated with an increased hydraulic safety (Lo Gullo *et al.* 1995, Eshel *et al.* 2000).

In this study, mean conduit diameters, hydraulically weighted conduit diameter and maximum vessel diameters in roots of the three olive varieties were mostly unaltered or only slightly decreased under moderate salt stress and even increased in high conductivity roots of Barnea under severe salt stress (Fig. 3.2a,c, Table 3.2). This discrepancy to previous studies might be a consequence of already remarkably small root conduits of olive under fresh water irrigation, compared to other Mediterranean species (Table 3.2; Martínez-Vilalta *et al.* 2002).

However, small mean conduit diameters may be a common adaptation to an increased tension of the water column in the conducting system (Baas *et al.* 1983, Stevenson and Mauseth 2001), and may explain the general drought and salinity tolerance of *Olea europaea*, but they cannot explain the differences in salt resistance between the three studied olive varieties.

Recently, the results of Schmitz *et al.* (2006) questioned the relevance of smaller mean conduit diameters for increasing hydraulic safety in favour of vessel density, which is

obviously interrelated to the fraction of small diameter conduits. Our results show an increased formation of smallest diameter conduits ($d = 5\text{--}10\ \mu\text{m}$) in salt-stressed fine roots of Barnea (highly tolerant) and Arbequina (tolerant) trees. In contrast, salt-sensitive Proline trees had a 10% smaller proportion of narrow conduits under moderate salinity and even 20% less narrow conduits than severely salt-stressed Barnea (Table 3.2). While 18% of the absorbed water was conducted in those smallest vessels in fine roots of moderately stressed Barnea, only half of that (9%) was transported in those small vessels in Proline (Table 3.3).

This is supposed to have major effects on the appearance and impact of embolism. Even though conduit diameters were thought to be rarely directly coupled to cavitation vulnerability (Hacke and Sperry 2001), narrow conduits may be advantageous with respect to embolism: they are typically associated with smaller pit membrane pores (Martínez-Vilalta *et al.* 2002), relatively larger wall strength (Hacke *et al.* 2001) and refill easier after embolism (Grace 1993, Holbrook and Zwieniecki 1999). In any case, a conduit population with an increased total number should improve its relative degree of safety since the impact of cavitation in single conduits on total loss of conductivity is lower (Mauseth and Stevenson 2004). Nevertheless, fine roots of Barnea under severe salt stress realised larger proportions of their conductivity with vessels $> 20\ \mu\text{m}$ in diameter, combining both safety and considerable conductivity in a more dimorphic conduit distribution pattern when severely stressed. The increased water use efficiency of a vascular system with both very small (safe) and large conduits (efficient) may account for its frequent occurrence in the flora of arid regions (Baas *et al.* 1983).

In addition, significantly larger conduit diameters were observed in specialized high conductivity roots of Barnea trees after exposure to severe salt stress (Figs. 3.1b, 3.2a,b). Different parts of a root system have been found to respond independently to salt stress (Waisel and Breckle 1987). While differentiation within the vessel population as discussed earlier may be a favourable adaptation to temporal changes in soil salinity, we suggest that the differentiation in ‘high conductivity’ and ‘normal’ roots (Fig. 3.1) poses an effective adaptation to soils varying spatially in salinity, such as drip-irrigated orchards (Mmolawa and Or 2000, Isla *et al.* 2003). Shani *et al.* (1993) have found a comparable ‘specialization’ in root hydraulics due to salinity, where most of the water uptake occurred by means of fresh water-accessing roots.

Does salinity affect conductivity in situ?

The specific conductivities (k_s) in roots and shoots of olive in this study were lower than k_s measured in other woody Mediterranean species (Martínez-Vilalta *et al.* 2002) but in accordance with k_s values found in olive coarse roots, recently published by Nardini *et al.* (2006). No significant differences in k_s were found between branches of fresh water and saline water irrigated trees (Fig. 3.3c, Table 3.4). This may indicate a lower sensitivity of the above-ground hydraulic system to salt stress in comparison with the significantly altered k_s in coarse roots of Arbequina and Proline.

No agreement has been revealed yet as to whether reduced (Shannon *et al.* 1994) or increased root conductivities (An *et al.* 2003) pose an adaptation to saline soils. Our results indicate that the more salt-resistant Barnea and Arbequina varieties possess lower axial conductivities in fine roots than salt-sensitive Proline trees, which is supporting the first assumption.

However, root conductivity increased with increasing salt stress, which contrasts previous result (Munns and Passioura 1984, Navarro *et al.* 2007). However, those studies were measuring total root conductivity, thereby including both radial and axial conductivity. Root radial conductivity is thought to be orders of magnitude smaller than axial conductivity (Frensch and Steudle 1989). Nevertheless, axial resistance can be a significant component of total resistance (Passioura 1972), especially in woody plants under water shortage (Hacke *et al.* 2000). The path length of radial water flow is much less than axial length, indicating the importance of axial conductivity especially in large woody plants (Addington *et al.* 2006).

Thus, increased axial conductivities are suggested to balance an increase of radial resistance by reducing resistance in another part of the root hydraulic system, or may have a 'compensatory effect' (West 1978) with regard to decreasing root biomasses or root numbers under salinity, as reported for several woody species (e.g. Krauss *et al.* 1999) and *Olea europea* var. Barnea in the same plot (Weissbein 2006). The importance of compensating increased resistances in small-sized root systems is underlined by a positive correlation between root hydraulic conductance and leaf surface area in olive (Nardini *et al.* 2006) and the reduced water uptake in salt stressed olive trees, resulting in limitation of photosynthesis (Loreto *et al.* 2003).

Considering the spreading of k_s in roots with increasing salinity (Fig. 3.3a,b), it is obvious that k_s of the bulk of Proline roots increased, whereas Barnea and Arbequina pos-

sess individual roots with increased and others with decreased conductivities under salt stress. The differentiation in more and less conductive roots in Barnea variety (Fig. 3.3a,b) is in accordance with detected anatomical adaptations of the xylem under severe salt stress (Table 3.3). It is suggested to be most favourable in environments with spatiotemporal heterogeneous water availabilities (see earlier in text). The amplitude of functional adaptations in response to heterogeneous environmental signals may indicate a different genetic potential of the three olive varieties, and the superiority of Arbequina and especially Barnea with regard to salt resistance. Although, those adaptations did not result in lower degrees of embolism in fine and coarse roots of Barnea and Arbequina trees than in Proline, branches of Barnea exhibited significantly lower embolism rates. This may underline the effectiveness of a dimorphic root system in preventing embolism in the shoot.

3.6 CONCLUSION

In previous studies, it has been demonstrated that differences in growth reduction caused by salt stress are the result of differences in root system structure (Lin and Sternberg 1994) or salt exclusion capacities (Mickelbart and Arpaia 2002). Shani *et al.* (1993) pointed to the importance of functionally differentiated root systems for water acquisition in heterogeneously saline soils. Our study underlined the importance of morphological adjustments and functional differentiation within the root hydraulic system. The highly salt tolerant olive variety Barnea showed major plastic adaptations at two levels of organisation: at a vascular level within an individual root (conduit size distribution) and between roots at the level of organ (diversification of roots with contrasting conductivities and ‘high conductivity’ roots). We conclude that high plasticity of the root hydraulic system in this variety of olive is an effective mechanism in adaptation to salinity.

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Chapter 4

BELOWGROUND COMPETITION IN A BROAD-LEAVED TEMPERATE MIXED FOREST - PATTERN ANALYSIS AND EXPERIMENTS IN A FOUR-SPECIES STAND

Boris Rewald and Christoph Leuschner

4.1 ABSTRACT

We investigated fine root biomass and distribution patterns in a species-rich temperate *Carpinus-Quercus-Fagus-Tilia* forest and searched for experimental evidence of symmetry or asymmetry in belowground competition. We conducted extensive root coring and applied the recently introduced *in situ*-root growth chamber technique for quantifying fine root growth under experimentally altered intra- and interspecific root neighbourhoods in the intact stand.

In 75% of all soil cores, fine roots of more than two tree species were present indicating a broad overlap of the root systems of neighbouring trees. *Quercus* trees had more than 10 times less fine root biomass in relation to aboveground biomass or productivity (stem growth) and a much higher leaf area index/root area index ratio than *Carpinus*, *Fagus* and *Tilia* trees. The root growth chamber experiments indicated a high belowground competitive ability of *Fagus* in interspecific interactions, but a low one of *Quercus*.

We conclude that (i) interspecific root competition is ubiquitous in this mixed stand, (ii) root competition between trees can be clearly asymmetric, and (iii) tree species may be ranked according to their belowground competitive ability. *Fagus* was found to be the most successful species in belowground competition, which matches with its superiority in aboveground competition in this forest community.

4.2 INTRODUCTION

A bulk of experimental and observational studies have provided convincing evidence that root competition is an important structuring force in many, if not most, terrestrial plant communities (Wilson 1988, Coomes and Grubb 2000). Current research focuses on the importance of root competition relative to other factors in determining growth and survival of plants and in affecting the diversity and species composition of plant communities (Rajaniemi *et al.* 2003, Ludwig *et al.* 2004). Because the mode of competition substantially influences population and community dynamics (Łomnicki 1980, Yokozawa *et al.* 1998, Aikio and Pakkasmaa 2003), there is a vital debate as to whether belowground competition is symmetric or asymmetric (de Kroon *et al.* 2003, Schenk 2006). Most experimental evidence suggests that soil resource acquisition by root systems of competing plants tends to be proportional to their sizes ('symmetric'; Weiner *et al.* 1997, Cahill and Casper 2000). In contrast to light competition, larger root systems *per se* cannot simply preempt nutrients or water at the expense of smaller plants. However, most of these results were obtained under artificial, homogeneous soil conditions (Hutchings and John 2004). It has been suggested that the picture of symmetric competition belowground may not be valid in patchy natural environments (Jackson and Caldwell 1993), where larger and faster growing root systems could exploit resources more completely (Campbell *et al.* 1991, Van Lear and Kapeluck 1995, Schwinning and Weiner 1998). Thus, the outcome of belowground competition in mixed stands may largely depend on the rate and degree as to which different species can access temporal or spatial resource patches in the soil (Thomas and Weiner 1989). In any case, experimental evidence for asymmetric belowground competition is still scarce (Blair 2001, Rajaniemi 2003, von Wettberg and Weiner 2003).

A second topic able to change our perception of belowground competition is the search for organic compounds released in root-root and root-soil interactions (Bais *et al.* 2003, Bonanomi *et al.* 2005, Falik *et al.* 2003). Chemical signals, yet unknown recognition systems in roots, and indirect root interactions involving other soil organisms may play an important role in the belowground interaction between tree root systems (Schenk 2006). Competition between roots of the same individual will lower resource use efficiency and possibly may reduce plant fitness (Schenk 2006). Indeed, roots have been found to avoid competition with roots of the same plant (Holzapfel and Alpert 2003,

Gruntman and Novoplansky 2004, Falik *et al.* 2005). On the other hand, a plant may increase its fitness by growing roots into soil shared with a competitor, allowing it to acquire resources from that space and also to decrease the competitors' fitness by reducing its resource supply (Robinson *et al.* 1999).

Various studies found a certain degree of niche partitioning in terms of rooting depth and placing of roots, root dynamics and resource acquisition strategies in mixed stands of herbs and grasses (Parrish and Bazzaz 1976, Mamolos *et al.* 1995, Nobel 1997, Fargione and Tilman 2005). Belowground interactions among woody plants have mostly been studied in agroforestry systems (Nambiar and Sands 1993). In forests, manipulative studies have mainly focused on root competition between adult trees and forest herbs or tree seedlings (Coomes and Grubb 2000, Barberis and Tanner 2005). Therefore, the significance of root competition between mature trees in intact stands, and the importance of root competition for tree growth, vitality and species coexistence in mixed forests is poorly understood. This is mainly a consequence of difficult access to the root system of trees and the lack of adequate techniques for studying root competition between trees experimentally.

Here, we present the results of a combined observational and experimental study in a *Carpinus-Quercus-Fagus-Tilia* temperate mixed forest, which investigated the abundance and horizontal distribution and the relative growth rate of fine roots in different competitive neighbourhoods.

Study aims were (i) to relate aboveground structure (leaf area index, stem density, basal area, stem growth) to belowground structure (fine root biomass and root area index) in the four coexisting tree species, (ii) to quantify the extent of root system overlap, (iii) to assess the evidence for symmetry or asymmetry in fine root competition, and (iv) to attempt a ranking of the four species with respect to belowground competitive ability in this mixed stand. We tested the hypotheses that (1) trees with a large aboveground biomass have a roughly proportional biomass belowground, (2) tree root systems are spatially segregated, i.e. territorial in the sense of Schenk *et al.* (1999), and (3) belowground competition is symmetric in forests.

4.3 METHODS

Study site

The study was carried out in 2002 in a four-species mixed forest consisting of 120- to 130-yr-old *Fagus sylvatica* L. (European beech) and *Quercus petraea* (MATT.) LIEBL. (Sessile oak) trees, and of 70- to 90-yr-old *Tilia cordata* MILL. (linden) and *Carpinus betulus* L. (hornbeam) trees in the Ziegelrodaer Forst south of the city of Eisleben in Saxony-Anhalt, Central Germany (51°25'N, 11°31'E). Forty-seven percent of the tree individuals (diameter at breast height: DBH \geq 7 cm) belonged to *Carpinus*, 40% to *Quercus*, 10% to *Fagus* and 3% to *Tilia* (Table 4.1).

Table 4.1 Stand structural characteristics of the *Carpinus*, *Fagus*, *Quercus* and *Tilia* trees (DBH \geq 7 cm) in the 0.37 ha study plot. Significant differences between the species are indicated by different letters (mean \pm SE, DBH and leaf area index: U-test after Mann and Whitney, tree height: Scheffé test, $P < 0.05$).

	Stem density [n ha ⁻¹]	Mean DBH [cm]	Mean tree height [m]	Stem basal area [m ² ha ⁻¹]	Leaf area index [m ² m ⁻²]
<i>Carpinus</i>	166	23.0 \pm 0.9 a	19.0 \pm 0.6 a	8.6	1.7 \pm 0.1 a
<i>Fagus</i>	36	46.2 \pm 2.5 b	30.1 \pm 0.8 b	6.6	2.3 \pm 0.1 b
<i>Quercus</i>	140	39.7 \pm 0.8 b	27.9 \pm 0.2 b	18.3	3.3 \pm 0.1 c
<i>Tilia</i>	10	39.0 \pm 2.9 ab	26.1 \pm 1.1 ab	1.3	0.5 \pm 0.1 d
Stand total	352	-	-	34.8	7.8 \pm 0.2

Located in the transition zone between the sub-oceanic and sub-continental regions of Central Europe, the stand represents a community, which is intermediate between a beech forest on eutrophic Cambisol (Galio-Fagetum community after Ellenberg 1996) and an oak-hornbeam-linden forest (Tilio-Carpinetum). The forest has been managed with the prime goal to produce *Quercus* logs in the past centuries. A substantial reduction in management intensity in the last three decades favoured the regrowth of *Carpinus*, which now forms a second tree layer under the upper canopy of *Quercus* and *Fagus* trees. Total stem density was 352 ha⁻¹ (all stems with DBH \geq 7 cm) with *Carpinus* contributing most of the thinner stems. *Fagus*, *Quercus* and *Tilia* did not differ significantly with respect to DBH (39-46 cm) and mean tree height (26-30 m), whereas the *Carpinus* trees were, on average, less tall and had a lower DBH (Table 4.1).

While a shrub layer was nearly absent (< 2% cover), about 10% of the forest floor was occupied by forest herbs (*Anemone nemorosa* L., *Stellaria holostea* L., *Athyrium filix-femina* (L.) ROTH and other species).

Mean annual precipitation was 462 mm at the nearby weather station of Allstedt; it is assumed that the study plot at a somewhat higher elevation received about 520 mm yr⁻¹ with approximately 55% of the annual precipitation falling from May to September (300 mm in the study year 2002). The mean annual temperature was 8.6 °C. The soils were meso- to eutrophic Cambisols (pH(H₂O): 4.3-4.4, base saturation about 40% in the topsoil) derived from Triassic sandstone (Upper Bunter) covered by a thin layer of Pleistocene eolic loess deposits. Atop of the mineral soil, a thin (5-30 mm) layer of ectorganic material (humus form: mull) was present. The groundwater horizon was far below the rooting zone.

Selection criteria for the study plot were (i) absence of canopy gaps, (ii) a representative tree species composition with respect to the forest community, and (iii) only minor soil disturbance by wild boar. A plot of 0.37 ha (45 x 92 m), which fulfilled these criteria, was selected and fenced, and all stems ≥ 7 cm DBH were mapped. Diameter at breast height was measured with dendrometer tapes at 1.3 m height, tree height with an ultrasonic Vertex III height meter (Haglöf, Sweden). For monitoring stem increment, 4 to 12 stems per species were instrumented with dendrometer tapes and read seven times during a period of 12 months. The stems used for increment measurement were selected in direct proximity to the root coring transects (see below); the stems represented the most abundant diameter classes of the species in the stand. We used allometric regressions based on DBH and stem form to estimate annual stem growth of the four species using the single-tree modelling software BWinPro (Nagel and Schmidt 2006). The leaf area index (LAI) was measured by litter sampling in autumn. Litter fall was collected with 30 litter buckets of 0.29 m² aperture placed in the plot at random distances along the root coring transects (see below). The material was sorted into leaf mass and non-leaf material (including bark, twigs and reproductive organs). Twenty leaves per bucket were selected by random and analyzed individually for their area with the software WinFolia 2001a (Régent, Quebec, Canada).

Analysis of fine root mass, morphology and distribution

Soil coring and associated fine root analysis was conducted for three purposes, (i) to estimate the root biomass and necromass of the four tree species in the stand,

(ii) to analyse the vertical and horizontal fine root distribution by species, and (iii) to compare the four coexisting species with respect to fine root morphological properties.

Fine root ($d \leq 2$ mm) sampling was conducted in June 2002 with sharp soil corers ($d = 35$ mm) that were manually driven into the topsoil to a depth of 250 mm. Coring was conducted at 60 locations that were selected by random on three transects of 30 m length (20 locations per transect). The transects were demarcated at a distance of about 5 m to each other in the north-western part of the study plot where all four tree species occurred in quantities corresponding to their presence in the entire plot, where the mean stem distance was about 7 m and no marked clumping of stems occurred. A clumping of stems would have complicated a spatial analysis of fine root mass in the stand. The exact position of the root coring locations in the plot was recorded with the aim to analyse the dependence of root biomass on the distance to the closest stem, tree species identity, and basal area of the surrounding stems. In the analysis of the relationship between belowground and aboveground biomass structure, all stems within a radius of 5 m around a coring location were considered.

The soil cores were sliced into organic layer, upper (0-10 cm) and lower (10-20 cm) mineral soil horizons, transferred to plastic bags, sealed, and transported to the laboratory where the processing of the stored samples (4°C) took place within four weeks (Tierney and Fahey 2001). We restricted root coring to the organic layer and the 0-20 cm layer of the mineral soil, since earlier investigations in the Ziegelrodaer Forst had shown that fine root biomass decreases exponentially with soil depth and that the 0-20 cm section of the soil profile contained about 60% of the total fine root biomass of the stand (Hertel 1999).

The samples were cleaned from soil using a water jet and a 0.25 mm sieve. Fine roots of the four tree species were separated under the binocular (16-40×) according to colour, periderm surface structure and ramification. Hertel (1999), Hölscher *et al.* (2002) and Korn (2004) developed a preliminary key for distinguishing fine roots of *Fagus*, *Quercus*, *Carpinus* and *Tilia* based on a set of morphological criteria, which was applied here. Live (biomass) and dead rootlets (necromass) were distinguished by colour, root elasticity and the degree of cohesion of cortex, periderm and stele. A non-turgid cortex and stele, an air-filled stele, or the complete loss of the stele and cortex with only the periderm being present, were used as indicators of root death (Leuschner *et al.* 2004). Herb roots occurred only at very low densities in the stand; they were discarded. Large fine root fragments (length ≥ 10 mm) were extracted by hand, smaller fragments

were determined in sub-samples ($n = 8$ per soil horizon) by spreading the remaining sieve content on a piece of filter paper (730 cm^2) with 36 squares marked on it (Van Praag *et al.* 1988). Six of the squares were randomly selected and analysed in a time-consuming procedure under the binocular for even smallest fine root fragments. The mass of small fragments was then extrapolated to all samples by quantifying the ratio between large and small root fragments in a sub-sample. All samples were oven-dried (48 h, 70°C) to constant weight.

The root mass data were expressed per ground area (g m^{-2} to a depth of 20 cm) and as biomass/necromass ratio for each tree species. Coring locations, where all surrounding stems within a 5 m radius belonged to one species, were termed ‘mono-specific coring locations’; ‘multi-species coring locations’ were surrounded by stems of two to four tree species.

For investigating root morphology, 29 to 49 fresh fine root samples per species and soil horizon were extracted and analysed for specific fine root surface area (SRA, in $\text{cm}^2 \text{g}^{-1}$, only fraction ≤ 2 mm in diameter considered) using a flat-bed scanner and the image analysis program WinRhizo 2002a (Régent, Quebec, Canada). By multiplying SRA with fine root biomass in the horizons, a fine root area index (RAI, in m^2 per m^2 ground area) was obtained. The specific abundance of live fine root tips (n per mg root dry mass) was also counted under a stereo-microscope.

Root chamber experiments on fine root competition

Hertel and Leuschner (2006) introduced the *in situ*-root growth chamber technique for monitoring fine root growth of trees in the soil of mature forests under conditions of manipulated root neighbourhoods (see Fig. A 3). This approach allows conducting replicated experiments on competitive interactions between tree fine roots under field conditions in intact forests. Our chambers partly resemble the root chambers developed by Mahall and Callaway (1991), Espeleta *et al.* (1998), and Escamilla and Comerford (1998) for studying nutrient depletion, root communication or the functioning of mycorrhizal roots in the rhizosphere. We applied this technique for quantifying competition between fine roots of all four species (interspecific competition) and compared the results with the outcome of intraspecific competition treatments. The technique and its application are described in detail in Hertel and Leuschner (2006). Briefly, 335 root growth chambers manufactured from opaque PVC plates with a volume of 189 cm^3 (90 x 70 x 30 mm length, height and width; Fig. A 3) were used in the stand. The cham-

ber's front and back sides were perforated with 36 holes ($d = 1$ mm) each, and the top and bottom consisted of plastic gauze ($d = 1.5$ mm) to permit sufficient water percolation and gas exchange but to prevent root ingrowth from the surrounding soil.

We investigated ten different competitive root interactions (six possible interspecific interactions between each two species, four intraspecific interactions) by placing two terminal fine roots in each chamber and exposing them for 180 to 210 d in the topsoil *in situ*. The chambers were covered by a layer of soil or litter. Live terminal fine roots were carefully uncovered in the uppermost soil with a pair of tweezers and small spoons, and inserted through one of the two openings ($d = 6.5$ mm) at the two opposite side walls. By this procedure, the mycorrhizal mycelium in the rhizosphere was cut but the terminal finest roots and their root tips remained intact and typically continued growth within a few weeks inside the chamber (Hertel and Leuschner 2006). After 6 months of exposure in the chambers, the majority of roots were intensively reinfected by mycorrhizal fungi and showed vital growth. The roots selected for study had a diameter at the point of insertion of 2 mm; approximately 30 mm of the terminal root section was enclosed in the chamber. Since the two root endings partly overlapped in the chamber, competitive interactions must have occurred in the experiments. The species identity of the roots was detected *in situ* from periderm morphology and colour as described above. In the case of experiments on interspecific root competition, the study objects were fine roots of two different species; intraspecific competition was investigated with two conspecific roots in a chamber. The chambers were filled with root-free mineral soil extracted from the direct vicinity and the roots were carefully embedded in this substrate which more or less resembled the undisturbed soil environment in the stand.

We attempted to accommodate each of the ten studied interaction types with at least 30 chambers to allow for a statistical analysis of the data. At the date of harvest, the branch roots were cut at the insertion holes, carefully extracted from the chamber and their dry mass (48 h, 70°C) and length increment were determined in the laboratory. Root performance was assessed as root relative growth rate (RGR in $\text{mg g}^{-1} \text{d}^{-1}$) between insertion date and date of harvest. The initial biomass of the two inserted fine roots was estimated non-destructively by photographing the root in front of a graph paper at the beginning of the experiment and calculating root length/dry mass relationships from root samples taken close to the chambers.

For quantifying a species' ability to compete successfully with the roots of other tree species for soil space and soil resources, we defined a competitive ability index (CA) which uses fine root RGR as a fitness parameter in the belowground compartment. We assumed that root growth is closely linked to an increase in absorbing surface area and thus to a growing nutrient and water absorption capacity of the fine root system. A species' RGR in interspecific interaction (two-species chambers, RGR_{mix}) was contrasted with its RGR in intraspecific interaction (single-species chambers, RGR_{mono}) with

$$(1) \quad CA = (RGR_{\text{mix}} - RGR_{\text{mono}}) \times RGR_{\text{mono}}^{-1}$$

Positive CA values stand for a better root growth with an allospecific root than with a conspecific one. For assessing the competitive ability of a tree species in all possible interspecific interactions in this four-species stand, all three CA values of a species were averaged. Similar CA values of two competing species were interpreted as an indication of a quasi-symmetric competitive interaction, irrespective of the absolute size of RGR of the two species. On the other hand, we assumed the larger the species differences in CA, the more asymmetric the interaction to be.

Using root RGR as criterion to assess belowground competitive ability follows the general practice in competition experiments with herbaceous pot-grown plants (Grace 1995). This species-centred approach of belowground competitive ability contrasts with the concept adopted by Schenk (2006) who focuses on the community-level consequences of belowground competition by defining root competition to be 'a reduction in the availability of a soil resource to roots that is caused by other roots'.

We were not able to reach a balanced experimental design in the root chamber study because the fine roots of the four species occurred at different abundances in the soil. Additionally, root species identification in the field was erroneous in various cases. Thus, several species combinations were represented with only a few chambers, while others could be accommodated with more than 30 replicates because the root species combination was particularly abundant. Furthermore, it turned out upon harvest that, in about 5% of the chambers, the roots had not grown at all, or the experiment was disturbed by the ingrowth of additional fine roots from the surrounding soil (3%). Possible causes of zero root growth were root damage during the insertion process, assumed low

vitality of the roots at the start of the experiment, or other unknown factors. Therefore, chambers with relative growth rates $< 0.001 \text{ mg g}^{-1} \text{ d}^{-1}$ were excluded from the analysis.

Statistical analysis

All data sets were tested for Gaussian distribution with a Shapiro-Wilk test. We used a parametric Scheffé's multiple comparison procedure to test for significant differences in tree height and fine root biomass among the four species. A non-parametric Mann and Whitney (Wilcoxon) two-sample test was used to determine if (i) tree species had different DBH means, (ii) root growth rates were different in the root chamber treatments, (iii) the species differed with respect to fine root morphology, and (iv) the species differed in their relative competitive abilities. These calculations were conducted with the SAS System for Windows 8.02 (SAS Institute, Cary, NC, USA). Linear and non-linear regressions were calculated with the program Xact 8.03 (SciLab, Hamburg, Germany).

4.4 RESULTS

Aboveground forest structure and productivity of the four tree species

The four-species mixed stand in the Ziegelrodaer Forst showed very different stem numbers and basal areas for *Carpinus*, *Fagus*, *Quercus* and *Tilia*. *Quercus* was the most abundant tree species with 40% of the stems and 53% of the basal area in this stand, followed by *Carpinus* (stems: 47%, basal area: 25%) and *Fagus* (10 and 19%, respectively). *Tilia* contributed less than 4% of the stems and of the basal area (Table 4.1). In contrast, relative basal area increment (in ‰ of the existing basal area) in the period January to September 2002 tended to be higher in *Fagus* than in all other species (Fig. 4.1, only the difference *Fagus-Tilia* significant), and thus was not related to a species' abundance in the stand. The leaf area index (LAI) was significantly different between the four species; LAI of all trees in the stand totalled at $7.8 \text{ m}^2 \text{ m}^{-2}$ (Table 4.1).

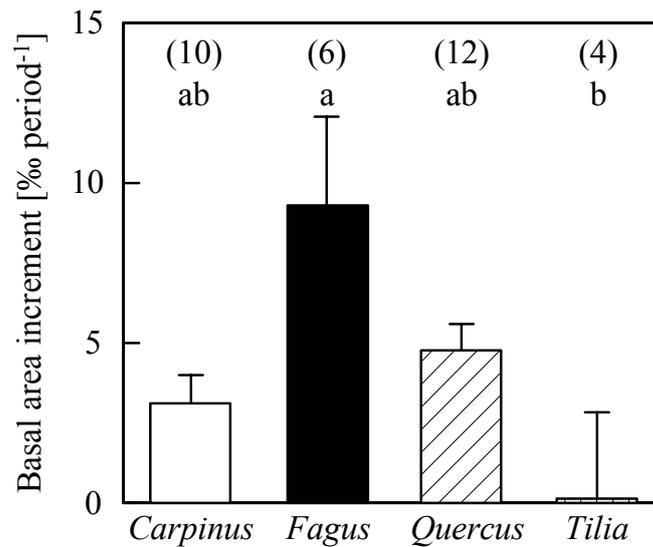


Fig. 4.1 Mean basal area increment (in % of the existing basal area) in the period January – September 2002 of the four tree species in the study plot (mean+SE, $n = 4-12$ trees per species). Significant differences between the species are indicated by different letters (U-test after Mann and Whitney, $p < 0.05$).

Fine root mass of the four species

No significant relationship between a species' basal area and its fine root biomass existed in the stand. *Quercus* with 53% of the basal area and an annual stem wood production of 1.2 Mg ha⁻¹ contributed only 11% of the stand total of fine root biomass, whereas *Fagus* (19% of basal area) and *Carpinus* (25%) with 0.4 and 0.1 Mg ha⁻¹ of stem wood production were over-represented in root biomass (32 and 51%, respectively; Fig. 4.2).

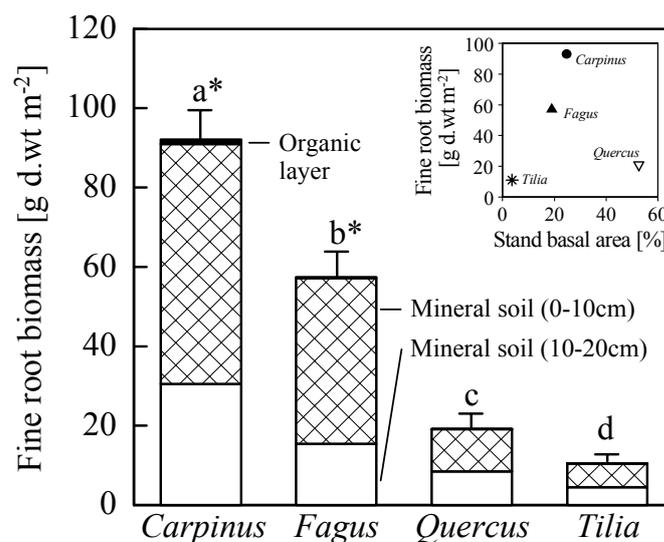


Fig. 4.2 Fine root biomass of the four tree species in the organic layer and two mineral soil horizons (0-10 and 10-20 cm) of the study plot ($n = 59$, mean+SE). Inlet: relationship between relative stand basal area and fine root biomass for the four species in the stand. Significant differences between the species are indicated by different letters (U-test after Mann and Whitney, $p < 0.05$). Asterisks denote significant differences between upper and lower mineral soil horizon.

Relating fine root biomass to stem increment yielded quotients of 150 to 1000 g root biomass per Mg ha⁻¹ of stem increment in *Carpinus*, *Fagus* and *Tilia*, but only 17 g per Mg ha⁻¹ in *Quercus*.

We found twice as much fine root necromass in the profile to 20 cm depth than root biomass with *Carpinus* contributing by far the largest proportion (> 50%) of dead roots (Table 4.2). *Fagus* had a significantly higher biomass/necromass ratio (0.84) than *Tilia*, *Carpinus* and *Quercus* (0.45-0.79).

Table 4.2 Necromass, biomass:necromass ratio, and root area index (RAI) of fine roots of the four tree species in soil profiles (organic layer and 0-20 cm of mineral soil) of the study plot (mean±SE, $n = 59$). Significant differences between the species are indicated by different letters (U-test after Mann and Whitney, $p < 0.05$).

	Fine root necromass [g d.wt m ⁻²]	Fine root bio- mass:necromass ratio	Fine root area index [m ² m ⁻²]
<i>Carpinus</i>	190.4 ± 16.8 a	0.45 ± 0.03 b	2.4 ± 0.4 a
<i>Fagus</i>	94.4 ± 19.2 b	0.84 ± 0.08 a	1.4 ± 0.3 b
<i>Quercus</i>	57.0 ± 4.1 b	0.54 ± 0.10 b	0.5 ± 0.3 c
<i>Tilia</i>	21.4 ± 5.7 c	0.79 ± 0.16 b	0.2 ± 0.2 d

Fine root morphology was not significantly different between the four species with respect to specific root surface area (SRA), the relative proportion of finest roots (≤ 1 mm in diameter) in fine root biomass, and specific root tip frequency (Table 4.3).

Table 4.3 Proportion of finest roots (diameter $d \leq 1$ mm) in fine root biomass ($d \leq 2$ mm), specific fine root surface area (SRA), and specific root tip frequency of the four tree species in the mineral soil (0-20 cm, mean±SE, $n =$ sample size). Different letters indicate significant differences between the species (U-test after Mann and Whitney, $p < 0.05$).

	n	Proportion of finest roots [%]	Specific root area [cm ² g ⁻¹]	Specific root tip fre- quency [n mg ⁻¹]
<i>Carpinus</i>	44	88.2 ± 1.8 a	349.2 ± 28.8 a	26 ± 4 a
<i>Fagus</i>	49	90.2 ± 2.1 a	315.4 ± 19.0 a	17 ± 2 a
<i>Quercus</i>	36	95.7 ± 1.4 a	325.5 ± 39.1 a	23 ± 4 a
<i>Tilia</i>	29	90.0 ± 3.6 a	415.9 ± 73.3 a	18 ± 5 a

However, *Tilia* tended to have a higher SRA, and *Fagus* and *Tilia* a lower root tip frequency than the other species. The fine root area index (RAI) of all trees in the stand totalled at 4.5 m² m⁻² (profile to 20 cm soil depth) with particularly large contributions by *Carpinus* and *Fagus* (Table 4.2). The ratio between LAI and RAI varied considera-

bly between 6.5 for *Quercus* and 0.7 for *Carpinus*. The ratios of *Fagus* and *Tilia* (1.6 and 2.4) were much more balanced.

Spatial distribution of fine roots and overlap among different species

The identification of fine roots by species allowed us to analyse species-specific fine root abundances in horizontal and vertical direction in the soil of the mixed stand. All species exhibited stem-centred distribution patterns with the highest biomass of a species regularly occurring at distances of less than 5 m around the stem (Fig. 4.3).

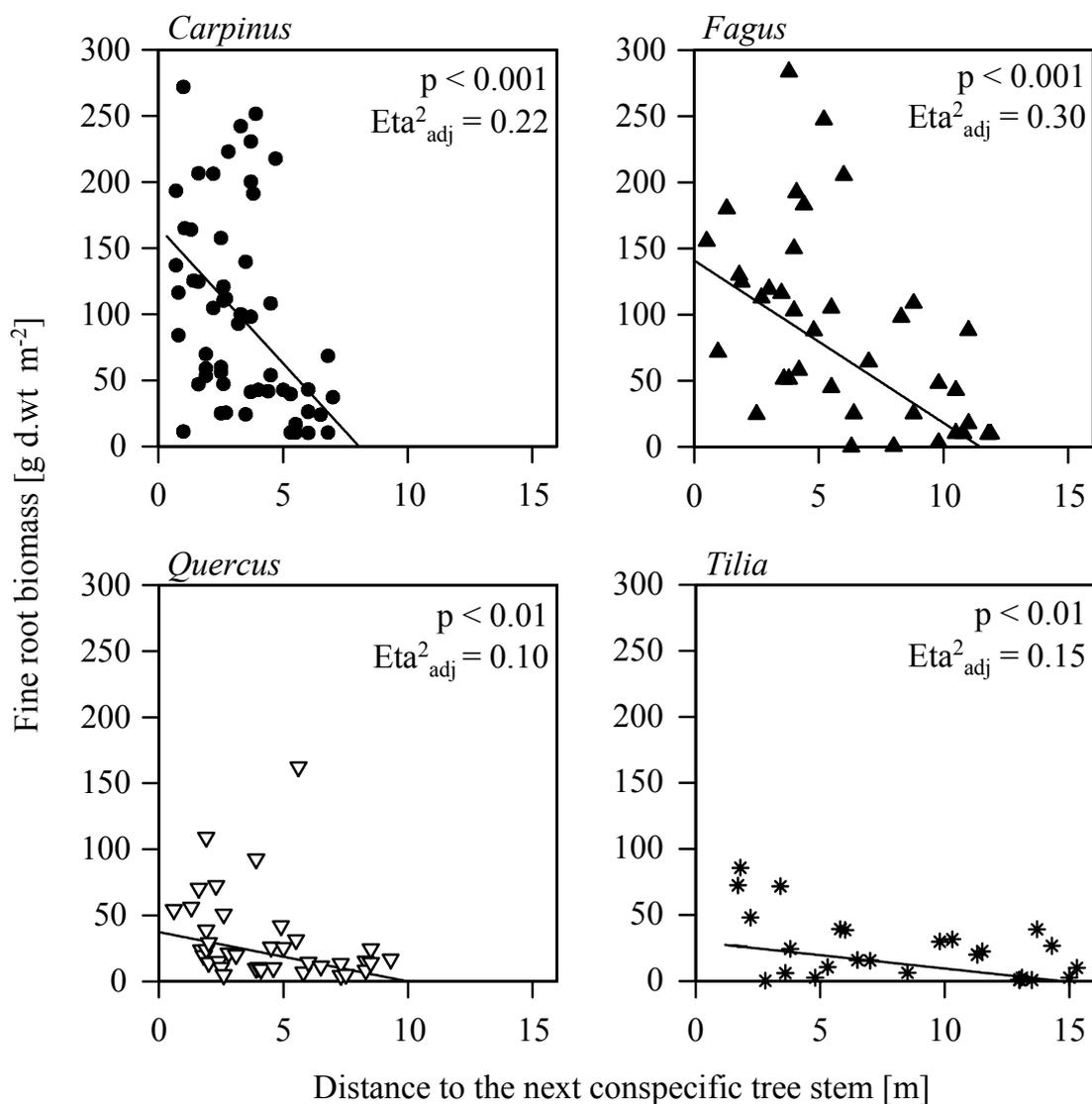


Fig. 4.3 Relation between cumulative fine root biomass of a species in the soil (organic layer and 0-20 cm of mineral soil) of the study plot and distance to the nearest conspecific stem ($n = 59$ soil samples).

Species-specific fine root density decreased more rapidly with stem distance in *Carpinus* and *Fagus*, which generally had higher fine root biomasses in the stand, than

in *Quercus* and *Tilia*, species with a comparably low density. The maximum horizontal extension of fine roots was estimated at 15 m for *Tilia*; in the other three species, we were not able to detect root system radii > 7-12 m because distances between conspecific stems were shorter than in the rare species *Tilia*.

The 0-20 cm mineral soil was densely explored by tree fine roots, and the root systems of the four species overlapped extensively. More than 50% of all investigated soil samples contained roots of two species; about 25% were explored by 3 or 4 species. Only one species was present in about 25% of the samples. The thin organic layer (5 to 30 mm in depth) contained only roots of *Fagus* and *Carpinus*, the two species with the largest total fine root biomass in the stand (Table 4.4).

Table 4.4 Relative frequency of soil samples containing fine roots of 1 to 4 tree species (or no roots at all) in three soil layers (in percent, $n = 59$).

Number of tree species present with their fine roots	Organic layer	Mineral soil (0-10 cm)	Mineral soil (10-20 cm)
No fine roots	59.3	0	0
1	33.9	23.4	17.2
2	6.8	48.3	60.3
3	0	23.3	15.6
4	0	5.0	6.9

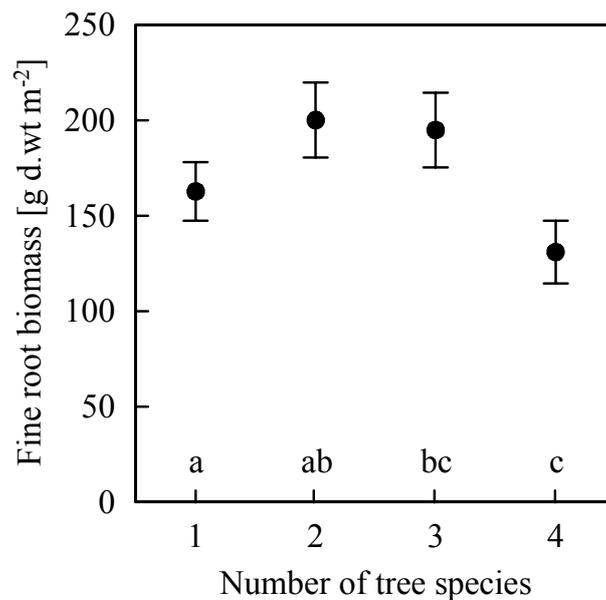


Fig. 4.4 Cumulative fine root biomass (of all four tree species) in the soil (organic layer and 0-20 cm of mineral soil) as dependent on the number of tree species being present by their roots in that location (mean±SE, $n = 59$). Significant differences between locations with 1, 2, 3 or 4 root species are indicated by different letters (U-test after Mann and Whitney, $p < 0.1$).

Soil patches, in which fine roots of two or three species were present in the profile to 20 cm depth, tended to have higher total fine root biomasses than patches with the roots of one or four tree species (Fig. 4.4). However, the difference between soil patches with one and two, or between three and four species, was significant only at $p < 0.1$.

Apparent neighbour effects on fine root biomass

Different root abundances of a target species in forest patches, in which either conspecific or allospecific tree species were dominant aboveground, may give hints on a species' belowground competitive ability in interspecific interactions. For each of the four species, we compared the fine root biomass in forest patches, where either all surrounding trees in a 5 m radius were conspecific (M_{mono} , 'mono-specific coring locations'), with patches, where part of the trees were allospecific (M_{mix} , 'multi-species coring locations'). As expected, a species' fine root biomass in the 0-20 cm profile tended to be higher in the mono-specific coring locations than in the multi-species locations for all four species (Table 4.5).

Table 4.5 Fine root biomass (in g d.wt m⁻²) in soil profiles (organic layer and 0-20 cm of mineral soil) in soil patches surrounded either by conspecific stems ('mono-specific coring locations') or by one or more allospecific stems ('multi-species coring locations') within a 5 m radius. The biomass ratio in multi-species to mono-specific locations is given as well. Significant differences between the fine root biomass in mono-specific and multi-species locations are indicated by different small letters (Scheffé test, $p < 0.05$), significant differences between the tree species by different capitals (Scheffé test, $p < 0.1$, mean \pm SE, n = sample size).

Species	Mono-specific coring locations	<i>n</i>	Multi-species coring locations	<i>n</i>	Multi-species/ mono-specific ratio
<i>Carpinus</i>	144.8 \pm 18.9 Aa	14	122.8 \pm 14.9 Aa	22	0.84 \pm 0.10
<i>Fagus</i>	149.2 \pm 12.8 ABa	4	121.0 \pm 23.6 Aa	9	0.81 \pm 0.19
<i>Quercus</i>	68.3 \pm 14.9 Ba	5	32.8 \pm 11.2 Ba	14	0.48 \pm 0.16
<i>Tilia</i>	60.6 \pm 10.0 Ba	5	9.9 \pm 7.4 Bb	5	0.16 \pm 0.13

However, only in the case of *Tilia*, the $M_{\text{mix}} - M_{\text{mono}}$ difference was large and significant at $p < 0.05$. In *Quercus*, the difference was marginally significant ($p < 0.1$). *Carpinus* and *Fagus* showed only non-significant differences in root biomass between mono-specific and multi-species coring locations. A large root biomass reduction in the presence of allospecific trees is reflected by small $M_{\text{mix}}/M_{\text{mono}}$ ratios as in *Tilia* and *Quercus* (0.16 and 0.48), a small reduction by high ratios as in *Carpinus* and *Fagus* (0.84 and 0.81).

In situ-root competition experiments

In the *in situ*-root growth chamber experiments, *Quercus*, *Tilia* and, in part, *Carpinus* showed highest relative growth rates (RGR) of their fine roots when exposed with a conspecific root (the differences in growth rates between intra- and interspecific competition treatments were only partly significant at $p < 0.05$, Table 4.6). *Fagus* fine roots, in contrast, grew significantly better in the neighbourhood of a *Quercus* or *Carpinus* root than in proximity to a conspecific root (the differences in growth rates between intra- and interspecific competition treatments were only partly significant at $p < 0.05$).

Table 4.6 Relative growth rate of fine roots (RGR, $\text{mg g}^{-1} \text{d}^{-1}$) of target species (rows) as dependent on the presence of roots of competitors (columns) in *in situ*-root growth chambers that were exposed for 180-210 d in the topsoil. Mixed-species chambers contained fine roots of two species (intraspecific competition), single-species chambers two fine roots of the same species (intra-specific competition, in frames). Significant differences in root RGR of a target species in the four treatments are indicated by different letters (U-test after Mann and Whitney, $p < 0.05$, mean \pm SE, number of replications given in parentheses).

Competitor	Target Species			
	<i>Carpinus</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Tilia</i>
<i>Carpinus</i>	1.8 \pm 0.1 a (153)	1.6 \pm 0.2 ab (64)	1.0 \pm 0.2 c (29)	1.1 \pm 0.2 bc (35)
<i>Fagus</i>	2.0 \pm 0.2 a (64)	1.1 \pm 0.2 b (82)	1.5 \pm 0.5 ab (16)	0.7 \pm 0.3 b (16)
<i>Quercus</i>	1.7 \pm 0.3 a (29)	2.1 \pm 0.5 a (16)	2.4 \pm 0.6 a (6)	1.3 \pm 0.7 a (5)
<i>Tilia</i>	1.6 \pm 0.3 a (35)	1.5 \pm 0.3 a (16)	1.8 \pm 0.5 a (5)	1.9 \pm 0.7 a (65)

The competitive ability index CA, which is defined as fine root RGR of the target species in intraspecific interaction vs. interspecific interaction with the three other tree species, showed large differences between the four species and was highest for *Fagus* (+0.30) and lowest for *Quercus* (-0.25); *Tilia* and *Carpinus* ranked in-between (+0.03 and -0.15; Fig. 4.5).

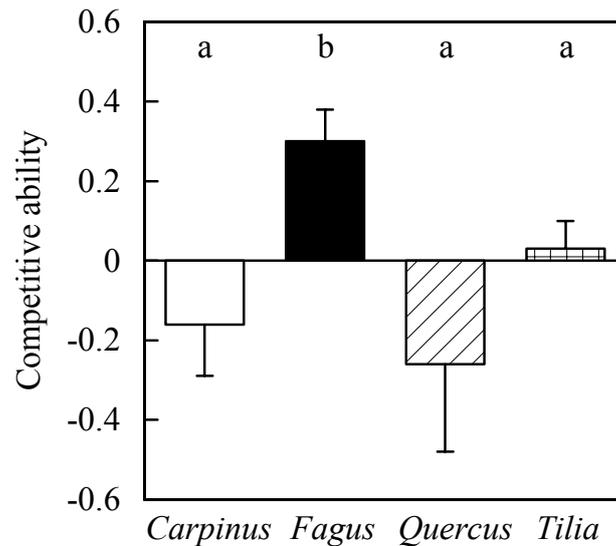


Fig. 4.5 Competitive ability CA (for definition see text) for interspecific competitive interactions of fine roots in relation to intraspecific interactions in the four tree species according to fine root growth experiments in *in situ*-root growth chambers. The CA values for all possible three interspecific interactions per species were averaged to obtain a species mean. Different letters indicate significant differences in CA values between the species (U-test after Mann and Whitney, $p < 0.05$). Mean \pm SE for 128, 96, 50, and 56 interspecific chambers of *Carpinus*, *Fagus*, *Quercus* and *Tilia*, respectively.

4.5 DISCUSSION

Relationship between aboveground and belowground structures

The fine root systems had a far larger horizontal extension than the corresponding tree crowns in the four-species mixed stand. This observation is in accordance with various other root inventories in forests, orchards and agroforestry systems (Kochenderfer 1973, Atkinson *et al.* 1976, Mou *et al.* 1995, Johnsen *et al.* 2005). *Tilia* trees spread their fine roots over an area of about 700 m² (radius \approx 15 m), which is roughly ten times the size of the crown projection area (data not shown). A much larger size of the root system compared to the crown area was already reported for deciduous trees by Stout (1956) who found a mean ratio of 4.5 : 1 for crown vs. root system area. For *Fagus*, *Quercus* and *Tilia*, we found a gradual decrease in fine root density with increasing stem distance within a radius of 10 m or more, but not a strict stem-centred distribution pattern as it was observed, for example, in spruce forests by Bédéneau and Auclair (1989) and Nielsen and Mackenthun (1991). Only in the case of *Carpinus*, fine root biomass showed a steep decrease within a 7 m-radius around the stems. We assume that stem-centred fine root distributions as in *Carpinus* are a consequence of the numerous pre-mature hornbeam trees in this stand which are forming a second canopy layer and may

not have reached the root system's maximum size in this stand. Given the high degree of root system overlap with 75% of the soil volume being explored by at least two or three different species, there are no indications of a spatial segregation ('territoriality') of whole fine root systems in this stand as was suggested by Lyford and Wilson 1964, Schenk *et al.* (1999) and others. Our results, based on soil core analyses, are not precluding root segregation at a millimetre or centimetre scale as reported by Caldwell *et al.* (1996).

The four tree species differed largely with respect to their presence in terms of fine root biomass and root surface area in the soil volume of the mixed stand. Relating fine root biomass to aboveground structural parameters, *Carpinus* had a very high fine root biomass in relation to its aboveground biomass and productivity in the stand, followed by *Fagus* with slightly lower fine root biomass/stem increment biomass (FRB/ST) ratios. In contrast, *Quercus* was highly under-represented in the belowground compartment with more than 10 times smaller FRB/ST and FRB/stem biomass ratios than *Carpinus*. Although fine root biomass does not necessarily reflect belowground productivity, the very large differences in the belowground/aboveground carbon partitioning patterns between *Quercus* and the other three species are unexpected because nutrient and water availability in the shared soil volume are imposing similar constraints on the functionality of the root system of the four species in this stand. Other biometric parameters such as the sapwood area/leaf area ratio (Huber value) or the LAI to basal area ratio are also known to differ between coexisting tree species in mixed stands, but they are not different by a factor of ten (Ammer 2003, Burkes *et al.* 2003)

These apparent tree species differences in carbon allocation patterns may have genetic causes expressing different physiological constitutions, or they can be a consequence of asymmetric interspecific competition, which may lead to a suppression of inferior competitors belowground. Evidence for the second explanation will be assessed in the following.

Evidence of asymmetry in belowground competition

We found two lines of evidence for the existence of asymmetry in belowground competition in this mixed forest, (i) indirect evidence from a comparison of fine root abundances in mono-specific and multi-species patches of the stand, and (ii) direct evidence from root growth experiments in contrasting root neighbourhoods using root growth chambers.

Our observation of an over-proportional reduction in fine root biomass of *Quercus petraea* in species-rich allospecific compared to monospecific stand patches in the Ziegelrodaer forest is supported by other studies in Central Europe. Büttner and Leuschner (1994) and Leuschner et al. (2001) found a 20% contribution of *Quercus* fine roots to the stand total of fine root biomass in a *Fagus-Quercus* forest, even though oak held 50 % of the basal area and 46 % of the total leaf area in the stand. Over-proportional reduction in fine root biomass of target tree species in mixed stands has also been reported by e.g. Hendriks and Bianchi (1995), Rust and Savill (2000), and Schmid and Kazda (2002) for stands including *Pseudotsuga menziesii*, *Fraxinus excelsior* and *Picea abies*. Most likely, these patterns are the outcome either of asymmetric root competition or of indirect competitive interactions involving unknown negative third-party effects on the roots of the inferior species.

A comparatively low belowground competitive ability of *Quercus* is strongly supported by the results of our root competition experiments. Even though we were not able to accommodate all treatments with a sufficient number of replicates, which partly reduced the statistical significance of the results, there was a tendency for *Quercus* roots to grow slower when placed with *Carpinus*, *Fagus* and *Tilia* roots than when growing with conspecific roots. This fits to the root abundance data indicating that *Quercus* root RGR tended to be reduced in the presence of competing *Carpinus* or *Fagus* roots. A high belowground competitive ability of *Fagus* in mixture with *Quercus* is supported by an earlier competition experiment with root growth chambers in a two-species *Fagus-Quercus* stand on sandy soil (Hertel and Leuschner 2006).

Although the root growth chambers employed here were designed to simulate fine root growth in a soil environment as close to nature as possible, several artefacts are inherent to this method, most notably an initial disturbance of the mycorrhizosphere (see discussion in Hertel and Leuschner 2006). The growth experiments may also be biased by temporal patterns of fine root growth that could differ between the competing species, thereby influencing the outcome of competition experiments (Eissenstat and Caldwell 1988, Burke and Chambers 2003). However, the long period of exposure (180 to 210 d) should have minimised this type of error in our experiment. Because the large majority of chambers showed vital fine root growth, resulting in largely overlapped root systems at harvest time, we believe that this method, if applied with a large number of replicates (> 30 per treatment), represents a promising approach to analyse root competition between trees with a statistically sound design in intact stands. Other approaches to study

fine root growth *in situ* such as the minirhizotron technique (Hendrick and Pregitzer 1996, Majdi 1996) are not suitable for investigating root competition because they do not allow root neighbourhood manipulation. Walk-in rhizotron facilities provide a better opportunity for manipulative studies, but the root boxes are rarely large enough to accommodate mature trees (Lyford and Wilson 1966, Atkinson 1985, Smit *et al.* 1994).

Our empirical data are support for more recent spatial modelling studies and theoretical analyses which concluded that belowground competition should rather be asymmetric than symmetric when resources are distributed heterogeneously in the soil, thereby contradicting earlier assumptions on the outcome of root competition (Schwinning 1996, Schwinning and Weiner 1998, Bauer *et al.* 2004). For example, asymmetric root competition could take place where larger plants are able to occupy nutrient-rich soil patches (Van Lear and Kapeluck 1995). Indeed, *Fagus* and *Carpinus*, the two species with the largest total fine root biomass in the investigated stand, were the only trees species present in the organic layer. Furthermore, larger plants could have access to deeper soil water reserves and deplete them before smaller plants can gain access providing them with a disproportionate part of the soil resources (Robinson *et al.* 1999). Asymmetry of competition for nutrients and water should increase when resource supply is high but uptake kinetics differ between the species (Raynaud and Leadley 2005). The yet existing evidence of asymmetric root competition is from herbaceous plants and not from mature trees, and it is contradicting (Blair 2001, Fransen *et al.* 2001, Cahill and Casper 2000, Facelli and Facelli 2002, Rajaniemi 2003, von Wettberg and Weiner 2003). Our data seem to be among the first to prove asymmetric belowground competition in forests. They are supported by sap flow measurements in small-diameter absorbing roots which indicated different water uptake rates by the roots of co-occurring tree species in a temperate mixed stand (Korn, Burk and Leuschner, unpublished data).

Fine root biomass of mixed forests - evidence for 'belowground overyielding'?

In-depth analyses of tree root distribution in natural and managed mixed forests, orchards and agroforestry systems have produced growing evidence that root systems of coexisting species are often vertically stratified (Lyford and Wilson 1964, Casper and Jackson 1997, Schenk *et al.* 1999, Bennett *et al.* 2002, Yang *et al.* 2002, Bolte and Villanueva 2006, Li *et al.* 2006). However, observational studies as those cited cannot provide unequivocal evidence of the action of belowground competition. Species differences in root distribution or rooting depth in a shared soil volume could be the conse-

quence of species differences in rooting patterns, thus reflecting a partial complementarity of the fundamental belowground niches (Connell 1980), or they could result from niche partitioning, i.e. a shift in the realized niches in response to asymmetric competition (Leuschner *et al.* 2001). This question can only be answered by comparing mixed and pure stands of the respective tree species (if they exist in nature) or, more directly, by experimental studies of synthetic tree stands differing in tree species composition (such as the 'BIOTREE' or the Sardinilla project, e.g. Scherer-Lorenzen *et al.* 2005). Alternative approaches are small-scale root neighbourhood manipulation experiments in the soil of intact stands as done in the present study.

A comparison of a tree species' root system in monospecific and mixed stands has only been conducted in a few case studies including McQueen (1968), Schmid (2002), Morgan *et al.* (1992), Leuschner *et al.* (2001) and Brandtberg *et al.* (2000). These studies produced controversial results with respect to increased belowground biomass production ('belowground overyielding') in species mixtures relative to monocultures. Schmid (2002) found a higher, Morgan *et al.* (1992) a lower fine root biomass in the two-species stands compared to the respective mono-specific stands, while Brandtberg *et al.* (2000) and Leuschner *et al.* (2001) observed a similar fine root mass in one- and two-species stands. While most of these studies compared one- and two-species stands, the present study is, to our knowledge, the only one which investigated a four-species stand. By comparing forest patches, where roots of one to four tree species coexisted in the soil, the present study provided only weak evidence of the existence of an 'overyielding' effect in the soil of this mixed forest. Soil patches containing the roots of two or three species tended to have a higher overall fine root biomass than patches with only one root species being present. However, this difference was only significant at $p < 0.1$. Moreover, the fact that patches containing the roots of four species tended to have particularly small total fine root biomasses and an often reduced root RGR in experiments with interspecific root neighbourhoods, does not support the hypothesis of 'belowground overyielding'. Further, the average profile total of fine root biomass in the Ziegelrodaer Forst (181 g m⁻² to 20 cm depth) was remarkably small compared to other mono-specific broad-leaved forests in the region (Hertel 1999, Leuschner and Hertel 2003) which makes belowground overyielding unlikely.

Clearly, data on fine root biomass are not comparable to hay yield data which were used to detect overyielding in synthetic grassland communities; by definition, overyielding exist when mixed stands show a higher aboveground productivity than any monoculture

of the constituting species (Hector *et al.* 1999, Lambers *et al.* 2004, Roscher *et al.* 2005). Nevertheless, given the large methodological problems associated with fine root production measurements in mixed stands due to species identification, fine root biomass may serve as a first approximation of belowground productivity and tree fitness in forests.

In conclusion, not much evidence yet exists which shows a higher fine root biomass in temperate mixed forests compared to pure stands and, more important, the few available records are partly contradicting.

Do the four tree species form a belowground competitive hierarchy?

We used the contrasting fine root growth rates in intra- and interspecific competition treatments as a measure of a species' belowground interspecific competitive ability. According to the classical Lotka-Volterra competition model, stable coexistence between a pair of species will occur if both species inhibit their own growth through intraspecific competition more than they inhibit that of the other species through interspecific competition. Accordingly, the root growth patterns of *Fagus* in the root chambers with a lower RGR in single-species chambers than in the two-species chambers must be judged as a clear indication of a superior belowground competitive ability of beech in this stand. Alternative measures of competitive ability such as overall plant fitness or total productivity are not applicable in root competition studies with tall trees, although they would be more consistent with the widely accepted standard of measuring competition effects on plants (Grace 1995). Our root growth-related approach yielded a species ranking with respect to competitive ability in the sequence *Fagus* > *Tilia* > *Carpinus* > *Quercus*.

Accordingly, root competition is size-asymmetric with superior and inferior species in this stand. Our experiments do not allow conclusions on the underlying mechanisms of this belowground interaction. In theory, at least three mechanisms are possible. (1) Different species may differ in their surface-specific water and/or nutrient uptake rates leading to resource pre-emption by the superior competitor (see the contrasting water uptake rates in trees discussed above, and Craine *et al.* 2005). (2) Unknown growth-reducing effects could act directly on the competitively inferior *Quercus* roots. (3) Self-self-discrimination could have occurred in the case of *Fagus* roots. Roots of the same species have been found to self-inhibit each other in certain herbaceous and shrubby species (Falik *et al.* 2003, 2005, Gruntman and Novoplansky 2004); this would

lead to a lower growth rate in treatments with intra- compared to interspecific competition.

According to root biomass data in mono-specific and mixed *Fagus/Picea* forests, beech seems to be a superior competitor belowground not only in mixture with oak but also with spruce (Schmid and Kazda 2002). Hence, it appears that *Fagus* is a successful competitor belowground in a variety of Central European mixed forests, even though it is known that the competitive ability of a species can vary in dependence of the environment and the identity of the competing species. Moreover, in European beech, high belowground and aboveground competitive abilities seem to be linked to each other (Leuschner 1998) supporting Grime's (2001) hypothesis of a positive correlation between these two components of plant competition.

4.6 CONCLUSION

Our results show that, in this four-species stand, (i) the fine root systems of different tree species do not seem to be territorial but are broadly overlapping, (ii) root competition between trees can clearly be asymmetric, and (iii) tree species may be ranked according to their belowground competitive ability. Future experimental studies in the rhizosphere of forests have to reveal whether these findings apply to other mixed forests as well, and what mechanisms (including resource competition, self-self inhibition, facilitation, allelopathy, or indirect competitive interactions through other organisms or agents) underlie the observed root growth responses in the chambers.

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Chapter 5

DOES ROOT COMPETITION ASYMMETRY INCREASE WITH WATER AVAILABILITY?

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5.1 ABSTRACT

Competition as a major structuring force in plant communities can be either symmetric or asymmetric with important consequences for the coexistence of plants in species assemblages. There is a vital debate as to whether belowground competition is symmetric or is similarly asymmetric as aboveground competition. Experimental evidence for asymmetric root competition is still scarce, in particular in communities of long-lived woody plants. Moreover, it is a matter of controversy if asymmetry in competition increases with resource availability or not.

We applied the *in situ*-root growth chamber approach to investigate the outcome of root competition between adult trees in a mixed beech-oak forest by altering the competitive neighbourhoods of fine roots and water availability experimentally. We tested the hypotheses that root competition between beech and oak is asymmetric and that asymmetry depends on soil moisture. Intact branch fine roots of beech and oak were allowed to grow for 365-390 d in root growth chambers while they were exposed to competition by either a conspecific (single-species chambers) or an allospecific root (two-species chambers). Species differences in relative root growth rate and fine root surface area increment were used to determine asymmetry in root competition. Different soil moisture regimes were considered by conducting a throughfall reduction experiment and by including data from earlier root competition experiments in beech-oak stands with contrasting soil water regimes.

Our results show that (i) the competitive interaction between beech and oak fine roots is clearly asymmetric, (ii) root morphology seems to depend on the competitor present, and (iii) the degree of asymmetry in root competition varies with soil moisture. We conclude that belowground competition in temperate broad-leaved mixed forests can be asymmetric as is competition for light with asymmetry decreasing with increasing water shortage.

5.2 INTRODUCTION

In the past, experimental and observational studies have provided much evidence that competition is a major structuring force in most terrestrial plant communities (Schoener 1983). Competition is an active process whose outcome is dependent on the relative abilities of the species to obtain resources such as light (Donald 1958), water (Moore 1929, Riegel *et al.* 1995, Seabloom *et al.* 2003) or nitrogen (Bartelheimer *et al.* 2006, Fargione and Tilman 2006). Although competition for light has been considered for long to be decisive for the performance of plants, nowadays there is growing evidence that root competition can have an influence as great as aboveground competition or even greater (Wilson 1988, Coomes and Grubb 2000, Kajimoto *et al.* 2007).

A variety of interaction processes in and between root systems have been identified which seem to be important in structuring the coexistence of root systems in the presence of intensive competition for soil resources. Chemical interference through allelopathy, so far unknown recognition systems, and indirect root interactions involving soil microorganisms and fauna may play an important role in the interaction between tree root systems (Mahall and Callaway 1991, Bonkowski *et al.* 2000, Schenk 2006). Presumably for improving resource use efficiency, roots have been found to avoid competition with roots of the same plant (Holzapfel and Alpert 2003, Gruntman and Novoplansky 2004, Falik *et al.* 2005). Under variable soil conditions, highly plastic responses of the root system's structure and of root morphology have been observed which may lead to an increased environmental tolerance and should affect uptake efficiency (Bradshaw 1965, Hodge 2006). Absorption rates of water and nutrients may change with specific root area, the number of root tips or the degree or type of mycorrhization (Gebauer and Stadler 1990, Taylor and Peterson 2005, Fargione and Tilman 2006).

There is a vital debate on the influence of resource availability on root competition. Two contrasting hypotheses have been formulated: (i) belowground competitive intensity is different in infertile and fertile, and in dry and moist soils (Grime 1979, Huston 1979, Keddy 1989, Wilson and Tilman 1993), or (ii) competition intensity is independent of water and nutrient availability (Newman 1973, Welden *et al.* 1988, Peltzer *et al.* 1998). Belowground and aboveground competition are fundamentally different with respect to the nature of the resources plants are competing for. In contrast to above-

ground competition, where larger individuals can obviously pre-empt light at the expense of smaller plants and symmetric competition is the exception, belowground competition has been found to be either size-symmetric (Weiner *et al.* 1997, Cahill and Casper 2000) or asymmetric (Fransen *et al.* 2001, Rajaniemi 2003, Rewald and Leuschner 2008). It has been suggested that the picture of symmetric competition belowground may not be valid in patchy soils (Jackson and Caldwell 1993, Schwinning and Weiner 1998), and if uptake kinetics differ between competing plant species (Aerts and Chapin 2000). In any case, experimental evidence for asymmetric belowground competition is still scarce (Blair 2001, Rajaniemi 2003, von Wettberg and Weiner 2003). Although there is a long record of research on competition for water in crop plantations and forest stands (Korstian and Coile 1938, Welbank 1961, Zegada-Lizarazu *et al.* 2006), little research has focused on the question how root competition is affected by changes in water availability in forests. This topic is gaining importance because climate change may lead to a higher drought frequency in certain regions of the temperate zone (Weltzin *et al.* 2003, IPCC 2007). In the past, belowground interactions among woody plants have mostly been studied in agroforestry systems (Nambiar and Sands 1993, Akinnifesi *et al.* 1999, Moreno *et al.* 2005) or between adult trees and tree seedlings (Coomes and Grubb 2000, Barberis and Tanner 2005, Powell and Borg 2006). Studies on root competition between adult trees in mixed forests are virtually lacking. This is partly a consequence of difficult access to the root systems of mature trees. Moreover, root competition has to be analysed by experimental approaches in order to distinguish between symmetric and asymmetric competition, which is difficult to achieve. Recently, Hertel and Leuschner (2006) introduced the *in situ*-root growth chamber technique, which allows for the monitoring of fine root growth of mature trees in the soil while altering competitive neighbourhoods and resource availability experimentally.

Here, we present the results of a comprehensive *in situ*-root growth chamber study in a temperate *Fagus-Quercus* mixed forest, which investigated the relative growth rate of fine roots in different competitive neighbourhoods while soil moisture was experimentally altered. The aims of the study were (i) to test whether belowground competition in this mature forest is symmetric or asymmetric, (ii) to compare the influence of reduced soil moisture and/or interspecific competition on root morphology, and (iii) to analyse whether the degree of root competition asymmetry changes with soil moisture availability.

5.3 METHODS

Study site

The study was carried out during 2005 and 2006 in a mixed forest consisting of 120 year-old *Fagus sylvatica* L. (European beech) and 200 year-old *Quercus petraea* (Matt.) Liebl. (Sessile oak) trees close to the village of Unterlüß (Lower Saxony, Germany, 52°14'50 N, 10°13'00 E; see Fig. A 4). Average stem density of mature trees was 220 ha⁻¹; maximum tree height was 30 m (Table 5.1). Situated in the diluvial lowlands of NW Germany (115 m a.s.l.), this site is characterized by acidic soil profiles (spodosystric cambisols) with thick organic layers (mean depth of the entire organic profile is 7.2 cm).

Table 5.1 Structural characteristics of the forest stands in Unterlüß and Ziegelroda.

	Age of dominant trees [yrs]	Stem density [ha ⁻¹]	Tree height [m]	Stem basal area [m ² ha ⁻¹]	LAI [m ² m ⁻²]
Unterlüß forest ^a					
<i>Fagus</i>	120	176	30	15.2	3.3
<i>Quercus</i>	200	44	28	12.3	1.6
Stand total	-	220	-	27.5	4.9
Ziegelrodaer forest ^b					
<i>Fagus</i>	125	36	30	6.6	2.3
<i>Quercus</i>	125	140	28	18.3	3.3
<i>Carpinus</i>	70-90	166	19	8.6	1.7
<i>Tilia</i>	70-90	10	26	1.3	0.5
Stand total	-	352	-	34.8	7.8

^aall trees > 10 cm dbh; ^ball trees > 7 cm dbh, data from Rewald and Leuschner (2008)

The climate is humid sub-oceanic (annual mean temperature: 8.1°C, average annual rainfall: 801 mm). The cumulative precipitation during the experimental period (May 2005 till the end of April 2006) was 818 mm, which is close to the long-term mean precipitation (DWD 2006). The root studies were conducted in patches on the forest floor, which were situated halfway between *Fagus* and *Quercus* stems with overlapping fine root systems. Two plots were chosen for study, which were comparable

with respect to stem density, tree height, and dbh. The stands on the two plots had a closed canopy and showed no signs of soil disturbance by wild boar. One of the two plots was equipped with a sub-canopy roof (8 m x 2.5 m, 1.6 m in height) made of a timber frame construction covered with transparent PVC plates which allowed to reduce soil moisture in a sufficiently large area (reduced soil moisture treatment). The roof was closed for a period of 11 months (June 2005 - April 2006) which resulted in a soil moisture reduction in the densely rooted topsoil by 5-15 vol% in this period compared to the uncovered soil (Table 5.2). The second plot served as a control with ambient soil moisture.

Table 5.2 Volumetric soil moisture (vol%) in the surface layer of the control and reduced soil moisture plots of the Unterlüß stand between May 2005 and April 2006. Monthly means (\pm SE) of six TDR measurements at two locations per plot are given.

Year	Month	Control	Reduced soil moisture
2005	May	26.5 \pm 0.6	27.7 \pm 0.9
	June	25.5 \pm 0.5	24.0 \pm 0.6
	July	23.6 \pm 0.4	14.5 \pm 1.1
	August	19.5 \pm 0.3	12.4 \pm 0.4
	September	15.6 \pm 0.6	10.8 \pm 0.2
	October	22.5 \pm 0.5	15.5 \pm 1.0
	November	24.6 \pm 0.4	15.5 \pm 0.4
2006	March	32.2 \pm 0.3	17.8 \pm 0.4
	April	29.6 \pm 0.7	16.8 \pm 0.5

Root chamber experiment

Hertel and Leuschner (2006) introduced the *in situ*-root growth chamber technique for monitoring fine root growth of trees in the soil of mature forests. This approach allows replicated experiments with branch fine roots of mature trees in forest soils by manipulating the fine root neighbourhood and thereby simulating different competitive situations among tree roots of two species. We applied this technique for quantifying the competitive ability of fine roots of *Fagus* and *Quercus* growing in mixture (interspecific competition) and compared the results with the outcome of intraspecific competition treatments. We used 180 root growth chambers that were manufactured from opaque PVC plates with a volume of 189 cm³ (9 x 7 x 3 cm length, height and width; see Fig. A 3). The chamber's front and back sides were perforated with holes, and the

top and bottom consisted of plastic gauze to permit sufficient water percolation and gas exchange between the chambers and the surrounding soil. Two terminal branch fine roots were carefully excavated in the uppermost soil layers and inserted through small holes into opposite side walls. The chambers were filled with homogenized and root-free mineral soil extracted in direct vicinity to the experimental plots. The chambers were then covered by a layer of soil and litter material and exposed for 365-390 days in the topsoil. At the point of insertion, the roots selected for study had a diameter of approx. 1 mm; 2-3 cm of the terminal root section was enclosed into the chamber. The species identity of the roots was detected *in situ* from periderm morphology and colour as described by Hertel (1999). With the root growth chamber experiment we tested three different types of root interactions: two interspecific (two *Fagus* roots, treatment A, or two *Quercus* roots, treatment B), and one interspecific setting (one *Fagus* root and one *Quercus* root, treatment C). These three treatments were conducted in both the control plot with ambient soil moisture and in the reduced soil moisture plot, yielding six treatments in total. The root growth chambers were inserted in the roofed plot and in the control plot at locations where fine roots of beech or oak, or both species had been traced in the forest floor. Soil water content was measured monthly (except for periods with snow or ground frost) with a mobile time domain reflectometry probe (Trime FM2, Imko, Ettlingen, Germany). On each occasion, two measuring locations per plot were chosen by random and each three TDR measurements were conducted in an area of 50 cm in diameter (Table 5.2). Temperature measurement under the roof (iButton DS1921, Maxim, Sunnyvale, USA) showed that the shelter resulted in an only small reduction of the soil temperature in the rooting horizon during summer (by 0.5-1.0 K in 7 cm depth) as compared to the uncovered plot (data not shown).

We attempted to accommodate each of the six studied interaction types with about 30 root chambers to allow for statistical analysis of the data. At the time of harvest, the branch roots were cut at the insertion holes and carefully extracted from the chamber. For investigating root morphology, all roots were analysed for specific fine root surface area (SRA, $\text{cm}^2 \text{g d.wt}^{-1}$) using a flat bed scanner and the image analysis program WinRhizo 2005b (Régent Instruments, Québec, Canada). Subsequently, root dry mass (48 h, 70°C) was determined in the laboratory. Root performance was assessed as relative growth rate (RGR, $\text{mg g}^{-1} \text{d}^{-1}$) between insertion date and day of harvest. The initial biomass of the two inserted fine roots was estimated non-destructively by photographing the roots in front of a graph paper at the beginning of the experiment and calculating

the initial tissue volume with WinRhizo. The initial dry mass of the root endings was estimated from root dry mass/volume relationships that were established for the two tree species. Since root surface area is a better estimator of resource uptake capacity than root mass, we determined root surface area increment (RSAI, $\text{m}^2 \text{m}^{-3} \text{d}^{-1}$) from the RGR and SRA data. We were not able to reach a fully balanced experimental design in the root chamber study because root species identification in the field was erroneous in some cases. Furthermore, approx. 20% of the chambers were disturbed by the ingrowth of additional fine roots from the surrounding soil, and thus had to be abandoned.

For quantifying a species' ability to compete successfully with the roots of other tree species for soil space and resources, we calculated a relative competitive ability index (CA), which uses fine root RGR as a belowground fitness parameter (Goldberg and Scheiner 1993, Wilson and Tilman 1993). We assumed that root growth is closely linked to an increase in absorbing surface area and thus to a growing nutrient and water absorption capacity of the fine root system (Grace 1995). A species' RGR in interspecific interaction (two-species chambers, treatment C, RGR_{mix}) was contrasted with its RGR in intraspecific interaction (single-species chambers, treatment A and B, RGR_{mono}) with

$$\text{CA} = (\text{RGR}_{\text{mix}} - \text{RGR}_{\text{mono}}) \times \text{RGR}_{\text{mono}}^{-1}. \quad (5.1)$$

By definition, a species has a positive CA value if, on average, it grows better with a root of the other species than with a conspecific root. Negative values indicate better growth with a conspecific than with an allospecific root. Our definition of the CA index resembles the 'relative competition intensity index' (RCI) as formulated by Grace (1995), which also compares plant performance in mixture with that in monoculture. However, in contrast to Grace (1995), we do not interpret a better growth in mixture as higher competition intensity in the community, but rather as evidence of competitive superiority in comparison to a second species, i.e. as competitive ability of the target plant or species in a two-species interaction. In fact, competition intensity may be equally high, or even higher, in monocultures compared to mixtures (Stoll and Prati 2001). The differences between the competitive abilities of *Fagus* and *Quercus* roots (ΔCA), growing in mixture, were used to assess competitive asymmetry. On the other hand, identical CA values in a given interaction would imply full symmetry in the out-

come of root interaction. In the present study, competition experiments were conducted under two contrasting soil moisture conditions (control treatment with moist soil, and reduced soil moisture treatment). In order to cover a broader range of soil moisture conditions, additional data on CA of *Fagus* and *Quercus* roots obtained in two earlier root competition experiments were included in the analysis as well. Hertel (1999) conducted an experiment in the same stand at Unterlüß in two periods with high and moderate rainfall. The second root competition experiment took place in a 100 year-old mixed *Fagus-Quercus-Carpinus-Tilia* forest at Ziegelroda, Saxony-Anhalt, Central Germany (Rewald and Leuschner 2008; Fig. A 6). Both stands contain patches with mature, 28-30 m tall *Fagus* and *Quercus* trees in close proximity to each other, which were selected for exposing the root growth chambers. However, the Ziegelrodaer forest experienced greater soil water deficits in summer than the Unterlüß forest (mean annual precipitation 801 vs. 520 mm). By combining the data from the two hydrological contrasting stands with the results of the throughfall exclusion experiment in 2005/2006, we were able to assemble the results of five *Fagus/Quercus* root competition experiments which differed with respect to soil moisture availability. For all five experiments, we calculated the cumulative soil water deficit for the period June 1 to October 31 based on volumetric soil moisture data of this study (Unterlüß forest) or from Burk (2006, Ziegelrodaer forest). The difference between monthly mean soil water content and water content at field capacity (soil matric potential = 100hPa) was added for the five months to obtain a cumulative deficit for the vegetation period. The ΔCA values of the five experiments were plotted against the cumulative soil water deficit.

Statistical analysis

All data sets were tested for Gaussian distribution with a Shapiro-Wilk test. We used a parametric Scheffé's multiple comparison procedure to test for significant differences in SRA between the different competition and soil moisture treatments. A non-parametric Mann-Whitney U test was used to detect if the tree species had a different RGR, and differed with respect to root surface area increment (RSAI) and competitive ability (CA). Calculations were conducted with SAS version 8.02 (SAS Institute, Cary, USA). Linear regressions were calculated with the program Xact 8.03 (SciLab, Hamburg, Germany).

5.4 RESULTS

Relative root growth rates in intra- and interspecific environments

In the *in situ*-root growth chamber experiment in the Unterlüß forest, *Quercus* roots showed the highest relative growth rate (RGR) when exposed with *Fagus* roots at ambient moisture conditions (Control: treatment C, Fig. 5.1). In contrast, the RGR of *Quercus* roots was significantly lower when growing together with a conspecific root (treatment B). In the single species chambers with ambient soil moisture (Control: treatment A and B), *Fagus* fine roots had a slightly higher RGR than *Quercus* roots (difference not significant). Moreover, *Fagus* roots grew not significantly better with allospecific than with a conspecific competitor, which contrasts with the behaviour of *Quercus* roots in the control treatment.

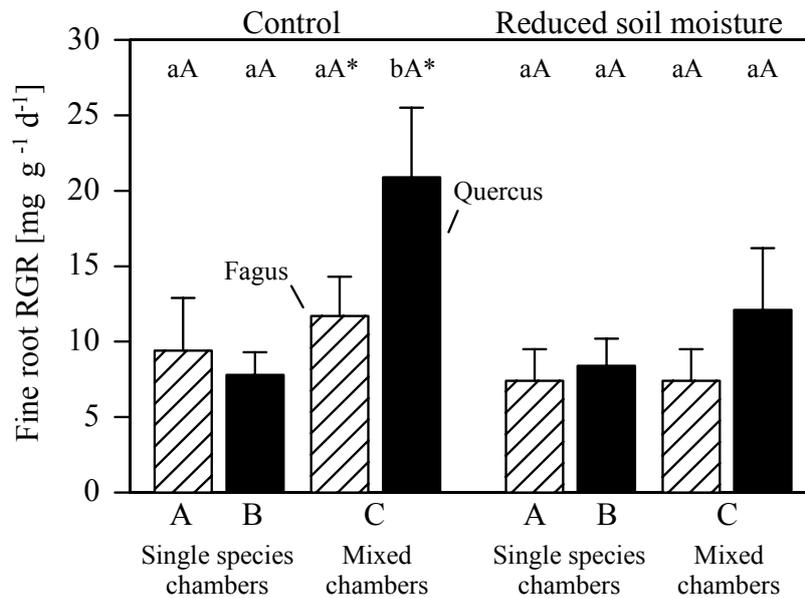


Fig. 5.1 Relative growth rate of *Fagus* and *Quercus* fine roots when being exposed for 365-390 d in *in situ*-root growth chambers in the field under different neighbourhoods (single species chambers: treatments A and B vs. two-species chambers: C) and soil moisture regimes (control vs. reduced soil moisture). Single species chambers contained two branch fine roots of the same species (*Fagus* or *Quercus*), mixed chambers each one *Fagus* and one *Quercus* root. The volumetric soil moisture was lowered by the roof in the reduced soil moisture plot by about 5-15 vol% compared to the control plot. Significant species-specific differences in root RGR within each moisture treatment are indicated by different lower case letters, significant differences between moisture treatments are indicated by capitals, and significant differences between species are marked by asterisks (Mann-Whitney U test, $p < 0.05$, mean+SE, $n = 23-46$).

In fact, RGR of *Quercus* in mixture was significantly higher than that of *Fagus*. Under experimentally reduced soil moisture, lower RGR values and no significant differences between intra- and interspecific treatments were found. The competitive ability index (CA), which is defined as fine root RGR of the target species in intraspecific interaction as compared to growth in interspecific interaction, showed significant differences between the species and soil moisture treatments. Both species shared small CA values (< 0.5) in the reduced soil moisture treatment in mixture, which indicates that the difference in the performance of the two species was small under water shortage. Moreover, our data shows that *Fagus* and *Quercus* roots behaved much more similar in the reduced soil moisture treatment than in the control treatment where the CA values revealed a larger difference (Table 5.3). Thus, ΔCA increased from the reduced soil moisture treatment to the control. By adding three more data points on ΔCA of similar root competition experiments conducted by Hertel (1999) and Rewald and Leuschner (2008) in the Unterlüß and Ziegelrodaer forests, a significant negative relationship between soil moisture deficit and ΔCA of *Fagus* and *Quercus* roots appeared (Fig. 5.2).

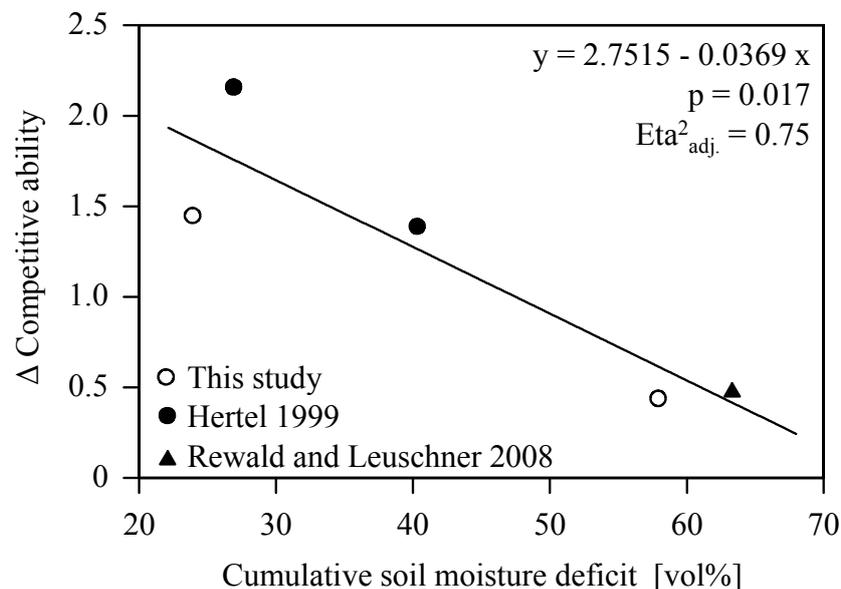


Fig. 5.2 Difference between the competitive ability (ΔCA) of *Fagus* and *Quercus* fine roots in interspecific competition as dependent on the cumulative soil moisture deficit in the period June to October (vol%). The accumulated soil moisture deficit was calculated as the sum of differences between monthly mean soil water content and water content at field capacity. In addition to the results from the present study (reduced soil moisture and control plots), we added data from other experiments conducted with *Fagus* and *Quercus* roots in *in situ*-root growth chambers (Hertel 1999, Rewald and Leuschner 2008). A competitive ability of zero stands for symmetric root competition, values above zero for superior growth either of *Fagus* or of *Quercus* roots in comparison to their competitor. The larger the ΔCA value, the more asymmetric was the outcome of the interaction.

Fine root morphology and root surface area increment

The highest mean SRA values of *Fagus* ($367 \pm 17 \text{ cm}^2 \text{ g}^{-1}$) and *Quercus* ($406 \pm 17 \text{ cm}^2 \text{ g}^{-1}$) occurred in the control treatment with ample soil moisture (Table 5.3). In this treatment, SRA of *Fagus* increased significantly under interspecific competition; in contrast, the SRA of *Quercus* roots was lower when exposed to allospecific roots. In the reduced soil moisture treatment, specific root area was either reduced or reached similar values as in the control. By calculating root surface area increment (RSAI) for the roots in the experiments, mass-related root growth rates were linked to root morphology (Table 5.3). In the control treatment with interspecific competition, both species showed highest RSAI rates. RSAI was significantly lower in the reduced soil moisture treatment. This difference was particularly large in the root chambers with interspecific competition.

Table 5.3 Specific root area (SRA), root surface area increment (RSAI) and competitive ability (CA) under different soil moisture treatments (control and reduced soil moisture) and competition treatments (single species chambers, treatments A and B: ‘Mono’, two-species chambers, treatment C: ‘Mix’). Significant differences between the two competition treatments within a soil moisture treatment are indicated by different lower case letters, significant differences between soil moisture treatments by different capitals and significant differences between competitive treatments of the same moisture treatment by asterisks (SRA: Scheffé test, RAI and CA: Mann-Whitney U test, $p < 0.05$, mean \pm SE, n = number of replicates).

Target species	Soil moisture treatment	Competition treatment	n	SRA [$\text{cm}^2 \text{ g}^{-1}$]		RSAI [$10^{-3} \text{ m}^2 \text{ m}^{-3} \text{ d}^{-1}$]		CA
<i>Fagus</i>	Control	Mono (A)	52	318 \pm 23	aA	4.4 \pm 0.8	aA	-
<i>Quercus</i>	Control	Mono (B)	36	367 \pm 17	aA	4.9 \pm 1.2	aA	-
<i>Fagus</i>	Control	Mix (C)	31	398 \pm 42	aA*	6.5 \pm 1.8	aA*	0.24 \pm 0.44 aA
<i>Quercus</i>	Control	Mix (C)	31	280 \pm 19	bA*	9.5 \pm 1.7	bA*	1.69 \pm 0.60 bA
<i>Fagus</i>	Reduced	Mono (A)	44	280 \pm 21	aA	2.4 \pm 0.5	aB	-
<i>Quercus</i>	Reduced	Mono (B)	32	289 \pm 16	aB	2.9 \pm 0.5	aA	-
<i>Fagus</i>	Reduced	Mix (C)	25	290 \pm 18	aB	1.7 \pm 0.4	aB*	0.0001 \pm 0.29 aB
<i>Quercus</i>	Reduced	Mix (C)	25	252 \pm 26	aA	3.4 \pm 0.6	aB*	0.44 \pm 0.49 bB

5.5 DISCUSSION

Evidence of asymmetric competition belowground?

Symmetry and asymmetry of competition have generally been defined by comparing the relationships between plant biomass and plant resource acquisition between the competing plants (usually measured as plant growth rate or nutrient uptake; Hara 1993, Grace 1995, Schwinning and Fox 1995). If the growth rates of competitors are in proportion to their initial plant biomass, competition is defined as being symmetric (Weiner 1990). Light, as a relatively unidirectional resource, may be pre-emptable by larger neighbours, leading to asymmetric competition, whereas water and mobile nutrients are generally thought to be less pre-emptable, resulting in more size-symmetric competition (Newbury and Newman 1978, Ford and Diggle 1981, Weiner 1986). However, it has recently been hypothesised that root competition may also be asymmetric (Schwinning 1996), while experimental results supporting this assumption are scarce and mostly refer to herbaceous plants (Blair 2001, Fransen *et al.* 2001, Facelli and Facelli 2002, Rajaniemi 2003, Rewald and Leuschner 2008). In contrast, the number of experiments suggesting symmetric competition belowground is much larger (Schwinning and Weiner 1998, Cahill and Casper 2000, von Wettberg and Weiner 2003). Our study provides evidence that the interaction between *Fagus* and *Quercus* roots in mature stands is asymmetric since the roots of the two species grew significantly different in two-species chambers, thus exhibiting different RGR and SRAI rates (Fig. 5.1, Table 5.3). This contrasts with the performance in single-species chambers, where *Fagus* and *Quercus* root growth was not different. Numerous earlier studies (Ross and Harper 1972, Elberse and de Kruyf 1979, Fowler 1984, Van Baalen *et al.* 1984) have demonstrated that an initial size advantage of one competitor can rapidly cause competitive inequality in any interaction. To avoid this shortcoming, we carefully selected equal-sized branch roots for the root growth chamber experiments to test for species-specific disproportionality effects.

We thus can exclude that the contrasting root growth rates in chambers with inter- and intraspecific competition are a consequence of initial differences in root size of the species. Rather, other non-size-symmetric factors must be responsible. Unfortunately, our experiments do not allow conclusions on the underlying mechanisms of this asymmetric belowground interaction. A number of processes may possibly be involved.

It has been suggested that asymmetric belowground competition may occur especially in patchy soil environments (Jackson and Caldwell 1993, Schwinning and Weiner 1998, Casper *et al.* 2000), where larger plants with a more extensive root system are able to occupy nutrient-rich soil patches over-proportionally (Van Lear and Kapeluck 1995) and pre-empt soil water and nutrient reserves before smaller plants can gain access (Robinson *et al.* 1999, Craine *et al.* 2005). Competitive ability seems to be closely related to the ability to rapidly fill a soil volume with roots (Rajaniemi 2007). Self-self-inhibition could also have occurred in the intraspecific treatments. Roots of the same species have been found to be self-inhibiting in certain herbaceous and shrubby species (Falik *et al.* 2003, 2005, Gruntman and Novoplansky 2004); this would lead to a lower growth rate in treatments with intra- compared to interspecific competition. Self-self-inhibition is thought to be favourable, because competition between roots of the same individual will lower resource use efficiency and thus may reduce plant fitness (Schenk 2006). Another mechanism that could have caused the observed non-proportionality in root growth are different water or nutrient uptake rates of the competing species (Eissenstat and Caldwell 1988b, Raynaud and Leadley 2005). It has been shown that nutrient uptake kinetics can differ between plant species under certain conditions of nutrient or soil water availability (Jackson and Caldwell 1991, 1996, Aerts and Chapin 2000, Raynaud and Leadley 2004, Wang and Cheng 2004).

Although the root growth chambers of this study were designed to simulate fine root growth in a soil environment as natural as possible, some artefacts are inherent to this method, e.g. an initial disturbance of the mycorrhizosphere and an artificially dense and homogeneous soil (Hertel and Leuschner 2006). The growth experiments may also be biased by species-specific temporal patterns of fine root growth (Eissenstat and Caldwell 1988a, Burke and Chambers 2003). However, the observed high degree of mycorrhizal infection of root tips and the long period of exposure (≥ 1 yr) indicate that these errors should have been less important. We believe that the *in situ*-ingrowth chamber technique is a promising experimental tool for analysing root interactions between mature trees with a statistically sound design. Other approaches for studying fine root growth *in situ* such as mini-rhizotrons are less suitable for investigating root competition of mature trees in forests (see Rewald and Leuschner 2008 for a detailed discussion).

Our experimental data on the outcome of root competition are support for more recent spatial modelling studies and theoretical analyses, which concluded that belowground

competition in mature forests should be rather asymmetric than symmetric (Aikio 2004, Raynaud and Leadley 2005). Taken together, these results contradict assumptions on mechanisms and the outcome of root competition, which have been obtained with herbs and grassland species (Weiner 1986, Schwinning 1996, Cahill and Casper 2000, Herben *et al.* 2007). In any case, symmetric and asymmetric competition must be viewed as the extremes of a continuum. In fact, roots compete simultaneously for several resources and their interaction may be a combination of all relevant resource-capturing processes (Schwinning and Weiner 1998).

Is root biomass increment an adequate parameter for quantifying belowground competition?

A large number of biotic and abiotic factors, including soil moisture and nutrient availability as well as mycorrhizal fungi, bacteria and other soil organisms, are known to influence the formation of the morphological characteristics of fine roots (Fitter and Stickland 1991, Kozłowski *et al.* 1991). As resource supply changes, changes in fine root biomass allocation and phenotype may lead to increased environmental tolerance and resource uptake efficiency (Robinson *et al.* 1994, Chiatante *et al.* 2005, De Lillis *et al.* 2005, Poyatos *et al.* 2007), which is likely to influence competitive ability (Grime *et al.* 1991). In particular, absorption rates of water and nutrients may change with specific root area, the number of root tips or the degree of mycorrhization (Gebauer and Stadler 1990, Taylor and Peterson 2005, Fargione and Tilman 2006). We found significantly different specific root areas (SRA) in different competition and soil moisture treatments (Table 5.3). *Quercus* roots have a significantly smaller SRA when subjected to reduced soil moisture, indicating that very fine branch roots were only present at ambient soil moisture. Interestingly, the finest root diameters were also missing at ambient moisture when *Quercus* roots competed with *Fagus* roots. Thus, SRA was not only depending on soil moisture characteristics but apparently also on competitive neighbourhood. This would shed a new light on how root surface area is controlled by the biotic and abiotic environment of the root (Löhmus *et al.* 1989, Ostonen *et al.* 1999). Plant morphology and architecture strongly determine how plants acquire and also deprive their neighbours of resources (Nye and Tinker 1977). Consequently, plant form has been found to influence the degree of competition symmetry (Geber 1989, Thomas and Weiner 1989, Hara 1993). We suggest that root surface area increment (RSAI) should be a more appropriate fitness parameter of competing roots than the mass-related

root growth rate (RGR), because RSAI is more directly linked to the absorbing surface than is root mass. However, the choice of the fitness parameter influences the result of asymmetry assessments. The significantly smaller SRA of *Quercus* roots in interspecific competition under ambient soil moisture counteracted the larger biomass increment of this species and led to a more symmetric root surface area increment among the two species. This finding is in accordance with Schwinning and Weiner (1998) who suggested a similarly plastic response to neighbour-induced resource depletion as to environmental gradients. These authors have hypothesised that plasticity in morphology and physiology can act to reduce asymmetry in competition by reducing the differences in resource uptake. In contrast to aboveground properties (Ballaré *et al.* 1994, Umeki 1997), we know much less about the mechanisms that may lead to neighbour-induced plastic responses in root morphology and root system structure. They must primarily be adaptations to avoid, or at least reduce, competitive suppression (Schwinning and Weiner 1998).

Previous studies have focused primarily on observed size-related effects in the outcome of competition among plants. Our results show that we need to replace generalising parameters such as biomass increase or relative growth rate by variables that are more directly related to water and nutrient uptake by considering root morphology and physiology as well, which ultimately determine success in root competition.

Does the degree of belowground competitive asymmetry vary with soil resource availability?

There is an ongoing controversy as to whether competition intensity varies along environmental gradients (Huston 1979, Keddy 1989, Wilson and Tilman 1993, Towland-Strutt and Keddy 1996, Goldberg *et al.* 1999), or is independent from abiotic factors such as water and nutrient availability (Newman 1973, Tilman 1988, Welden *et al.* 1988, Peltzer *et al.* 1998). In this study, we conducted a below-canopy throughfall reduction experiment to investigate whether the degree of root competition asymmetry changes with soil water availability. Our results, complemented by related data of the studies by Hertel (1999) and Rewald and Leuschner (2008), provided evidence that the asymmetry of root growth or surface area increment between competing *Fagus* and *Quercus* roots decreased with increasing soil moisture deficit. This analysis, based on five different experiments, revealed a significant correlation between competitive asymmetry (ΔCA), expressed as difference between species-specific competitive abili-

ties, and cumulative soil moisture deficit (Fig. 5.2). Thus, marked asymmetry in the outcome of root competition only developed when soil moisture in summer was sufficiently high. Resource limitation, i.e. drought, seems to hit both species in a similar manner with the consequence that species-specific differences in competitive ability in mixture are disappearing in the more stressful environment. Therefore, the overall importance of direct biotic interactions belowground seems to be reduced under limited soil water availability.

We are aware that competition experiments that differ in duration may create severe problems to any data analysis (Osenberg *et al.* 1999). Fortunately, all included studies of our meta-analysis of root competition experiments were running long-term (≥ 6 months), covering at least one vegetation period. Our findings are consistent with previous studies which indicated that ample supply of belowground resources, especially sufficiently high precipitation, lead to a more pronounced asymmetry in aboveground growth among competing plants (Skovsgaard 1997, Wichmann 2001). Raynaud and Leadley (2005) suggested that the asymmetry of competition should increase with increasing nutrient and water supply because, under high soil moisture, ion diffusivity increases and uptake rate depends mostly on root physiology (Williams and Yanai 1996, Raynaud and Leadley 2004). The model of Raynaud and Leadley (2005) suggests that the diffusivity of the soil is a major determinant of the size-symmetry or asymmetry of root competition and that this interaction can vary from near size-symmetry under conditions of low diffusivity to size asymmetry with increasing diffusive supply.

To test this hypothesis, we used data on soil pH and cation exchange capacity (CEC) as rough measures of soil nutrient availability to investigate a possible soil fertility dependence of competition asymmetry in the five experiments. We did not find a dependence of the degree of asymmetry on pH or CEC (data not shown). This indicates that, in these experiments, water availability, rather than nutrient availability per se, was controlling competition asymmetry, probably because a low diffusivity as caused by low soil moisture overrules differences in nutrient concentrations or mineralisation rates in the soil. Competition for water should be size symmetric only if each unit of root surface has the same specific uptake rate (Schwinning and Weiner 1998). However, *in situ* measurements with miniaturized sap flow gauges have provided increasing evidence that different tree species, root size classes, and different roots of the same tree can differ by an order of magnitude in water uptake rate or even more despite access to the same soil volume (Korn 2004, Leuschner *et al.* 2004). Thus, it becomes clear that sim-

ple models linking root biomass with competitive ability are most likely misleading in many forest ecosystems.

5.6 CONCLUSION

Our results show that (i) tree species competition belowground is clearly asymmetric in the studied stand, (ii) root morphology seems to depend on the competitor present, thereby modifying the degree of competitive asymmetry, and (iii) the degree of competitive asymmetry varies with soil moisture status. Asymmetry only develops in the absence of water shortage. Future experimental studies in the rhizosphere of forests have to reveal whether these findings apply to other resource gradients and species as well, and what mechanisms (including resource competition, self-self-inhibition, facilitation, allelopathy, or indirect competitive interactions through other organisms or agents) underlie the observed root growth responses in the chambers.

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Chapter 6

SYNTHESIS

6.1 BELOWGROUND ADAPTATIONS OF TREES TO WATER SHORTAGE AND THE ROLE OF COMPETITIVE INTERACTIONS

The flow of water into, through and ultimately out of plants is driven by transpiration and, thus, powered by the atmospheric demand for water vapour (Hellkvist *et al.* 1974, Tyree 1997). Water flow in the soil-plant-atmosphere continuum (SPAC) is not only characterised by the rate of transpiration, but hydraulic conductances of soil and plant tissues play important roles as well (Gardner 1965, Tyree and Zimmermann 2003). Approximately 50% of the whole-plant hydraulic resistance are located in the root system, which shows the outstanding importance of this organ of water uptake within the flow path (Boyer 1971, Zimmermann 1983).

Water transfer from the soil to the atmosphere is more complex in mixed forests than in monospecific stands because (i) competitive interactions can influence the abundance, distribution and morphology of root systems, and (ii) other species may increase or reduce soil moisture in a different manner than conspecific tree individuals do (McKay and Malcolm 1988, Caldwell *et al.* 1998, Schmid and Kazda 2002, Filella and Penuelas 2003).

This chapter synthesizes results on effects of (i) water shortage and (ii) soil salinity on the morphology and function of tree root systems with respect to water uptake. Since both water shortage and salinity reduce soil water potentials, plant responses to drought and salt stress bear striking similarities.

Root system biomass under water shortage and the role of inter-specific competition

Changes in root biomass are an important means of adjustment to altered soil moisture levels (Osunubi and Davies 1981). It has been well documented that tree species adapted to more xeric conditions have higher root:shoot ratios (e.g. Joslin *et al.* 2000), thus, increasing the ratio between water absorbing and transpiring surface. However, results for both seedlings and mature trees grown under experimentally altered moisture regimes, or studied along moisture gradients, are contradictory (see Tables A 1, A 2).

Apparently, direction and magnitude of root biomass response to drought largely depend not only on tree species or even variety, but also on study duration and/or study design (e.g. light regime, see Climent *et al.* 2006).

However, increases of root biomass increases in response to drought have mostly been found in conifer species, which are known to differ in their root growth strategies from deciduous broad-leaved trees (Bauhus and Messier 1999).

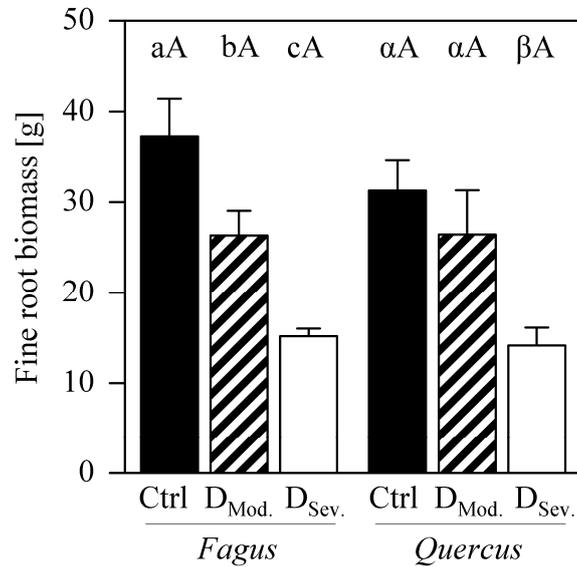


Fig. 6.1 Fine root biomass of *Fagus sylvatica* and *Quercus petraea* saplings after three years of different soil moisture treatment, i.e. well-watered Control (Ctrl), moderate drought stress (D_{Mod.}), and severe drought stress (D_{Sev.}; see Chapter 2). Significant differences within species are indicated by different Latin or Greek lower case letters, and significant differences within moisture treatments are indicated by capitals (Scheffé, $p < 0.05$, mean+SE, $n = 8-10$).

Studies on mature trees and saplings of *Fagus sylvatica*, *Quercus petraea* and *Olea europaea* indicate mostly unaltered or decreased fine root biomasses in response to drought or salinity (Tables A 1, A 2), which is in consistency with results obtained in this study (Figs. 6.1, 6.2). Several factors may be responsible for the observed decrease in root system size under water shortage: e.g. (i) reduced root elongation at low water potentials, and/or (ii) increased root mortality, and reduced root growth due to reduced carbohydrate supply, or, in the case of adult trees, a (iii) shift of root biomass into deeper, wetter soil horizons. Especially root growth of *Fagus sylvatica* may be hampered by carbon limitation whereas *Quercus petraea* is known to maintain high rates of photosynthesis even with low leaf water potentials (Raftoyannis and Radoglou 2002).

Root biomass is known to be influenced by belowground competition. This study and Leuschner *et al.* 2001 observed remarkably small fine root biomasses (Fig. 4.2) and an over-proportional reduction of root growth rates (Table 4.6) of *Quercus petraea* in mixed forests stands if compared to mono-specific oak woods. This finding has been attributed to competitive replacement of oak roots by beech roots and has been reported for other mixed forest stands as well (e.g. Schmid and Kazda 2002, Bolte

and Villanueva 2006). The competitive superiority of beech (Fig. 4.5), based on a putative correlation between fine root biomass and resource uptake, is especially astonishing in the Ziegelrodaer forest, where annual rainfall (mean annual precipitation: approx. 520 mm) is close to the assumed precipitation-induced range margin of *Fagus sylvatica* (Ellenberg 1996). However, a comparison of the belowground competitive abilities of beech and oak along a soil moisture gradient (Fig. 5.2) revealed, that the difference between intra- and interspecific competitive abilities of the two tree species decreased with increasing soil moisture deficits. Consequently, species-specific traits of water uptake strategies are assumed to be more important than the competitive abilities of the species under severe droughts.

Root topology and water redistribution in mixed and mono-specific forest stands

Root architecture and distribution in the soil are of great importance as they determine plant access to water (Ryel *et al.* 2004). Although fine root density mostly shows an exponential decrease with soil depth (Figs. 4.2, 6.2; Gale and Gringal 1987, Leuschner *et al.* 2004b), deeper root systems would enable access to subsurface resources of water (Köstler 1968, Kozłowski *et al.* 1991, Jackson *et al.* 1999). Especially *Quercus* spp. have been found to successfully avoid drought stress by deep rooting (Čermák *et al.* 1980, Badot *et al.* 1994, Bréda *et al.* 1995), whereas *Fagus sylvatica* roots are less frequent in greater depths (Leuschner *et al.* 2001).

Even though, this study (Fig. 6.2) and that of Leuschner *et al.* (2001) showed fine root biomass of oak and beech to be similar in conspecific patches of the Unterlüß forest, both species seem to respond differently to drought. While the fine root biomass of oak was significantly reduced after three months of experimentally-induced summer drought, beech was found to grow new fine roots in the upper soil horizons even under severe drought (Fig. 6.2; see Mainiero and Kazda 2006). Since there is no evidence for rapid root growth responses to drought stress in *Fagus sylvatica* (Mainiero and Kazda 2006) or *Quercus* spp. (Konôpka *et al.* 2005), this conservative strategy of fine root investment by *Fagus* is suggested to be only favourable under more mesic conditions (see Green and Clothier 1995). It is possible that a less flexible carbon-investment strategy and the subsequently increased fine root turnover (Mainiero and Kazda 2006) are partly involved in the higher drought sensitivity of beech.

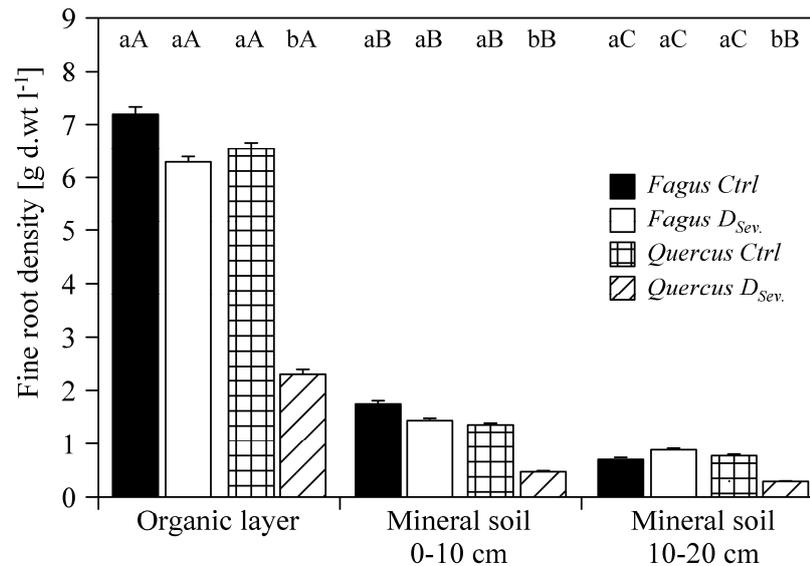


Fig. 6.2 Fine root densities of mature *Fagus sylvatica* and *Quercus petraea* trees after three month of different soil moisture treatment, i.e. ambient-watered Control (Ctrl), and severely drought-stressed (D_{Sev.}, see Chapter 2). Significant differences within the three soil horizons are indicated by different lower case letters, and significant differences between soil horizons are indicated by capitals (Scheffé, $p < 0.05$, mean+SE, $n = 20$; Rewald, Prigge and Leuschner, unpublished).

Soil moisture is often highly variable within soil horizons (Staelens *et al.* 2006), and the capability of root systems to explore the soil for heterogeneously distributed moisture might be crucial for successful water uptake (Fig. 4.3; Cole and Mahall 2006). Although it is known that water uptake of individual *Fagus* and *Quercus* roots can differ within soil horizons (Coners and Leuschner 2005), possibly resulting from moisture differences, studies about species-specific differences in the detection of water, e.g. via hydrotropism, are lacking. Such foraging traits might be very important in densely rooted mixed forests (Table 4.4, Fig. 5.1), where competitors could potentially pre-empt moist soil patches.

Rooting in soil patches with different moisture content can induce a transfer of water from wet soil to dry soil via ‘hydraulic lift’ (Caldwell *et al.* 1998) or ‘hydraulic redistribution’ (Burgess *et al.* 1998, Schulze *et al.* 1998). Hydraulic redistribution can re-wet dry topsoil layers, thus, possibly facilitating nutrient uptake, and buffering plants against water deficits. Moisture distributed more uniformly in the soil column may retard water uptake by reducing soil conductivity, thus, prolonging water availability during periods of drought (Richards and Caldwell 1987, Ryel 2004, Pereira *et al.* 2006). Furthermore, the effectiveness of water absorption by deep roots and the survival of shallow roots in dry soil are suggested to be increased by hydraulic lift (Caldwell and Richards 1989, Seyfried *et al.* 2005). A weakness of plant-mediated water relocation is

that water from moist soil horizons or even plant-internal water (Matyssek *et al.* 1991) may leak into dry soil along the flow path. ‘Hydraulic fuse’-mechanisms that are assumed to prevent or reduce such leakage are: (i) shedding of fine root branches (Head 1973, Pereira *et al.* 2004), (ii) suberization of the rhizodermis and/or aquaporin regulation, or (iii) increase of the resistance of the hydraulic pathway by cavitation (discussed below).

Influence of drought on root morphology

Root morphology is another parameter with the potential to adapt to altered soil moisture. Nevertheless, the overall root architecture is genetically determined (Zobel 1991, Gregory 2006). The detection of adaptational mechanisms is hampered by the large variation of root morphology and architecture within species or individuals, possibly caused by soil heterogeneity (Fitter 1994, Meier and Leuschner 2008a). In contrast to previous studies (e.g. Hertel 1999), this study neither revealed significant differences in the specific root area (SRA) between well-watered *Fagus* and *Quercus* trees in the Unterlüß forest (Table 5.3), nor between roots of both species from low rainfall areas such as the Ziegelrodaer forest (Table 4.3).

It is a general presumption that finest roots are most effective with regard to water uptake (e.g. Rieger and Litvin 1999, Lindenmair *et al.* 2004). Thus, SRA could be expected to increase during drought. In contrast to this assumption, SRA of *Fagus* and *Quercus* in the Unterlüß forest decreased under reduced water availability (Table 5.3), which is in accordance with previous findings for *Fagus* and other species (e.g. Aspelmeier and Leuschner 2006, Meier and Leuschner 2008b). The underlying mechanisms must remain speculative, but may include increased mortality/shedding of root tips and finest roots, the (re-)growth of less ramified roots by increased turnover rates (see Table A 2), and, for beech, increased root tissue densities (Table 2.3).

Root elongation rate, which is positively correlated with root diameter, is an even more important attribute for maximizing uptake rates of low-diffusive nutrients such as phosphorous than root surface area (Silberbush and Barber 1983, Raven and Edwards 2001). In order to tap more soil regions with plant-available water, higher elongation rates are suggested to be most favourable in soil with a heterogeneous distribution of moisture or in the case of inter-specific competition for water. *Quercus petraea* roots are suggested to be superior to *Fagus sylvatica* in accessing distinct water patches in heterogeneous soils, as indicated by their faster growth (RGR) and less ramified root branches

(SRA; Table 4.6, Fig. 5.1). Furthermore, roots of smaller diameter (and larger SRA) have higher construction and maintenance costs per unit biomass than larger roots (Eissenstat and Yanai 1997). Most likely, there must be a trade-off between the benefits of a large absorbing surface area per unit biomass and an increased contact with the soil, and the benefits of increased ‘long-distance’ foraging and reduced maintenance costs under water shortage.

Rates of water uptake per root surface area vary significantly between individual roots, species and sites with different climate (Korn 2004, Burk 2006). *Fagus* has been found to possess higher root-surface-area related sap-flow rates than *Quercus* (Coners and Leuschner 2002). Furthermore, even under well-watered conditions, beech roots showed lower root surface-specific flows on a site with a more oceanic climate than on a more continental site (Burk 2006), indicating a yet unknown, but highly plastic uptake pattern of beech roots growing on dryer sites. Unfortunately, no information is available about such plasticity in oak uptake kinetics. However, during periods of severe drought, this trait of *Fagus* might turn into a disadvantage, if water in the rhizosphere is depleted too fast, causing an interruption of the SPAC at the soil-root interface.

These reports on different surface-related water uptake rates substantiate the evidence of asymmetric competition between beech and oak (Table 4.6, Fig. 5.1). Whether water or nutrient uptake, allelopathic chemicals, soil fauna or microorganism are the underlying mechanism of these competitive interactions remains unclear, but different uptake kinetics are feasible explanations. Earlier studies and models, which indicate either symmetric or asymmetric competition belowground, are listed in Tables A 3 - A 5.

Adaptability of root physiology to water shortage

The capacity of roots for water uptake is determined not only by root surface area, but by other properties, in particular the resistance of tissues to water transport, as well. Drought and salinity are known to induce short- and long-term alterations of the radial pathway, usually resulting in an increase of radial resistance (Huang and Nobel 1993, Steudle 2000).

Water channel proteins in the cell membranes (aquaporins) mediate the short-term adjustment of the symplastic pathway to salt or drought stress (Yamada 1997, Katsuhara and Shibasaka 2007). Although data for woody plants is scarce (for olive see Lovisolo *et al.* 2007), studies on herbaceous plants suggest that aquaporins are present in virtually

all root types (Kirch *et al.* 2000, Otto and Kaldenhoff 2000, Kaldenhoff and Fischer 2006), and especially in cells that control water uptake and radial water flow (Schäffner 1998). The regulation of root aquaporins enables a very tight coupling between root water uptake and whole plant physiology, e.g. by facilitating water flow under moist conditions, or reducing water loss to the soil via unintended hydraulic redistribution by ‘more tight’ membranes. A higher expression of aquaporins, and, thus, higher root surface area-specific conductance, is suggested to compensate for a reduced root system size in salt- and drought-stressed olive trees, explaining in part the above-average drought- and salt-tolerance of this species (Lovisolo *et al.* 2007). Although no studies on aquaporins in *Fagus* and *Quercus* roots have been published yet, increased aquaporin densities are likely to be involved in the high surface area-related sap flow rates of *Fagus* roots.

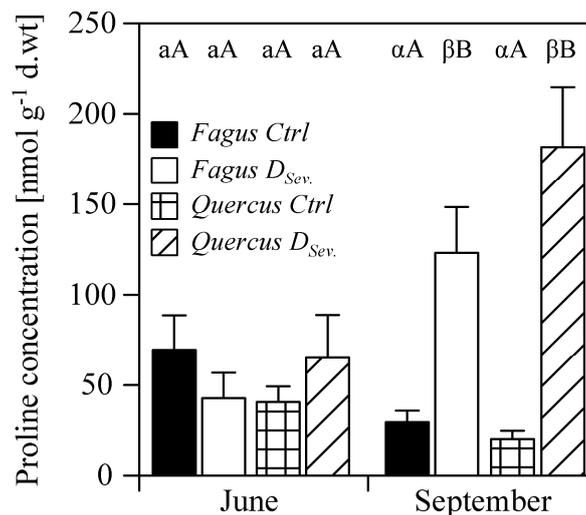


Fig. 6.3 Proline concentration in fine roots (diameter < 2 mm) of mature *Fagus sylvatica* and *Quercus petraea* trees before (June 2004) and after (September 2004) a three month-period of different soil moisture availability (see Chapter 2). Soil moisture treatments are ambient-watered Control (Ctrl), and severe drought stress (D_{Sev.}). Significant differences between species at one date are indicated by different Latin or Greek lower case letters, and significant differences between June and September are indicated by capitals (Scheffé, $p < 0.05$, mean+SE, $n = 2-5$; Rewald, Prigge and Leuschner, unpublished).

Another mechanism, supposedly allowing plants to tolerate periods of water shortage is osmotic adjustment (Chaves *et al.* 2003). Osmotic adjustment enables sustained root growth under moderate levels of drought stress by partial turgor recovery and maintenance of the ability to loosen cell walls (Hsiao and Xu 2000). Proline is an important component in osmoregulation, its concentrations have been found to increase strongly in response to drought or salt stress and have been suggested to explain differences in drought- and salt-tolerances (Hare *et al.* 1998, de Lacerda *et al.* 2003, Ennajeh 2006, Garcia-Sánchez *et al.* 2007). This study revealed a significant increase in proline con-

centrations in fine roots of mature *Fagus* and *Quercus* trees after three months of severe drought stress (Fig. 6.3). Although not statistically significant, drought-stressed oak roots exhibited a tendency to higher proline concentration than fine roots of beech, thus indicating higher levels of osmotic adjustment.

In general, water shortage is thought to facilitate suberization of the root rhizodermis, subsequently limiting the apoplastic by-pass and reducing the radial conductivity of roots (Zimmermann and Steudle 1998). However, previous studies provide convincing evidence of water uptake even by strongly suberized regions of woody roots (Chung and Kramer 1975, MacFall *et al.* 1990, 1991). Increased root suberization under drought or salt stress might therefore correlate better with general stress-tolerance (Cruz *et al.* 1992, Schreiber *et al.* 2005), instead of explaining different water uptake rates (Leuschner *et al.* 2003, Korn 2004).

Mycorrhizal fungi and drought stress

Considerable uncertainty exists about the influence of fungal hyphae on host hydraulics and water uptake (Hampp and Schaeffer 1999, Nardini *et al.* 2000) and responses of the fungal community to drought (Shi *et al.* 2002). Due to the large contact area between hyphae and soil particles, mycorrhiza formation has been suggested to improve water availability of the host plants (Duddridge *et al.* 1980, McFall 1991, Augé 2001), and to support acclimation to drought stress (Davies *et al.* 1996, George and Marschner 1996). While Steudle and Heydt (1997) found only a marginal influence of mycorrhization on beech saplings water uptake rate, oaks showed a strong decline in transpired water, derived by hydraulic lift, after severing the mycorrhizal hyphae net (Egerton-Warburton *et al.* 2003). Furthermore, hyphae were found to transfer water between roots of ‘donor’ *Quercus* individuals, performing hydraulic lift, and ‘receiver’ plants, possibly resulting in multiple benefits during drought as enhanced water and nutrient uptake and/or redistribution (Leake *et al.* 2004), or a rapid recovery from desiccation or refilling of embolized vessels. However, it has to remain open if similar mechanisms exist in beech and if the quantities of redistributed water account for significant reduction of drought stress in oak.

Changes in root axial conductivity under drought and salt stress

Different species or even genotypes of woody plants may differ substantially with respect to root axial conductivity (e.g. Huber 1956, Larcher 2001). However, the fine and coarse roots of ring-porous oak and diffuse-porous beech showed no systematic differences with regard to their specific conductivity (k_s) or sap flow density (Korn 2004), whereas root k_s of the three olive varieties partially differed. In contrast to these findings, *Quercus* shoots showed higher specific conductivities than *Fagus* shoots (see Fig. 2.2, and Steppe and Lemeur 2007), but only minor differences were found between shoot k_s of the three olive varieties. These results highlight the variability of axial hydraulic conductivity between organs.

A majority of previous studies has reported reduced root and shoot axial conductivities in response to drought and salinity (see Tables A 6, A 7), thereby improving plant water status by reducing water loss to the atmosphere and the soil (North and Nobel 1992, Meinzer *et al.* 1996, Trillo and Fernández 2005). While the reduced shoot conductivities under water shortage found in this study (Fig. 2.2) are in accordance with a bulk of earlier literature, no general reduction of fine and coarse root axial hydraulic conductivity in response to either drought or salt stress could be detected (Figs. 2.1, 3.3, Table 3.4).

An increase of root axial conductivity has been suggested to facilitate water uptake by reducing the flow resistance (Nardini and Pitt 1999). Although it has previously been considered a minor limiting factor of whole-root conductivity as compared to radial conductivity (Sands *et al.* 1982, Steudle 1994), Hacke *et al.* (2000) demonstrated that whole-plant water use and axial conductivity of woody plants during drought stress were in accordance. Especially the large root systems of adult trees with a great path length (West *et al.* 1999, Magnani *et al.* 2000, Addington *et al.* 2006) and reduced potential gradients due to large root:leaf area ratios (Grier *et al.* 1981, Vanninen *et al.* 1996) illustrate the importance of sufficient root axial conductivities. This fact is mirrored by the higher axial conductivities of roots of mature trees if compared to those of saplings (Table 2.3). Since knowledge about ontogenetic influences on the hydraulic system is still scarce (Ito *et al.* 1995, Mencuccini 2002), a non-competed metaxylem maturation in sapling roots could have caused these differences as well (Staubin *et al.* 1986, Vercambre *et al.* 2002, Tyree 2003).

Increases of root conductivity would be particularly straightforward adaptations in plants that respond to drought or salt stress with a reduction of fine root biomass (see Figs. 6.1, 6.2, and Weissbein 2006). The extent of root biomass reduction may ex-

plain the different response of root conductivity in mature beech and oak trees to drought (Fig. 2.1, Table 2.3). The minor reduction of root biomass of mature beech trees might have made an increase of root axial conductivity unnecessary (Fig. 6.2). Nevertheless, this study is one of very few reports that show that salinity- and drought-induced losses in root biomass may partly be compensated by increases of root hydraulic conductivity, when drought stress is not too severe (Figs. 2.1a, 3.3, Table 3.4). Although the underlying mechanisms must remain speculative, they are likely to include the re-growth of fine roots as indicated by the increased turnover rates (Table A 2), and modifications of secondary growth in coarse roots.

Another adaptation of the tree root hydraulic system to soil water shortage might be the development of root branches with diverging hydraulic properties, thereby exploring the spatial heterogeneity of water reserves, as is typical for temporally drought-exposed (Göttlein and Manderscheid 1998) and saline soils (Oron *et al.* 1999). In most of the beech, oak and olive roots examined in this study, a very large variation in root axial conductivity was found, with outliers showing up to 100 times higher k_s values than the sample mean (Figs. 2.1, 3.1, 3.3). Such high conductivity roots were found in the fresh- or well-watered control treatments as well as under salt/drought application, but the variability of fine root axial conductivity generally increased in root samples exposed to moderate or severe drought and in the salt-treated roots of Barnea variety (Fig. 3.1). Several previous studies have documented that root axial conductivity and water uptake rate can differ substantially within root systems, e.g. between deep and shallow roots (Pate *et al.* 1995, Korn 2004, Leuschner *et al.* 2004a). Since individual roots or root branches are thought to act as ‘physiologically autonomous units’ (Shani *et al.* 1993), the differentiation of the root population into high-conductivity and low-conductivity roots has been postulated as a favourable adaptation to heterogeneous environments. Consequently, the larger variability of hydraulic conductivity within the severely drought-stressed root systems of oaks if compared to beech, and the large intra-vascular and intra-root system variability in the roots of *Olea europaea* var. Barnea indicate their better adaptation to soil containing heterogeneous distributed moisture.

Influence of water shortage on root hydraulic safety

It has been thought for long that an increased axial conductivity is associated with an increasing risk to cavitation (Hargrave *et al.* 1994). Now there is convincing evidence that the susceptibility to drought stress-induced cavitation depends on the size of

pit membrane pores between adjacent conduits rather than vessel diameter (Jarbeau *et al.* 1995, Alder *et al.* 1996, Pockman and Sperry 2000). Accordingly, this study revealed no correlation between root axial conductivity and the degree of root embolism (Tables 2.3, 3.4) and consequently no conductivity-safety trade-off in roots, as has been found previously in beech branches by Cochard *et al.* (1999).

While some embolism may occur even in roots of well-watered plants (Table 2.3; see Alder *et al.* 1996, Domec *et al.* 2004), fine roots have been suggested to be weak, replaceable segments of the soil-plant-atmosphere continuum (Sperry and Saliendra 1994, Domec *et al.* 2004), expedient to uncouple parts of the SPAC in response to more severe water shortage. Acting as ‘hydraulic fuses’ (Zimmermann 1983), they are thought to prevent plant-wide cavitation and water loss to the soil, as resulting from unintended hydraulic redistribution (Nobel and North 1992, Sperry and Ikeda 1997, Hacke *et al.* 2000). As previously discussed, root shedding and probably aquaporin regulation, are involved in this function. Cavitation is suggested to be another, possibly reversible, ‘hydraulic fuse’ mechanism in roots. The slightly negative water potential inducing 50% loss of conductivity in beech and oak roots (Fig. 2.3, Table 2.4) support this hypothesis, as does the significant increase of Ψ_{PLC50} in drought-stressed *Quercus* roots (Table 2.4). There is now convincing evidence that embolism is reversible in many cases (Pickard 1989, Tyree *et al.* 1986, Zwieniecki and Holbrook 1998, Lovisolo and Schubert 2006). Although the mechanisms are still largely unknown, the active secretion of osmotic solutes, possibly via aquaporins, by adjacent living cells is likely to be involved (Holbrook and Zwieniecki 1999, Sakr 2003). The ability to repair cavitated vessels has profound implications, i.e. root embolism could be favourable if it prevents water loss to the soil without costly shedding of roots. Thus, the significantly increased vulnerability to cavitation in drought-stressed *Quercus petraea* roots seems to be a straightforward adaptation to drought rather than an impairment by drought, in particular if root system size is already reduced and further root shedding cannot be afforded.

6.2 CONCLUSIONS

The study of drought- and salt-resistance strategies has classically focused on the dynamics of stem and leaf water relations such as leaf water status (Lo Gullo and Salleo 1988, Fotelli *et al.* 2000, Aasamaa *et al.* 2004), stem sap flow (Čermák *et al.* 1993, Leuzinger *et al.* 2005), evaporative flux (Reich and Hinckley 1989), and stem and leaf vulnerability to cavitation (Harvey and van den Driessche 1997, Sperry and Tyree 1988). However, it is in the soil where water uptake occurs and plant individuals compete for water and other resources. Although an increasing number of studies has been addressing belowground traits (e.g. Levy *et al.* 1983, Hendriks and Bianchi 1995, McPhee 1998, Blake and Li 2003, de Kroon *et al.* 2003), a better understanding of the adaptability of tree root systems to water limitation and belowground competition is still urgently needed to enable predictions on the effects of climate change on mature forest stands.

Four main hypotheses were tested in this study to answer some important questions in this field:

i) The adaptive mechanisms of root hydraulic systems are analogue to those in above-ground organs.

This study suggests that *Quercus* fine and coarse roots are capable of responding more flexibly to drought in terms of root topology and physiology than beech roots: fine and coarse roots of *Quercus* generally responded with an increase of axial conductivity to moderate or severe drought, while those of *Fagus* mostly did not. The same pattern was found in salt-stressed *Olea europaea* roots, the conductivity of which increased with increasing salinity. This is in contrary to effects in shoots, where conductivity generally decreases in response to drought or salinity, disproving the hypothesis. Drought-adapted tree species such as *Quercus petraea* seem to be capable of partly compensating for drought-induced root biomass losses by increasing axial conductivity of the remaining roots, a mechanism rarely observed in aboveground organs.

ii) Fine roots act as 'hydraulic fuses' in the soil-plant-atmosphere continuum to prevent runaway cavitation in the whole plant.

In support of the hypothesis, this study provided evidence that small-diameter roots may indeed function as fuses in the SPAC of temperate trees. In addition to most previous studies, which suggest root shedding as the underlying mechanism, this study indicates cavitation as another, potentially reversible, 'hydraulic fuse' mechanism. This conclusion is based on the very high vulnerability of small-diameter roots of both oak and beech to cavitation and the further increase of this vulnerability in drought-stressed *Quercus* roots.

iii) Belowground competitive ability is symmetric and linked to root system size.

In contrast to the hypothesis, this study revealed two lines of evidence for the existence of asymmetry in belowground competition: fine root biomass of *Quercus petraea* was over-proportionally reduced in species-rich allospecific stand patches as compared to monospecific ones, and both root growth rates and root morphology depended on the competitor present but not on initial size differences. Although the experiments do not allow conclusions about the underlying mechanisms of this asymmetric belowground interaction, pre-emption of soil water and nutrient patches by plants with larger root systems, which gain access before smaller plants do, and species-specific uptake kinetics are likely to be involved.

iv) Belowground competition ability differs between tree species and is not modified by resource availability.

In support of the hypothesis, tree species may be ranked according to their belowground competitive ability. According to root biomass data and root growth in experimentally altered neighbourhoods, beech seems to be a superior competitor belowground. However, future experimental studies in the rhizosphere of forests have to reveal what mechanisms (including resource competition, self-self inhibition, facilitation, allelopathy, or indirect competitive interactions through other organisms or agents) form the basis of the observed pattern.

This study revealed a significant correlation between competitive asymmetry (ΔCA), expressed as difference between species-specific competitive abilities, and cumulative soil moisture deficit. Thus, in contrast to the formulated hypothesis, marked asymmetry

in the outcome of root competition only developed when soil moisture in summer was sufficiently high. Resource limitation, i.e. drought, seems to affect the competitive abilities of both *Fagus sylvatica* and *Quercus petraea* roots in a similar manner, with the consequence that species-specific differences in competitive ability in mixture disappear in the more stressful environment. Thus, the overall importance of direct biotic interactions belowground seems to be reduced under limited soil water availability.

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ANNEX

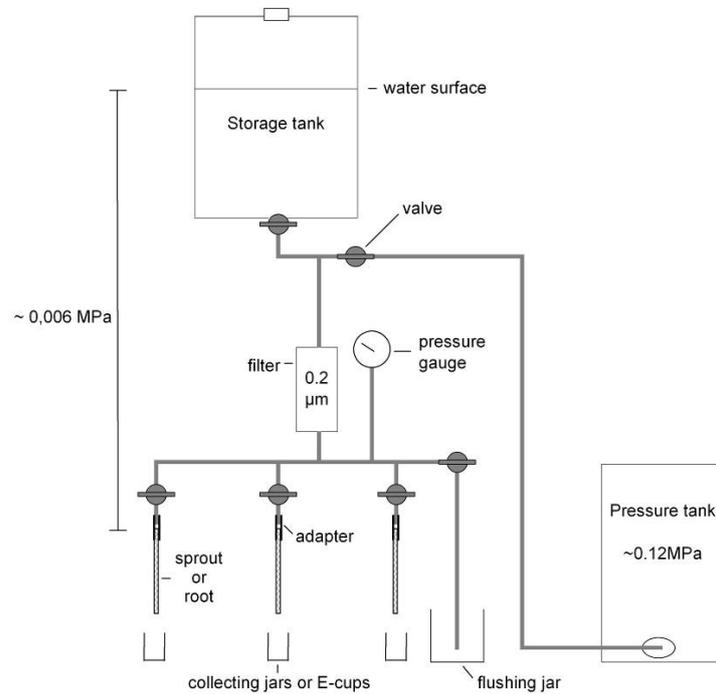


Fig. A 1 Apparatus for measurement of axial hydraulic conductivity and the degree of embolism according to the protocol given by Sperry *et al.* (1988). This method was used in Chapters 2 and 3.

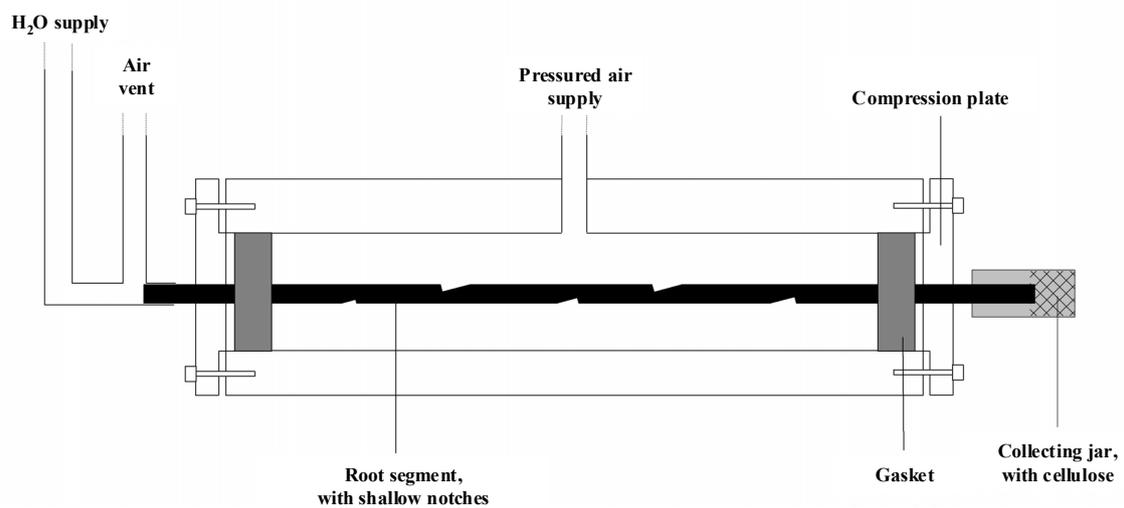


Fig. A 2 Apparatus to determine the vulnerability to embolism with the 'air injection method' according to the protocol given by Sperry and Saliendra (1994). This method was used in Chapter 2.

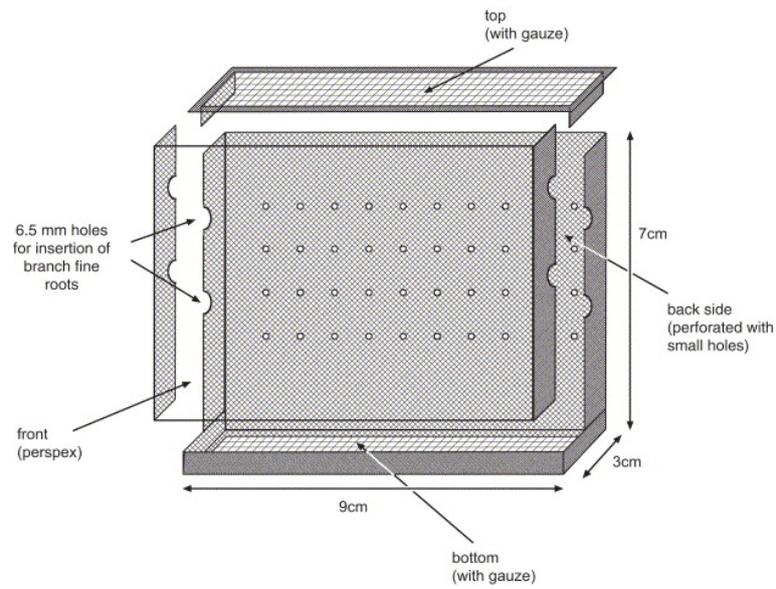


Fig. A 3 The *in situ*-root growth chamber as used for the assessment of competition belowground in Chapters 4 and 5. Reprinted from Hertel and Leuschner (2006).



Fig. A 4 The experimental sites: Sub-canopy roof in a beech patch of the Unterlüß forest, Lower-Saxony, Germany (left), and the saplings experiment at the Experimental Botanical Garden, University of Göttingen, Germany (right).



Fig. A 5 The experimental sites: Olive orchard at the Ramat Negev Experimental Station, South Israel.



Fig. A 6 The experimental sites: Mixed stand in the Ziegelrodaer forest, Saxony-Anhalt, Germany.

Table A 1 Effect of drought or salinity on root biomass, root:shoot ratio (or root:leaf ratio), rooting depth and fine root turnover in seedlings, compared to well-watered treatments.

Species	Duration, method, stress*	Root biomass	Root:shoot ratio	Root depth	Fine root turnover	Reference
<i>Quercus robur</i>	pot, d	+		++		Osunubi and Davies 1981
<i>Betula pendula</i>		ns	ns	ns		
<i>Pinus taeda</i>	pot, d	ns	++			Bongarten and Tesky 1987
<i>Fagus sylvatica</i>	12-wk, pot, d	--				Davidson <i>et al.</i> 1992
<i>Juglans nigra</i>	pot, d	ns	++			Pallardy and Rhoads 1993
<i>Quercus stellata</i>		ns				
<i>Quercus alba</i>		ns				
<i>Acer saccharum</i>		ns				
<i>Quercus robur</i>	3-wk, pot, d	--	ns			Fort <i>et al.</i> 1997
<i>Betula pendula</i>	2-wk, pot, d	--	-			Fort <i>et al.</i> 1998
<i>Picea abies</i> M clone	8-wk, pot, d	--				Karlsson <i>et al.</i> 1997
<i>Fagus sylvatica</i>	pot, d	ns	++			Van Hees 1997
<i>Quercus petraea</i>		ns	+			
<i>Quercus rubra</i>	12-wk, pot, d	ns	++			Tomlinson and Anderson 1998
<i>Pinus taeda</i>	4-wk, pot, d	ns	ns	+		Torreano and Morris 1998
<i>Fagus sylvatica</i>	12-wk, exp, d		-			Volkmer and Rennenberg 1999
<i>Fagus sylvatica</i>	2× 10/11-wk, pot, d	-	0			Thomas 2000
<i>Quercus petraea</i>		++	++			
<i>Quercus pubescens</i>		ns	+			
<i>Sorbus aria</i>		ns	+			
<i>Quercus robur</i>	14-wk, pot, d	ns	++	ns		Thomas and Gausling 2000
<i>Quercus petraea</i>		ns	++	ns		
<i>Fagus sylvatica</i>	7-wk, pot, d		--			Fotelli <i>et al.</i> 2001
<i>Prunus dulcis</i>	1-4-yr, pot, d	ns	ns			Heilmeyer <i>et al.</i> 2001
<i>Quercus robur</i>	8-wk, pot, d	ns	++			Gieger 2002, Gieger and Thomas 2002
<i>Quercus petraea</i>		ns	++			
<i>Thuja occidentalis</i>	2-yr, exp, d	-	--		ns	Pronk <i>et al.</i> 2002
<i>Quercus ilex</i>	12-wk, pot, d	--	+		+	Chiatante <i>et al.</i> 2005
<i>Fagus sylvatica</i>	pot, d	ns	++			Löf <i>et al.</i> 2005
<i>Prosopis argentina</i>	12-wk, pot, s	--	+/-			Villagra <i>et al.</i> 2005
<i>Prosopis alpataco</i>		-	+/-			
<i>Prosopis argentina</i>	12-wk, pot, d	-	++			Villagra <i>et al.</i> 2006
<i>Prosopis alpataco</i>		--	++			
<i>Betula pendula</i>	12-14-wk, pot, d	--	++			Aspelmeier and Leuschner 2006
<i>Quercus pubescens</i>	12-wk, pot, d	--	ns	-	+	Chiatante <i>et al.</i> 2006
<i>Fraxinus ornus</i>		--	+	--	+	
<i>Pinus canadiensis</i> SH*	22wk, pot, d	++	++			Climent <i>et al.</i> 2006
<i>Pinus canadiensis</i> FL		ns	ns			
<i>Fagus sylvatica</i>	12-wk, pot, d	--				Schumann 2006
<i>Fraxinus excelsior</i>		--				
<i>Quercus petraea</i>		--				
<i>Fagus sylvatica</i> var.*	12-wk, pot, d	--		ns		Rose 2007
<i>Pistacia lentiscus</i>	24-wk, pot, d	--	--		ns	Cortina <i>et al.</i> 2008
<i>Fagus sylvatica</i> var.*	2-yr, pot, d	-/--	+/ns	-		Meier and Leuschner 2008a
<i>Fagus sylvatica</i>	3-yr, pot, d	--	-			This study (Fig. 6.1)
<i>Quercus petraea</i>		--	-			

ns (not significant), + (marginal increase), ++ (significant increase), - (marginal decrease), -- (significant decrease), +/- or -/-- (data not consistent); * pot (pot experiment), exp (*in situ* experiment), d (drought), s (salt); SH (shaded), FL (full light), var. (different varieties).

Table A 2 Effect of drought or salinity on root biomass, root:shoot ratio (or root:leaf ratio), rooting depth and fine root turnover in stands or orchards of mature trees, compared to well-watered sites or treatments.

Dominant species	Duration, method, stress*	Root bio-mass	Root: shoot ratio	Root depth	Fine root turn-over	Reference
<i>Pseudotsuga menziesii</i>	grad, d	ns			+	Santantonio and Hermann 1985
<i>Fagus sylvatica</i>	grad, d	--				Kalisz <i>et al.</i> 1987
<i>Quercus rubra</i>						
<i>Carya spp.</i>						
<i>Liriodendron tulipifera</i>						
<i>Pinus contorta</i>	grad, d		+		+	Comeau and Kimmins 1989
<i>Pseudotsuga menziesii</i>	2-yr, exp, d	++	++		++	Gower <i>et al.</i> 1992
<i>Picea abies</i>	3-4-yr, exp, d	+	+		+	de Visser <i>et al.</i> 1994
<i>Pseudotsuga menziesii</i>		+	ns		+	
<i>Populus deltoides</i>	4-yr, exp, d	ns		++		Dickmann <i>et al.</i> 1996
<i>Pinus taeda</i>	grad, d	++				Parker and Lear 1996
<i>Picea abies</i>	3-yr, exp, d	ns	ns		ns	Bredemeier <i>et al.</i> 1998
<i>Hevea brasiliensis</i>	10-yr, exp, d	ns	++	--		Devakumar <i>et al.</i> 1999
<i>Pinus sylvestris</i>	grad, d	ns			+	Pietikäinen <i>et al.</i> 1999
<i>Picea abies</i>						
<i>Quercus prinus</i>	5-yr, exp, d	ns	ns		ns	Joslin <i>et al.</i> 2000
<i>Quercus alba</i>						
<i>Nyssa sylvatica</i>						
<i>Acer rubrum</i>						
<i>Fagus sylvatica</i>	grad, d	--				Leuschner and Hertel 2003
<i>Quercus petraea</i>						
<i>Fagus sylvatica</i>	grad, d	-				Leuschner <i>et al.</i> 2004
<i>Fagus sylvatica</i>	12-wk, exp, d	-				Prigge 2005, this study (Fig. 6.2)
<i>Quercus petraea</i>		--				
<i>Olea europea</i>	1-yr, exp, s	-			+	Weissbein 2006
<i>Cryptomeria japonica</i>	24-wk, exp, d	--			-	Konôpka <i>et al.</i> 2007
<i>Fagus sylvatica</i>	grad, d	--				Meier and Leuschner 2008b
<i>Fagus sylvatica</i>	2-yr, exp, d	-				This study (data not shown)
<i>Quercus petraea</i>		--				

ns (not significant), + (marginal increase), ++ (significant increase), - (marginal decrease), -- (significant decrease); *exp (*in situ* experiment), grad (moisture gradient), d (drought), s (salt).

Table A 3 Studies on herbaceous plants suggesting either symmetric or asymmetric competition below-ground.

Species	Type of study*	Main evidence†	Rationale	Reference
<i>Plantago lanceolata</i> <i>Holcus lanatus</i> <i>Lolium perenne</i> <i>Rumex acetosa</i> <i>Lolium perenne</i>	pot	asym	competitive advantage of smaller plants, species identity important determinant	Newbery and Newman 1978
<i>Agropyron spicatum</i> <i>Agropyron desertorum</i>	pot	asym	differences in phosphorus competition in similar-sized plants	Hofman and Ennik 1980, 1982, Ennik and Hofman 1983
<i>Ipomoea tricolor</i>	pot	sym	growth rates, size asymmetry	Weiner 1986
<i>Agrostis stolonifera</i> <i>Scirpus sylvaticus</i>	<i>in situ</i>	asym	nitrogen capture was not related to root system size	Crick and Grime 1987
<i>Solidago canadensis</i> Div. (old-field)	<i>in situ</i>	sym	per-unit-size effects; lack of species effect	Goldberg 1987
Div. (7 species)	<i>in situ</i>	sym	per-gram effect stronger than per-individual effects	Miller and Werner 1987
<i>Festuca ovina</i>	pot	asym	no effect of initial size advantage	Wilson 1988
<i>Ambrosia artemisiifolia</i> <i>Impatiens pallida</i> <i>Molina caerulea</i>	<i>in situ</i>	sym / asym	low root biomass	Thomas and Weiner 1989
Div. (8 species)	pot	asym	root biomass; high root:shoot ratio, root proliferation	Aerts <i>et al.</i> 1991
Div. (7 species, old-field and pasture)	pot	asym	species specific foraging mechanism (scale vs. precision)	Campbell <i>et al.</i> 1991a, b
<i>Agropyron cristatum</i> <i>Bouteloua gracilis</i> <i>Elaeagnus commutata</i> <i>Melilotus officinalis</i> <i>Potentilla pensylvanica</i> <i>Pennisetum americanum</i>	<i>in situ</i>	asym	per-gram effect stronger than per-individual effects	Goldberg and Landa 1991
<i>Agropyron cristatum</i> <i>Bouteloua gracilis</i> <i>Elaeagnus commutata</i> <i>Melilotus officinalis</i> <i>Potentilla pensylvanica</i> <i>Pennisetum americanum</i>	<i>in situ</i>	asym	no influence of initial biomass, species identity important determinant	Gerry and Wilson 1995
<i>Amaranthus retroflexus</i>	pot	sym	growth rates	Schwinning 1996
<i>Kochia scoparia</i>	pot	sym	relative growth rates	Cahill 1997
<i>Abutilon theophrasti</i>	pot	sym	biomass	Weiner <i>et al.</i> 1997
<i>Anthoxanthum odoratum</i> <i>Festuca rubra</i> <i>Holcus lanatus</i> <i>Lolium perenne</i>	pot	sym	growth rates, biomass	Casper <i>et al.</i> 1998
Div. (6 species, South Carolina coastal plain)	pot	asym	increased N uptake per biomass in heterogeneous soils; foraging characteristics	Fransen <i>et al.</i> 1998, 1999
Div. (7 species, British woodland)	<i>in situ</i>	asym	Species specific foraging scale and precision	Einsmann <i>et al.</i> 1999
	<i>in situ</i>	asym	differing abilities to locate and recognize patches of nutrients	Farley and Fitter 1999a,b

**in situ* (field experiment), pot (pot experiment); † asym (asymmetric competition), sym (symmetric competition).

Table A 3 (continuation) Studies on herbaceous plants suggesting either symmetric or asymmetric competition belowground.

Species	Type of study*	Main evidence [†]	Rationale	Reference
<i>Lolium perenne</i> <i>Poa pratensis</i>	pot	asym	root proliferation in heterogeneous environments	Hodge <i>et al.</i> 1999a,b
<i>Lolium perenne</i> <i>Poa pratensis</i>	pot	asym	root proliferation in heterogeneous environments	Robinson <i>et al.</i> 1999
<i>Amaranthus retroflexus</i>	<i>in situ</i>	sym	root biomass, no effect of soil heterogeneity	Cahill 1999, Cahill and Casper 2000
<i>Ipomea tricolour</i>	pot	sym	no influence of heterogeneous resources	Blair 2001
<i>Anthoxanthum odoratum</i> <i>Festuca rubra</i> <i>Holcus lanatus</i>	pot	sym / asym	biomass production (homogeneous / heterogeneous soil)	Fransen <i>et al.</i> 2001, Fransen and de Kroon 2001
Div. (59 species, Great Plains grassland)s	<i>in situ</i>	asym	species-specific nutrient foraging	Johnson and Biondini 2001
Div. (6 species)	pot	asym	no correlation between root system size and foraging precision	Wijesinghe <i>et al.</i> 2001
<i>Chaemaecrista nictitans</i> <i>Hypericum gantianoides</i> <i>Erechtites hieracifolia</i> <i>Solidago altissima</i>	pot	asym	foraging scale, precision and rate in heterogeneous environments	Bliss <i>et al.</i> 2002
<i>Trifolium subterraneum</i>	pot	asym	mycorrhizal infection promotes pre-emption of heterogeneous resources	Facelli and Facelli 2002
<i>Phaseolus variegatus</i>	pot	sym	higher root biomass under interspecific competition than in monoculture	Maina <i>et al.</i> 2002
Div. (grassland)	<i>in situ</i>	sym	competition is independent of species diversity	Cahill 2003
<i>Briza media</i> <i>Festuca ovina</i>	pot	asym	outcome of two-species competition may differ between patchy and homogeneous soils, foraging	Day <i>et al.</i> 2003
<i>Lolium perenne</i> <i>Plantago lanceolata</i> <i>Trifolium repens</i>	pot	asym	foraging for patchy resources, uptake kinetics	Hodge 2003
<i>Achillea millefolium</i> <i>Bromus inermis</i> <i>Hieracium caespitosum</i>	pot	asym	relative growth rates, foraging for patchy resources	Rajaniemi 2003
<i>Triticum aestivum</i>	pot	sym	no pre-emption of resources by larger plants	von Wettberg and Weiner 2003
Div. (8 species)	pot	asym	foraging scale, precision and rate; relative growth rate	Rajaniemi and Reynolds 2004
<i>Andropogon gerardii</i> <i>Schizachyrium scoparium</i> <i>Sorghastrum nutans</i> <i>Sporobolus heterolepis</i>	<i>in situ</i>	asym	influence of mycorrhization on plant-plant interactions	Casper and Castelli 2007
Div. (6 species)	<i>in situ</i>	asym	foraging scale and precision in patchy soils	Rajaniemi 2007

**in situ* (field experiment), pot (pot experiment); [†]asym (asymmetric competition), sym (symmetric competition).

Table A 4 Studies on woody plants suggesting either symmetric or asymmetric competition below-ground.

Species	Type of study*	Main evidence [†]	Rationale	Reference
<i>Artemisia tridentata</i>	pot	asym	differences in phosphorus competition in similar-sized plants	Caldwell <i>et al.</i> 1985
<i>Erica tetralix</i> <i>Calluna vulgaris</i>	pot	asym	spatial arrangement, phenotypic plasticity	Aerts <i>et al.</i> 1991
<i>Fraxinus pennsylvanica</i>	<i>in situ</i>	asym	no influence of initial biomass, species identity important determinant	Gerry and Wilson 1995
<i>Acer rubrum</i> Div.	<i>in situ</i> / pot	asym	genomic difference in the nutrient uptake kinetics	Kelly <i>et al.</i> 1994, 2000
<i>Pinus taeda</i>	<i>in situ</i>	sym	root distribution	Mou <i>et al.</i> 1995
<i>Diospyrus virginiana</i> <i>Euonymus americanus</i> <i>Liquidambar styraciflua</i> <i>Pinus taeda</i>	pot	asym	Species specific foraging scale and precision	Einsmann <i>et al.</i> 1999
<i>Fagus sylvatica</i> <i>Quercus petraea</i>	<i>in situ</i>	asym	growth rate, biomass	Hertel 1999
<i>Grevilla robusta</i> <i>Senna spectabilis</i>	<i>in situ</i>	asym	morphological plasticity	Livesley <i>et al.</i> 2000
<i>Betula alleghaniensis</i>	pot	sym	size-uptake relationship	Berntson and Wayne 2000
<i>Citrus paradise</i> <i>Malus domestica</i>	<i>in situ</i>	asym	influence of root age on uptake kinetics	Bouma <i>et al.</i> 2001
<i>Acer rubrum</i> <i>Prunus serotina</i> <i>Quercus rubra</i>	pot	asym	nutrient net gain not related to root surface area	Kelly <i>et al.</i> 2001
<i>Fagus sylvatica</i> <i>Quercus petraea</i>	<i>in situ</i>	asym	growth rate, biomass	Leuschner <i>et al.</i> 2001
<i>Pinus taeda</i> <i>Liquidambar styraciflua</i>	pot	asym	foraging scale, precision and rate in heterogeneous environments	Bliss <i>et al.</i> 2002
<i>Fagus sylvatica</i> <i>Picea abies</i>	pot	asym	species-specific uptake kinetics	Gessler <i>et al.</i> 2002
<i>Fagus sylvatica</i> <i>Picea abies</i> <i>Quercus petraea</i>	<i>in situ</i>	asym	species-specific water uptake kinetics	Coners and Leuschner 2005
<i>Vitis rupestris</i> x <i>Vitis riparia</i> cv. 3309 C	pot	asym	declining nitrate uptake with root age	Volder <i>et al.</i> 2005
<i>Fagus sylvatica</i> <i>Picea abies</i>	<i>in situ</i>	sym	biomass	Bolte 2006
<i>Carya illinoensis</i> <i>Gossypium hirsutum</i>	<i>in situ</i>	asym	morphological plasticity	Zamora <i>et al.</i> 2007
<i>Fagus sylvatica</i> <i>Quercus petraea</i>	<i>in situ</i>	asym	relative growth rate; foraging scale, morphological plasticity	This study (Table 4.6, Fig. 5.1)

**in situ* (field experiment), pot (pot experiment); [†]asym (asymmetric competition), sym (symmetric competition).

Table A 5 Reviews and models suggesting either symmetric or asymmetric competition belowground.

Species	Type of study	Main evidence [†]	Rational	Reference
	review	sym	unchanged or lower size inequality at higher densities	Weiner and Thomas 1986
	review	asym	superior competitive ability varies according to ecological circumstances	Tilman 1988
	review	sym	patchy resources	Weiner 1990
	review	asym	nitrogen capture was not related to root system size	Grime <i>et al.</i> 1991
<i>Larrea tridentate</i>	<i>in situ</i> / model	asym	heterogeneous resources	Brisson and Reynolds 1994
	review	asym	non-biomass-dependend, species-specific response to nutrient patches	Robinson 1994
	model	asym	uptake kinetics	Jackson and Caldwell 1996
	review	sym	resource uptake, growth, fecundity	Casper and Jackson 1997
Div.	model / review	asym	plasticity in root demography	Eissenstat and Yanai 1997
	review	sym / asym	density, resource uptake, biomass increment	Schwinning and Weiner 1998
	review	sym	no effects of soil heterogeneity; root biomass	Casper <i>et al.</i> 2000
<i>Glycine max</i>	model	asym	foraging, uptake kinetics	Gersani <i>et al.</i> 2001
<i>Fagus sylvatica</i>	review	asym	space sequestration, uptake kinetics	Grams <i>et al.</i> 2002
<i>Picea abies</i>				
<i>Abutilon theophrasti</i>	model	sym	advances of nutrient rich patches are counter-balanced by a higher root production	Casper <i>et al.</i> 2003
	review	sym	resource availability	de Kroon <i>et al.</i> 2003
	review	asym	foraging in heterogeneous soils	Hutchings <i>et al.</i> 2003
	model	asym	plants outcompete other plants by pre-empting nutrient supply	Craine <i>et al.</i> 2005
	review	sym	no benefits of foraging precision; foraging scale (biomass) matters	Kembel and Cahill 2005
	model	sym / asym	space occupation, uptake rates	Raynaud and Leadley 2004, 2005
	model	sym	maximizing root length in the presence of competitor	Craine 2006
<i>Fagus sylvatica</i>	model	asym	Richard equation	Nord-Larsen <i>et al.</i> 2006
	review	asym	patchy resources	Schenk 2006
Div.	review	asym	species specific nutrient uptake rates	Lucash <i>et al.</i> 2007
	model	asym	distance costs, resource heterogeneity	O'Brien <i>et al.</i> 2007

[†]asym (asymmetric competition), sym (symmetric competition).

Table A 6 Short- and long-term influence of drought or salt stress on axial conductivity and sap flow in conifers.

Gymnosperm tree species	Type of study*	Duration / type	Organ [‡]	Cause	Effect on conductivity [†]	Reference
<i>Pinus ponderosa</i>	M, F, d	gradient	S	lower leaf:sapwood area ratio	+ (LSC)	Callaway <i>et al.</i> 1994
<i>Abies lasiocarpa</i> <i>Larix laricina</i> <i>Picea glauca</i>	M, F, d	2 summers	B	embolism	- (k_h)	Sperry <i>et al.</i> 1994
<i>Tsuga heterophylla</i>	S, F, d	10-wk	S	embolism	-- (LSC)	Kavanagh and Zaerr 1997
<i>Abies concolor</i> <i>Pseudotsuga menziesii</i>	M, F, lab		B, FR, CR	embolism	-- (k_h)	Sperry and Ikeda 1997
<i>Pinus halepensis</i> , mesic ecotype	S, P, d	summer	shoot	embolism	-- (LSC) -- (k_h)	Tognetti <i>et al.</i> 1997
<i>Pinus halepensis</i> , xeric ecotype	S, P, d	ecotype	shoot	less embolism, osmotic adjustment	- (LSC) - (k_h)	Tognetti <i>et al.</i> 1997
<i>Pinus halepensis</i>	M, F, d	12-mth	B, S	embolism	-- (WP)	Borghetti <i>et al.</i> 1998
<i>Pinus sylvestris</i>	M, F, d	summer	S	embolism	- (K) - (LSC)	Irvine <i>et al.</i> 1998
Div. (10 species, semi-arid → rain forest)	S, L, d	gradient, species	shoot	Ψ_{PLC50} was correlated with habitat moisture	- to -- (k_h)	Brodribb and Hill 1999
<i>Pinus sylvestris</i>	M, F, s	summer	R	shift of water uptake to deeper soil horizons	+ (K)	Plamboeck <i>et al.</i> 1999
Div. (17 species)	review, d	VPD gradient	S	lower leaf:sapwood area ratio (only <i>Pinus</i>)	+ (LSC, only <i>Pinus</i>)	DeLucia <i>et al.</i> 2000
<i>Pinus taeda</i>	S, P, d	9-yr	S, R	lower leaf:sapwood area ratio, increased root biomass	+ (LSC) 0 (WP) - ($k_{h\text{root}}$)	Ewers <i>et al.</i> 2000
<i>Pinus ponderosa</i> (mesic, xeric)	M, F, d	ecotype		larger tracheids, lower leaf:sapwood area ratio	+ (k_s) + (LSC)	Maherali and DeLucia 2000
<i>Pinus sylvestris</i>	S, P, d	3-wk	S		- (k_s)	Croise <i>et al.</i> 2001
<i>Pinus sylvestris</i>	M, F, d	gradient	S	lower leaf:sapwood area ratio	+ (LSC)	Mencuccini and Bonosi 2001
<i>Picea abies</i> (dominant, suppressed trees)	M, F, d	summer	S	embolism	-- (K)	Sellin 2001

*Mature trees (M) or seedlings/saplings (S), in the field (F), pot (P), laboratory (L), or in aeroponics (A), drought stress (d) or salt stress (s). [‡]Manual induction of embolism in the laboratory (air injection/dehydration), diurnal rhythm (diurnal), comparison of ecotypes in contrasting environments (ecotype), comparison of a species along a moisture gradient (gradient), comparison of species in contrasting environments (species), summer drought (summer). [‡]Branch (B), coarse root (CR) fine root (FR), leaf (L), petiole (P), root (R), shoot/stem (S), whole plant (WP). [†]0 (not influenced), + (marginal increase), ++ (significant increase), - (marginal decrease), -- (significant decrease), Huber value (HV), hydraulic conductivity (k_h), specific conductivity (k_s), sap flow (K), radial and axial conductivity (L_{pr}), leaf specific conductivity (LSC), and conductivity of the whole plant (WP).

Table A 6 (continuation) Short- and long-term influence of drought or salt stress on axial conductivity and sap flow in conifers.

Gymnosperm tree species	Type of study*	Duration / type	Organ [‡]	Cause	Effect on conductivity [†]	Reference
<i>Pinus laricio</i>	M, F, d	3-yr	S	embolism, lower leaf:sapwood area ratio	-- (K) 0 (k_h) + (LSC)	Cinnirella <i>et al.</i> 2002
<i>Pinus ponderosa</i> (same ecotype from 7 mesic → xeric habitat)	M/S, F/P, d	9-mth	S	embolism, lower leaf:sapwood area ratio	-- (k_h) - (k_s) - (LSC)	Maherali <i>et al.</i> 2002
<i>Picea banksiana</i> <i>Pinus mariana</i>	S, A, d	5× 3-d	S	embolism	-- (k_h) -- (k_s) - (LSC)	Blake and Li 2003
<i>Pinus pinaster</i>	S, F, d	3-wk	R	degradation of fungal symbiont	- (k_h)	Bogeat-Triboult <i>et al.</i> 2004
<i>Pseudotsuga menziesii</i> <i>Pinus ponderosa</i>	M, F, d	summer	R	embolism, hydraulic redistribution	-- (k_h) + (K)	Domec <i>et al.</i> 2004
<i>Pinus sylvestris</i>	M, F, d	11-mth	B, S	embolism	- (k_h)	Perks <i>et al.</i> 2004
<i>Picea abies</i>	M, F, d	4-mth	R		-- (K)	Leuschner <i>et al.</i> 2004a
<i>Cedrus atlantica</i> <i>C. brevifolia</i> <i>C. libani</i>	S, F, d	2× 10-wk	B, L, S	embolism, decreased tracheid size, lower Ψ_{PLC50}	-- (k_s) 0/+ (LSC) ++ (HV)	Ladjal <i>et al.</i> 2005
<i>Pinus echinata</i> <i>P. palustris</i> <i>P. taeda</i>	S, P, d	28-d	R	decreased re-growth of roots	-- (L_{pr})	Sword Sayer <i>et al.</i> 2005
<i>Pinus palustris</i> (mesic, xeric habitat)	M, P, d	gradient	L, R	higher leaf:sapwood area ratio, higher root:leaf area ratio	0 (LSC) 0 ($k_{s\text{ root}}$) + (K)	Addington <i>et al.</i> 2006
<i>Pinus sylvestris</i>	M, F, d	summer, gradient	R		-- (K)	Burk 2006

*Mature trees (M) or seedlings/saplings (S), in the field (F), pot (P), laboratory (L), or in aeroponics (A), drought stress (d) or salt stress (s). [‡]Manual induction of embolism in the laboratory (air injection/dehydration), diurnal rhythm (diurnal), comparison of ecotypes in contrasting environments (ecotype), comparison of a species along a moisture gradient (gradient), comparison of species in contrasting environments (species), summer drought (summer). [‡]Branch (B), coarse root (CR) fine root (FR), leaf (L), petiole (P), root (R), shoot/stem (S), whole plant (WP). [†]0 (not influenced), + (marginal increase), ++ (significant increase), - (marginal decrease), -- (significant decrease), Huber value (HV), hydraulic conductivity (k_h), specific conductivity (k_s), sap flow (K), radial and axial conductivity (L_{pr}), leaf specific conductivity (LSC), and conductivity of the whole plant (WP).

Table A 7 Short- and long-term influence of drought or salt stress on axial conductivity and sap flow in woody angiosperms.

Angiosperm tree species	Type of study*	Duration / type	Organ [‡]	Cause	Effect on conductivity [†]	Reference
<i>Citrus jambhiri</i>	S, P, d	18-d	R	permeability of the root cell membrane	-- (L _{pr})	Ramos and Kaufmann 1979
<i>Citrus</i> spp. (7 species)	S, P, d/s	5-mth	R		- (L _{pr})	Zekri and Parsons 1989
<i>Quercus alba</i> <i>Quercus rubra</i>	M, F, d	summer	B	embolism	-- (k _h)	Cochard 1990
<i>Ceratonia siliqua</i>	S, P, d	3-wk	S	embolism	-- (k _h)	Lo Gullo and Salleo 1991
<i>Fraxinus pennsylvanica</i>	S, P, d	summer	S	decreased leaf area	0 (k _s) + (LSC)	Shumway <i>et al.</i> 1991
<i>Quercus petraea</i> <i>Q. pubescens</i> <i>Q. robur</i>	M, F, d	summer	B, P	embolism	-- (LSC)	Cochard <i>et al.</i> 1992b
<i>Populus deltoides</i>	S, L, d		B	embolism	-- (k _h)	Lo Gullo and Salleo 1992
<i>Quercus rubra</i> <i>Populus deltoides</i>	S, P/L, d		B	embolism	-- (k _h)	Tyree <i>et al.</i> 1992c
<i>Quercus rubra</i> <i>Liriodendron tulipifera</i>	S, P, d	2 summers	S	decreased leaf:sapwood area ratio & xylem area, embolism	-- (K) - (LSC)	Shumway <i>et al.</i> 1993
<i>Betula occidentalis</i>	S, P	air injection	B	embolism	-- (k _h) - (LSC)	Sperry and Pockman 1993
<i>Juglans regia</i>	M, F, d	summer	P, S	embolism	-- (k _h petiole) - (k _h stem)	Tyree <i>et al.</i> 1993
Div. (7 species)	M, F, d	summer	B	embolism	-- (k _h)	Sperry <i>et al.</i> 1994
<i>Salvia mellifera</i>	M, F/L, d	summer	B	embolism	-- (k _h)	Hargrave <i>et al.</i> 1994
<i>Salvia mellifera</i> <i>Ceanothus megacarpus</i>	M, F/L, d	summer, air injection	S	embolism, reduced leaf area	-/-- (K _h) + (LSC)	Kolb and Davis 1994
<i>Pseudobombax septenatum</i> <i>Ochroma pyramidale</i>	M, F, d	summer	P, R, S	embolism	-- (K)	Machado and Tyree 1994
<i>Quercus robur</i>	S, P, d	summer	B, P	embolism	-- (k _h)	Simonin <i>et al.</i> 1994
<i>Betula occidentalis</i>	M/S, F/L, d	summer, air injection	B, S	embolism	-- (k _h)	Sperry and Saliendra 1994
<i>Populus deltoides</i> <i>P. balsamifera</i> <i>P. angustifolia</i>	S, P, d	summer	S	embolism	-- (k _h)	Tyree <i>et al.</i> 1994
<i>Malosma laurina</i> <i>Heteromeles arbutifolia</i>	M, F/L, d	air injection	B	embolism	-- (k _h)	Jarbeau <i>et al.</i> 1995

*Mature trees (M) or seedlings/saplings (S), in the field (F), pot (P), laboratory (L), or in aeroponics (A), drought stress (d) or salt stress (s). [‡]Manual induction of embolism in the laboratory (air injection/dehydration), diurnal rhythm (diurnal), comparison of ecotypes in contrasting environments (ecotype), comparison of a species along a moisture gradient (gradient), comparison of species in contrasting environments (species), summer drought (summer); [‡]Branch (B), coarse root (CR) fine root (FR), leaf (L), petiole (P), root (R), shoot/stem (S), whole plant (WP). [†]0 (not influenced), + (marginal increase), ++ (significant increase), - (marginal decrease), -- (significant decrease), Huber value (HV), hydraulic conductivity (k_h), specific conductivity (k_s), sap flow (K), radial and axial conductivity (L_{pr}), leaf specific conductivity (LSC), and conductivity of the whole plant (WP).

Table A 7 (continuation) Short- and long-term influence of drought or salt stress on axial conductivity and sap flow in woody angiosperms.

Angiosperm tree species	Type of study*	Duration / type [§]	Organ [‡]	Cause	Effect on conductivity [†]	Reference
<i>Hevea brasiliensis</i>	S, P/L, d	air injection	P, S	embolism	-- (k_h)	Ranasinghe and Milburn 1995
<i>Olea europaea</i>	S, P, d	25-45-d	R		-- (L_{pr})	Rieger 1995
<i>Prunus persica</i>						
<i>Poncirus trifoliata</i> × <i>Citrus paradisi</i>						
<i>Pistachia integerrima</i>						
<i>Fagus sylvatica</i> (mesic, xeric ecotypes)	S, P, d	8/10-d	S	embolism	-- (k_h) -- (LSC)	Tognetti <i>et al.</i> 1995
<i>Acer grandidentatum</i>	M, F, d	gradient	S	embolism	-- (k_h)	Alder <i>et al.</i> 1996
<i>Populus</i> (mesic, xeric ecotypes)	M, F, d	gradient	S	larger Ψ_{PLC50} & vessels in xeric ecotypes	+ (k_h)	Blake <i>et al.</i> 1996
<i>Populus trichocarpa</i>	S, P, d	species	S	larger vessels in drought-resistant clone, embolism	+ ($k_{s\ theo}$) -- (k_h)	Harvey and van der Driessche 1997
<i>P. deltoides</i> (drought-sensitive and – resistant clones)						
<i>Rhus laurina</i>	M, F, d	summer	S	embolism	-- (k_h)	Langan <i>et al.</i> 1997
<i>Ceanothus megacarpus</i>						
<i>Olea oleaster</i>	S, P, d	6-mth	R	suberization	-- (L_{pr})	Lo Gullo <i>et al.</i> 1998
<i>Vitis vinifera</i>	M, P, d	40-d	S	decreased leaf area, rel. higher xylem area	0/- (LSC) 0/- (k_s) - (k_h)	Lovisol and Schubert 1998
<i>Quercus pubescens</i>	M, F, d	summer	B	embolism	-- (k_h)	Tognetti <i>et al.</i> 1998
<i>Q. ilex</i>					- (K)	
<i>Ceanothus</i> spp (3 species, mesic → xeric habitats)	M, F, d	gradient	S	embolism	-- (k_h)	Davis <i>et al.</i> 1999
<i>Quercus pubescens</i>	S, F/P, d	summer	R, S	embolism	0 ($k_{h\ root}$) -- ($k_{h\ shoot}$)	Nardini and Pitt 1999
<i>Populus trichocarpa</i> (4 mesic → xeric habitats)	M, P/L, d	gradient, air injection	S	lower Ψ_{PLC50} & k_s in xeric ecotypes	0 (k_h)	Sparks and Black 1999
<i>Acer rubrum</i>	M, F, d	diurnal	P	embolism	-/-- (k_h)	Zwieniecki <i>et al.</i> 2000
<i>Liriodendron tulipifera</i>						
<i>Vitis labrusca</i>						
<i>Avicennia germinans</i>	M, F, s	6-mth	S	embolism	-- (LSC) -- (k_s)	Sobrado 2001
<i>Quercus robur</i>	S, P, d	8-wk	B	decreased sapwood, embolism	0/-- (k_h) -- (k_s)	Gieger 2002, Gieger and Thomas 2002
<i>Quercus petraea</i>						

*Mature trees (M) or seedlings/saplings (S), in the field (F), pot (P), laboratory (L), or in aeroponics (A), drought stress (d) or salt stress (s). [§]Manual induction of embolism in the laboratory (air injection/dehydration), diurnal rhythm (diurnal), comparison of ecotypes in contrasting environments (ecotype), comparison of a species along a moisture gradient (gradient), comparison of species in contrasting environments (species), summer drought (summer). [‡]Branch (B), coarse root (CR) fine root (FR), leaf (L), petiole (P), root (R), shoot/stem (S), whole plant (WP). [†]0 (not influenced), + (marginal increase), ++ (significant increase), - (marginal decrease), -- (significant decrease), Huber value (HV), hydraulic conductivity (k_h), specific conductivity (k_s), sap flow (K), radial and axial conductivity (L_{pr}), leaf specific conductivity (LSC), and conductivity of the whole plant (WP).

Table A 7 (continuation) Short- and long-term influence of drought or salt stress on axial conductivity and sap flow in woody angiosperms.

Angiosperm tree species	Type of study*	Duration / type	Organ [‡]	Cause	Effect on conductivity [†]	Reference
<i>Populus tremuloides</i>	S, P, d	16-d	R	embolism, aquaporin expression	-- (L _{pr})	Siemens and Zwiazek 2003
<i>Pistacia lentiscus</i> <i>Quercus coccifera</i>	S, P/L, d	summer, dehydration	B	embolism	-- (LSC) -- (k _h)	Vilagrosa <i>et al.</i> 2003
<i>Fagus sylvatica</i> <i>Quercus petraea</i>	M, F, d	summer	R		-- (K)	Leuschner <i>et al.</i> 2004a
<i>Eucalyptus crebra</i> <i>E. xanthoclada</i>	M/S, F/L, d	summer, air injection	S	embolism	-- (k _h)	Rice <i>et al.</i> 2004
<i>Eucalyptus grandis</i> <i>E. sideroxylon</i> <i>E. occidentalis</i>	S, P, d	6-wk	S	reduced vessel size and density	- (k _{s theo})	Searson <i>et al.</i> 2004
<i>Populus tremuloides</i>	S, A, d	17-20-h	R	aquaporin expression	+/- (L _{pr})	Siemens and Zwiazek 2004
<i>Fagus sylvatica</i> <i>Betula pendula</i>	M, F, d	summer	R		-- (K)	Burk 2006
<i>Populus euphratica</i> <i>P. × canescens</i>	M, F, s	6-wk	S	reduced vessel size	0/- (k _{h theo})	Junghans <i>et al.</i> 2006
<i>Rhizophora mucronata</i>	M, F, s	gradient	S	increased vessel density, decreased vessel size	- (k _{s theo})	Schmitz <i>et al.</i> 2006
<i>Olea europaea</i> (3 varieties)	S, P, d	15-wk	S	increased vessel density, vessel diameter: inconsistent	0/+ (k _{h theo})	Bacelar <i>et al.</i> 2007
<i>Vitis berlandieri</i> × <i>rupestris</i>	M, F, d	7-d	S	aquaporin expression	+ (k _h)	Galmes <i>et al.</i> 2007
<i>Arbutus unedo</i>	S, P, s	16-wk	R		-- (L _{pr})	Navarro <i>et al.</i> 2007
<i>Vitis</i> spp. (5 varieties)	M, F, d	summer	S	embolism	-- (k _h)	Pire <i>et al.</i> 2007
<i>Laguncularia racemosa</i>	S, P, s		S	increased vessel density, decreased vessel size	-- (k _h) -- (k _s)	Sobrado 2007
<i>Olea europea</i> var. (3 varieties)	M, F, s	7-yr	R, S	increased vessel density, high conductivity roots	++ (k _{h root}) ++ (k _{s root}) 0 (k _{s shoot})	This study (Tables 3.1, 3.4)
<i>Fagus sylvatica</i> <i>Quercus petraea</i>	M/S, F/P, d	2/3-yr	R, S	embolism, xylem anatomy	-- (k _{s shoot}) -/++ (k _{s root})	This study (Figs. 2.1, 2.2, 2.3, Table 2.3)

*Mature trees (M) or seedlings/saplings (S), in the field (F), pot (P), laboratory (L), or in aeroponics (A), drought stress (d) or salt stress (s). [§]Manual induction of embolism in the laboratory (air injection/dehydration), diurnal rhythm (diurnal), comparison of ecotypes in contrasting environments (ecotype), comparison of a species along a moisture gradient (gradient), comparison of species in contrasting environments (species), summer drought (summer). [‡]Branch (B), coarse root (CR) fine root (FR), leaf (L), petiole (P), root (R), shoot/stem (S), whole plant (WP). [†]0 (not influenced), + (marginal increase), ++ (significant increase), - (marginal decrease), -- (significant decrease), Huber value (HV), hydraulic conductivity (k_h), specific conductivity (k_s), sap flow (K), radial and axial conductivity (L_{pr}), leaf specific conductivity (LSC), and conductivity of the whole plant (WP).

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